DIGITAL ACCESS TO SCHOLARSHIP AT HARVARD
DASH.HARVARD.EDU

HARVARD LIBRARY
Office for Scholarly Communication

The Biomechanics and Evolution of High-Speed Throwing

Citation

Roach, Neil. 2012. The Biomechanics and Evolution of High-Speed Throwing. Doctoral dissertation, Harvard University.

Permanent link

http://nrs.harvard.edu/urn-3:HUL.InstRepos:9822375

Terms of Use

This article was downloaded from Harvard University's DASH repository, and is made available under the terms and conditions applicable to Other Posted Material, as set forth at http://nrs.harvard.edu/urn-3:HUL.InstRepos:dash.current.terms-of-use#LAA

Share Your Story

The Harvard community has made this article openly available.
Please share how this access benefits you. Submit a story .

Accessibility

© *2012 Neil Thomas Roach*

All rights reserved.

Advisor: Daniel Lieberman Neil Thomas Roach

The Biomechanics and Evolution of High-Speed Throwing

Abstract

Throwing with power and accuracy is a uniquely human behavior and a potentially important mode of early hunting. Chimpanzees, our closest living relatives, do occasionally throw, although with much less velocity. At some point in our evolutionary history, hominins developed the ability to produce high performance throws. The anatomical changes that enable increased throwing ability are poorly understood and the antiquity of this behavior is unknown.

In this thesis, I examine how anatomical shifts in the upper body known to occur during human evolution affect throwing performance. I propose a new biomechanical model for how humans amplify power during high-speed throwing using elastic energy stored and released in the throwing shoulder. I also propose and experimentally test a series of functional hypotheses regarding how four key shifts in upper body anatomy affect throwing performance: increased torso rotational mobility, laterally oriented shoulders, lower humeral torsion, and increased wrist hyperextensability.

These hypotheses are tested by collecting 3D body motion data during throws performed by human subjects in whom I varied anatomical parameters using restrictive braces to examine their effects on throwing kinematics. These data are broken down using inverse dynamics analysis into the individual motions, velocities, and forces acting around each joint axis. I compare performance at each joint across experimental conditions to test hypotheses regarding the relationship between skeletal features and throwing performance. I also developed and tested a method for predicting humeral torsion using range of motion data, allowing me to calculate torsion in my subjects and determine its effect on throwing performance.

My results strongly support an important role for elastic energy storage in powering humans' uniquely rapid throwing motion. I also found strong performance effects related to anatomical shifts in the torso, shoulder, and arm. When used to interpret the hominin fossil record, my data suggest high-speed throwing ability arose in a mosaic-like fashion, with all relevant features first present in *Homo erectus.* What drove the evolution of these anatomical shifts is unknown, but as a result the ability to produce high-speed throws was available for early hunting and likely provided an adaptive advantage in this context.

Table of Contents

Abstract..... iii

List of Figures..... vii

List of Tables..... viii

Acknowledgements..... ix

Chapter 1 – An Introduction..... 1
- 1.1. Why throwing?..... 1
- 1.2. Thesis Overview..... 1
- 1.3. Literature Cited..... 6

Chapter 2 – The Effect of Humeral Torsion on Rotational Range of Motion in the Shoulder and Throwing Performance..... 7
- 2.1. Chapter Summary..... 7
- 2.2. Introduction..... 9
- 2.3. Model..... 13
- 2.4. Materials and Methods..... 17
- 2.5. Results..... 22
- 2.6. Discussion..... 25
- 2.7. Acknowledgements..... 31
- 2.8. Literature Cited..... 32

Chapter 3 – Elastic Energy Storage in the Shoulder and the Evolution of High-Speed Throwing in *Homo*..... 37
- 3.1. Chapter Summary..... 37
- 3.2. Introduction..... 38
- 3.3. Model..... 39
- 3.4. Materials and Methods..... 40
- 3.5. Results..... 44
- 3.6. Discussion..... 48
- 3.7. Acknowledgements..... 50
- 3.8. Literature Cited..... 51

Chapter 4 – The Biomechanics of Power Generation during Rapid, Overhand Throwing in Humans..... 54
- 4.1. Chapter Summary..... 54
- 4.2. Introduction..... 55
- 4.3. Model..... 58
- 4.4. Hypotheses..... 60
- 4.5. Materials and Methods..... 65
- 4.6. Results..... 71
- 4.7. Discussion..... 80

4.8. Acknowledgements…… 89
4.9. Literature Cited…… 90

Chapter 5 – Throwing and the Evolution of the Hominin Forelimb…… 95
5.1. Chapter Summary…… 95
5.2. Introduction…… 96
5.3. Who throws?…… 99
5.4. How do we throw?…… 104
5.5. Who threw first?…… 110
5.6. Why do we throw?…… 135
5.7. What questions remain?…… 142
5.8. Acknowledgements…… 144
5.9. Literature Cited…… 145

Appendix 1 – Supplemental Data for Chapter 2…… 168

Appendix 1 – Supplemental Material for Chapter 3…… 169

List of Figures

Figure 2.1: Humeral torsion vs. retroversion…….. 10
Figure 2.2: Predicting humeral torsion from rotational range of motion…… 15
Figure 2.3: Measuring humeral torsion using computed tomography..... 19
Figure 2.4: Measuring range of motion at the shoulder…….. 20
Figure 2.5: Torsion prediction regressions…….. 24
Figure 3.1: Model of throwing differences between *Pan* and *Homo*…….. 41
Figure 3.2: Shoulder and elbow power during throwing…….. 45
Figure 3.3: Brace-restricted power during throwing…….. 47
Figure 3.4: Humeral torsion and throwing performance…….. 49
Figure 4.1: Free-body diagram of the arm during cocking…….. 59
Figure 4.2: Critical upper body motions during throwing.…….. 61
Figure 4.3: Reflective markers and kinetic model…….. 66
Figure 4.4: Arm-cocking and acceleration phases…….. 70
Figure 4.5: Kinematic and kinetic data for 4 critical motions.…….. 72
Figure 5.1: Chimpanzee throwing…….. 100
Figure 5.2: Arm-cocking and acceleration phases…….. 103
Figure 5.3: Critical upper body motions during throwing.…….. 106
Figure 5.4: Free-body diagram of the arm during cocking…….. 108
Figure 5.4: Humeral torsion…….. 125
Supplemental Figure 3.1: Reflective markers…….. 170
Supplemental Figure 3.2: Kinetic model…….. 174
Supplemental Figure 3.3: Residual analysis – full trial…….. 177
Supplemental Figure 3.4: Residual analysis – critical period…….. 177
Supplemental Figure 3.5: Phase duration…….. 183
Supplemental Figure 3.6: Maximum ball speed…….. 188
Supplemental Figure 3.7: Shoulder sham power…….. 189
Supplemental Figure 3.8: Free-body diagram of the arm during cocking…. 196
Supplemental Figure 3.9: Static optimization…….. 197

List of Tables

Table 4.1: Segment definitions..... 67
Table 4.2: Torso restriction data..... 73
Table 4.3: Clavicle restriction data..... 75
Table 4.4: Shoulder restriction data..... 77
Table 4.5: Wrist restriction data..... 79
Supplemental Table 2.1: Measurement reliability data..... 168
Supplemental Table 3.1: Segment definitions..... 172
Supplemental Table 3.2: Joint definitions..... 175
Supplemental Table 3.3: Cutoff frequency data..... 179
Supplemental Table 3.4: Shoulder muscle volumes..... 185
Supplemental Table 3.5: Modeled power comparison..... 186
Supplemental Table 3.6: Chimpanzee throwing velocity..... 191

Acknowledgements

The process of completing a PhD is long, at times difficult, and could not be done alone. I owe a great debt of gratitude to many friends, colleagues, and mentors for their support and encouragement during the past seven years. You have made my time in graduate school interesting and enjoyable. Thank you!

First and foremost, I would like to thank my advisor, Dan Lieberman. Over the last seven years Dan has been my strongest advocate, provided good advice (and a healthy dose of nudging), read innumerable drafts of variable quality, and has always been available to talk about ideas, plans, or anything else that was on my mind. That I frequently find myself in academic talks thinking, "What is your model?" is terrifying, but also a testament to the sound, experimentalist approach to science that Dan has imparted to me. I am forever indebted to him for his continued belief in me and my abilities, for his patience in the face of my epic stubbornness, and for his being an excellent mentor and friend.

Many thanks are owed to my thesis committee: Richard Wrangham, for his constant encouragement and for always advocating on behalf of chimpanzee throwing abilities; Andy Biewener, whose biomechanical expertise and careful review of my work has made this thesis immeasurably better; L Mahadevan, whose ideas about throwing have changed my thinking; Tom Gill III, whose guidance through complicated hospital procedures and IRB protocols made a difficult process seamless; and finally Susan Larson, whose work I have followed and learned from

over the years, and whose careful reading and interrogation of my research has helped strengthen my work and clarified my thinking.

Completing this dissertation would not have been possible without the help and excellent ideas of my collaborators. Madhu Venkadesan was my partner in throwing related crimes during his time at Harvard. His ideas and help were critical in my thinking about elastic energy storage, the heart of my thesis. I count Madhu a good friend and look forward to our continued collaboration. Many thanks are due to Tom Gill IV, whose help and financial support made data collection at MGH possible. I would also like to thank Bill Palmer, who reached out numerous time on my behalf to cut through hospital red tape and get me access to hospital equipment. Finally, I would like to thank Mike Rainbow, whose biomechanical expertise made difficult data analysis easy. Mike's excellent ideas and careful review of my work have also vastly improved my writing and thinking. I look forward to our continued work together.

Many individuals were also vital in making my data collection and analysis possible. Leia Stirling and the Wyss Institute Motion Capture Lab were incredibly generous in allowing me to collect my kinematic data in their facility. Processing this data was a titanic endeavor and would never have been completed if not for the hundreds of hours spent by many Harvard students who tirelessly turned tiny little dots on a computer screen into my thesis data. For this I am indebted to Matt Vincent, Gulus Emre, Randi Griffin, Adanma Ekeledo, Wesley Gordon, and George

Karas. I am also very grateful to the many subjects who have participated in my experiments for kindly sharing their valuable time with me.

I am also very grateful to have been a part of the close-knit Human Evolutionary Biology department these past years. I have greatly enjoyed all of the many beer hours, Tuesday lunch talks, and getting to know and interact with so many interesting people. Special thanks are due to the members of the Skeletal Biology Lab past and present (Brian Addison, Meir Barak, Eric Castillo, Adam Daoud, Maureen Devlin, Carolyn Eng, Brenda Frazier, Kristi Lewton, Herman Pontzer, Dave Raichlen, Campbell Rolian, Madhu Venkadesan, Anna Warrener, Katherine Whitcome, Sara Wright, and Katie Zink) who taught me a great many things and made my life at Harvard enjoyable. I count you all as good friends and will (and do) miss seeing you all every day.

To Meg Lynch, Meg Jarvi, and Laura Christoffels (the best departmental staff anywhere): Thank you, Thank you, a thousand times…Thank you. Your help sorting out the intricacies of university bureaucracy, grant renewals, paycheck issues, and the thousands of other tasks I have bothered you with has been invaluable.

Many thanks are owed to my other mentors, David Pilbeam and Sally McBrearty. Throughout my time at Harvard, David has always been there to provide good advice, listen to me vent, and help me when I needed it. David has generously written countless recommendations, made many phone calls, and procured many ASPR dollars on my behalf. His help and support have always been graciously given and were always much appreciated. Sally McBrearty has been my mentor and friend

since I walked into her office at UConn in the fall of 2001, declared that I was interested in human evolution, and asked if she would advise me. Sally took me under her wing, brought me to do fieldwork in Kenya (an experience that changed the course of my life), and treated and trained me as one of her own graduate students. Sally's unshakable belief in me, her continued support, and the doors she has opened for me are debts I will never be able to repay. I am forever grateful.

I also want to thank my parents, Brian and Kathy Roach, and siblings, Lee, Jessica, and Thomas, for their encouragement, support, and love during this process. While my parent's interest and love of the natural world was passed to all of us kids, my father's fascination with dinosaur bones has mutated a bit in its passage to me. Nonetheless, I always had an interested audience during visits home, who thought what I worked on was cool and encouraged me when I needed it most.

Finally, I owe the greatest debt of gratitude to my wife, Amanda Lobell. Meeting Amanda in graduate school was by far the best thing that has ever happened to me and she has filled my time in Cambridge with love, caring, and unreasonable amounts of fun. Amanda's impact on this thesis is not quantifiable. She has acted as my research assistant, my editor, my confidant, my advisor, and my therapist. She has been there for me through every step of this process. I owe her more than I can hope to repay (although she reminds me frequently that a vacation would be a good way to start). I consider myself immensely lucky to call her my best friend, my colleague, and my wife.

Chapter 1 – An Introduction

1.1 Why throwing?

How and why do humans throw projectiles with both considerable accuracy and high velocities? Human throwing ability is unique among animals and universal to all human cultures. High-speed throwing was likely important during human evolution, enabling hominin throwers to hunt more effectively and safely, to drive off predators, and to interact aggressively with other individuals from a safer distance than more direct forms of fighting. Despite the potential adaptive importance of high performance throwing, little is known about the evolution of this unique and critical behavior. This thesis investigates the biomechanics of how humans produce high-speed throws and examines how differences in skeletal and soft tissue anatomy affect throwing performance. The results of these analyses are applied to the hominin fossil record in hopes of gaining insight into the evolutionary history and antiquity of high-speed throwing.

1.2 Thesis Overview

This dissertation includes four related studies. Chapter 2 considers the effects of humeral torsion on the range of rotational motion in the shoulder and throwing performance. Chapter 3 proposes and tests a model for elastic energy storage in the shoulder. Chapter 4 presents and tests a model of anatomical variations that improve the biomechanics of power generation during rapid, overhand throwing in humans. Finally, Chapter 5 integrates the evidence from

Chapters 2-4 with fossil and archaeological evidence to review how and when throwing evolved and how selection for throwing may have helped modify the hominin upper body and forelimb.

In Chapter 2, I examine the effect of humeral torsion of rotational range of motion at the shoulder. Humeral torsion is a highly variable angular measure that quantifies the difference between the orientation of the humeral head and the axis around which flexion and extension occur in the elbow. Previous studies have shown that throwing athletes have lower levels of humeral torsion than non-throwing athletes, and lower levels of torsion in their throwing versus non-throwing arms (1-4). Some of these studies have also shown that throwing athletes with higher than expected torsion are more likely to experience pain and injuries to their shoulders (1). While these studies have attempted to link torsion values with biomechanically meaningful measures such as rotational range of motion in the shoulder, they have only partially confirmed these relationships. Chapter 2 investigates the relationship between humeral torsion and active range of motion by regressing actual computed tomography (CT) derived humeral torsion values against predicted values calculated from range of motion data (both goniometric and 3D kinematic data). My findings show that range of motion measures are significantly correlated with underlying humeral torsion values and can be used to predict these values when medical imaging is not possible.

In Chapter 3, I propose a biomechanical model for how humans achieve rapid throws in part by using elastic energy stored in the ligaments, tendons, and muscles

crossing the shoulder. According to the model, elastic energy is used to amplify power production by muscles, resulting in very rapid motions in the forelimb. I further hypothesize that anatomical differences between humans and chimpanzees compromise chimpanzees' ability to use this elastic energy storage mechanism and help to explain why our closest extant relatives throw so poorly. I use three lines of evidence to test these hypotheses: 1. a kinetic analysis of humeral rotation during throwing; 2. a quantitative comparison of actual power production at the shoulder with modeled estimates of shoulder muscle power generation capacity; 3. an experimental perturbation of the proposed elastic energy storage mechanism. The results from these studies show that during normal throwing, the humerus first externally rotates passively, stretching the elastic elements at the shoulder. Furthermore, during this stretching a large opposing muscular force is generated by the shoulder muscles, resulting in a sustained period of energy absorption during which elastic energy is stored. When released, this energy can account for more than half of the total energy required to generate the rapid internal rotation of the humerus that follows. Mathematical modeling of shoulder joint power shows that forces generated by shoulder muscles alone are insufficient to explain the rapid motions of the arm, confirming the importance of the elastic energy mechanism. Finally, a perturbation of this elastic storage mechanism using a shoulder brace shows that storage of elastic energy at the shoulder affects the velocity of the arm and of the projectile. We infer from these data that a mobile waist and hips, "relaxed" laterally oriented shoulder, and low humeral torsion all increase throwing performance by enabling more elastic energy storage and release. The presence of

all of these functionally important morphologies in *Homo erectus* suggests that these hominins could throw projectiles with high-speed, and may have done so during hunting.

Chapter 4 focuses on power generation, by testing how variations in upper body skeletal anatomy would affect the four key motions that previous studies (5) have shown to contribute the most to projectile velocity: 1. internal rotation of the humerus; 2. elbow extension; 3. torso rotation; 4. wrist flexion. The performance effects of the throwing motion were perturbed using braces that restrict particular movements, allowing me to quantify the effects of specific components of normal throwing using an observed vs. expected framework. I use three-dimensional inverse dynamics analysis to decompose the complex throwing motion into the individual rotations occurring at each joint and the forces that drive those rotations. These joint performance data are then used to test a set of discrete hypotheses of how joint motions are interrelated. The results suggest that high-velocity during throwing is achieved using a combination of kinetic energy transfer between adjacent body segments — a "kinetic chain" (6-9) — combined with substantial power amplification from elastic energy stored at the shoulder. Restriction of proximal joint motions at the torso and shoulder lead to significant reductions in throwing performance measures not only in the restricted joint but also more distal joints. These results provide insight into why the shoulder and elbow frequently suffer repetitive stress injuries in throwing athletes.

Finally, in chapter 5, I review what is known about the mechanics of throwing and interpret the hominin fossil record in light of these data. I assess my own functional hypotheses as well as previous functional morphological interpretations of hominin fossil material relating to throwing performance and address the biomechanical support for those interpretations. I conclude that the morphological shifts that enable high-speed throwing behavior emerge in a mosaic-like fashion in *Australopithecus* and early *Homo.* By *Homo erectus*, all the relevant features appear to be present, suggesting that this species had modern human-like throwing performance abilities. I conclude that such throwing ability would have provided significant adaptive benefits for early hunting, although further research is necessary to determine the extent to which selection for throwing or other behaviors led to the evolution of these features.

1.3 Literature Cited

1. Pieper HG (1998) Humeral torsion in the throwing arm of handball players. *Am J Sports Med* 26(2):247-253.

2. Osbahr DC, Cannon DL, & Speer KP (2002) Retroversion of the humerus in the throwing shoulder of college baseball pitchers. *Am J Sports Med* 30(3):347-353.

3. Reagan KM*, et al.* (2002) Humeral retroversion and its relationship to glenohumeral rotation in the shoulder of college baseball players. *Am J Sports Med* 30(3):354-360.

4. Chant CB, Litchfield R, Griffin S, & Thain LM (2007) Humeral head retroversion in competitive baseball players and its relationship to glenohumeral rotation range of motion. *J Orthop Sports Phys Ther* 37(9):514-520.

5. Hirashima M, Kudo K, Watarai K, & Ohtsuki T (2007) Control of 3D limb dynamics in unconstrained overarm throws of different speeds performed by skilled baseball players. *J Neurophysiol* 97(1):680-691.

6. Hirashima M, Yamane K, Nakamura Y, & Ohtsuki T (2008) Kinetic chain of overarm throwing in terms of joint rotations revealed by induced acceleration analysis. *J Biomech* 41(13):2874-2883.

7. Higgins JR (1977) *Human Movement: an integrated approach* (The C.V. Mosby Company, Saint Louis).

8. Feltner ME (1989) 3-Dimensional Interactions in a 2-Segment Kinetic Chain .2. Application to the Throwing Arm in Baseball Pitching. *Int J Sport Biomech* 5(4):420-450.

9. Atwater AE (1979) Biomechanics of overarm throwing movements and of throwing injuries. *Exerc Sport Sci Rev* 7:43-85.

Chapter 2 – The Effect of Humeral Torsion on Rotational Range of Motion in the Shoulder and Throwing Performance

2.1 Chapter Summary

Several recent studies have found that throwing athletes typically have lower humeral torsion (retroversion) and a greater range of external rotation at the shoulder than non-athletes. How these two parameters are related is debated. This study uses data from a sample of both throwers and non-throwers to test a new model that predicts torsion values from range of motion data. The model proposes a series of predicted regressions, which can help provide new insight into the factors affecting rotational range of motion at the shoulder.

Humeral torsion angles were measured from computed tomography scans collected from 25 male subjects. These values are compared to predicted torsion values for the same subjects calculated from both kinematic and goniometric range-of-motion data. Results show that humeral torsion is negatively correlated (*Goniometric:* $r = -0.409$, $p = 0.047$; *Kinematic:* $r = -0.442$, $p = 0.035$) with external rotational range of motion and positively correlated (*Goniometric:* $r = 0.741$, $p < 0.001$; *Kinematic:* $r = 0.559$, $p = 0.006$) with internal rotational range of motion. The predicted torsion values are highly correlated (*Goniometric:* $r = 0.815$, $p < 0.001$; *Kinematic:* $r = 0.617$, $p = 0.006$) with actual torsion values. Deviations in the data away from predicted equations highlight significant differences between high torsion and low torsion individuals that may have significant functional

consequences. The method described here may be useful for non-invasively assessing the degree of torsion in studies of the evolution and biomechanics of the shoulder and arm, and for testing hypotheses about the etiology of repetitive stress injuries among athletes and others who throw frequently.

2.2 Introduction

Humeral torsion describes the angular difference between the orientation of the proximal humeral head and the axis of the elbow at the distal humerus. This angle is measured at the intersection of two lines: one that evenly bisects the articular surface of the humeral head proximally, and the second being the transepicondylar line distally (Figure 2.1). In the clinical literature, this angle is measured in the opposing direction and is referred to as humeral retroversion. Therefore, a measured increase in retroversion is the same as a decrease in torsion. These two terms simply represent different assumptions about the neutral position of this angle (1-5). The use of alternative terms has led to some confusion in the literature (1, 2). For clarity, we will here use exclusively the term humeral torsion and have translated the results of previous studies cited as needed.

In humans, humeral torsion is highly variable. Torsion values have been shown to differ between western and non-western populations (4, 6-8), males and females (6-9), and by side of the body (6, 8, 10). Torsion also varies ontogenetically, with younger individuals having less torsion, which then increases during postnatal growth (5, 11-13). During normal postnatal ontogeny, torsion steadily increases by an average of 23.4 degrees until the completion of skeletal growth (11). Much of this change in torsion seems to occur at the proximal humerus, which is one of the last bones in the body to fuse: only 20 percent of individuals have achieved fusion by 18 years of age (14).

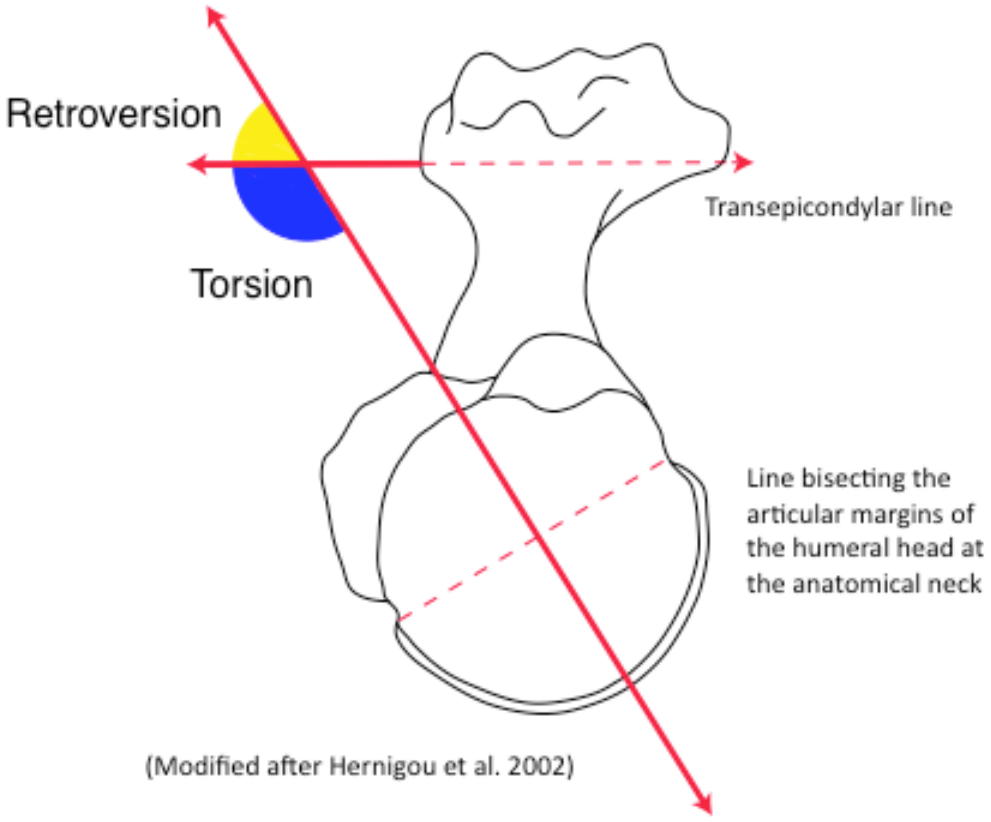


Figure 2.1. Humeral torsion (in blue) is determined by measuring the angle between the orientation of the humeral head and the distal condyle of the humerus. In the clinical literature, the same angle is referred to as humeral retroversion (in yellow) and is measured in the opposite direction.

Many previous functional studies of humeral torsion have focused on the relationship between torsion and habitual throwing activity (15-19). Athletes who habitually throw tend to have 10-20 degrees less torsion in their dominant, throwing arm compared to their non-dominant arm and the arms of non-throwing controls (15-25). No statistical difference has been found between arms in non-throwing controls (15, 16, 19). Furthermore, Pieper (19) shows that when throwing athletes are subdivided into those with and without chronic pain, those reporting

chronic pain did not show this reduction in dominant arm torsion. Other studies have sought to further clarify the relationship of torsion to injury by linking torsion to rotational range-of-motion (ROM) in the shoulder (15, 17, 18).

Deficits to rotational ROM in the shoulder have long been suggested as a potential cause of shoulder injury in throwing athletes (26-31). A recent study by Wilk et al (26) showed that a deficit to the total rotational ROM at the shoulder of as little as 5 degrees led to a twofold increase in the likelihood of injury. Previous work has shown that, much like torsion, rotational ROM also differs between dominant and non-dominant arms in throwing athletes (15-18, 22, 23, 28, 32, 33). Throwing athletes typically have an externally shifted ROM arc in the throwing arm, with an increase in external rotational ROM of between 9-13 degrees and a similar deficit to the internal rotational ROM (15-18).

Beyond its relevance to understanding injury, rotational range of motion at the shoulder may also have significant performance consequences. Glenohumeral rotation is known to be a significant contributor to power generated during the throwing motion (22, 34-37). Reaching angular velocities in excess of 7000 degrees per second, the rapid internal rotation of the humerus is the fastest motion produced by the human body and this rotation can generate very high torques (22, 35, 36). Whether modifications to the rotational ROM allow additional acceleration of the arm and torque production at the shoulder is unknown and is an important avenue for future research.

What factors contribute to variations in the rotational ROM arc is unclear. Numerous authors have posited that these modifications result primarily from changes to the soft tissues of the shoulder capsule (22-25, 38-43). These same studies note the high prevalence of severe laxity in the anterior glenohumeral capsule of throwing athletes. Burkhart and colleagues have further suggested that this anterior laxity is accompanied by tightening of the ligaments in the posterior portion of the capsule (31, 38). Still others have suggested that skeletal remodeling of the proximal humerus is the major cause of modifications to the rotational ROM at the shoulder (15-19). Several studies investigating the relationship between humeral torsion and rotational ROM have found significant correlations between these two variables in professional and collegiate throwing athletes (15, 17, 18). However, these correlations have not been consistent in either strength or directionality between studies.

Although the studies noted above have all found significant negative correlations between external rotational ROM and torsion, the relationship between internal rotational ROM and torsion is less clear. Osbahr et al (17) and Reagan et al (18) found no statistically significant relationship between internal rotational ROM and torsion in baseball pitchers. In contrast, Reagan et al (18) found these variables to be significantly, negatively correlated in baseball players playing field positions. This result contrasts with another study of baseball players of unspecified positions in which internal rotational ROM and torsion were significantly, positively correlated (15).

We sought to clarify and generalize the relationship between humeral torsion and rotational range of motion at the shoulder using a sample of both collegiate athletes and non-athletes. We propose a simple, new model to predict expected torsion values from ROM data collected using both standard goniometry and kinematics. Our method is then validated against observed (actual) torsion values derived from computed tomography (CT). This observed versus expected framework allows us to generate testable predictions and move beyond simple strength of correlation results. Using this method, we can begin to address the complex interplay between how soft and hard tissues affect ROM at the shoulder joint, how this interplay may relate to injury, and the possible functional consequences of these tradeoffs. This method also provides a means to assess ranges of motion in the fossil record, allowing us to test some hypotheses about the evolution of throwing capabilities.

2.3 Model

We tested a model that uses ROM measures to predict torsion values and vice versa. Our model is based on a set of simple assumptions.

We begin with the assumption that the total rotational ROM (internal + external) is not correlated significantly with the degree of torsion, as shown by previous studies (15, 17, 18). We therefore would expect any angular change at the external end of the ROM arc must be coupled with a commensurate, opposing angular change at the internal end of the ROM arc. Thus, while the values for internal and external rotational ROM will change, the sum of these to values will not.

This requires a one-to-one tradeoff between internal and external rotational ROM, which accounts for the constant total ROM value, and leads to all regression predictions between torsion and any range of motion value in our analyses having an absolute slope of 1.0. This predicted slope allows for changes in torsion to affect changes in the position of the ROM arc relative to the body without affecting the total ROM. Furthermore, this assumption of a constant total ROM leads to the prediction that the regression relationships between external rotational ROM/torsion and internal rotational ROM/torsion should also be inversely related (as one increases the other decreases).

Predicting torsion values from ROM data further requires the assumption that the midpoint of the total ROM arc represents the neutral, resting position of the humerus in relation to the scapular glenoid. If this is correct, then the location of this neutral position should provide an indication of the degree of humeral torsion. Individuals with a total ROM midpoint that is internally shifted are predicted to have a higher torsion value than individuals with more externally shifted total ROM midpoints. Using the measured external and internal rotational ROM maxima, expected torsion values are generated using the formula below (see also Figure 2.2). Note: The addition/subtraction of 180 degrees in all formulas allows our results to be reported using a common convention for human torsion values, eg. (7, 44).

Equation 2.1.

$$\text{Torsion (predicted)} = 180 - \left(\frac{\chi_{\max\ Ext\ ROM} - \chi_{\max\ Int\ ROM}}{2} \right)$$

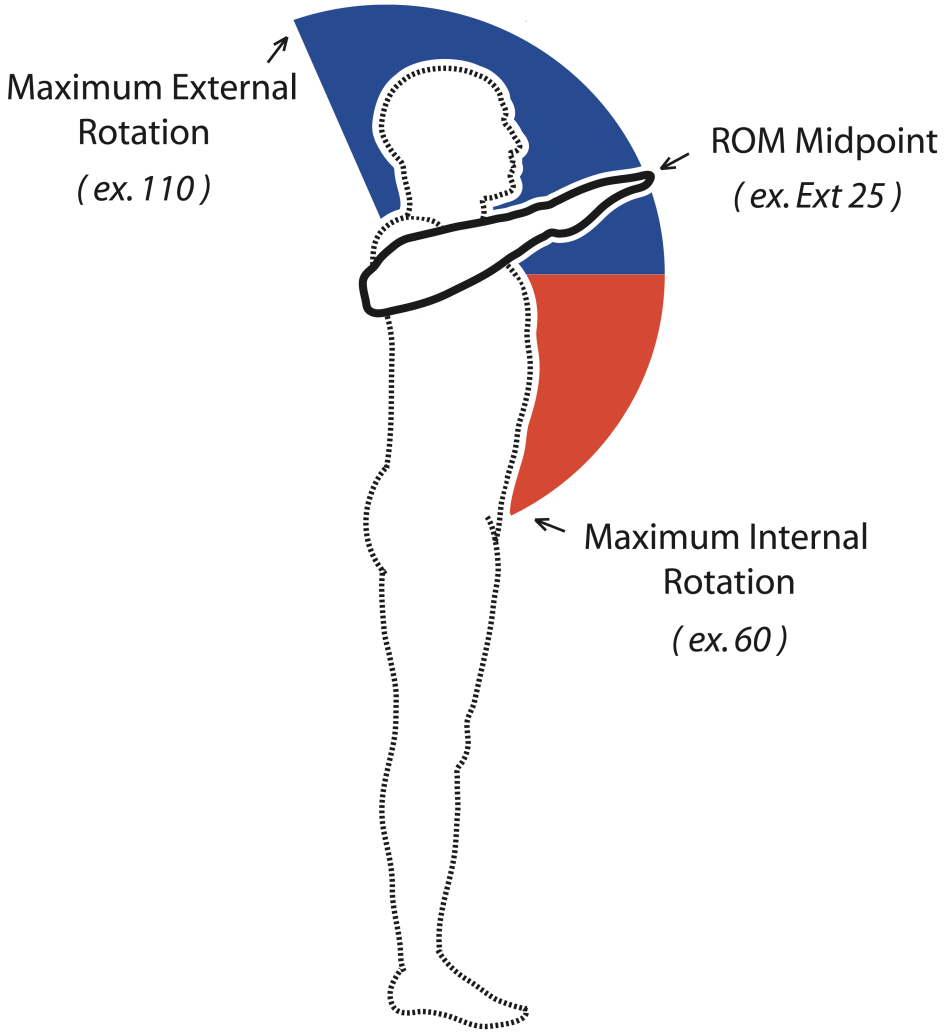


Figure 2.2. Torsion is predicted from mean ROM maxima data. The difference between external and internal rotation (in the example – 25 degrees) is equal to the ROM midpoint. The use of the 180-degree term allows the torsion value to be reported according to prior convention. Note: Following clinical definition, external rotational ROM is illustrated in blue and internal rotational ROM is illustrated in red.

To test our assumptions, these expected values are regressed against actual torsion values. If our model is accurate, the predicted torsion values will closely match the

actual values. Thus, for the predicted torsion (y)/actual torsion (x) regression we predict a regression equation of y=x.

Although predicting torsion values from ROM data is useful, when the actual regressions differ from our predictions it becomes important to accurately address the discrepancy. By running our model in the reverse direction and predicting external and internal rotational ROM from actual torsion values we can better identify the source of the discrepancy. These reverse predictions again rely on the assumption that the midpoint of the total rotational ROM reflects the underlying torsion. Given this assumption, a predicted ROM midpoint can be generated from actual torsion values. By adding/subtracting half of the mean total ROM from this midpoint, external and internal ROM maxima can be generated. The formula used to generate predicted external ROM values is:

Equation 2.2.

$$\textit{External ROM (predicted)} = -\textit{Actual torsion} + \left(180 + \frac{\textit{total ROM}}{2}\right)$$

The regression equation derived from this formula is y = -x + (180+ ½ total ROM); with (y) as predicted external ROM and (x) as actual torsion. For our calculations, we use the mean total ROM value across all subjects (reported below). According to our model, as torsion increases there should be a commensurate decrease in external ROM maxima (hence the slope of -1.0). This prediction is tested against the actual external rotational ROM maxima/torsion regression. The formula used to

generate predicted internal ROM values is:

Equation 2.3.

$$\text{Internal ROM (predicted)} = \textit{Actual torsion} - \left(180 - \frac{\textit{total ROM}}{2}\right)$$

The regression equation derived from this formula is y = x - (180 - ½ total ROM); with (y) as predicted internal ROM and (x) as actual torsion. Accordingly, as torsion increases, so too should the internal ROM maxima (hence the slope of 1.0). This prediction is tested against the actual internal rotational ROM maxima/torsion regression.

2.4 Materials and Methods

Subjects - Twenty-five adult male subjects (ages 18-35) were recruited to participate in the study. Thirteen of the subjects were collegiate athletes (6 baseball players from a variety of positions, 7 athletes from non-throwing sports) and the remaining 12 subjects were non-athletes. The proportions of the study sample were chosen to maximize the variance in torsion values surveyed and to reduce the effects of pathological ROM often found in throwing athletes (26, 29, 38). Institutional review board approval was obtained from both Massachusetts General Hospital and Harvard University. Subjects provided written consent and completed an injury history and physical activity questionnaire prior to participation in the study.

Computed Tomography (CT) Imaging - All subjects were CT scanned at the Massachusetts General Hospital Imaging Center using a GE 8-slice Lightspeed Computed Tomography Imager. A low dose scanning technique was used to minimize radiation exposure to the subjects. Subjects were positioned on the scanner examination table with their dominant arm fully adducted at their side and their elbow flexed 90 degrees with their forearm resting on their abdomen. The arm was then immobilized by wedging a stiff pillow between the arm and the examination table. Two separate scans were targeted and collected at the shoulder and the elbow. Each scan covered approximately 5 cm of the arm, capturing each end of the humerus with 5mm think image slices. The images were processed using Image J software and the humeral torsion angle calculated (following (45)) by subtracting the angle of the transepicondylar line from the axis of the humeral head (Figure 2.3). The humeral torsion angle was calculated using the mean of the three best superior and inferior scans. The measurement reliability was calculated (see supplemental data) and the mean torsion angle was used in the analysis as the actual, CT derived torsion value.

Range of Motion (ROM) measures - Active ROM was measured using both standard goniometry and three-dimensional kinematic imaging. Active ROM, where subjects rotate their arm to the limits of their ROM using their own muscular power, was used instead of passive ROM because it most closely approximates the functional ROM available for actions such as throwing and also reduces the effects of any anisotropy in the capsular ligaments. The two different methods for collecting

ROM data were used to maximize the utility of our method for a variety of research and clinical contexts.

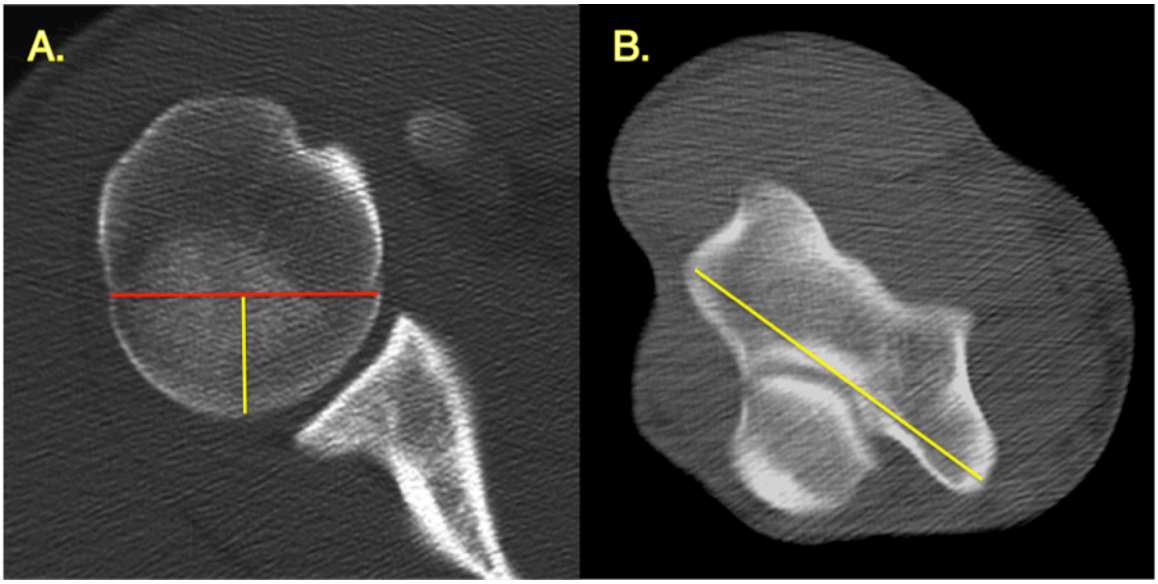


Figure 2.3. Humeral torsion was measured in Image J by creating transects between the inflection points marking the anatomical neck proximally (A) and along the distal transepicondylar line (B).

For goniometric ROM measurements, subjects were positioned on an examination table with their dominant arm off the side of the table (Figure 2.4). The arm was positioned in line with both shoulders in a neutral shoulder flexion/extension posture. The shoulder was abducted 90 degrees and the elbow flexed 90 degrees. The subject was instructed to keep their shoulder pressed to the examination table to prevent scapular movement. The subject then rotated his arm to both its maximal external and internal rotation position and held this position for 5 seconds for goniometric measurement taken along the length of the forearm. The measurements were taken using a Jamar 12 ½" goniometer, which was modified to

include a weighted plumb line to serve as a vertical arm. The rotational motion and measurements were repeated twice. Measurement repeatability was calculated using the interclass correlation (see supplemental material). The mean of both external and internal ROM maxima measures were taken and the predicted, goniometry derived torsion value was calculated using equation 1.

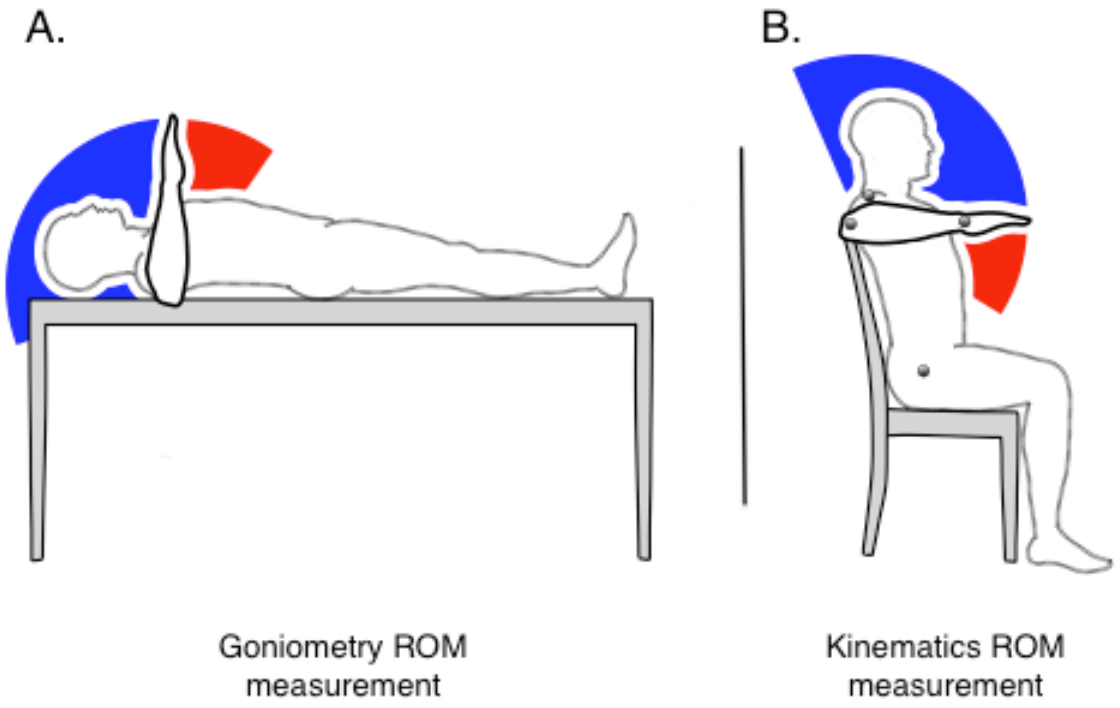


Figure 2.4. For the ROM calculations, each subject was measured using a standard goniometer (A) and a kinematic imaging system (B). For the goniometric measurement, the subject was in a supine position on an examining table. For the kinematic measurement, the subject was seating in an armless chair. External rotational ROM is illustrated in blue and internal rotational ROM is illustrated in red.

For the kinematic ROM measurements, data was collected using an eight-camera Qualisys Motion Capture 3D Infrared Oqus camera system collecting at 500Hz. All subjects were fitted with nine 25cm passive reflective markers. The markers were placed on C7 prominens, both hips (at the greater trochanter of the femora), both scapular acromion, the lateral and medial epicondyles of the dominant side distal humerus and both ulnar and radial styloid processes in the dominant side wrist. The subject was then seated in an armless, high backed office chair in an upright posture with the back firmly against the chair back. The subject was again instructed to position his arm out to the side of his body, in line with both shoulders. The shoulder was abducted 90 degrees and the elbow flexed 90 degrees. The subject was then instructed to again rotate their arm to both its maximal external and internal rotation position with as little scapular motion as possible (to limit scapular protraction or retraction). The motion was repeated between 4-6 times during 30 seconds of data capture. Raw 3D marker positional data was processed using Qualisys Task Manager software and exported for analysis to MATLAB 7.6. Custom written MATLAB code was used to calculate external and internal ROM maxima while correcting for minor deviations in elbow and shoulder position. Measurement reliability was calculated and the means of both external and internal rotational maxima were used to generate predicted, kinematics derived torsion values using equation 1.

Statistical analysis - Pearson correlation coefficients were calculated and the presence of outliers tested (using Mahalanobis distances at a 95% confidence

interval) with JMP version 5 software. Intraclass correlations were calculated to assess measurement reliability using SPSS version 19 software.

2.5 Results

Total rotational ROM was calculated first as an initial test of the validity of our model. Total ROM values, calculated as the external ROM maxima plus the internal ROM maxima, ranged from 108.5 - 205.5 degrees (*Goniometric*: mean – 153.4, st. dev. – 18.2; *Kinematic*: mean – 142.3, st. dev. – 21.5). As hypothesized, no statistically significant correlation was found between actual torsion and the total rotational ROM (*Goniometric:* $r = 0.229$, $p = 0.293$; *Kinematic:* $r = 0.328$, $p = 0.127$). This lack of a significant relationship between torsion and total rotational ROM is consistent with previous studies (15, 17, 18) and provides support for our model's initial assumption.

The measured values of both internal and external rotation ROM were then regressed against actual, CT derived torsion values. These regressions were compared to the predicted regression relationship derived from the model to assess any potential skew in our model.

Measured external ROM values ranged from 70.5-120.5 degrees (*Goniometric*: mean -100.7, st. dev. – 10.9; *Kinematic*: mean – 105.4, st. dev. – 7.9). In keeping with previous work (15, 17, 18) and our model's predictions, external rotational ROM is significantly negatively correlated with actual torsion using both goniometric ($r = -0.409$) and kinematic ($r = -0.442$) measures. However, the slope of the measured external ROM/torsion regression is significantly lower than our

predicted slope of -1.0 (Figure 2.5A & 2.5D). This deviation from the predicted equation appears to be driven primarily by lower than predicted external ROM values in low torsion individuals.

Measured internal ROM values ranged from 1-99.5 degrees (*Goniometric*: mean -51.5, st. dev. – 15.5; *Kinematic*: mean – 34.8, st. dev. – 22.4). As hypothesized, internal rotational ROM is significantly positively correlated with actual torsion using both goniometric ($r = 0.741$) and kinematic ($r = 0.559$) measures. The internal ROM/actual torsion regression equations are not significantly different than the predicted equation and the predicted slope of 1.0 (Figure 2.5B & 2.5E).

Finally, predicted torsion values were calculated from both ROM data sets and regressed against actual torsion. The actual (CT derived) torsion values ranged from 111.6 – 184.1 degrees (mean - 141.1, st. dev. – 18.3). Both predicted torsion measures are significantly correlated with actual torsion (Figure 2.5C & 2.5F). Goniometric predictions are more highly correlated ($r = 0.815$) with actual values than are the kinematic predictions ($r = .617$). Beyond the strength of the correlations, it is worth noting that neither predicted versus actual torsion regressions has the slope of 1.0 expected in our model. Both predicted/actual torsion regressions show significantly higher predicted values in individuals with low actual torsion. This is in keeping with the deviation from expected values found in the external ROM maxima in low torsion individuals. While the strength of the correlations varies between the ROM collection methods, the regression equations

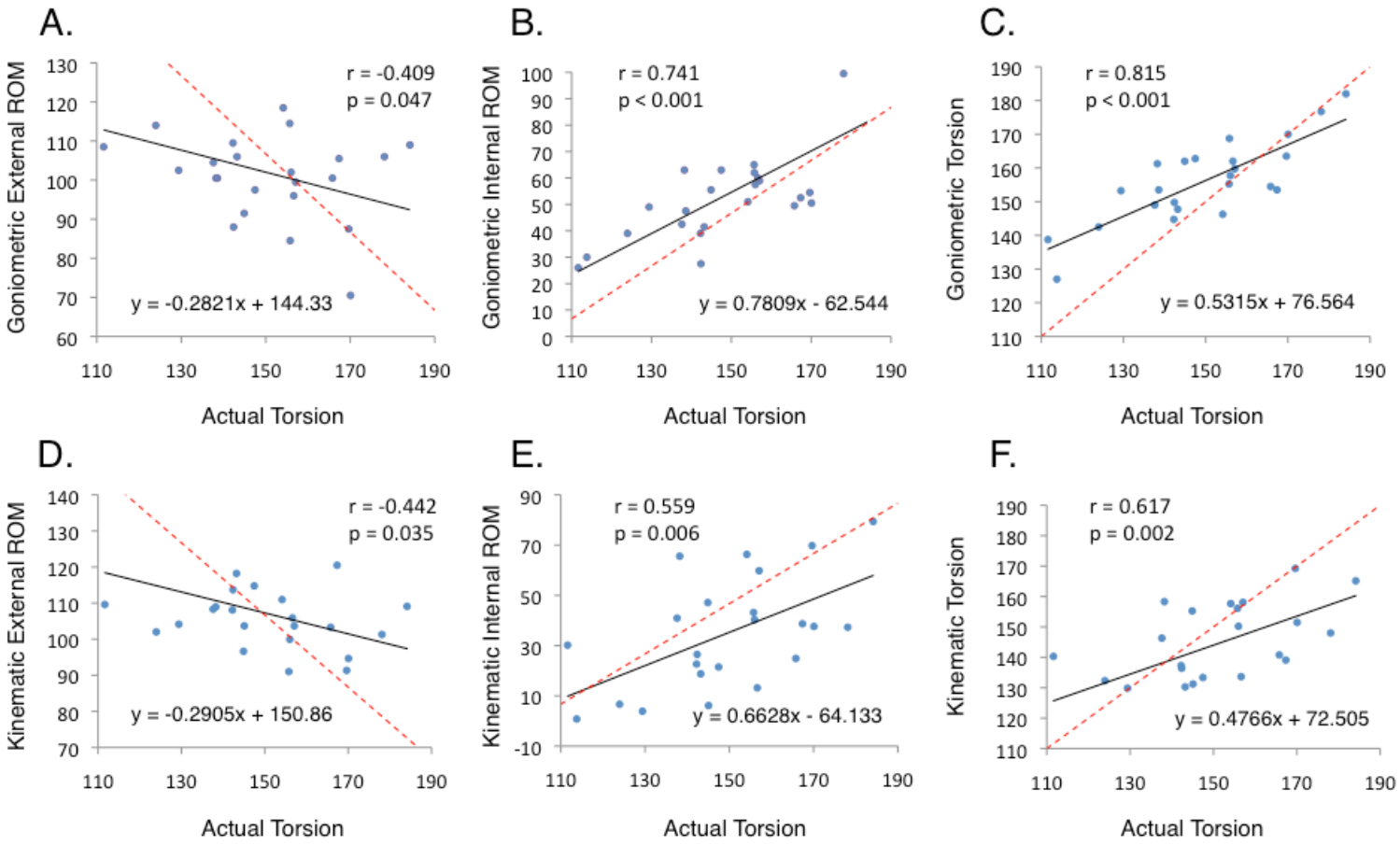


Figure 2.5. Regression relationships, Pearson's correlation coefficients (r) and significance values (p) are shown for all statistically significant parameters. The red dashed line illustrates the expected regression equations for each parameter. Note: The number of subjects (N) represented in each graph is variable. For graphs A & C; N = 24 as goniometry data was missing for 1 subject. For graph B; N = 23 due to the same lack of data from 1 subject and the exclusion of a significant outlier. For graphs D, E & F; N = 23 as maker occlusion prevents calculation for 2 subjects.

for both predicted/actual torsion regressions are statistically indistinguishable from each other.

2.6 Discussion

As predicted, the above results show that the ROM available for internal rotation increases with humeral torsion. Further, this increase is accompanied by a decrease in the ROM available for external rotation. This finding supports the inverse tradeoff between internal and external rotation and humeral torsion found by Chant et al. (2007). The strength of the correlations reported here between ROM and torsion are equivalent to previous published values for external rotation ROM and significantly higher than previously published values for internal rotation ROM (15, 17, 18). This improved correlation coefficient for the relationship between internal rotational ROM and torsion may partly result from increasing the variance in the sample by including non-throwers in the study population.

As in previous studies, no significant relationship was found between total rotational ROM and humeral torsion (15, 17, 18). This result supports the validity of our model's assumptions. It should be noted that there is a non-significant trend in this relationship towards a slight increase in total rotational ROM with increased torsion from both ROM data sets. A power test indicates that significantly larger samples would be required to test the statistical validity of this trend (needed sample, *Goniometric:* 197; *Kinematic:* 92). If this trend were supported, it would seem to defy clinical expectations that low torsion throwing athletes might be

expected to extend their total rotational ROM with increased laxity of the anterior shoulder capsule. However, in the light of its current non-significance this trend should be interpreted with caution until a larger, balanced sample of throwers and non-throwers is available.

The strength of the correlation coefficients reported here suggests that the hard tissue contributions to rotational ROM are significant, but that soft tissue contributions may also be substantial. However, caution should be exercised before attributing the remaining variance to soft tissue effects as some of this variance is likely explained by the co-occurrence of other small shoulder motions that accompany humeral rotation (46). These small scapular motions can reduce the accuracy of humeral rotation measures and may account for some of the differences in capsular laxity reported in previous studies (27, 29, 38). Furthermore, given the near spherical shape of the articular surface of the humeral head and the rotational nature of the motion investigated here, it seems likely that in a neutral shoulder flexion/extension posture that the anterior and posterior ligaments of the glenohumeral capsule would be stretched roughly equally. Only when these humeral rotations are accompanied by deviations from this neutral flexion/extension posture, such as during the maximal shoulder extension seen in the windup of a pitch, would we expect the asymmetrical stretching of the capsular ligaments and the resulting laxity.

The strength of the predicted torsion values reported here strongly validate our method of estimating torsion using simple kinematic measures and without the

use of costly radioactive imaging. While the goniometric predictions were significantly stronger in this analysis than the kinematic method, this difference in strength may very well be due to small scapular protraction/retraction that occurred during the kinematic imaging trials. While scapular movement was limited by contact with the table during goniometric data collection, this was not possible during the kinematic trials. Although our marker setup allowed us to identify protraction and retraction of the scapula, without additional markers collecting scapular movement data it was not possible to correct for the minor scapular rotations that accompanied these movements. Another potential factor affecting the strength of our regressions could result from not providing external support for the weight of the arm. Minor deviations in humeral position could introduce noise into our data. However, due to the short duration of data collection fatigue effects are unlikely and humeral movements are thought to be quite minimal and evenly applied to both data sets. While these small movements apparently reduced the strength of the regressions (more noticeably in the kinematic data), they do not significantly alter the slope of the regression equations. The consistency of the slope between both ROM data sets provides further confidence in the predictive model.

A key result is that the predicted torsion values deviate from the predicted regression equation ($y = x$), especially in the low torsion individuals. These low torsion individuals showed more internal rotation than expected and lower external rotation. In the kinematic ROM measures the high torsion individuals also deviate from the predicted regression with higher than expected external ROM and lower internal ROM. What factors are responsible for these residuals is unclear. Covarying

changes in the carrying angle of the elbow (45) could be responsible for these differences, as might some non-ligamentous soft tissue constraint such as differences in muscle mass. Further research is needed to resolve this problem.

Based on our empirical data (reported in Figure 5C & 5F), we propose that a better linear regression for predicting torsion would be (y = .5x + ½ total ROM). This regression equation represents a simplification of the empirically derived slopes (0.4766x, 0.5315x) to a slope of 0.5x and the empirical intercepts (72.505, 76.564) to an intercept equal to half of the total ROM (for our data - 71.2, 76.7 respectively). Using this modified regression equation to predicting torsion from ROM maxima, we derive:

Equation 2.5.

$$\text{Torsion (predicted)} = \left(\frac{180 - \left(\frac{\chi_{\max\ Ext\ ROM} - \chi_{\max\ Int\ ROM}}{2} \right) - \left(\frac{total\ \ ROM}{2} \right)}{0.5} \right)$$

This predictive equation is useful in kinematic studies and when imaging of subjects is not possible. It could also be a useful clinical tool for quickly identifying throwing athletes with high torsion values who might be at increased risk of shoulder and elbow injury.

This non-invasive assessment of torsion may be particularly important for juvenile athletes. Little league players (especially pitchers) have been shown to have high rates of injury both to the shoulder and elbow (47-55). It has been suggested that these injuries are the result of overuse of the shoulder and arm during the

throwing motion (38, 39, 56, 57). It is also possible that the risk of injury in juveniles is further increased due to the incomplete torsion of their throwing arm. Such incomplete torsion could lead to compensations in the throwing motion, which in turn could put additional stresses on downstream joint such as the elbow leading to injury.

It is also noteworthy that there are some significant differences between the correlation values reported in this study and other studies (15, 17, 18). These may in fact represent important differences in functional constraints between differing study populations. Our study found correlation coefficients for external rotation ROM and torsion that were equal to or slightly lower than previous studies. Conversely, for the relationship between internal rotation ROM and torsion we found significantly higher correlation values. This may be due to the fact that our study surveyed a wide variety of torsion values and included many non-throwers while previous work has largely focused on throwing athletes. It is possible that these groups have different functional requirements when it comes to humeral rotation. Non-throwers may require more internal rotational movement for manipulative tasks and power generation for actions such as pounding and prying. Conversely, throwing athletes, for whom high projectile velocity is imperative, may benefit greatly from increased external rotational ROM. An increase in external rotational ROM could allow throwers to achieve a much greater range of rotational motion prior to the release of the projectile and still maintain accuracy. Given that humeral rotation is known to occur very quickly and is a significant contributor to projectile velocity at release, a change in rotational ROM could have significant

performance effects during throwing. These potential differences in functional constraint may explain some important differences in the literature and are a relevant avenue of future study.

In short, humeral torsion significantly affects rotational ROM at the shoulder. Low torsion (high retroversion) is strongly associated with reduced internal rotational ROM and a greater range of external rotational ROM. We present a simple metric for assessing humeral torsion using non-invasive, easily obtained ROM data which can be helpful clinically in diagnosing individuals with high risk of shoulder and elbow injuries and useful for kinematic studies of shoulder motion. This method also allows for the assessment of rotational ROM at the shoulder from the skeleton itself. Assessing ROM using skeletal material allows for estimates of ROM at the shoulder in fossil hominins, which show considerable variability in this feature. For example, two recently published *H. erectus* skeletons have been shown to have low degrees of humeral torsion (58, 59). These values are similar to or lower than those found in the dominant arm in elite throwing athletes, suggesting a comparable or even more externally shifted ROM in these hominin shoulders. If it is the case, as we propose, that greater external rotational ROM at the shoulder increases throwing velocity, then it is possible that the uniquely human capacity for high performance throwing may have evolved by 2 million years ago. Testing this hypothesis, however, requires additional data on how rotational ROM at the shoulder relates to throwing velocity, as well as how other anatomical changes in the upper body that occur in *H. erectus* affect the ability to throw with power and accuracy.

2.7 Acknowledgements

I would like to thank Dan Lieberman, Tom Gill, III, Bill Palmer, and Tom Gill, IV for their help in designing and implementing this study. I would also like to thank the subjects who volunteered their time, the staff at the MGH Imaging Service, Michelle Cardillo, Louise Borda & Isabella Suzarte for their help making this study possible. The authors would also like to thank the two reviewers for their helpful comments and criticisms. Generous funding for the Qualisys Oqus camera system was provided by the Hintze Family Charitable Trust and the American School for Prehistoric Research. External funding was provided by the National Science Foundation (BCS 0961943).

2.8 Literature Cited

1. Larson SG (2007) The definition of humeral torsion: a comment on Rhodes (2006). *American Journal of Physical Anthropology* 133(2):819-820; discussion 820-821.

2. Rhodes JA (2007) Humeral torsion and retroversion in the literature: A reply to Larson. *American Journal of Physical Anthropology* 133:819-821.

3. Hill JA, Tkach L, & Hendrix RW (1989) A study of glenohumeral orientation in patients with anterior recurrent shoulder dislocations using computerized axial tomography. *Orthop Rev* 18(1):84-91.

4. Evans FG & Krahl VE (1945) The torsion of the humerus: a phylogenetic study from fish to man. *American Journal of Anatomy* 76:303-307.

5. Krahl VE (1947) The torsion of the humerus; its localization, cause and duration in man. *Am J Anat* 80(3):275-319.

6. Broca P (1881) Le torsion de l'humerus et le tropometre. *Revue d'Anthropologie* 4:193-210; 385-423.

7. Martin CP (1933) The Cause of Torsion of the Humerus and of the Notch on the Anterior Edge of the Glenoid Cavity of the Scapula. *J Anat* 67(Pt 4):573-582.

8. Krahl VE & Evans FG (1945) Humeral Torsion in Man. *American Journal of Physical Anthropology* 3(3):229-253.

9. Edelson G (1999) Variations in the retroversion of the humeral head. *J Shoulder Elbow Surg* 8:142-145.

10. Kronberg M, Brostrom LA, & Soderlund V (1990) Retroversion of the humeral head in the normal shoulder and its relationship to the normal range of motion. *Clin Orthop Relat Res* 253:113-117.

11. Cowgill LW (2007) Humeral torsion revisited: a functional and ontogenetic model for populational variation. *Am J Phys Anthropol* 134(4):472-480.

12. Scheuer L & Black S (2000) *Developmental Juvenile Osteology* (Elselvier Academic Press, New York).

13. Edelson G (2000) The development of humeral head retroversion. *J Shoulder Elbow Surg* 9(4):316-318.

14. McKern TW & Stewart TD (1957) Skeletal age changes in young american males. (Quartermaster research & development command, Natick, MA).

15. Chant CB, Litchfield R, Griffin S, & Thain LM (2007) Humeral head retroversion in competitive baseball players and its relationship to glenohumeral rotation range of motion. *J Orthop Sports Phys Ther* 37(9):514-520.

16. Crockett HC*, et al.* (2002) Osseous adaptation and range of motion at the glenohumeral joint in professional baseball pitchers. *Am J Sports Med* 30(1):20-26.

17. Osbahr DC, Cannon DL, & Speer KP (2002) Retroversion of the humerus in the throwing shoulder of college baseball pitchers. *Am J Sports Med* 30(3):347-353.

18. Reagan KM*, et al.* (2002) Humeral retroversion and its relationship to glenohumeral rotation in the shoulder of college baseball players. *Am J Sports Med* 30(3):354-360.

19. Pieper HG (1998) Humeral torsion in the throwing arm of handball players. *Am J Sports Med* 26(2):247-253.

20. Borsa PA, Dover GC, Wilk KE, & Reinold MM (2006) Glenohumeral range of motion and stiffness in professional baseball pitchers. *Med Sci Sports Exerc* 38(1):21-26.

21. Borsa PA*, et al.* (2005) Correlation of range of motion and glenohumeral translation in professional baseball pitchers. *Am J Sports Med* 33(9):1392-1399.

22. Bigliani LU*, et al.* (1997) Shoulder motion and laxity in the professional baseball player. *Am J Sports Med* 25(5):609-613.

23. Brown LP, Niehues SL, Harrah A, Yavorsky P, & Hirshman HP (1988) Upper extremity range of motion and isokinetic strength of the internal and external shoulder rotators in major league baseball players. *Am J Sports Med* 16(6):577-585.

24. King J, Brelsford HJ, & Tullos HS (1969) Analysis of the pitching arm of the professional baseball pitcher. *Clin Orthop Relat Res* 67:116-123.

25. Magnusson SP, Gleim GW, & Nicholas JA (1994) Shoulder weakness in professional baseball pitchers. *Med Sci Sports Exerc* 26(1):5-9.

26. Wilk KE*, et al.* (2011) Correlation of glenohumeral internal rotation deficit and total rotational motion to shoulder injuries in professional baseball pitchers. *Am J Sports Med* 39(2):329-335.

27. Torres RR & Gomes JL (2009) Measurement of glenohumeral internal rotation in asymptomatic tennis players and swimmers. *Am J Sports Med* 37(5):1017-1023.

28. Ellenbecker TS, Roetert EP, Bailie DS, Davies GJ, & Brown SW (2002) Glenohumeral joint total rotation range of motion in elite tennis players and baseball pitchers. *Med Sci Sports Exerc* 34(12):2052-2056.

29. Dines JS, Frank JB, Akerman M, & Yocum LA (2009) Glenohumeral internal rotation deficits in baseball players with ulnar collateral ligament insufficiency. *Am J Sports Med* 37(3):566-570.

30. Burkhart SS, Morgan CD, & Kibler WB (2003) The disabled throwing shoulder: spectrum of pathology Part III: The SICK scapula, scapular dyskinesis, the kinetic chain, and rehabilitation. *Arthroscopy* 19(6):641-661.

31. Burkhart SS, Morgan CD, & Kibler WB (2003) The disabled throwing shoulder: spectrum of pathology Part I: pathoanatomy and biomechanics. *Arthroscopy* 19(4):404-420.

32. Ellenbecker TS, Roetert EP, Piorkowski PA, & Schulz DA (1996) Glenohumeral joint internal and external rotation range of motion in elite junior tennis players. *J Orthop Sports Phys Ther* 24(6):336-341.

33. Kibler WB, Chandler TJ, Livingston BP, & Roetert EP (1996) Shoulder range of motion in elite tennis players. Effect of age and years of tournament play. *Am J Sports Med* 24(3):279-285.

34. Hirashima M, Kudo K, Watarai K, & Ohtsuki T (2007) Control of 3D limb dynamics in unconstrained overarm throws of different speeds performed by skilled baseball players. *J Neurophysiol* 97(1):680-691.

35. Fleisig GS, Andrews JR, Dillman CJ, & Escamilla RF (1995) Kinetics of baseball pitching with implications about injury mechanisms. *Am J Sports Med* 23(2):233-239.

36. Fleisig GS, Barrentine SW, Escamilla RF, & Andrews JR (1996) Biomechanics of overhand throwing with implications for injuries. *Sports Med* 21(6):421-437.

37. Dillman CJ (1990) Proper mechanics of pitching. *Sports Med Update* 5:15-20.

38. Burkhart SS, Morgan CD, & Kibler WB (2000) Shoulder injuries in overhead athletes. The "dead arm" revisited. *Clin Sports Med* 19(1):125-158.

39. Jobe CM, Pink MM, Jobe FW, & Shaffer B (1996) Anterior shoulder instability, impingement, and rotator cuff tear: theories and concepts. *Operative Techniques in Upper Extremity Sports Injuries*, ed Jobe FW (Mosby, St. Louis, MO).

40. Kvitne RS & Jobe FW (1993) The diagnosis and treatment of anterior instability in the throwing athlete. *Clin Orthop Relat Res* 291:107-123.

41. Meister K (2000) Injuries to the shoulder in the throwing athlete. Part two: evaluation/treatment. *Am J Sports Med* 28(4):587-601.

42. Meister K (2000) Injuries to the shoulder in the throwing athlete. Part one: Biomechanics/pathophysiology/classification of injury. *Am J Sports Med* 28(2):265-275.

43. Pappas AM, Zawacki RM, & McCarthy CF (1985) Rehabilitation of the pitching shoulder. *Am J Sports Med* 13(4):223-235.

44. Larson SG (1988) Subscapularis function in gibbons and chimpanzees: Implications for interpretation of humeral head torsion in hominoids. *American Journal of Physical Anthropology* 76:449-462.

45. Hernigou P, Duparc F, & Hernigou A (2002) Determining humeral retroversion with computed tomography. *J Bone Joint Surg Am* 84-A(10):1753-1762.

46. McCully SP, Kumar N, Lazarus MD, & Karduna AR (2005) Internal and external rotation of the shoulder: effects of plane, end-range determination, and scapular motion. *J Shoulder Elbow Surg* 14(6):602-610.

47. Larson RL, Singer KM, Bergstrom R, & Thomas S (1976) Little League survey: the Eugene study. *Am J Sports Med* 4(5):201-209.

48. Adams JE (1966) Little league shoulder: osteochondrosis of the proximal humeral epiphysis in boy baseball pitchers. *Calif Med* 105(1):22-25.

49. Axe MJ, Snyder-Mackler L, Konin JG, & Strube MJ (1996) Development of a distance-based interval throwing program for Little League-aged athletes. *Am J Sports Med* 24(5):594-602.

50. Keeley DW, Hackett T, Keirns M, Sabick MB, & Torry MR (2008) A biomechanical analysis of youth pitching mechanics. *J Pediatr Orthop* 28(4):452-459.

51. Klingele KE & Kocher MS (2002) Little league elbow: valgus overload injury in the paediatric athlete. *Sports Med* 32(15):1005-1015.

52. Ricci AR & Mason DE (2004) Little league shoulder: case report and literature review. *Del Med J* 76(1):11-14.

53. Stein CJ & Micheli LJ (2011) Overuse injuries in youth sports. *Phys Sportsmed* 38(2):102-108.

54. Gugenheim JJ, Jr., Stanley RF, Woods GW, & Tullos HS (1976) Little League survey: the Houston study. *Am J Sports Med* 4(5):189-200.

55. Olsen SJ, 2nd, Fleisig GS, Dun S, Loftice J, & Andrews JR (2006) Risk factors for shoulder and elbow injuries in adolescent baseball pitchers. *Am J Sports Med* 34(6):905-912.

56. Lyman S, Fleisig GS, Andrews JR, & Osinski ED (2002) Effect of pitch type, pitch count, and pitching mechanics on risk of elbow and shoulder pain in youth baseball pitchers. *Am J Sports Med* 30(4):463-468.

57. Fleisig GS*, et al.* (2011) Risk of serious injury for young baseball pitchers: a 10-year prospective study. *Am J Sports Med* 39(2):253-257.

58. Larson SG (2007) Evolutionary Transformation of the Hominin Shoulder. *Evolutionary Anthropology* 16:172-187.

59. Lordkipanidze D*, et al.* (2007) Postcranial evidence from early Homo from Dmanisi, Georgia. *Nature* 449(7160):305-310.

Chapter 3 - Elastic Energy Storage in the Shoulder and the Evolution of High-Speed Throwing in *Homo*

3.1 Chapter Summary

Humans are uniquely able to throw overhand with considerable accuracy and high velocity, with much of the power coming from the shoulder. How and when humans evolved the ability to generate high-speed throws is poorly understood. Here, we show that much of the power necessary to throw objects with high velocity comes from elastic energy stored at the shoulder in combination with decreased humeral torsion. Low torsion and other anatomical features that would have improved throwing performance are all present two million years ago in *Homo erectus*, suggesting that throwing ability was selected for early hunting.

3.2 Introduction

Humans are the only species that throws objects with high speed and accuracy. Some primates, including chimpanzees, our closest extant relatives, occasionally throw objects with moderate accuracy but little velocity (1). Darwin speculated that the evolution of bipedalism made high-speed throwing possible by freeing the arms (2). Since Darwin, it is widely believed that hunting, first evident in the archaeological record by at least 1.8 million years ago, was the most likely selective context for the evolution of throwing (3, 4). However, when, how, and why hominins evolved high-powered throwing capabilities remain subjects of much conjecture (5-7).

Throws are powered by rapid, sequential activation of many muscles, starting in the legs and progressing through the body (8-10). At each joint, torques are generated that accelerate segmental masses, creating rapid angular movements, which accumulate kinetic energy in the projectile until its release. One especially important movement is internal (medial) rotation around the long axis of the humerus, which occurs in a few milliseconds and can exceed 9,000°/sec (10). This rotation is the fastest motion the human body produces and the largest contributor to projectile velocity (11). Previous research has focused on the shoulder muscles' role in generating internal humeral rotation (8, 12). Although internal rotator muscles are very important in generating this rapid rotation, these muscles alone may not explain how humans generate so much internal rotational power. Peak internal rotation moments have been shown to occur well before the humerus starts to rotate internally (9). In addition, electromyography data show that the internal rotators are variably active during the critical acceleration phase (13, 14). Further, three of the human internal rotator muscles appear ill-suited to producing the high torques

required for rapid rotation because their fibers are oriented so that the majority of the torque produced is for actions other than humeral rotation (*Pectoralis major*, *Latissimus dorsi*, *Deltoid*).

3.3 Model

We propose that humans generate much of the power needed for rapid humeral rotation using several evolutionarily novel features in the shoulder that help store and release elastic energy. We postulate that energy storage occurs during the arm-cocking phase (Figure 3.1A), which begins with completion of a large step towards the target. As the foot hits the ground, the arm is already externally rotated, horizontally extended, and abducted nearly 90° at the shoulder, with forearm flexion approaching 90° at the elbow (10). As the cocking phase begins, the torso rotates rapidly towards the target and the major shoulder horizontal flexor, *Pectoralis major*, is activated (8, 10). Together, these motions generate large torques around the vertebral axis. When the arm's mass is positioned away from the shoulder and elbow prior to the initiation of these torques, the arm's moment of inertia is increased around the long axis of the humerus and lags behind the accelerating torso (Figure 3.1B). Further, flexing the elbow during the cocking phase allows passive inertial forces to externally rotate the arm, stretching all of the short, parallel tendons, ligaments, and elastic components of muscles that cross the shoulder (27), potentially storing elastic energy in the large aggregate cross-sectional area of these structures. Then, when the biceps deactivate and elbow extension begins, the arm's moment of inertia is reduced, allowing stretched elements to recoil, releasing energy, and powering the extremely rapid internal rotation of the humerus.

Compared to apes (27), humans have three derived morphological features that can help store and release elastic energy during throwing. First, humans' tall, mobile waists decouple the hips and thorax, permitting more torso rotation than is found in chimpanzees (15), in turn contributing to the torque needed to load the shoulder's elastic elements. Second, humeral torsion, the angle between humeral head orientation and the axis of the elbow, is 10-20° lower in human throwers' dominant arms compared to chimpanzee humeri (5). Decreased torsion extends the rotational range-of-motion (ROM) at the shoulder externally (16), potentially enabling more elastic energy storage during the cocking phase. Finally, humans have a more laterally oriented glenohumeral joint, which aligns the *P. major* flexion moment around the same axis as the torso rotation moment. This orientation allows humans to increase the arm's moment of inertia by abducting the humerus in line with the torso rotation and shoulder flexion torques, maximizing resistance to both (Figure 3.1B/C). In contrast, chimpanzees' more cranially oriented glenohumeral joint and limited ability to produce torso rotation torque requires them to maximize inertial loading by abducting their humeri more than humans' to bring their arm in line with the *P. major* flexion moment. This increased abduction, however, forces chimpanzees to position their elbow in a more extended posture to maximize the arm's moment of inertia resulting in a costly reduction in elbow extension during the throw.

3.4 Materials and Methods

Subjects - Data were collected from 24 male subjects (ages 19-23). Nineteen of the subjects were collegiate athletes (16 baseball players, 3 non-throwing athletes). Prior to enrollment in the study, all participants were required to pass a throwing performance task (27) in order to eliminate poor throwers. For all subjects, we collected weight,

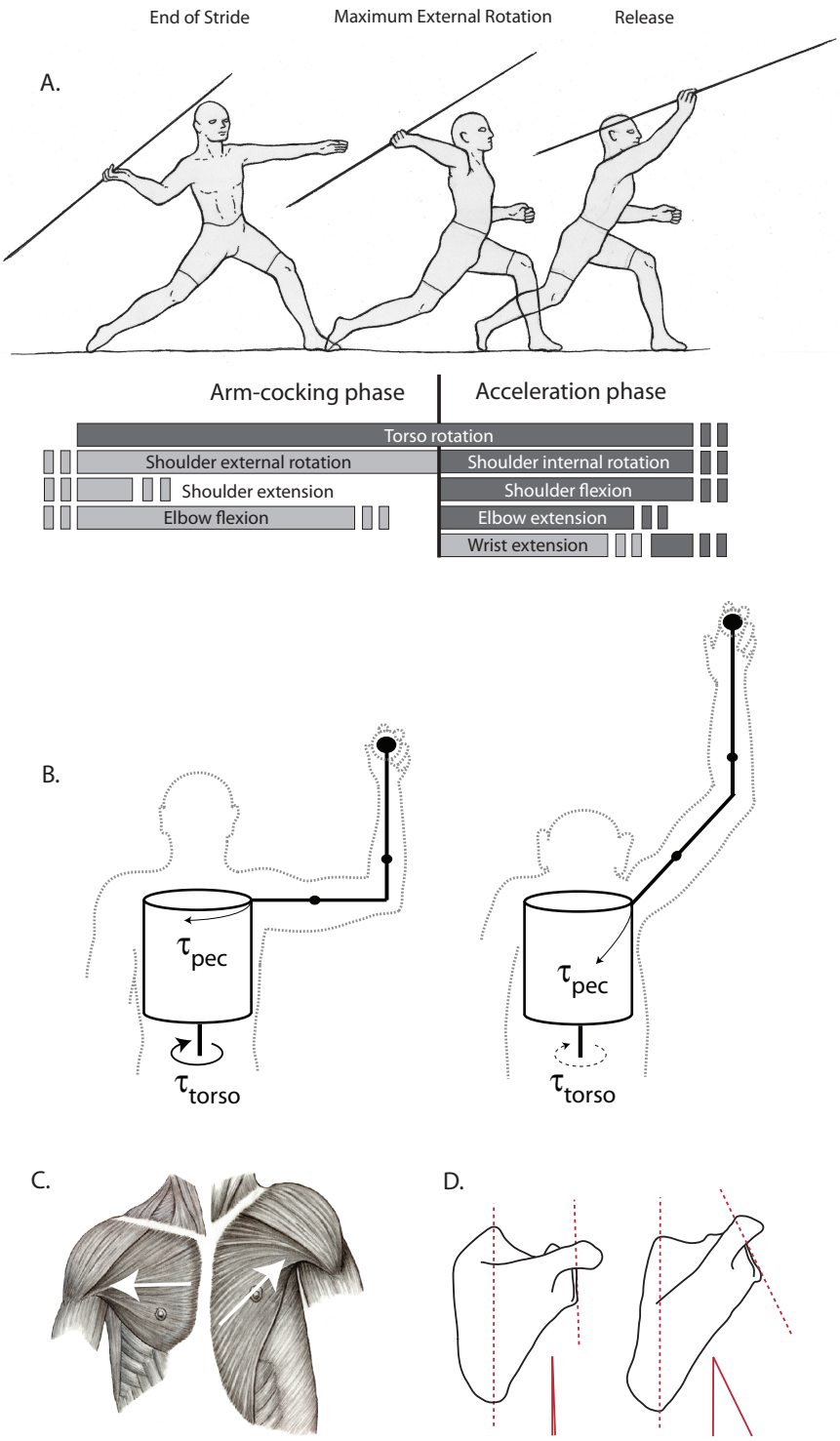


Figure 3.1. Arm-cocking and acceleration phases of the overhand throw (A). Humans (left) and chimpanzees (right) differ in arm abduction and elbow flexion during throwing (B) because of differences in shoulder orientation, which alters the major line of action of the *Pectoralis major* (C). Aligning the long axis of the humerus with the major axis of *P. major*

and flexing the elbow maximizes inertia to shoulder flexion torque and loads the elastic ligaments in the shoulder. However, chimpanzee morphology is compromised between maximizing humeral rotation or elbow extension. Signatures of shoulder orientation found in the scapula (D) can be used to reconstruct hominin shoulder orientation.

information on relevant injury/medical history, and basic anthropometric data (height, segment lengths and circumferences, joint range of motion). Humeral torsion was estimated using range of motion measures (16). All subjects provided informed written consent in accordance with the Harvard Committee on the Use of Human Subjects.

Kinematics - Kinematic data were collected at 1000 Hz using an eight-camera Vicon T10s 3D infrared motion capture system (Vicon Inc, Centennial CO, USA). Each subject had twenty-one passive reflective markers taped on the throwing arm and torso (27). Subjects were given approximately 5 minutes to stretch and warm up before recording. After the warm up period, subjects were tasked to throw a 144g baseball at a 1m-radius target from 10m away. The subject then threw 8-10 normal pitches and 8-20 pitches using a Donjoy Shoulder Stabilizer (Donjoy Inc, Vista, CA) brace that restricts external rotational range of motion at the shoulder. As a sham, data from an intermediate condition in which the brace was applied but not tightened were also collected (27). Ball speed was measured using a Sports Radar Model 3600 radar gun. Ball release was timed using a synched FlexiForce A201 force sensor (Tekscan Inc, Boston MA, USA) collected at 1000 Hz taped to the palmar side of the distal phalanx of the third digit and synched with a 30 Hz Canon Vixia HV30 digital video camera (Canon Inc, Tokyo, Japan). In order to filter the kinematic data, a residual analysis (17) of the entire throwing trial and the critical period during the humeral internal rotation motion was calculated in MATLAB (version R2010b) (27). A Butterworth 2^{nd} order low-pass filter (cutoff 25Hz) was applied and marker gaps up to 100 frames were

interpolated using C-Motion Visual3D software (v4). For analysis, each motion was then subdivided into five standard phases of the throw: windup/stride, arm cocking, arm acceleration, arm deceleration, and follow-through (18).

Kinetics – Joint Euler angles were calculated and inverse dynamics analyses were performed using mass distribution data from Dempster (19) in Visual3D. Joint angular velocities, moments, and power were calculated using each joint's instantaneous axis of rotation. The sequence of rotations at each joint is described in the Supplemental text. Joint work was calculated in MATLAB using the trapz function.

Muscular power modeling – The work of humeral rotation during the acceleration phase of the throw was calculated as the area under the humeral rotation power curve. This measurement of work was divided by the duration of the acceleration phase to calculate average power of humeral rotation. This power value (W) was then standardized to W kg^{-1} by dividing by the summed maximum masses of all muscles which potentially contribute to internal rotation at the shoulder: *Pectoralis major*, *Latissimus dorsi*, anterior *Deltoid*, *Subscapularis*, and *Teres major* (27). These masses were calculated by multiplying the largest recorded volumes for each muscle (20) by the known density (1.06 g/cm^3) of mammalian muscle (21). The resulting average actual power of humeral rotation during the acceleration phase (W kg^{-1}) was then compared to published maximum power values for skeletal muscle (22-24).

Statistics – Kinetic data were standardized to phase length, interpolated, and resampled using custom MATLAB code to yield comparable data across all trials and subjects (27). Individual subject means were compared across experimental conditions using repeated measures ANOVA or MANOVA where appropriate. All statistical analyses

were conducted using JMP software (v.5). Differences were considered to be significant at alpha < 0.05.

3.5 Results

To test this model, we used high-speed, 3D kinematic and kinetic data from 20 experienced human throwers to quantify power production at the shoulder during overhand baseball throwing (25). During the arm-cocking phase, the throwers' humeri externally rotate 57±15° past the active ROM limit achieved using their own muscular power, indicating passive stretching of the ligaments, tendons, and muscles crossing the shoulder. Inverse dynamics analysis shows that during this period, the shoulder produces an opposing internal rotation torque, causing a sustained period of power absorption (Figure 3.2). By integrating the area under the power curve during arm-cocking, we calculate that the negative work of shoulder rotation averages -201±70J, with an average power of -631±337W. In contrast, the total rotational work of the subsequent internal rotation motion is 346±120J, with power during acceleration averaging 3,847±1,697W. If 90% of the negative work during arm-cocking is stored and returned elastically (26), this energy can account for 54±15% of the internal humeral rotation work done during a typical throw.

Without using invasive techniques such as sonomicrometry, we cannot precisely partition how much of this power is generated by muscles versus how much is returned from elastic structures. However, to infer how much shoulder rotational power is provided by elastic energy during throwing, we compared estimates of the maximum power production capacity of all shoulder internal rotator muscles with actual calculated power (27). Dividing average shoulder rotation power during acceleration by an estimate of total

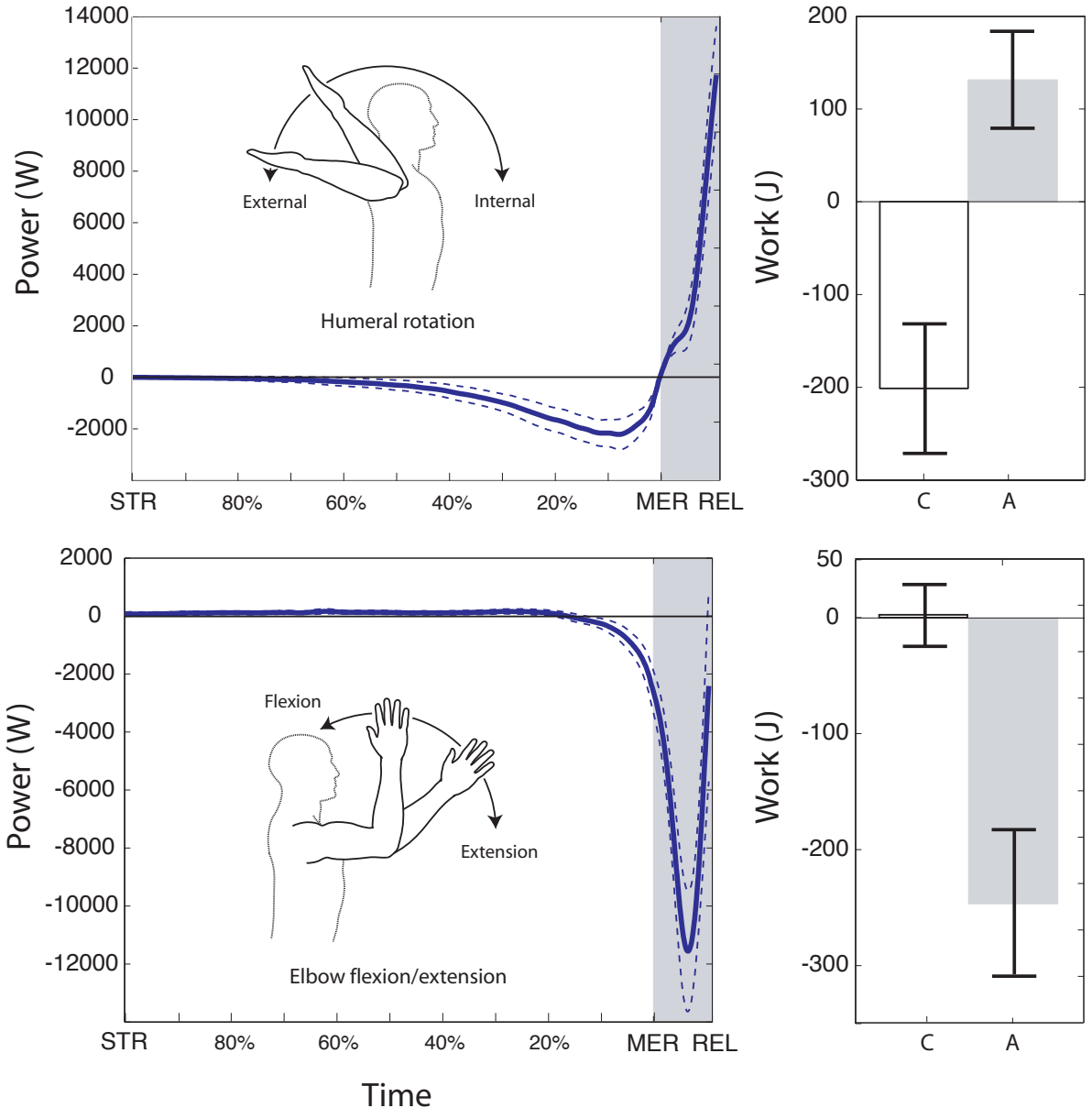


Figure 3.2. Mean shoulder rotational power (with 95% confidence intervals) shows a sustained period of negative power and work during arm-cocking, between stride (STR) and maximum external rotation (MER) - white. This negative work is recovered during acceleration, between MER and release (REL) - gray. Recovered work powers both internal rotation at the shoulder and extension of the elbow.

internal rotator muscle volume, shows that average rotational power per kilogram at the shoulder is between three and seven times greater than muscle's maximum isotonic power

production capacity (22). Even when the modeled muscle power values are increased to account for force enhancement during active muscle stretching (28), the average rotational power we measured still exceeds those increased muscle power estimates by two to four fold. Therefore, shoulder muscles alone are incapable of powering the rapid internal rotation motion observed during overhand throwing. Instead, throwing power is amplified through elastic recoil in a manner similar to the way extremely rapid and forceful movements are generated in other animals (29, 30).

Elastic energy storage at the shoulder also affects the generation of joint velocity and power at the elbow. During acceleration, the elbow extends at very high angular velocities (2,434±552°/sec) despite large amounts of negative power and work (-246±63J), indicating that the triceps are not powering this rapid extension (Figure 3.2). As previous studies have shown, elbow extension is powered primarily by more proximal segments (11), especially the shoulder.

A third line of evidence for the importance of elastic energy storage comes from experimentally limiting shoulder rotational ROM with therapeutic braces (15), which restricted external rotation by 24±9°. During brace trials, shoulder rotation beyond the active ROM decreased by 50±36% and shoulder work during arm-cocking decreased by 45±17% (rmANOVA $p < 0.001$) (Figure 3.3). Shoulder rotation work during the subsequent acceleration phase was not significantly different between conditions, but average shoulder rotation power during acceleration decreased significantly (-16±35%, rmANOVA $p = 0.036$). Wearing a shoulder brace also decreased elbow negative work during acceleration by 20±21% (rmANOVA $p < 0.001$). Overall, these work and power reductions from less elastic energy exchange significantly reduced humeral rotation

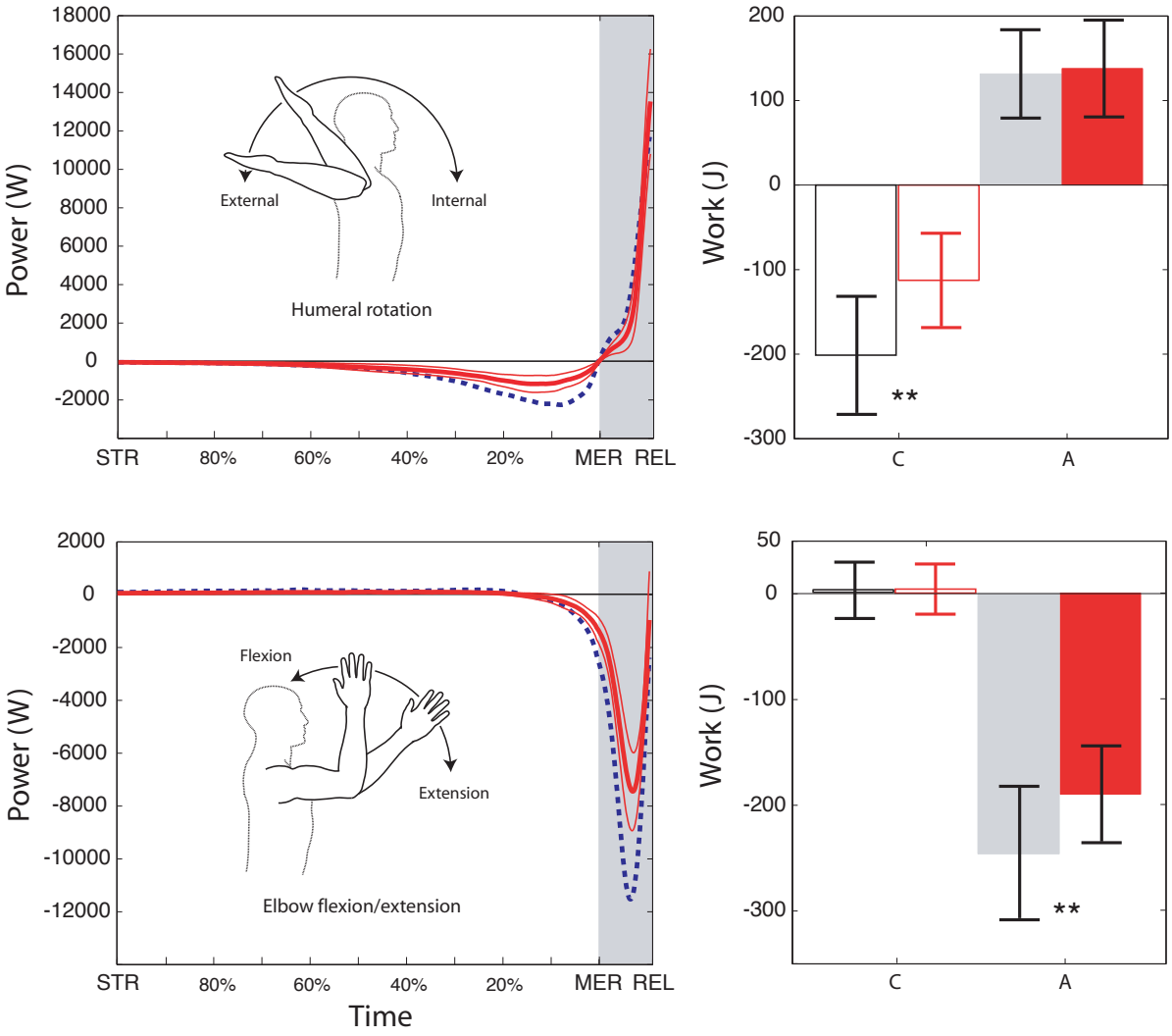


Figure 3.3. Brace restricted mean power (with 95% confidence intervals) for shoulder rotation and elbow flexion/extension are plotted in red alongside normal values in dashed blue. Significant reductions ($p < 0.05$) in shoulder rotation work occur during arm-cocking and in elbow flexion/extension work during acceleration.

angular acceleration (-24±29%, rmANOVA $p < 0.001$) and elbow extension angular velocity (-21±10%, rmANOVA $p < 0.001$), reducing ball speed by 10±8% (MANOVA, $p < 0.001$).

Natural variation in humeral torsion shows similar performance effects. By maintaining relatively lower, juvenile levels of torsion into adulthood, throwing athletes increase power generation by shifting the humerus' rotational ROM externally (16). This

shift allows further external rotation during arm-cocking and increases internal rotation during acceleration (Figure 3.4A), permitting more elastic energy storage and release. It is unknown whether the plasticity of humeral torsion is greater in humans than in other taxa, but plasticity in humans may be beneficial, enabling low torsion to persist in the throwing arm, while higher torsion (useful for manipulative tasks) develops in the non-throwing arm (5, 31).

3.6 Discussion

When high-speed throwing first evolved is difficult to test because the first projectiles were probably rocks and untipped wooden spears. However, the derived morphological features that help human throwers store elastic energy can be assessed in the fossil record. These features evolved in a mosaic-like fashion, some predating the evolution of *Homo*. Tall, decoupled waists first appear in *Australopithecus* as adaptations for locomotion (15). Low humeral torsion also appears in *Australopithecus,* likely resulting from the release of the forelimbs from weight-bearing during quadrupedal locomotion, and is present in early *Homo* (5) (Figure 3.4D). Although variation in glenoid orientation exists within *Australopithecus* (32), a fully lateral glenoid position is definitively present in *Homo erectus*. Such laterally oriented shoulders probably decreased the mechanical advantage of the scapular rotator muscles during climbing, probably had little or negative effects on stone tool production , and are best explained as an adaptation for throwing. Low, wide shoulders, long legs, and hyperextendable wrists are also present in *H. erectus* (15, 33). While some of these features were selected for functions other than throwing, their combined configuration, first present in *H. erectus,* would have benefited throwing

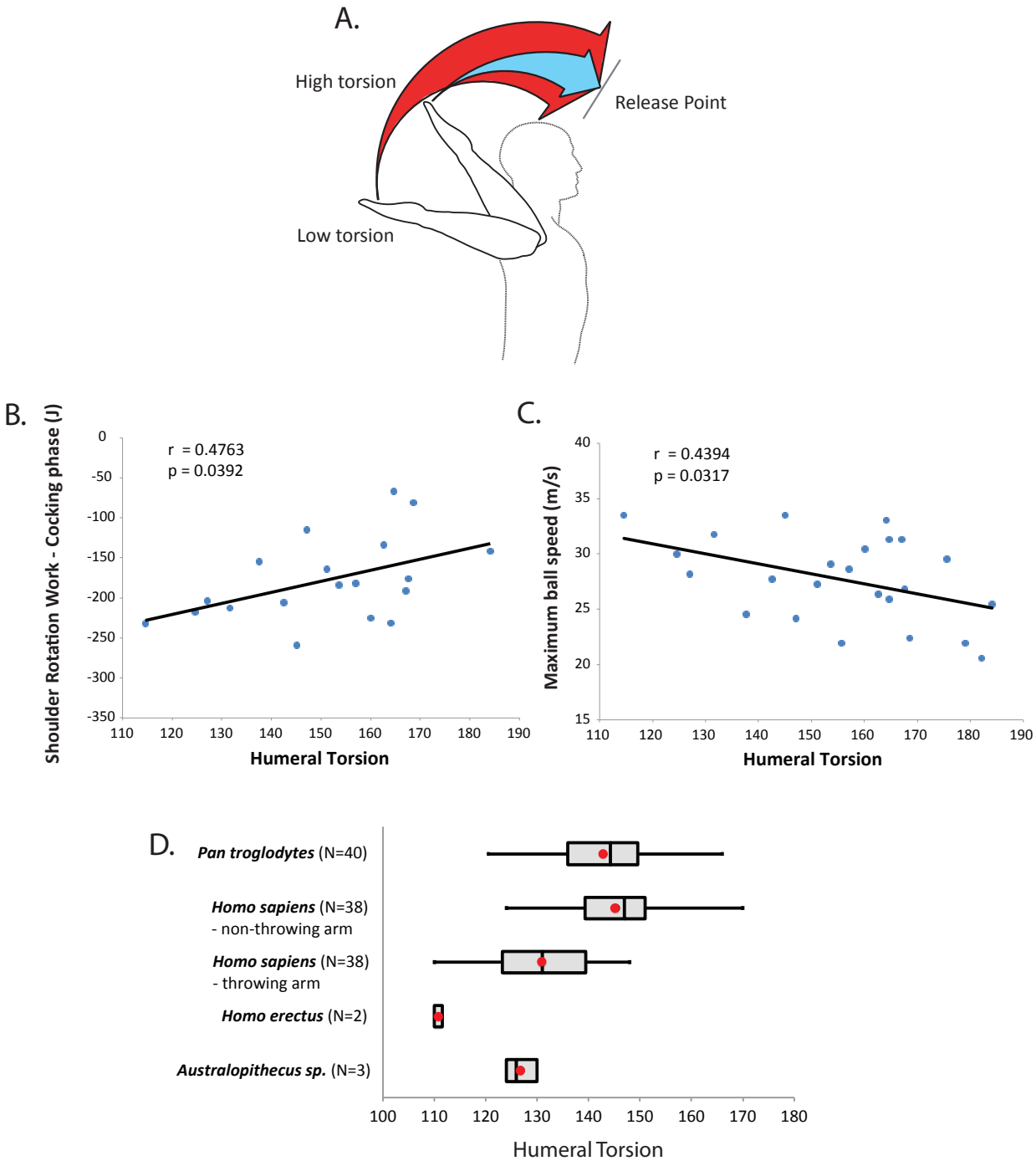


Figure 3.4. Low humeral torsion shifts the shoulder rotational ROM externally (A), allowing increased negative work during arm-cocking to be stored as elastic energy (B), resulting in faster projectile speed (C). Humans and chimpanzees show comparable degrees of torsion (data from: 5), although throwing athletes have reduced dominant arm torsion (data from: 31) consistent with low torsion in *Australopithecus* and *Homo erectus* (D) (data from: 5).

performance by enabling elastic energy storage in the shoulder, providing a strong selective advantage during hunting.

An evolutionary perspective on throwing has implications for the high prevalence of injuries in throwing athletes. While most throwing today occurs in the context of sports, humans most likely evolved to throw spears using the same mechanics (17). However, Paleolithic hunters almost certainly threw less frequently than modern athletes. The repeated stretching of ligaments and tendons in the shoulder and resulting downstream torques at the elbow can lead to laxity and tearing (9). While humans' unique ability to power high-speed throws using elastic energy may have been critical in enabling early hunting, repeatedly overusing this ability can result in serious injuries in modern throwing athletes.

3.7 Acknowledgments

I would like to thank Madhu Venkadesan, Mike Rainbow, and Dan Lieberman for all of their invaluable help in developing and testing this model, analyzing the data, and editing this chapter. I would also like to thank the Wyss Institute, Leia Stirling, Kate Saul, Andy Biewener, Richard Wrangham, Susan Larson, Brian Roach, Laszlo Meszoly, Amanda Lobell, and many undergraduate research assistants for their help and support.

Funding was generously provided by the National Science Foundation (BCS-0961943) and the American School for Prehistoric Research.

3.8 Literature Cited

1. Goodall J (1986) *The Chimpanzees of Gombe: Patterns of Behavior* (Harvard University Press, Cambridge).

2. Darwin C (1871) *Descent of Man* (John Murray, London).

3. Braun DR, *et al.* (2010) Early hominin diet included diverse terrestrial and aquatic animals 1.95 Ma in East Turkana, Kenya. *Proc Natl Acad Sci U S A* 107(22):10002-10007.

4. McPherron SP, *et al.* (2010) Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* 466(7308):857-860.

5. Larson SG (2007) Evolutionary Transformation of the Hominin Shoulder. *Evolutionary Anthropology* 16:172-187.

6. Calvin WH (1983) *The Throwing Madonna: Essays on the Brain* (Bantam, New York).

7. Rhodes JA & Churchill SE (2009) Throwing in the Middle and Upper Paleolithic: inferences from an analysis of humeral retroversion. *J Hum Evol* 56(1):1-10.

8. Hirashima M, Kadota H, Sakurai S, Kudo K, & Ohtsuki T (2002) Sequential muscle activity and its functional role in the upper extremity and trunk during overarm throwing. *J Sports Sci* 20(4):301-310.

9. Fleisig GS, Andrews JR, Dillman CJ, & Escamilla RF (1995) Kinetics of baseball pitching with implications about injury mechanisms. *Am J Sports Med* 23(2):233-239.

10. Pappas AM, Zawacki RM, & Sullivan TJ (1985) Biomechanics of baseball pitching. A preliminary report. *Am J Sports Med* 13(4):216-222.

11. Hirashima M, Kudo K, Watarai K, & Ohtsuki T (2007) Control of 3D limb dynamics in unconstrained overarm throws of different speeds performed by skilled baseball players. *J Neurophysiol* 97(1):680-691.

12. Jobe FW, Tibone JE, Perry J, & Moynes D (1983) An EMG analysis of the shoulder in throwing and pitching. A preliminary report. *Am J Sports Med* 11(1):3-5.

13. DiGiovine NM, Jobe FW, Pink M, & Perry J (1992) An electromyography analysis of the upper extremity in pitching. *J Shoulder Elbow Surg* 1:15-25.

14. Gowan ID, Jobe FW, Tibone JE, Perry J, & Moynes DR (1987) A comparative electromyographic analysis of the shoulder during pitching. Professional versus amateur pitchers. *Am J Sports Med* 15(6):586-590.

15. Bramble DM & Lieberman DE (2004) Endurance Running and the Evolution of Homo. *Nature* 432:345-352.

16. Roach NT, Lieberman DE, Gill TJ, IV, Palmer WE, & Gill TJ, III (2012) The effect of humeral torsion on rotational range of motion in the shoulder and throwing performance. *J Anat* 220:293-301.

17. Winter DA (1990) *Biomechanics and motor control of human movement* (Wiley-Interscience, New York) 2nd Ed.

18. Dillman CJ, Fleisig GS, & Andrews JR (1993) Biomechanics of pitching with emphasis upon shoulder kinematics. *J Orthop Sports Phys Ther* 18(2):402-408.

19. Dempster WT (1955) *Space requirements for the seated operator* (Wright Air Development Center, Wright-Patterson Air Force Base, OH).

20. Garner BA & Pandy MG (2003) Estimation of musculotendon properties in the human upper limb. *Ann Biomed Eng* 31(2):207-220.

21. Mendez J & Keys A (1960) Density and composition of mammalian muscle. *Metabolism* 9:184-188.

22. McGowan CP, Baudinette RV, Usherwood JR, & Biewener AA (2005) The mechanics of jumping versus steady hopping in yellow-footed rock wallabies. *J Exp Biol* 208(Pt 14):2741-2751.

23. Lutz GJ & Rome LC (1994) Built for jumping: the design of the frog muscular system. *Science* 263(5145):370-372.

24. Peplowski MM & Marsh RL (1997) Work and power output in the hindlimb muscles of Cuban tree frogs Osteopilus septentrionalis during jumping. *J Exp Biol* 200(Pt 22):2861-2870.

25. see Materials and Methods

26. Bennett MB, Ker RF, Dimery NJ, & Alexander RM (1986) Mechanical properties of various mammalian tendons. *Zool. Lond. (A)* 209:537-548.

27. see Supplemental Data

28. McMahon TA (1984) *Muscles, Reflexes, and Locomotion* (Princeton University Press, Princeton, NJ).

29. Roberts TJ & Marsh RL (2003) Probing the limits to muscle-powered accelerations: lessons from jumping bullfrogs. *Journal of Experimental Biology* 206:2567-2580.

30. Biewener AA, Konieczynski DD, & Baudinette RV (1998) In vivo muscle force-length behavior during steady-speed hopping in tammar wallabies. *J Exp Biol* 201(Pt 11):1681-1694.

31. Pieper HG (1998) Humeral torsion in the throwing arm of handball players. *Am J Sports Med* 26(2):247-253.

32. Haile-Selassie Y, *et al.* (2010) An early Australopithecus afarensis postcranium from Woranso-Mille, Ethiopia. *Proc Natl Acad Sci U S A* 107(27):12121-12126.

33. Richmond BG, Begun DR, & Strait DS (2001) Origin of Human Bipedalism: The Knuckle-Walking Hypothesis Revisited. *Yearbook of Physical Anthropology* 44:70-105.

Chapter 4 - The Biomechanics of Power Generation during Rapid, Overhand Throwing in Humans

4.1 Chapter Summary

High-speed throwing is a distinctive human behavior, but the biomechanical bases of how humans produce high-speed throws are not completely understood. Using inverse dynamics analyses of high-speed kinematic data from 20 baseball players fitted with 4 different braces, each of which inhibits specific motions, we test a model for how power is generated at key joints during the throwing motion. We show that achieving high projectile speeds during throwing requires a combination of elastic energy storage at the shoulder that generates rapid internal rotation of the humerus, as well as the transfer of kinetic energy from proximal body segments to distal segments. Most of the work produced during throwing is generated at the hips, and much of this work (combined with work from the *Pectoralis major*) is used to load elastic elements in the shoulder and power the rapid acceleration of the projectile. Our data indicate that, despite very high angular velocities generated at the elbow and wrist, a large percentage of the work to power these motions is generated passively. Furthermore, heavy reliance on elastic energy storage can help explain why throwing athletes frequently suffer from shoulder labrum tears, shoulder instability, and damage to the ulnar collateral ligament.

4.2 Introduction

The human forelimb is quite derived relative to other hominoids and our hominin ancestors (1, 2). Understanding how and why the human shoulder is so different requires consideration of humans' unique ability to throw objects overhand with both remarkable accuracy and high velocity. Today most high-speed throwing occurs during sports activities, but in the past throwing was crucial for hunting, defense against predators, and aggressive interactions such as warfare. Regardless of their purpose, high-speed overhand throws are produced using a stereotypic, whip-like motion involving the whole body. The throw begins with movement of the legs and progresses quickly up the trunk and arm, ending with rapid movement of the throwing hand as the projectile is released (3-6). There has been considerable inquiry into how this complex motion generates high linear velocities of projectiles, and which joints and joint-specific angular motions are primarily responsible (5, 7-9). Previous work shows that large angular velocities of torso rotation, shoulder internal rotation, elbow extension, and wrist flexion all occur at the moment of release (4, 6, 8, 10) and significantly contribute to projectile speed (8). This study focuses on how these large angular velocities in the upper body are produced.

Angular movements and the angular velocities of those movements are produced when torques act across joints, generating mechanical work and power. Muscles are the source of most torques and thus key contributors to joint power production and angular velocity. As expected, electromyography (EMG) patterns of

muscle activity during the throwing motion show sequential activation of muscles mirroring the progression of the throwing motion (11). However, a report of an individual with a paralyzed *Triceps brachii* who can still achieve rapid elbow extension during throwing (12) calls into question whether this muscle alone powers this elbow extension. In addition, EMG data on shoulder internal rotator muscles show variable activity during the rapid acceleration of the internal rotation motion (13, 14). Given there is no simple relationship between EMG intensity, muscle force production, and whether a muscle is contracting concentrically or eccentrically (15, 16), it is reasonable to question whether muscle torques alone are solely responsible for the large angular velocities produced in the upper body.

Previous researchers has suggested that additional sources of torque to power these large angular velocities during throwing come from movements generated at other joints in adjacent, connected body segments, which can be transferred from joint to joint via a "kinetic chain" (6, 7, 17-19). These interaction torques can result directly from muscular actions at other joints or from velocity-dependent forces such as centrifugal and Coriolis forces (7). Mathematical decomposition of throwing kinematics using the equations of motion have shown that the high angular velocities observed in the elbow and wrist joints at release are largely due to these interaction torques (5, 8, 9, 20, 21). An induced acceleration study by Hirashima and colleagues (7) further deconstructed these interaction torques showing that elbow extension during throwing was largely driven by velocity-dependent forces generated by torso rotation and shoulder internal rotation. The same study also found that wrist flexion during throwing is driven

primarily by velocity-dependent forces generated by elbow extension. These data provide strong support for the hypothesis that power generated at more proximal joints (such as the hips, torso, and shoulder) can be transferred to the throwing arm producing very, rapid "whip-like" accelerations of the arm and hand (9, 17, 20, 22). However, like all kinetic analyses, these studies have only estimated the contributions of joint rotational motions (ie. shoulder rotation) and cannot determine the extent to which muscles are responsible for those motions or how much of a role elastic energy storage plays in generating those motions.

Several studies have suggested that the storage and release of elastic energy plays a role in power enhancement during the throwing motion. Wilk et al. (23) argued that throwing athletes enhance the torque production of numerous throwing muscles by "pre-stretching" those muscles just prior to their activation, resulting in elastic energy storage in the muscle itself. Similarly, the analyses described in chapter 3 found that the posture of the arm as it is "cocked" (externally rotated) just prior to the rapid shoulder internal rotation motion passively stretches the elastic elements (including ligaments, tendons, and muscles) that cross the shoulder. By comparing actual power production during throwing to modeled maximum power values for all muscles potentially involved, I inferred that this passive stretching results in significant amounts of elastic energy being stored and released, powering the rapid internal rotation of the humerus that follows. One limitation of these studies, however, is that they can only indirectly infer elastic energy storage from other data, because *in vivo* imaging of soft tissues during the throwing motion is difficult and more invasive methods that measure muscle strain such as

sonomicrometry (24, 25) are not possible in human subjects. Furthermore, *in vivo* measurement of ligament and tendon strains and elastic energy storage is difficult, if not impossible, in a structure such as the shoulder (26-29).

4.3 Model

I propose that humans power high-speed throws by combining the transfer of kinetic power between segments, active muscle force produced throughout the body, and large amounts of elastic energy stored and released at the shoulder. The propulsive portion of the throwing motion begins with a large stride in the goal direction (3, 4), which serves to generate linear velocity in the upper body (8) and also to position the pelvis and torso for the rotation that follows. As the contralateral-side foot contacts the ground, the pelvis and torso begin to rapidly rotate the throwing-side arm towards the target (3, 4). The large hip rotator muscles are likely responsible for powering the majority of the rapid rotation of both the pelvis and torso, with less significant contributions from the torso rotators. While the torso rotation motion accelerates, the forelimb is moved to its "cocking" position. The humerus is abducted nearly 90° at the shoulder, horizontally extended, and externally rotated to its actively achieved ROM limit, while the elbow is flexed nearly 90° (3, 4). Chapter 3 suggests that this positioning of the arm and forearm maximizes the forelimb's moment of inertia around the humeral rotation axis (Figure 4.1). This large moment of inertia thus causes the arm to lag behind, passively externally rotating the humerus, potentially storing elastic energy in the

ligaments, tendons, and muscles crossing the shoulder. As torso rotation angular velocity peaks and the largest

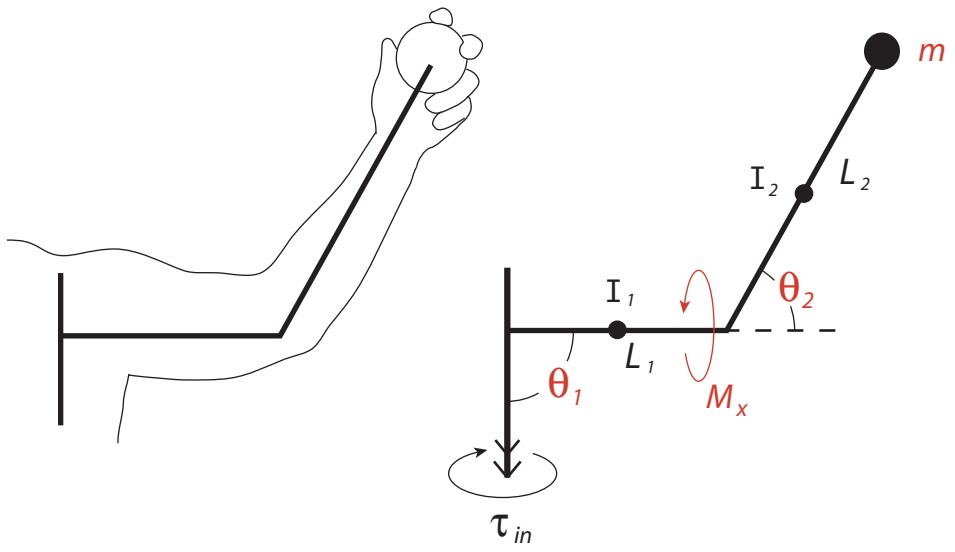


Figure 4.1. Free-body diagram of the throwing arm during cocking. During the cocking phase, the arm is abducted (θ_1) nearly 90° at the shoulder, positioning the mass of the arm, forearm, hand, and projectile away from the rotational axis of the torso. By flexing the elbow (θ_2) slightly less than 90°, the moment of inertia (M_x) is maximized around the long axis of the humerus. As torso rotation accelerates and the *Pectoralis major* contracts (increasing τ_{in}) the forelimb's large moment of inertia cause it to lag behind the accelerating torso, passively externally rotating the humerus, and stretching the elastic elements crossing the shoulder.

shoulder flexor, *Pectoralis major*, is activated, the passive external rotation of the arm reaches its maximal extent. The biceps then briefly deactivate allowing the triceps and large centrifugal forces from the torso rotation motion to rapidly extend the elbow (7, 11). As the elbow is extended, the moment of inertia around the long axis of the humerus drops allowing the stretched elastic elements to recoil. This recoil recovers the stored elastic energy, and in combination with the internal

rotator muscles of the shoulder, powers the rapid internal rotation the humerus, further extension of the elbow, and flexion of the wrist in a whip-like sequence that terminates in projectile release.

4.4 Hypotheses

Here we use a novel experimental approach to test our model of how human throwers generate power. We examined experimentally the effects of four key motions primarily responsible for projectile speed (torso rotation, shoulder internal rotation, elbow extension, and wrist flexion – Figure 4.2) by inducing variation in throwing kinematics through the use of therapeutic braces that limit joint range of motion (ROM) or modify joint position. Using braces allows us to experimentally test the effects of morphologies that are associated with performance differences in a study group where all individuals have comparable, high skill levels. Furthermore, this approach allows for a within-subjects experimental design, which can be valuable in analyzing complex motions such as throwing that can differ significantly in kinematics between individuals. Braces can also be used to induce variation where none currently exists. Using such braces to generate variation is necessary because collecting kinematic data from closely related species that vary in forelimb morphology, such as chimpanzees, is difficult and from extinct hominins is impossible. Further, since chimpanzees throw poorly and with very different kinematics than humans (30-33), we lack appropriate natural variation in the form of intermediate morphologies and throwing performance to adequately address the evolution of this complex behavior.

Another advantage of using braces is that we can use kinematic data from these experiments in combination with inverse dynamics analysis (which uses Newtonian physics to break down complex motions into the individual rotations

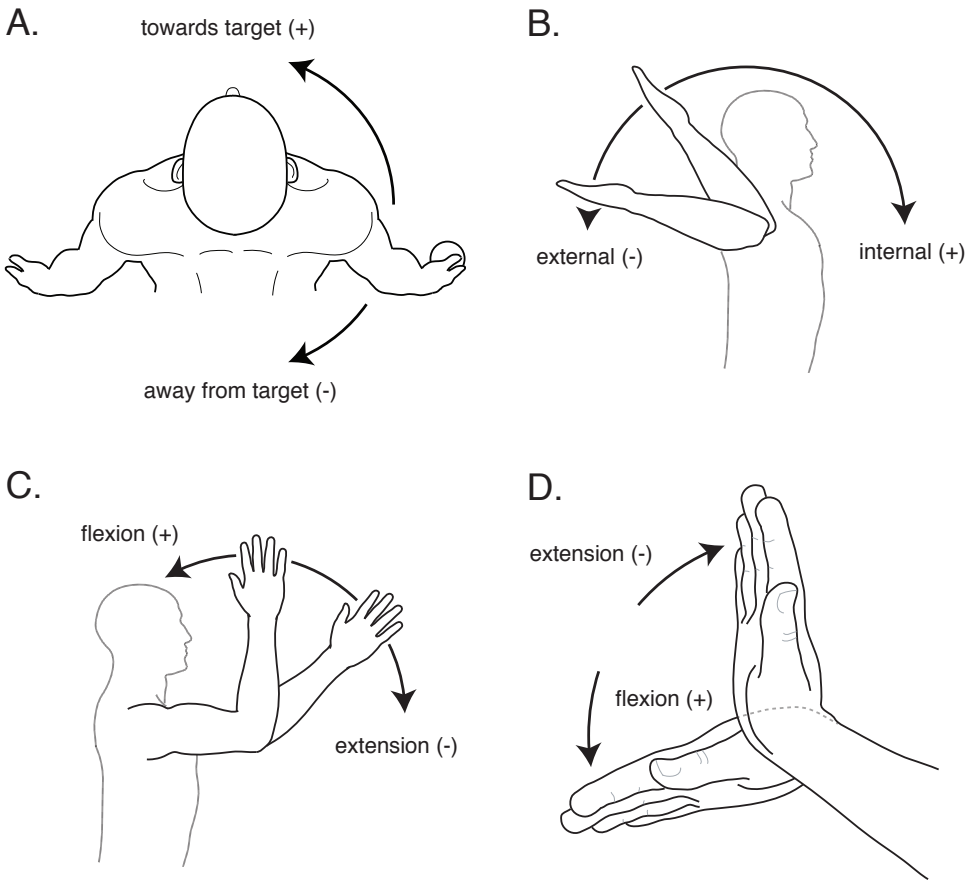


Figure 4.2. The four critical upper body motions examined in this study are: A. torso rotation; B. shoulder rotation; C. elbow flexion/extension; D. wrist flexion/extension. The + and – senses in the diagram show the convention used to describe the directionality of the angular velocities and torques. Note: the torso rotation senses are dependent upon handedness, as the description is relative to the throwing side.

occurring around each joint axis and the forces that drive those motions) to test discrete hypotheses about how particular motions and morphologies contribute to

throwing performance. By combining the use of braces with inverse dynamics, we test five related hypotheses using an observed versus expected framework.

Hypothesis 1: *The hip rotator muscles generate much of the torso rotation power during throwing.* Previous work has shown that hip rotation is an important component of the throwing motion and is correlated with throwing performance (34-36). We propose that by stabilizing the torso relative to the pelvis through bilateral contraction of the intrinsic spinal rotator muscles, the large hip rotators can power the rapid rotation of the torso and pelvis together. Both the medial hip rotators (*Gluteus medius and minimus, Tensor fasciae latae*) and lateral hip rotators (*Gluteus maximus, Quadratus femoris,* both *Gemelli,* both *Obturator*, *Piriformis, Sartorius*) can be active at the same time during the throwing motion at the contralateral and throwing-side hips respectively. We test this hypothesis by limiting intervertebral rotation using a back brace, which is predicted to lead to significant reductions in torso rotation angular velocity, torque, power, and work. However, given that we are only limiting torso rotational motion generated between the vertebrae and not at the hips, we expect the reductions in these throwing performance measures to be minor.

Hypothesis 2: *Torso rotation powers the storage of elastic energy at the shoulder.* Chapter 3 proposed that by abducting the shoulder and flexing the elbow as torso rotation reaches its peak angular velocity, the forelimb's mass is positioned away from the shoulder, increasing its moment of inertia, and causing the forelimb to lag behind the accelerating torso. This lag causes further external rotation of the

shoulder beyond the active muscularly driven ROM and into the passive range (37-39). It is reasonable to hypothesize that this passively, externally rotated and horizontally extended shoulder position results in stretching of the elastic elements that cross the shoulder and the storage of elastic energy (39). Although future work is necessary to determine which structures store and release this elastic energy, we can document the occurrence of elastic energy storage by comparing actual performance to estimates of maximum performance potential (39)**.** When actual performance exceeds even generous models of maximum performance, we will infer that elastic energy recovery accounts for the difference. Furthermore, when the production of negative work at joints of interest, indicating energy loss or absorption by elastic structures, is immediately followed by rapid, powerful motions, the presence of elastic recoil can again be inferred. Consequently, this study tests the hypothesis that torso rotation contributes to the elastic storage mechanism by examining how the torso brace restriction affects throwing performance at the shoulder. If elastic energy is stored as predicted, then we expect that when the brace is applied, minor reductions in torso rotation performance will lead to reductions in the amount of negative work done at the shoulder during the cocking phase. This reduction in shoulder rotation work during cocking should further result in large reductions in shoulder rotation angular velocity, torque, power, and work during acceleration.

Hypothesis 3: *Pectoralis major powers the storage of elastic energy at the shoulder.* Much like the torso rotation motion, we propose that when the forelimb is in its cocked position (3) muscular action by the largest shoulder horizontal flexor, *P.*

major, will result in substantial torque generated around the same shoulder axis as the torso rotation torque, causing the forelimb's mass to lag and stretch the elastic elements at the shoulder. Mathematical decomposition of the projectile's speed into the angular velocity contributions of each joint motion in the upper body show that horizontal flexion at the shoulder actually contributes negatively to projectile speed at release (8). However, individuals with a congenital absence of the *P. major* (Poland's syndrome) have been noted to throw poorly (40). Further, action by the horizontal flexors as the arm is cocked may generate useful torque and power around the same axis as the torso rotation motion and help load the elastic storage mechanism at the shoulder. To test this hypothesis, we use a clavicle brace to modify the orientation of *P. major* and alter its major line of action. When restricted the brace should cause a suboptimal realignment by cranially rotating this muscle's major line of action, which we expect will again result in a significant reduction in the amount of negative work done at the shoulder during cocking, and thus reductions in shoulder rotation angular velocity, torque, power, and work during acceleration.

Hypothesis 4: *Rapid elbow extension and wrist flexion at the end of the throw are generated passively.* Previous research has suggested that the extremely rapid motions at these distal joints just prior to projectile release result from the kinetic transfer of power from more proximal body segments, such as the torso and shoulder (7-9, 20, 21). To further test this hypothesis, we examine data from three proximal joint brace restrictions (torso, shoulder – which limits external rotational

ROM, and clavicle). We expect that for each of these proximal restrictions elbow extension and wrist flexion angular velocity and work will drop significantly.

Hypothesis 5: *Wrist hyperextension allows release to occur later in the throwing motion enabling the shoulder internal rotation and elbow extension motions to attain higher angular velocities.* Kinematic data on the overhand throwing motion have shown that while the arm is cocking, the wrist slowly hyperextends and then rapidly flexes as the arm accelerates towards the target (8, 10). This wrist hyperextension could enable other more proximal joint actions (eg. elbow flexion) to continue to accelerate prior to release and still achieve an accurate release trajectory. We test this hypothesis by restricting hyperextension using a wrist brace, which we expect will result in a significant decrease in the duration of the final acceleration phase of the throw, as well as significant reductions in wrist flexion, elbow extension, and shoulder internal rotation angular velocities and work.

Finally, we expect that projectile speed will drop significantly during all brace restricted conditions.

4.5 Materials and Methods

Subjects - Throwing data were collected from 24 male subjects (ages 19-23). All subjects included in the study met pre-determined inclusion criteria based on throwing performance. Prior to the study, they had 5 tries to hit a 1m x 1m target from 10m away at 22.35 m/s (50mph) or higher. In addition, during data collection, at least one throw across all conditions had to reach 22.35 m/s or higher. These performance criteria were designed to exclude poor throwers and resulted in the

exclusion of three subjects. An additional subject was excluded because his abnormal responses to the braces caused his kinematics to be more than 2 standard deviations away from the mean performance measures in all brace conditions.

Data collection - Three-dimensional, kinematic data were collected at 1000Hz using an eight-camera Vicon T10s 3D infrared motion capture system (Vicon Inc,

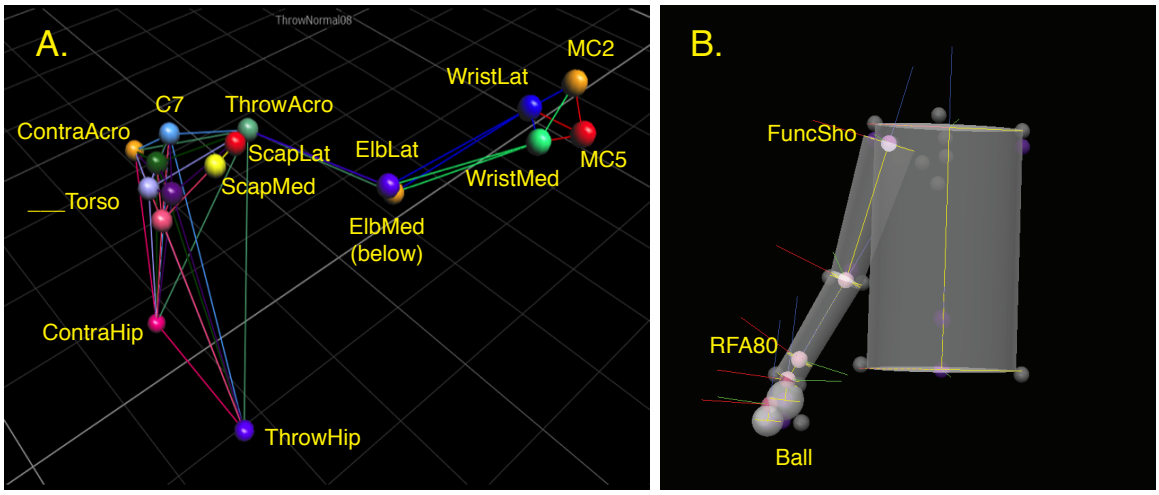


Figure 4.3. Reflective markers (A) and kinetic model (B) used in data collection and analysis. Note: The markers labeled ___Torso are a rigid cluster of 4 markers (SupTorso, ContraTorso, InfTorso & ThrowTorso). A second rigid ___Arm cluster is missing from this trial. In B, the light gray kinetic model shows the segments used in the inverse dynamics analysis. The Ball segment was a non-independent point mass added to the hand segment at the approximate ball position of a split-finger throw. This mass was dropped to zero in the analyses after the ball was released. The FuncSho marker highlighted is the functional joint center of the shoulder joint defined using a conical motion trial. RFA80 refers to another functional joint used to solve a tracking problem resulting from the different joint centers for flexion/extension and pronation/supination in the elbow (39).

Centennial CO, USA). Each subject had twenty-one passive reflective markers taped on the throwing arm and torso (Figure 4.3, Table 4.1). Subjects were first given the opportunity to warm up and then asked to throw a 144g baseball at a 1m radius

Segment Definitions				
Segment	**Segment Geometry**	**Defining Markers**	**Tracking Markers**	**Axes**
Thorax/Pelvis	Cylinder	Proximal: ThrowHip, ContraHip Distal: ThrowAcro, ContraAcro	midHip (calc) ThrowAcro ContraAcro	X: axial flex/extension Y: lateral flex/extension Z: axial rotation
Arm	Cone	Proximal: FuncSho (calc), ThrowAcro Distal: ElbMed, ElbLat	FuncSho (calc) ElbMed EldLat	X: flex/extension Y: ab/adduction Z: int/external rotation
ForearmUpper	Cone	Proximal: ElbMed, ElbLat Distal: RFA80 (calc)	ElbMed ElbLat RFA80 (calc)	X: flex/extension
ForearmLower	Cone	Proximal: RFA80 (calc) Distal: WriMed, WriLat	RFA80 (calc) WriMed WriLat	Z: pro/supination
Hand	Sphere	Proximal: WriMed, WriLat Distal: MC5, MC2	midWrist (calc) MC5 MC2	X: flex/extension Y: ulnar/radial deviation
Ball	Sphere	Single marker: Ball Prox (calc)	midWrist (calc) MC5 MC2	No independent motion

Table 4.1. Segment parameters used in the kinetic model. Segment length and diameter is obtained using the defining marker sets. Segmental movements are recorded using the tracking markers around the defined axes.

target positioned 10m from the subject. Each subject threw approximately 10-20 pitches in each of five randomly ordered experimental conditions (see below). Ball

speed was measured using a Sports Radar Model 3600 radar gun, and ball accuracy was calculated using Image J software (v 1.41) from digital video collected with a 30 Hz Canon Vixia HV30 digital video camera (Canon Inc, Tokyo, Japan) recording the ball impacting the target. Ball release was timed using a synched FlexiForce A201 force sensor (Tekscan Inc, Boston MA, USA) collecting at 1000Hz taped to the palmar side of the distal phalanx of the third digit.

Experimental treatments - Five different experimental treatments were used: normal unrestricted, torso restricted, clavicle restricted, shoulder restricted, and wrist restricted. All restricted conditions were accompanied by sham trials in which the brace was applied but not tightened to test the effect of the brace itself independent of the restriction (except for the torso restriction condition for which this was not possible). All brace conditions used commercially available therapeutic braces. Subjects were given *ad libitum* practice throws to acquaint themselves with both the sham and restricted portions of each condition. The torso restriction condition employed a DonJoy Dual TLSO back brace (DonJoy Inc., Vista, CA) to limit intervertebral motion from T2/T3 to the sacrum. This back brace uses wide, elastic Velcro straps to fasten a rigid plastic plate on the dorsal side of the body with a similar, smaller plate on the ventral side. A steel bar with a wide, padded end extends cranially from the ventral plate and is fixed against the clavicles to prevent rotational motion in the torso. The clavicle restriction condition used a DonJoy Clavicle Posture Support brace to hold the shoulder in a superiorly rotated, "shrugged" posture. This brace contains two self-adhering straps that run over the shoulders, under the armpits, and join in the back. During brace tightening, the

subject was requested to shrug his shoulders and the clavicle brace was tightened to prevent a relaxation. For the shoulder restriction condition, a DonJoy Shoulder Stabilizer brace was used to limit external rotational ROM at the shoulder. This shoulder brace is comprised of a tight, elastic Velcro vest with a single, elastic half-sleeve on the throwing arm. To restrict external rotation of the humerus, the arm was internally rotation and a Velcro strap was affixed from the dorsal side of the vest to the ventral side of the sleeve. The wrist restriction condition employed an Allsport Dynamics IMC Wrist brace (Allsport Dynamics Inc., Nacogdoches, TX) with the 0° extension stop either employed (restricted) or absent (sham). This brace affixed a rigid plastic sleeve and a small plastic plate to the dorsal side of the distal forearm and hand respectively. When the extension stop was screwed into place, the plastic sleeve contacted the hand plate and prevented the wrist from hyperextending.

Analysis - Raw marker data were identified using Vicon Nexus software (v 1.7.1) and exported to C-Motion Visual3D software (v4) for additional analysis. A Butterworth 2nd order low-pass filter with a cutoff frequency of 25Hz was chosen and applied after a residual analysis (41) of the data was conducted (39). Marker gaps of up to 100 frames were interpolated using Visual3D. Joint Euler angles were calculated and inverse dynamics analyses were performed using mass distribution ratios from Dempster (42) in Visual3D. Joint angular velocities, moments, and power were calculated using each joint's instantaneous axis of rotation. The Cardan sequence of rotations at each joint was XYZ. Joint work was calculated in MATLAB (v 7.11.0) using the trapz function. To help simplify analysis, each throwing motion

was divided into five standard throwing phases: windup/stride, arm-cocking, arm acceleration, arm deceleration, and follow-through (3). Because positive projectile linear velocity is generated during the arm-cocking and acceleration phases (Figure 4.4), we present data from just these two phases. Individual subject means from a number of performance measures were compared across experimental conditions using repeated measures ANOVA or MANOVA when variances were not equal

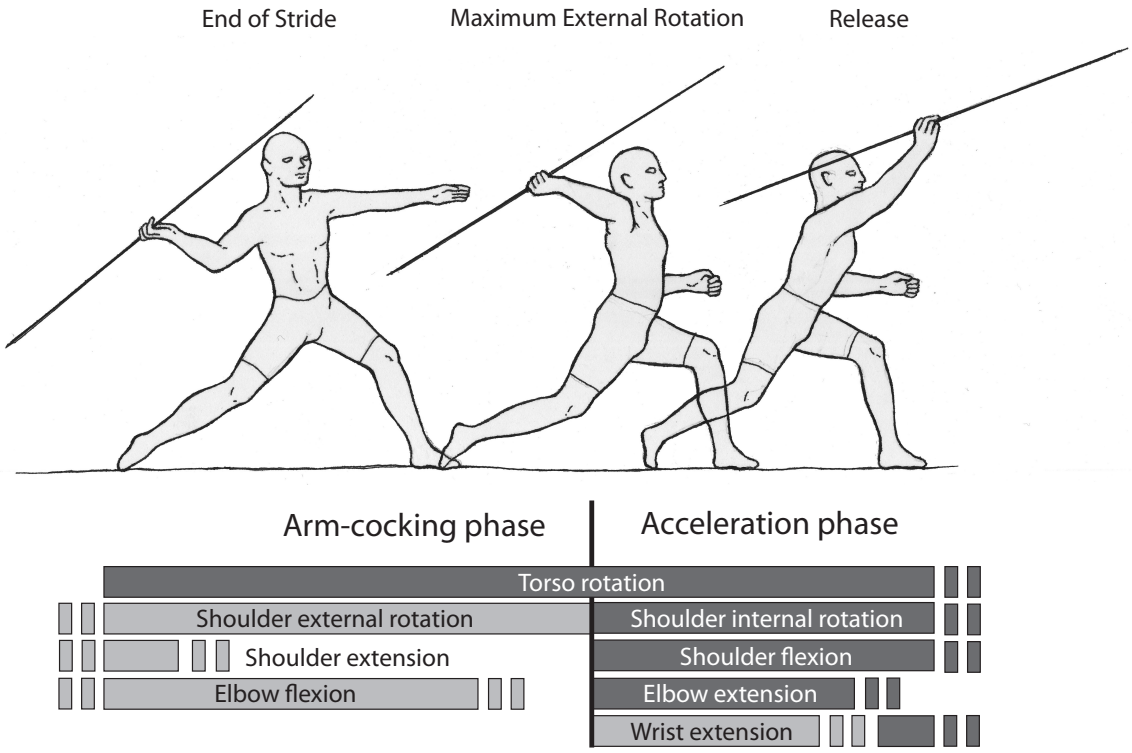


Figure 4.4. The arm-cocking and acceleration phases of the throw. Arm-cocking begins with the contralateral foot touching the ground at the end of a large stride (STR) in the target direction. During the cocking phase, the humerus externally rotates until it reaches maximum external rotation (MER). Following MER, the very brief acceleration phase occurs in which the humerus rapidly internally rotates, the elbow extends and the wrist is flexed. Acceleration ends with the release (REL) of the projectile.

(Mauchley's sphericity chi-square $p < 0.05$). Differences were taken as significant at the alpha < 0.05 level. Post-hoc matched pairs t-tests were used to determine which condition (normal, sham, and/or restricted) accounted for any significance. Given that the torso restriction condition does not have sham, all reported statistics for this condition are matched pairs t-tests.

4.6 Results

Normal unrestricted condition: During normal unrestricted throwing, maximum ball speed was 27.7±3.8 m/s (mean of all subject means±st. dev. of subject means) with the ball striking the target on average 0.3±0.2 m from the bullseye. The angular velocity of torso rotation peaked (848±160 °/s) during the latter half of the cocking phase (Figure 4.5), before producing an opposing braking torque during the brief acceleration phase. This opposing torque resulted in a short period of power absorption during acceleration, generating net negative work during this phase (-74±44 J). During the cocking phase at the shoulder, the humerus was externally rotated while simultaneously a large, opposing internal rotation torque was generated. This resulted in a sustained period of power absorption and negative work (-201±70 J) at the shoulder. As the acceleration phase began, with the initiation of shoulder internal rotation, the shoulder rotation torque and angular velocity became in-phase resulting in very high angular velocities (4290± 1127 °/s) and peak power (11838±4170 W). At the elbow, the cocking phase began with the elbow continuing to flex, while a moderate flexion torque was produced. However,

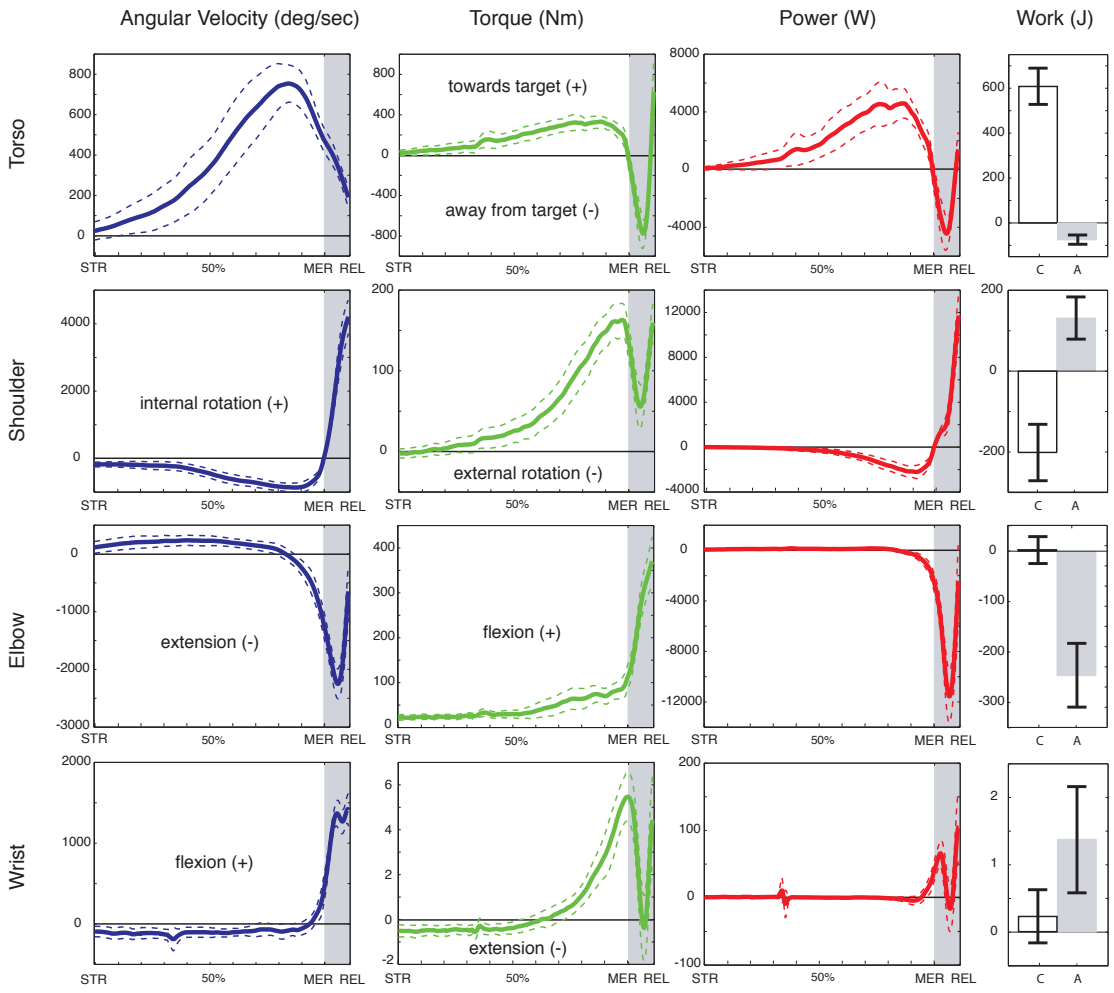


Figure 4.5. Joint kinematic and kinetic data from the four critical joint axes during normal throwing. Mean data across all subjects are shown with bolded lines, while 95% confidence intervals are reported with dashed lines. Differences in phase timing between individuals were standardized by interpolation each phase 1000 fold and subsequently down sampling each throw to a standard length. The length ratio of the two phases was kept proportional to the normal, unrestricted phase duration ratio. The arm-cocking phase (between STR and MER) is shown in the white field and labeled C in the work plots, while the acceleration phase (between MER and REL) is shown in a gray field and labeled A in the work plots.

during the last quarter of the cocking phase the elbow began to extend rapidly (-2434±552 °/s), peaking midway through the acceleration phase. During this rapid extension, the opposing flexion moment at the elbow intensified, resulting in large

Torso Restriction			
		Normal	**Torso Restriction**
Performance	Max. ball speed (m/s)	27.7(± 3.8)	**26.3(± 4)***
	Accuracy (m from bullseye)	0.3(± 0.2)	0.4(± 0.3)
Timing	Duration of Cocking (ms)	387(± 182)	*303(± 122)**
	Duration of Acceleration (ms)	40(± 12)	37(± 12)
Torso rotation	Peak Ang. Vel. (deg/s)	848(± 160)	***835(± 158)***
(+ throw arm torwards target,	Peak Torque (Nm)	828(± 437)	***773(± 424)***
- away from target)	Peak Power (W)	6207(± 2190)	***5968(± 2166)***
	Work - Cocking (J)	609(± 171)	**536(± 149)***
	Work - Acceleration (J)	-74(± 44)	-79(± 40)
Shoulder rotation	Peak Ang. Vel. (deg/s)	4290(± 1127)	**3970(± 1226)***
(+ internal, - external)	Peak Torque (Nm)	206(± 42)	***178(± 42)***
	Peak Power (W)	11838(± 4170)	**9872(± 4005)***
	Work - Cocking (J)	-201(± 70)	**-184(± 73)***
	Work - Acceleration (J)	132(± 52)	**100(± 56)***
Elbow flexion/extension	Peak Ang. Vel. (deg/s)	-2434(± 552)	**-2284(± 582)***
(+ flexion, - extension)	Peak Torque (Nm)	392(± 116)	357(± 121)
	Peak Power (W)	2028(± 3983)	2473(± 4498)
	Work - Cocking (J)	2(± 27)	-1(± 22)
	Work - Acceleration (J)	-246(± 63)	**-218(± 53)***
Wrist flexion/extension	Peak Ang. Vel. (deg/s)	1593(± 336)	**1645(± 280)**
(+ flexion, - extension)	Peak Torque (Nm)	7(± 3)	6(± 3)
	Peak Power (W)	138(± 90)	155(± 109)
	Work - Cocking (J)	0.2(± 1)	0.3(± 1)
	Work - Acceleration (J)	1(± 2)	**1(± 2)**

Table 4.2. Kinematic and kinetic performance measures for the four critical joint axes during normal and torso restriction conditions. Given that no sham was possible for this condition, restricted values that statistically differ ($p < 0.05$) from normal values are indicated with *. Bold values indicate hypothesized reductions from normal values, while italic values indicate unexpected changes.

amounts of power being absorbed and negative work generated (-246±63 J). Finally, at the wrist, a sustained extension occurred until the very end of the cocking phase,

when the wrist began to rapidly flex, continuing through the acceleration phase. A small flexion moment was produced (peak - 7±3 Nm) at the end of cocking, which then dropped to near zero and recovered during the acceleration phase. This oscillating power resulted in a small, net positive amount of work (1±2 J) generated during acceleration. Importantly, while there was considerable variation between subjects in the timing and duration of the throwing phases, as well as significant differences in overall performance, there was very little variation in the pattern of throwing kinematics across subjects.

Torso restriction condition: The torso restriction brace completely restricted intervertebral rotational motion, allowing only the hip rotators to rotate the trunk. Given the design of the torso brace, no sham condition was possible. Contrary to expectations, there were no significant reductions in torso rotation peak power, angular velocity, or torque (Table 4.2). However, a significant drop in torso rotation work during cocking (-11±18%) was recorded. As expected, significant reductions were seen in shoulder rotation peak angular velocity (-7±13%), power (-14±20%), and work (cocking: -7±25%; acceleration: -19±30%). Reductions also occurred in elbow extension peak angular velocity (-6±7%) and elbow work during acceleration (-7±14%). No significant reductions were measured in any performance variables at the wrist. As hypothesized, when the torso restriction brace was applied, maximum ball speed dropped -5±6%.

Clavicle restriction condition: When applied, the clavicle brace superiorly rotated the scapula 7±4° and also limited scapular protraction. The clavicle sham

Clavicle Restriction				
		Normal	**Clavicle Sham**	**Clavicle Restriction**
Performance	Max. ball speed (m/s)	27.7(± 3.8)	*27(± 4.2)**	**26.3(± 4.1)*†**
	Accuracy (m from bullseye)	0.3(± 0.2)	0.4(± 0.2)	0.4(± 0.2)
Timing	Duration of Cocking (ms)	387(± 182)	*300(± 72)**	*306(± 93)**
	Duration of Acceleration (ms)	40(± 12)	*32(± 9)**	34(± 11)
Torso rotation	Peak Ang. Vel. (deg/s)	848(± 160)	862(± 144)	870(± 155)
(+ throw arm torwards target, - away from target)	Peak Torque (Nm)	828(± 437)	580(± 167)	588(± 240)
	Peak Power (W)	6207(± 2190)	6869(± 2617)	6492(± 2159)
	Work - Cocking (J)	609(± 171)	638(± 177)	607(± 174)
	Work - Acceleration (J)	-74(± 44)	*-109(± 53)**	*-107(± 63)**
Shoulder rotation	Peak Ang. Vel. (deg/s)	4290(± 1127)	*3852(± 1175)**	***3778(± 1126)****
(+ internal, - external)	Peak Torque (Nm)	206(± 42)	180(± 38)	**169(± 37)*†**
	Peak Power (W)	11838(± 4170)	*8431(± 4455)**	***8958(± 4552)****
	Work - Cocking (J)	-201(± 70)	-188(± 60)	**-173(± 63)*†**
	Work - Acceleration (J)	132(± 52)	*54(± 35)**	***58(± 32)****
Elbow flexion/extension	Peak Ang. Vel. (deg/s)	-2434(± 552)	-2326(± 517)	**-2220(± 517)*†**
(+ flexion, - extension)	Peak Torque (Nm)	392(± 116)	357(± 80)	*336(± 84)†*
	Peak Power (W)	2028(± 3983)	631(± 1050)	630(± 1064)
	Work - Cocking (J)	2(± 27)	4(± 21)	5(± 22)
	Work - Acceleration (J)	-246(± 63)	*-225(± 58)**	**-206(± 59)*†**
Wrist flexion/extension	Peak Ang. Vel. (deg/s)	1593(± 336)	1505(± 255)	**1510(± 276)**
(+ flexion, - extension)	Peak Torque (Nm)	7(± 3)	6(± 2)	6(± 2)
	Peak Power (W)	138(± 90)	113(± 80)	107(± 73)
	Work - Cocking (J)	0.2(± 1)	0.4(± 1)	0.3(± 1)
	Work - Acceleration (J)	1(± 2)	1(± 1)	**1(± 1)**

Table 4.3. Kinematic and kinetic performance measures for the four critical joint axes during normal and clavicle brace restricted conditions. Restricted and sham values that statistically differ ($p < 0.05$) from normal values are indicated with *, while restricted values that statistically differ from the sham are shown with †. Bold values indicate hypothesized reductions from normal values, while italic values indicate unexpected changes.

showed no significant effects on joint motion. However, data from the sham trials (Table 4.3) indicate some perturbation of the normal throwing motion as there were

reductions in: mean maximum ball speed (-3±5%), phase duration (cocking -12±27%, acceleration -16±27%), torso rotation work – acceleration (-42±42%), elbow extension work – acceleration (-10±17%), shoulder rotation work – acceleration (-56±25%), and shoulder rotation angular velocity (-11±12%) and power (-28±32%). When the restriction was added, there was a further drop in maximum ball speed of -3±6%. Reductions in shoulder rotation peak torque (-13±31%) and work during acceleration (-9±10%) were recorded relative to normal values. Elbow extension angular velocity dropped -4±8% relative to normal, while elbow work during acceleration dropped -8±13% relative to the reduced sham values. No significant changes were observed in the wrist.

Shoulder restriction condition: When tightened, the shoulder brace reduced shoulder external rotation by 24±9°. However, when acting as a sham, the shoulder brace also restricted external rotation by 11±7°, much like a tight jacket. During the sham trials, there were also slight reductions in mean maximum ball speed (-3±5%), shoulder rotation work during the cocking phase (-9±13%), and a slight lengthening of the duration of the cocking phase (3±5%) (Table 4.4). However, for each of these significant changes in the sham condition, the shoulder restriction condition statistically differed from both the sham and normal conditions. The restricted trials showed a reduction in maximum ball speed from the sham trials of -8±6%. The duration of the cocking phase of the restricted trials shortened (-9±14%), while the

Shoulder Restriction

		Normal	Shoulder Sham	Shoulder Restriction
Performance	Max. ball speed (m/s)	27.7(± 3.8)	*27(± 4)**	**24.9(± 4)*†**
	Accuracy (m from bullseye)	0.3(± 0.2)	0.4(± 0.3)	0.4(± 0.3)
Timing	Duration of Cocking (ms)	387(± 182)	392(± 167)	*354(± 196)*†*
	Duration of Acceleration (ms)	40(± 12)	*38(± 14)**	*55(± 27)*†*
Torso rotation	Peak Ang. Vel. (deg/s)	848(± 160)	859(± 161)	833(± 156)
(+ throw arm torwards target, - away from target)	Peak Torque (Nm)	828(± 437)	827(± 404)	890(± 453)
	Peak Power (W)	6207(± 2190)	6111(± 2036)	5559(± 2000)
	Work - Cocking (J)	609(± 171)	587(± 152)	*513(± 154)*†*
	Work - Acceleration (J)	-74(± 44)	-78(± 42)	*-42(± 57)*†*
Shoulder rotation	Peak Ang. Vel. (deg/s)	4290(± 1127)	4261(± 1106)	4038(± 1141)
(+ internal, - external)	Peak Torque (Nm)	206(± 42)	206(± 45)	198(± 45)
	Peak Power (W)	11838(± 4170)	12145(± 4628)	13566(± 6141)
	Work - Cocking (J)	-201(± 70)	-181(± 63)*	-113(± 57)*†
	Work - Acceleration (J)	132(± 52)	124(± 63)	138(± 58)
Elbow flexion/extension	Peak Ang. Vel. (deg/s)	-2434(± 552)	-2341(± 505)	**1923(± 471)*†**
(+ flexion, - extension)	Peak Torque (Nm)	392(± 116)	355(± 88)	326(± 100)
	Peak Power (W)	2028(± 3983)	1229(± 2050)	1180(± 2383)
	Work - Cocking (J)	2(± 27)	3(± 20)	4(± 24)
	Work - Acceleration (J)	-246(± 63)	-236(± 58)	**-190(± 46)*†**
Wrist flexion/extension	Peak Ang. Vel. (deg/s)	1593(± 336)	1549(± 490)	**1515(± 332)**
(+ flexion, - extension)	Peak Torque (Nm)	7(± 3)	6(± 2)	6(± 2)
	Peak Power (W)	138(± 90)	128(± 74)	127(± 70)
	Work - Cocking (J)	0.2(± 1)	0.4(± 1)	*-0.1(± 1)*†*
	Work - Acceleration (J)	1(± 2)	1(± 2)	***2(± 1)*†***

Table 4.4. Kinematic and kinetic performance measures for the four critical joint axes during normal and shoulder brace restricted conditions. Restricted and sham values that statistically differ ($p < 0.05$) from normal values are indicated with *, while restricted values that statistically differ from the sham are shown with †. Bold values indicate hypothesized reductions from normal values, while italic values indicate unexpected changes.

acceleration phase lengthened (38±56%). Reductions in torso rotation work were recorded for both phases (cocking -14±20%, acceleration -41±57%). Although

shoulder rotation work during the cocking phase dropped significantly (-45±17%) from normal values, no further significant reductions occurred in shoulder rotation peak angular velocity, torque, power, or work during acceleration. As predicted there were significant reductions in elbow extension angular velocity (-21±10%) and elbow work during acceleration (-20±21%). Wrist flexion peak angular velocity remained unchanged, but a significant reduction in wrist work during cocking was followed by a significant increase in wrist work during acceleration.

Wrist restriction condition: When restricted by a brace, wrist extension ROM was reduced 62±7°, but there was no significant reduction in the sham condition. However, the wrist restriction sham trials showed numerous significant reductions in the measured performance variables (Table 4.5). Although the restricted condition showed significant reductions in ball speed and phase duration from normal values, these reductions were not significantly different from the sham condition. Similarly, while torso rotation performance metrics differed from normal values, only torso rotation work during acceleration differed between the sham and restricted trials (-6±17%). However, restricted shoulder rotation peak angular velocity dropped -6±8% from sham values, while shoulder rotation peak power and work values all dropped relative to normal and increased relative to sham trials. Elbow extension peak angular velocity did not differ between sham and restricted conditions, although restricted elbow work during acceleration dropped -19±14% from sham levels. The wrist flexion peak angular velocity dropped -34±37% relative

to the sham trials, while wrist flexion/extension peak power and work during acceleration increased relative to the sham.

Wrist Restriction				
		Normal	**Shoulder Sham**	**Shoulder Restriction**
Performance	Max. ball speed (m/s)	27.7(± 3.8)	*26.1(± 3.9)**	***25.8(± 4)****
	Accuracy (m from bullseye)	0.3(± 0.2)	0.4(± 0.2)	0.4(± 0.2)
Timing	Duration of Cocking (ms)	387(± 182)	*309(± 72)**	*311(± 95)**
	Duration of Acceleration (ms)	40(± 12)	*34(± 9)**	***33(± 10)****
Torso rotation	Peak Ang. Vel. (deg/s)	848(± 160)	838(± 175)	831(± 188)
(+ throw arm torwards target, - away from target)	Peak Torque (Nm)	828(± 437)	*431(± 96)**	*409(± 101)**
	Peak Power (W)	6207(± 2190)	5488(± 1670)	5676(± 2149)
	Work - Cocking (J)	609(± 171)	*541(± 136)**	*550(± 155)**
	Work - Acceleration (J)	-74(± 44)	-69(± 42)	*-62(± 39)*†*
Shoulder rotation	Peak Ang. Vel. (deg/s)	4290(± 1127)	*3799(± 1237)**	**3579(± 1217)*†**
(+ internal, - external)	Peak Torque (Nm)	206(± 42)	191(± 53)	185(± 53)
	Peak Power (W)	11838(± 4170)	*3534(± 1415)**	*4852(± 2614)*†*
	Work - Cocking (J)	-201(± 70)	*-181(± 66)**	*-192(± 68)†*
	Work - Acceleration (J)	132(± 52)	*33(± 27)**	**49(± 31)*†**
Elbow flexion/extension	Peak Ang. Vel. (deg/s)	-2434(± 552)	*-2308(± 587)**	***-2261(± 588)****
(+ flexion, - extension)	Peak Torque (Nm)	392(± 116)	351(± 116)	*276(± 81)*†*
	Peak Power (W)	2028(± 3983)	537(± 466)	354(± 178)
	Work - Cocking (J)	2(± 27)	*15(± 19)**	*-0.5(± 24)†*
	Work - Acceleration (J)	-246(± 63)	*-215(± 63)**	**-174(± 61)*†**
Wrist flexion/extension	Peak Ang. Vel. (deg/s)	1593(± 336)	*1406(± 331)**	**881(± 243)*†**
(+ flexion, - extension)	Peak Torque (Nm)	7(± 3)	*3(± 2)**	6(± 2)†
	Peak Power (W)	138(± 90)	*24(± 28)**	***47(± 29)*†***
	Work - Cocking (J)	0.2(± 1)	0.5(± 1)	0.5(± 0.4)
	Work - Acceleration (J)	1(± 2)	*-3(± 2)**	***1(± 1)†***

Table 4.5. Kinematic and kinetic performance measures for the four critical joint axes during normal and wrist brace restricted conditions. Restricted and sham values that statistically differ ($p < 0.05$) from normal values are indicated with *, while restricted values that statistically differ from the sham are shown with †. Bold values indicate hypothesized reductions from normal values, while italic values indicate unexpected changes.

4.7 Discussion

Overall, the results of the brace restriction trials are largely consistent with our model of power generation during throwing. We found support for both the use of an elastic energy storage mechanism at the shoulder as well as the importance of a kinetic chain in transferring power between body segments. These data also show some unanticipated responses to sham conditions, especially in the wrist, which bear further explanation and investigation.

We hypothesized (H1) that by restricting rotational movement between the vertebrae by using a brace, measures of throwing performance would experience small, but significant reductions. However, despite the fact that the restriction of intervertebral motion was essentially complete, we saw a significant reduction in torso rotation work during only the cocking phase. All other torso performance measures remained unchanged. This result suggests that during normal throwing, most (~90%) of the work required to achieve high projectile velocity is generated at the hips. The reduction seen in torso rotation work during the cocking phase may be driven by a significant reduction in the duration of this phase. However, the fact that other brace conditions result in similar changes in phase duration without affecting the amount of torso rotation work performed suggest this is not the case. These data strongly support the hypothesis that the hip rotators are almost wholly responsible for powering the rapid rotation of the torso (34-36). Further work is necessary to determine which hip rotator muscles are primarily responsible for generating this power.

Although the torso brace restriction resulted in mostly minor, non-significant reductions in performance at the torso, the effects of this brace do seem to be amplified at the shoulder. We had hypothesized (H2) that if torso rotation was in fact powering the elastic storage mechanism at the shoulder (39), even minor reductions in torso rotation performance should result in less elastic energy stored at the shoulder and, consequently, large reductions in shoulder rotation performance. The data from the torso restriction trials support this hypothesis. Negative shoulder rotation work during the cocking phase, which can be used as a proxy for elastic energy storage, is reduced by more than 10% during the torso brace trials. Further reductions in shoulder rotation angular velocity, power, and work during the acceleration phase accompany this reduction in work during the cocking phase. While it is again possible that a reduction in the duration of the cocking phase is partly responsible for changes in the shoulder performance measures, data from other experimental conditions in which the cocking phase shortened without affecting these same measures make this unlikely. Furthermore, no change is seen in the duration of the acceleration phase in which peak shoulder rotation angular velocity and power are achieved. These results provide support for torso rotation contributing to elastic energy storage in the shoulder during the arm-cocking phase.

The other potential source of power we proposed (H3) could contribute to elastic energy storage at the shoulder is *Pectoralis major*. By using the clavicle brace to hold the shoulder complex in a superiorly rotated position, we sought to change this muscle's major line of action, effectively excluding contributions from the

inferior fibers of the muscle to horizontal flexion at the shoulder. While no significant effects of the sham were measured on static shoulder ROM, significant changes in performance measures during the sham trials suggest that the unloaded brace did cause some restriction potentially by limiting scapular protraction around the moment of release. However, despite the unexpected restriction caused by the sham and the performance responses that resulted during the sham trials, the restricted trials did show further significant decreases in shoulder rotation work during the critical cocking phase and also in peak shoulder torque. Shoulder rotation angular velocity, power, and work during acceleration all changed relative to the normal condition, but did not differ from the sham trials. While the reductions in shoulder rotation torque and work during cocking confirm the effect of the restriction and support the role of *P. major* in loading the elastic elements in the shoulder, the lack of significant shifts in the other performance measures (e.g. shoulder rotation angular velocity, power, and work during acceleration) leaves this hypothesis only partially supported. It is possible that the minor superior rotation the brace induced was insufficient to yield a large enough effect on these performance measures to overcome the high degree of variance they show. However, it is worth noting that the clavicle brace restriction did lead to performance reductions in peak elbow extension angular velocity and work during the acceleration phase.

It has long been thought that, despite very rapid angular velocities at the distal elbow and wrist joints, the work and power necessary to achieve rapid angular movements in these joints during throwing are derived from power

generated at more proximal joints (7-9, 20, 21). As hypothesized (H4), work during both the cocking and acceleration phases of a normal throw is very low at the wrist and low or negative at the elbow. This finding suggests that both motions are largely passive. Furthermore, when examining all brace conditions (torso, clavicle, shoulder) in which proximal joint actions (torso rotation and/or shoulder rotation) were affected, significant performance reductions were seen at the elbow, but not the wrist. These data suggest that the elbow is likely powered primarily by kinetic transfer from upstream joints (7-9, 20). This kinetic chain may also apply to the wrist, although the lack of response to the restrictions at the wrist suggests some compensatory action is possible. It is worth noting that given the brevity of the acceleration phase, having multiple passive components in the shoulder, elbow, and wrist could serve to simplify the difficult neural control problem that rapid throwing poses. Such reduced complexity would allow the throwing motion to be more easily, effectively, and consistently produced.

Another hypothesis (H5) was that wrist hyperextension allows throwers to delay projectile release, enabling additional acceleration of the proximal joints, while still maintaining an accurate release trajectory. Although the wrist brace restriction did show a reduction in the duration of the acceleration phase relative to the normal condition, it did not differ from the reduction seen during the sham trials. In fact, unlike responses to the other brace's sham conditions, the performance effects of the wrist sham were pervasive and severe. Significant performance reductions were seen in all segments analyzed during the wrist sham condition. Given that no measurable effect of wrist ROM was noted with the sham, it is likely

that the effects seen during the sham trials were due to the addition of the brace's mass to the distal forelimb. Although the mass of the brace was ~165 g, this additional mass more than doubles the previously added ball's mass at the hand. These sham result suggest that the elastic storage mechanism at the shoulder could be quite sensitive to changes in projectile or distal forearm mass. Without postural adjustments, such a change in mass could significantly increase the forelimb's moment of inertia during the critical cocking phase and disrupt a system finely tuned for passive action.

The wrist brace restriction did show significant performance effects relative to the wrist sham where expected (shoulder rotation angular velocity, elbow extension work – acceleration, and wrist flexion angular velocity). However, these reductions appear to be independent of any change in phase duration. Furthermore, a number of performance variables that were predicted to drop because of the restriction (shoulder rotation work - acceleration, wrist peak power and work - acceleration) actually increased over the sham values, potentially because of compensation for the restriction. While these data do not lead to the outright rejection of our wrist hyperextension hypothesis, further data on adding mass at the wrist without using a brace are needed to address the effects of both factors on throwing performance.

While the use of braces to induce variation in joint ROM can be an effective way to address how skeletal morphology can contribute to complex motions such as throwing, such an approach is not without limitations. Although all brace

restrictions (except for the wrist) showed significant reductions in ball speed relative to both their sham and normal trials, these reductions were relatively minor (0.5-9%). Such minor reductions highlight the ability of the subjects - all accomplished throwers - to compensate for minor to moderate disruptions of their normal throwing motion. Brace restrictions can also lead to unintended responses, such as limiting scapular protraction (clavicle brace) or causing compensatory flexion action at the wrist (shoulder brace). Our experimental design targeted key motions responsible for projectile speed, but the effect of these braces were not restricted to only the motions reported here. Furthermore, even when tasked to throw as hard as possible in all brace restricted conditions, the tendency of some subjects to fight through the restrictions in order to maintain performance can lead to variable effort between trials. Despite these drawbacks of our experimental approach, both the kinematic data and the fact that accuracy remained unchanged across all conditions does provide some confirmation that the normal throwing motion was mostly preserved.

In conclusion, the results of this study confirm previous findings that power generation during rapid overhand throwing is strongly affected by two phenomena: the transfer of power/work from proximal segments to distal joints via a kinetic chain (6, 7, 17, 20, 43) and elastic energy storage at the shoulder (23, 39). The hips rotators were shown to account for most of the torso rotation power and work produced during throwing. Through a kinetic transfer of power, torso rotation enabled the passive loading of the elastic elements in the shoulder during the cocking phase. Much of the energy absorbed at the shoulder during cocking was

then recovered in the acceleration phase, resulting in faster shoulder internal rotation and elbow extension just prior to release (39). The *Pectoralis major* was also shown to contribute to the amount of energy absorption (negative work) at the shoulder during the cocking phase and again showed significant effects on elbow extension angular velocity. Kinetic power transfers like that used to load the elastic storage mechanism are also likely driving the rapid elbow extension and wrist flexion motions that occur at the end of the throw (7-9, 20). Both the wrist and elbow show little to no positive work performed during either the cocking or acceleration phases suggesting that both motions are powered by more proximal joint actions. The effects of wrist hyperextension on the throwing motion remain unclear. While there are clearly some performance benefits to hyperextension, the unexpected effects of adding mass at the wrist makes interpreting these results difficult.

A number of important questions remain unanswered and need further study. While the storage and use of elastic energy at the shoulder is strongly supported, where this energy is stored in unknown. There are numerous short, elastic ligaments in the shoulder capsule and broad, flat muscles tendons crossing the shoulder joint that, when stretched, could store elastic energy. There are also elastic components within the muscle tissue of the many shoulder muscles that could also contribute. Further investigation of these elastic elements using *in vivo* soft tissue imaging during the throwing motion would be invaluable in addressing which elements are storing elastic energy. It is also unknown how variations in throwing kinematics would affect elastic energy storage. Increasing the variance in

subjects' throwing performance or including alternative throwing styles, such as windmill-type cricket bowls, could provide important insights into differences in elastic energy storage and throwing performance.

Finally, how power is generated during throwing may be used to better understand common throwing injuries. Three of the most common injuries in throwing athletes occur at the shoulder (shoulder labrum tears, shoulder instability) and elbow (medial epicondylitis) (6, 10, 44-50). Damage to the superior portion of the shoulder labrum at the attachment site of the biceps (a SLAP lesion/tear) likely results from a high degree of passive external rotation of the humerus during the arm-cocking phase (51, 52). During arm-cocking, the biceps are activated in order to maintain the flexed elbow that is vital for elastic energy storage (11). However, the combination of bicep flexion and passive external rotation of the humerus cause high concentrations of stress at the biceps' tendinous insertion on the labrum. Such stretching and sometimes tearing of the biceps tendon suggests that this tendon may in fact provide some elastic storage potential irrespective of the role of the biceps in positioning the forearm. Similarly, shoulder instability and the problems it can cause (anterior ligament laxity, increased likelihood of dislocation (48)) may be driven by use of the capsular ligaments to store elastic energy at the shoulder to power rapid throwing. During cocking, the arm is abducted in line with the shoulders, horizontally extending, and externally rotated. This arm position pulls taut the anterior band of the inferior glenohumeral ligament, the middle glenohumeral ligament, and the coracohumeral ligament (53). When the arm is then passively externally rotated as its mass lags behind the accelerating

torso, these ligaments are stretched. Such stretching could enable the storage of elastic energy in these ligaments, although with overuse it could lead to deformation of these ligaments and, consequently, shoulder instability. Finally, the elbow flexion positioning vital to increase the forelimb's moment of inertia and enable elastic energy storage also results in very high valgus torques at the elbow during both the arm-cocking and early acceleration phases (10, 54-56). This high, out-of-the-joint-plane torque stretches the ulnar collateral ligament, which stabilizes the elbow, and can lead to damage and painful inflammation (6, 10, 50). All of these injuries directly result from forelimb positioning necessary to maximize elastic energy storage. Other frequent shoulder injuries, such as rotator cuff tears, are less directly related to power generation, but likely result from forces generated to decelerate the rapidly moving forelimb after the projectile is released (10, 49, 57).

Although the elastic energy used to power the throwing motion is vital to throwing performance, the results from this study suggest steps that might be taken to reduce the risk of injury to throwers. A number of studies have shown that limiting the frequency of high-speed throwing does have some protective effect against these overuse injuries (6, 47, 50, 55, 58, 59). Furthermore, it has been shown that the amount of passive external rotation at the shoulder during the arm-cocking phase (when elastic energy is stored) is correlated with injury (37, 38). This result suggests that using mildly restrictive garments (such as a compression shirt) would have some protective effect against over-rotation injuries. However, it should be cautioned that because the same factors that enhance throwing performance also

increase the risk of injury, completely preventing these injuries is probably impossible.

4.8 Acknowledgements

I would like to thank Dan Lieberman for his help in designing this study and tirelessly commenting on this manuscript; the National Science Foundation, the American School for Prehistoric Research, and the Harvard Department of Human Evolutionary Biology for generously funding this research; our subjects for generously giving their time; the Wyss Institute Motion Capture lab for the use of their equipment and facilities; Mike Rainbow, Madhu Venkadesan, Leia Stirling, Matt Vincent, George Karas, Randi Griffin, Gulus Emre, Wes Gordon, Adanma Ekeledo, and Amanda Lobell for their invaluable help.

4.9 Literature Cited

1. Larson SG (1993) Functional Morphology of the Shoulder in Primates. *Postcranial Adaptation in Non-human Primates*, ed Gebo DL (Northern Illinois University Press, Chicago, IL), pp 45-69.

2. Larson SG (2007) Evolutionary Transformation of the Hominin Shoulder. *Evolutionary Anthropology* 16:172-187.

3. Dillman CJ, Fleisig GS, & Andrews JR (1993) Biomechanics of pitching with emphasis upon shoulder kinematics. *J Orthop Sports Phys Ther* 18(2):402-408.

4. Pappas AM, Zawacki RM, & Sullivan TJ (1985) Biomechanics of baseball pitching. A preliminary report. *Am J Sports Med* 13(4):216-222.

5. Hong DA, Cheung TK, & Roberts EM (2001) A three-dimensional, six-segment chain analysis of forceful overarm throwing. *J Electromyogr Kinesiol* 11(2):95-112.

6. Fleisig GS, Barrentine SW, Escamilla RF, & Andrews JR (1996) Biomechanics of overhand throwing with implications for injuries. *Sports Med* 21(6):421-437.

7. Hirashima M, Yamane K, Nakamura Y, & Ohtsuki T (2008) Kinetic chain of overarm throwing in terms of joint rotations revealed by induced acceleration analysis. *J Biomech* 41(13):2874-2883.

8. Hirashima M, Kudo K, Watarai K, & Ohtsuki T (2007) Control of 3D limb dynamics in unconstrained overarm throws of different speeds performed by skilled baseball players. *J Neurophysiol* 97(1):680-691.

9. Putnam CA (1993) Sequential motions of body segments in striking and throwing skills: descriptions and explanations. *J Biomech* 26 Suppl 1:125-135.

10. Fleisig GS, Andrews JR, Dillman CJ, & Escamilla RF (1995) Kinetics of baseball pitching with implications about injury mechanisms. *Am J Sports Med* 23(2):233-239.

11. Hirashima M, Kadota H, Sakurai S, Kudo K, & Ohtsuki T (2002) Sequential muscle activity and its functional role in the upper extremity and trunk during overarm throwing. *J Sports Sci* 20(4):301-310.

12. Roberts EM (1971) Cinematography in biomedical investigation. *Selected Topics in Biomedical Invesitgation. Proceedings of the C.I.C. Symposium on Biomechanics*, ed Cooper JM (The Athletic Institute, Chicago), pp 71-81.

13. DiGiovine NM, Jobe FW, Pink M, & Perry J (1992) An electromyography analysis of the upper extremity in pitching. *J Shoulder Elbow Surg* 1:15-25.

14. Gowan ID, Jobe FW, Tibone JE, Perry J, & Moynes DR (1987) A comparative electromyographic analysis of the shoulder during pitching. Professional versus amateur pitchers. *Am J Sports Med* 15(6):586-590.

15. Gans C (1992) Electromyography. *Biomechanics - Structures and Systems: A Practical Approach*, ed Biewener AA (Oxford University Press, Oxford), pp 123-147.

16. Bell DG (1993) The influence of air temperature on the EMG/force relationship of the quadriceps. *Eur J Appl Physiol Occup Physiol* 67(3):256-260.

17. Atwater AE (1979) Biomechanics of overarm throwing movements and of throwing injuries. *Exerc Sport Sci Rev* 7:43-85.

18. Hore J, O'Brien M, & Watts S (2005) Control of joint rotations in overarm throws of different speeds made by dominant and nondominant arms. *J Neurophysiol* 94(6):3975-3986.

19. Kibler WB & Sciascia A (2004) Kinetic chain contributions to elbow function and dysfunction in sports. *Clin Sports Med* 23(4):545-552, viii.

20. Feltner ME (1989) 3-Dimensional Interactions in a 2-Segment Kinetic Chain .2. Application to the Throwing Arm in Baseball Pitching. *Int J Sport Biomech* 5(4):420-450.

21. Hirashima M, Ohgane K, Kudo K, Hase K, & Ohtsuki T (2003) Counteractive relationship between the interaction torque and muscle torque at the wrist is predestined in ball-throwing. *J Neurophysiol* 90(3):1449-1463.

22. Alexander RM (1991) Optimum timing of muscle activation for simple models of throwing. *J Theor Biol* 150(3):349-372.

23. Wilk KE, *et al.* (1993) Stretch-shortening drills for the upper extremities: theory and clinical application. *J Orthop Sports Phys Ther* 17(5):225-239.

24. Newman S, *et al.* (1984) Respiratory muscle length measured by sonomicrometry. *J Appl Physiol* 56(3):753-764.

25. Biewener AA, Corning WR, & Tobalske BW (1998) In vivo pectoralis muscle force-length behavior during level flight in pigeons (Columba livia). *J Exp Biol* 201 (Pt 24):3293-3307.

26. Finni T, Komi PV, & Lepola V (2000) In vivo human triceps surae and quadriceps femoris muscle function in a squat jump and counter movement jump. *Eur J Appl Physiol* 83(4 -5):416-426.

27. Komi PV, Salonen M, Jarvinen M, & Kokko O (1987) In vivo registration of Achilles tendon forces in man. I. Methodological development. *Int J Sports Med* 8 Suppl 1:3-8.

28. Lewis JL, Lew WD, & Schmidt J (1982) A note on the application and evaluation of the buckle transducer for the knee ligament force measurement. *J Biomech Eng* 104(2):125-128.

29. Pourcelot P, Defontaine M, Ravary B, Lematre M, & Crevier-Denoix N (2005) A non-invasive method of tendon force measurement. *J Biomech* 38(10):2124-2129.

30. Goodall J (1986) *The Chimpanzees of Gombe: Patterns of Behavior* (Harvard University Press, Cambridge).

31. Goodall J (1964) Tool-Using and Aimed Throwing in a Community of Free-Living Chimpanzees. *Nature* 201:1264-1266.

32. Kohler W (1925) *The Mentality of Apes* (Harcourt and Brace, New York).

33. Sugiyama Y & Koman J (1979) Tool-using and making behavior in wild chimpanzees at Bossou, Guinea. *Primates* 20:513-524.

34. Wight J, Richards J, & Hall S (2004) Influence of pelvis rotation styles on baseball pitching mechanics. *Sports Biomech* 3(1):67-83.

35. Stodden DF, Fleisig GS, McLean SP, Lyman SL, & Andrews JR (2001) Relationship of pelvis and upper torso kinematics to pitched baseball velocity. *J Appl Biomech* 17(1):164-172.

36. Matsuo T, Escamilla RF, Fleisig GS, Barrentine SW, & Andrews JR (2001) Comparison of kinematic and temporal patterns between different pitch velocity groups. *J Appl Biomech* 17(1):1-13.

37. Miyashita K, *et al.* (2008) Relationship between maximum shoulder external rotation angle and throwing and physical variables. *J Sports Sci Med* 7:47-53.

38. Miyashita K, *et al.* (2008) The role of shoulder maximum external rotation during throwing for elbow injury prevention in baseball players. *J Sports Sci Med* 7:223-228.

39. Roach NT (2012) Chapter 3 - Elastic energy storage in the shoulder and the evolution of high-speed throwing in *Homo;* in The Biomechanics and Evolution of High-Speed Throwing *PhD dissertation* (Harvard University, Cambridge, MA).

40. Lee YH & Chun SI (1991) Congenital absence of pectoralis major: a case report and isokinetic analysis of shoulder motion. *Yonsei medical journal* 32(1):87-90.

41. Winter DA (1991) *The biomechanics of motor control of human gait: normal, elderly and pathological* (University of Waterloo Press, Waterloo, Ontario).

42. Dempster WT (1955) *Space requirements for the seated operator* (Wright Air Development Center, Wright-Patterson Air Force Base, OH).

43. Higgins JR (1977) *Human Movement: an integrated approach* (The C.V. Mosby Company, Saint Louis).

44. Altchek DW & Dines DM (1995) Shoulder Injuries in the Throwing Athlete. *J Am Acad Orthop Surg* 3(3):159-165.

45. Anz AW, *et al.* (2010) Correlation of torque and elbow injury in professional baseball pitchers. *Am J Sports Med* 38(7):1368-1374.

46. Badia A & Stennett C (2006) Sports-related injuries of the elbow. *J Hand Ther* 19(2):206-226.

47. Fleisig GS, *et al.* (2011) Risk of serious injury for young baseball pitchers: a 10-year prospective study. *Am J Sports Med* 39(2):253-257.

48. Meister K (2000) Injuries to the shoulder in the throwing athlete. Part one: Biomechanics/pathophysiology/classification of injury. *Am J Sports Med* 28(2):265-275.

49. Jobe CM, Pink MM, Jobe FW, & Shaffer B (1996) Anterior shoulder instability, impingement, and rotator cuff tear: theories and concepts. *Operative Techniques in Upper Extremity Sports Injuries*, ed Jobe FW (Mosby, St. Louis, MO).

50. Rizio L & Uribe JW (2001) Overuse injuries of the upper extremity in baseball. *Clin Sports Med* 20(3):453-468.

51. Burkhart SS, Morgan CD, & Kibler WB (2003) The disabled throwing shoulder: spectrum of pathology Part I: pathoanatomy and biomechanics. *Arthroscopy* 19(4):404-420.

52. Burkhart SS, Morgan CD, & Kibler WB (2000) Shoulder injuries in overhead athletes. The "dead arm" revisited. *Clin Sports Med* 19(1):125-158.

53. Clemente C (1985) *Gray's Anatomy of the Human Body* (Lea & Febiger, Philadelphia) 30th American Ed.

54. Loftice J, Fleisig GS, Zheng N, & Andrews JR (2004) Biomechanics of the elbow in sports. *Clin Sports Med* 23(4):519-530, vii-viii.

55. Sabick MB, Torry MR, Lawton RL, & Hawkins RJ (2004) Valgus torque in youth baseball pitchers: A biomechanical study. *J Shoulder Elbow Surg* 13(3):349-355.

56. Werner SL, Fleisig GS, Dillman CJ, & Andrews JR (1993) Biomechanics of the elbow during baseball pitching. *J Orthop Sports Phys Ther* 17(6):274-278.

57. Andrews JR & Angelo RL (1988) Shoulder arthroscopy for the throwing athlete. *Tech Orthop* 3(1):75-82.

58. Gainor BJ, Piotrowski G, Puhl J, Allen WC, & Hagen R (1980) The throw: biomechanics and acute injury. *Am J Sports Med* 8(2):114-118.

59. Feltner M & Dapena J (1986) Dynamics of the Shoulder and Elbow Joints of the Throwing Arm during a Baseball Pitch. *Int J Sport Biomech* 2(4):235-259.

Chapter 5 - Throwing and the Evolution of the Hominin Forelimb

5.1 Chapter Summary

High-speed, accurate throwing is a uniquely human behavior that is universal across all cultures. The ability to produce high-speed throws was likely important in the past, but when high-speed throwing ability evolved is unknown. Archaeological data addressing this question remain incomplete as the earliest projectiles, untipped spears and stones, are rarely preserved or identified. An alternative approach to testing when and how throwing evolved is to integrate comparative anatomy of apes and humans, biomechanical models of throwing, and experiments that test predicted relationships between anatomical variation among humans and throwing performance. When applied to the hominin fossil record, these insights on the functional morphology of throwing suggest that high-speed throwing first appears in *Homo erectus*. This enhanced throwing ability results from the accumulation of exapted morphological changes in the hominin torso and forelimb as well as a novel, adaptive shift in the position of the shoulder. High-speed throwing by *Homo erectus* was likely a vital component of a flexible early hunting/scavenging strategy that radically altered hominin diet, morphology, and life history.

5.2 Introduction

In his 1871 book, *The Descent of Man and Selection in Relation to Sex*, Darwin noted that, "To throw a stone with as true an aim as a Fuegian in defending himself, or in killing birds, requires the most consummate perfection in the correlated action of the muscles of the hand, arm, and shoulder, and further, a fine sense of touch" (1). Darwin's observation, made over 100 years ago, highlights both humans' unique ability to throw objects with speed and accuracy and the mechanical complexity of the throwing motion. Since Darwin, throwing has played a major role in our thinking about the course of human evolution. Humans' unique ability to throw probably had significant effects on the evolution of hunting, which represents a major transition in the hominin diet (2-5). The ability to throw projectiles such as sticks, stones, or crude spears with accuracy and force almost surely helped hominins to kill or disable prey (6, 7) or drive off other predators from their own kills (8, 9). However, other adaptive arguments have been proposed for the evolution of throwing. Fifer (10) postulates that the use of high-performance throws very early in hominin evolution was an important defensive strategy for driving off dangerous terrestrial predators, allowing early hominins to traverse more open habitats safely. He further suggests that morphological modifications in the upper body to improve throwing performance eventually made quadrupedalism less effective and drove the adoption of habitual bipedalism. Carrier (11) has also proposed that advantages in generated force from a bipedal versus quadrupedal posture during intraspecific aggression bouts, involving striking and throwing behavior, may have favored early bipedal posture. Other researchers have suggested that although high-speed throwing may

have evolved in the context of hunting/scavenging, the more important adaptive context was social competition (9, 12, 13). The ability to throw well could be a low risk way of punishing non-cooperators (9, 12) or serve to equalize body size differences by emphasizing skill over strength (13, 14), fostering social cooperation and improving group bonds. Bingham (9, 15, 16) further suggests that human's unique throwing ability and the role this ability plays in the evolution of cooperation had significant effects well into recent human history. The complexity and rapidity of the throwing motion are also thought to be very neurologically demanding and some authors have suggested this complexity created strong selection pressures for a larger brain and contributed to cognitive advances such as language ability long assumed to be linked to increased brain size (13, 17-19).

Despite the likely adaptive importance of high-speed, accurate throwing in our evolutionary past, we actually know very little about the evolution of this behavior. We not only do not know when high performance throwing arose, but we also do now know what morphological features evolved to improve throwing performance, and whether these features were adaptations for throwing or for other derived behaviors.. The inability to recognize and date the origins of this important behavior limits our capacity to evaluate hypotheses regarding why throwing evolved and what selective pressures drove its emergence. The most direct evidence for the antiquity of throwing comes from the presence of projectiles in the archaeological record. However, lithic projectile points appear only recently in hominin evolution (20, 21) and preservational and identification biases make the recovery of early projectiles such as untipped wooden spears, stones, and throwing

sticks sporadic and uninformative. In the absence of useful data from the archaeological record, more indirect evidence of throwing behavior must be gleaned from functional morphological analyses of hominin fossils. However, analyses of the skeletal signatures of throwing behavior are necessarily correlational and often their effects on throwing performance have been based on untested models (10, 22). Furthermore, many of these functional studies focus primarily on differences between more recent taxa (especially *H. neanderthalensis* versus *H. sapiens*) and are unable to address the antiquity of throwing behavior in hominin evolution.

The approach I adopt here is to evaluate what is currently known about throwing behavior and mechanics in a comparative context. Comparing differences in throwing behavior and anatomy in humans and non-human primates provides a starting point for examining how shifts in morphology during hominin evolution affect throwing performance. Biomechanical data on how humans generate high-speed throws are used to further refine these hypotheses by linking morphological shifts to actual measures of throwing performance. Because of interest in the fossil record, I specifically focus on morphological shifts evident in the skeleton that most significantly affect throwing performance and evaluate their occurrence in the hominin fossil record. The timing of these shifts provides insight into why high-speed throwing evolved and what role this behavior may have played in the evolution of our genus.

5.3 Who throws?

A good place to begin considering the evolution of human's unique ability to throw projectiles at high-speeds is to examine the comparative evidence for throwing among non-human animals and within livings humans. Although we tend to think of throwing as a distinctively human behavior, there are many accounts of animals using projectiles for defense (23, 24), prey capture (25, 26), play (27), and even to maintain hygiene (28). However, aimed throwing of solid projectiles, in which an object such as a stick or stone is directed along an elevated trajectory towards another object or individual, is far less common. With the single exception of lone African elephant using her trunk to hurl large branches at a nearby rhinoceros (29), only primates have been observed to produce aimed throws (30-40). In addition, throwing behavior among non-human primates is actually quite rare. Even the most prolific non-human throwers, the common chimpanzee (*Pan troglodytes*), throw very infrequently.

Despite the infrequency of chimpanzee throwing, this behavior among chimpanzees is important to consider because chimps still throw more frequently than other non-human primates and because they are humans' closest relatives (41-44). Furthermore, the last common ancestor (LCA) of chimpanzees and humans must have been chimpanzee-like in some respects (45). Chimpanzees of both sexes and all ages have been observed to throw objects both overhand (bipedally) and underhand (tripedally) (33, 34, 36, 37, 46). Bipedal throws are typically performed with an overhand, windmill-type motion (Figure 5.1), in which the throwing arm is

Figure 5.1. Juvenile male chimpanzee throwing a rock overhand, bipedally (from (33)). Note the high arm abduction angle, extended elbow, and stride with the throwing side leg.

abducted 135° or more and the elbow is close to fully extended. During these overhand throws, a chimpanzee will take a step in the direction of the target with the throwing side leg, which is followed by flexion at the hips and shoulder prior to release of the projectile. Tripedal throws are typically accomplished using a sidearm-type motion that sweeps the projectile under the quadrupedally positioned torso by internally rotating and adducting the humerus and flexing the elbow.

Researchers have qualitatively noted that although chimpanzee throws are generally fairly accurate in terms of direction, they tend to lack power and often fall short of their intended targets (33, 34, 37). Preliminary quantitative data on the throwing performance of two juvenile male chimpanzees, 3 and 9 years old, that had been trained to throw baseballs overhand bipedally support these assessments. The throws of both individuals averaged only 6±1 m/s over 17/18 throws, and were generally within a meter of the target. Given the impressive strength of chimpanzee upper bodies (47-49), this lack of throwing power raises the hypothesis that their poor performance is more than just a lack of familiarity or training, but rather results from morphological limitations that limit power production during throwing (50).

The context and frequency of chimpanzee throwing behavior are known to vary by sex and age. Although there are no known sex differences in throwing performance, adult male chimps throw three times more frequently than females, and juvenile males throw at least eight times more frequently than their adult counterparts (33). Furthermore, adult male chimps direct most of their throws at conspecifics during aggressive displays, while female chimpanzees direct most of their throws towards interspecifics (such as baboons) in competition for resources (33). Juveniles show no such targeting preferences.

Compared to other animals, including apes, humans are remarkably good throwers capable of throwing with both great accuracy and high velocity. Humans throw using a variety of kinematic styles including underhand tosses, sidearm

throws, windwill or cricket style throws, dart-throwing or wrist-flick motions, and overhand throws. The fastest throws humans generate are produced using the overhand style. Elite male professional baseball players routinely throw 44m/s or faster during competition. Although such speeds represent the pinnacle of human throwing performance, even the average maximum throwing speed in 12-year old little league athletes (23±2 m/s)(51) far exceeds what chimpanzees can do.

The human overhand throwing motion also differs kinematically from the chimpanzee overhand throw (52, 53). In humans, the throwing motion begins with a windup phase, in which the throwing side torso and pelvis are rotated away from the target. The windup is followed by a large stride in the goal direction with the contralateral leg (Figure 5.2). As the striding leg contacts the ground, the pelvis and torso begin to rapidly rotate towards the target in quick succession. At the same time, the arm is "cocked," defined as when the shoulder is abducted approximately 90°, fully horizontally extended, and externally rotated and the elbow flexed approximately 90°. As the humerus reaches its maximum external rotation, the arm-cocking phase ends and is following by a brief acceleration phase, lasting approximately 30-35ms for a 25m/s throw (54). During this acceleration phase, the humerus internally rotates very rapidly, reaching angular velocities of up to 9000°/s (53). This rotation is the fastest motion the human body produces. At the same time, the shoulder horizontally flexes, the elbow rapidly extends, and the wrist flexes as the projectile is released by decreasing digital flexor force in the hand.

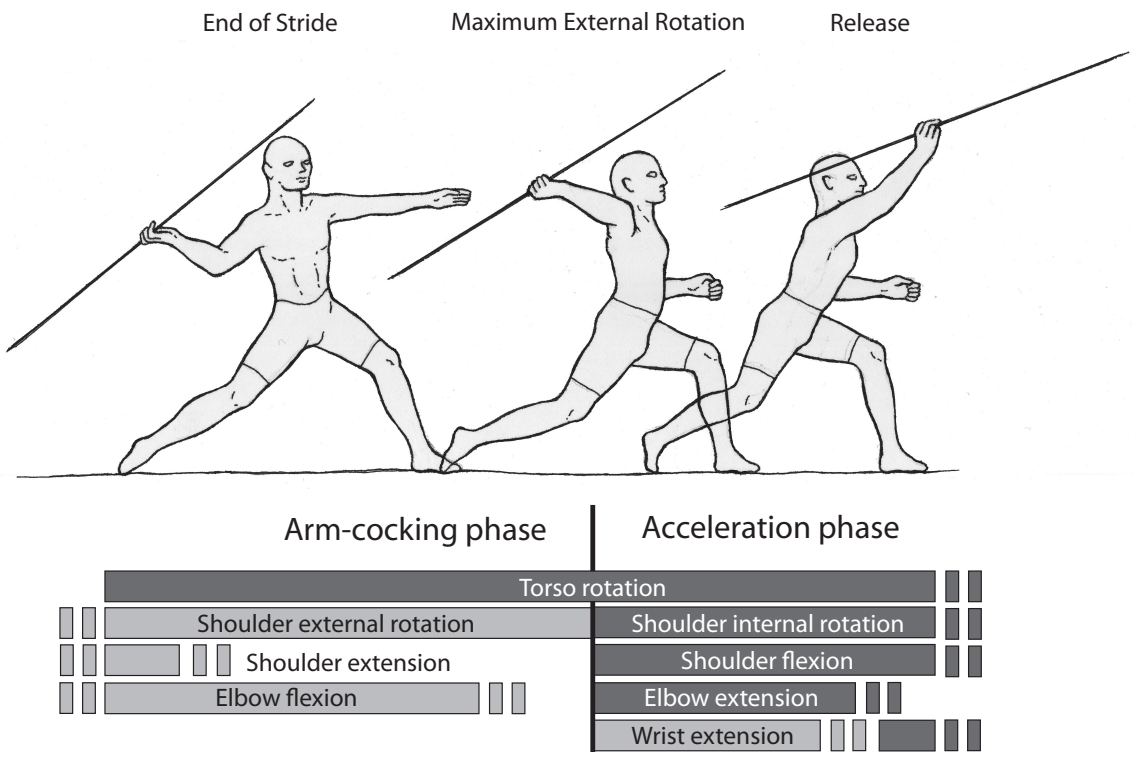


Figure 5.2. The arm cocking and acceleration phases of the human throwing motion. Arm-cocking begins with the contralateral foot touching the ground at the end of a large stride in the target direction. During the cocking phase that follows, the humerus externally rotates until it reaches maximum external rotation. Cocking is followed by a very brief acceleration phase in which the humerus rapidly internally rotates, the elbow extends and the wrist is flexed. Acceleration ends with the release of the projectile.

Although all humans are capable of throwing well compared to other species, there is much variation in human throwing ability, especially between the sexes. Men typically throw with higher average velocity than do comparably aged women (55-58). Additionally, heterosexual men have also been shown to throw with higher average speed and accuracy than homosexual men (59). That sex differences in throwing performance appear well before hormonal changes during puberty (as early as 3 years of age (60-62)) and seem to be weaker in non-Western children

(63) strongly suggest that environmental and social factors are critical in the development of these differences. Although most throws performed by both men and women today are in the context of sports and recreation, these sex differences likely mirror the historical context of differences in throwing behaviors. There are numerous ethnographic reports of men and boys throwing in the context of hunting (64-71), warfare (72-79), ritualized aggression (80-82), enforcement of social norms (81, 83-85), driving off predators and nuisance animals (86-88), and sports (76, 89, 90). Ethnographic reports of women throwing in any context are rare or absent suggesting a long-standing sex bias in this behavior.

Such differences in gender roles, and the sexual division of labor with which they are associated, have been at the foundation of early theoretical studies addressing the origins of human hunting (2, 91). Given the important role throwing may have played in early hunting behavior (2, 6), it is not unreasonable to infer that the gender differences in throwing behavior and performance are ancient and may represent a strategy for mitigating failure risks by hunters (92). However, it is important to note that although men are typically responsible for more hunting activity than women, women do also hunt in some societies (93). Furthermore, gender differences in throwing behavior may be a relatively recent behavioral innovation designed to increase group hunting/foraging efficiency (94).

5.4 How do we throw?

How humans power high-velocity throws has been the subject of considerable research (50, 54, 95-105). Electromyography (EMG) studies

consistently reveal that during throwing a rapid sequential activation of muscles occurs, starting in the distal segments (legs and hips) and proceeding to the proximal segments (forearm and hand) (98). The torques which these muscular contractions generate produce angular motions around many joint axes throughout the body. Analyses of the angular velocity contributions of all upper body joint motions to projectile speed show that the largest contributors at the moment of release are internal rotation of the humerus, elbow extension, torso rotation, and wrist flexion (Figure 5.3) (99). However, there are reasons to believe that these rapid motions are not all powered solely by contractions of the muscles crossing each joint. For example, despite humeral internal rotation during the acceleration phase of the throw being the fastest motion the human body produces, EMG studies of contractile intensity in the shoulder internal rotator muscles show very high variability across the internal rotators (106, 107), and modeling of these muscles power generation capabilities indicates that they cannot provide all of the power actually generated (Chapter 3). Furthermore, one report of an individual with a paralyzed *Triceps* muscle shows that this athlete could still achieve more than 80% of his pre-injury throwing velocity. We can therefore conclude that muscles of the shoulder alone cannot account for all of the joint power necessary to achieve these high angular velocities (108).

There are two complementary factors that may help amplify muscular power contributions, allowing humans to produce very large amounts of joint power during throwing. The first is the transfer of power between body segments or a "kinetic chain". An illustrative example of this principle is the use of nunchucks,

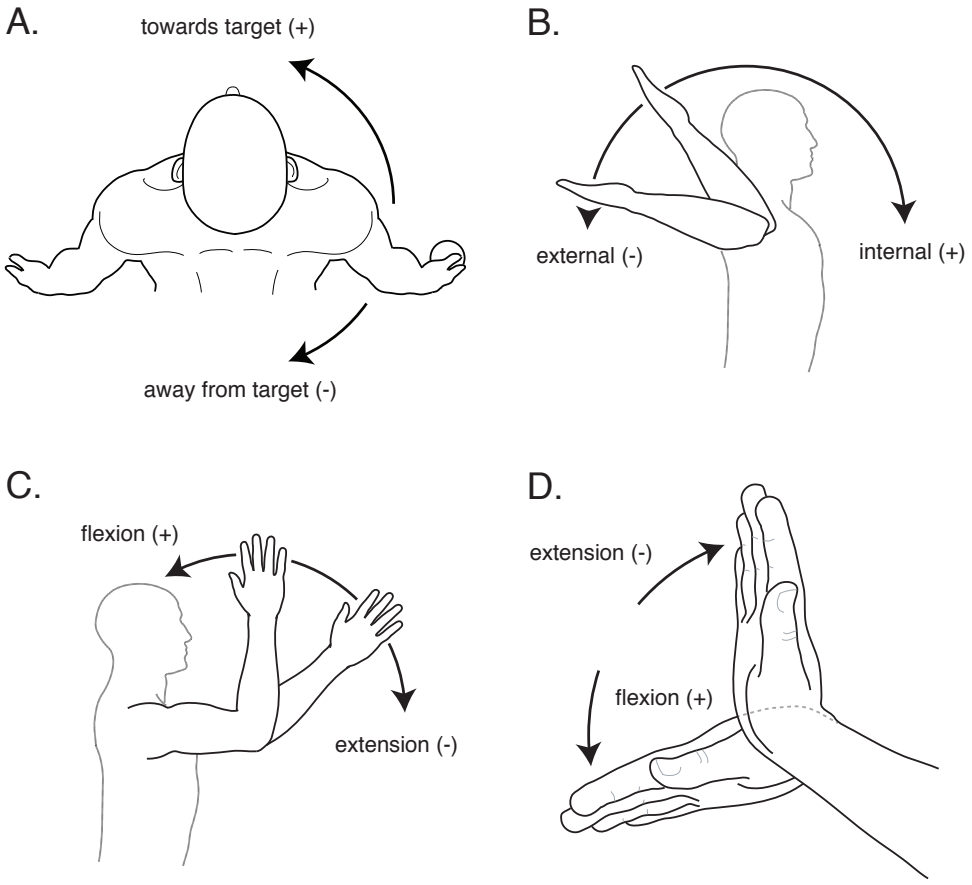


Figure 5.3. The four critical upper body motions for generating high speed throws are: A. torso rotation; B. shoulder rotation; C. elbow flexion/extension; D. wrist flexion/extension.

where a muscular force is applied to one end of the nunchucks, generating centrifugal forces that are transferred to the opposite side via a chain connection, resulting in rapid movement of the opposite end. Biomechanical analyses investigating how power is generated at each joint and the contributions of adjacent body segments to this power generation show that both elbow extension and wrist flexion during the acceleration phase are primarily driven by passive forces generated in more proximal segments (50, 54, 100, 101, 104). These studies

highlight the importance of the transfer of kinetic power between adjacent segments, or the kinetic chain, which has long been thought to be an important component of throwing performance (105, 109).

Chapters 2 and 3 suggest another source of power enhancement at the shoulder: the storage and release of elastic energy. Elastic energy is stored when two opposing forces are separated by a stretchy, elastic material that lengthens and absorbs some of the energy of both forces. For example, elastic energy is stored when one hand pulls the pouch of a slingshot back, while the other hand holds the handle, resisting the pull of the rubber bands. When one of the two opposing forces drops (ie. the slingshot pouch is released), the stretched elastic material will recoil, rapidly releasing it stored energy. This thesis proposes that a such a mechanism is employed at the shoulder during the human overhand throwing motion (50, 54). By positioning the arm and forearm during the arm-cocking phase, the forelimb's moment of inertia is increased (Figure 5.4). Thus, when the torso rotation motion accelerates and the largest shoulder horizontal flexor (*P. major*) is activated, this large rotation force is resisted by the inertial forces from the forelimb. These inertial forces cause the forelimb to externally rotate passively, stretching the elastic elements (ligaments, tendons, elastic components of muscle) that cross the shoulder, storing elastic energy. Only when the *Biceps* are briefly deactivated at the beginning of the acceleration phase (98), does the elbow begin to extend, reducing the forelimb's moment of inertia and allowing the elastic elements to recoil and release their stored energy. Chapter 2 shows that during arm-cocking a large amount of negative work (or energy absorption) occurs at the shoulder (50, 54). We infer that

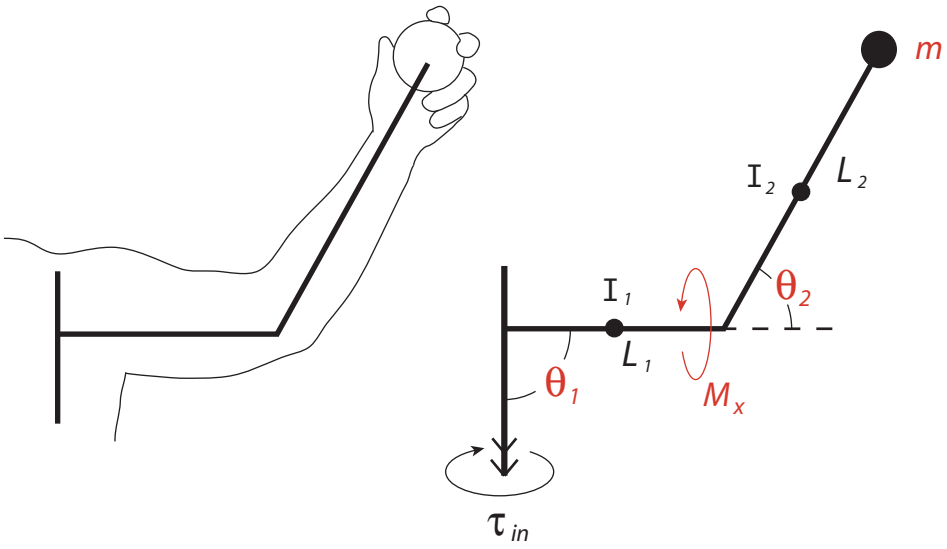


Figure 5.4. Free-body diagram of the throwing arm during cocking. During the cocking phase, the arm is abducted (θ_1) nearly 90° at the shoulder, positioning the mass of the arm, forearm, hand, and projectile away from the rotational axis of the torso. By flexing the elbow (θ_2) slightly less than 90°, the moment of inertia (M_x) is maximized around the long axis of the humerus. As torso rotation accelerates and the *Pectoralis major* contracts (increasing τ_{in}) the forelimb's large moment of inertia cause it to lag behind the accelerating torso, passively externally rotating the humerus, and stretching the elastic elements crossing the shoulder.

this energy is recovered elastically because the internal rotation power production at the shoulder during the following acceleration phase far exceeds the capacity of the shoulder internal rotator muscles to produce such a rapid motion. Elastic energy storage (EES) has been shown in humans previously (110-112). However, these instances of elastic energy usage are typically associated with locomotion and often serve to increase energetic efficiency. Although reported instances of elastic energy usage for power amplification in humans are rare (111, 113, 114), such usage is well documented in other taxa (115-117).

If correct, the EES model for throwing helps explain how humans can produce so much power at the shoulder, but exactly where this elastic energy is stored is not currently known. The clinical literature suggests that energy storage most likely occurs in the muscles, tendons, and ligaments that cross the anterior surface of the shoulder. Repetitive injury data from throwing athletes show an increased prevalence of shoulder instability and stretching related tears and laxity in the glenohumeral ligaments and at the origin of the biceps tendon on the superior glenoid labrum (103, 118, 119). Such stretching related injuries to elastic tissues suggest (but do not prove) that they could store elastic energy. Furthermore, remodeling of the glenohumeral ligaments in those suffering from shoulder instability show higher amounts of elastin present in these ligaments and an increase in the number of large diameter collagen fibrils (120), effectively making these ligaments more tendon-like. Although these elastic structures are not typical of those used by many animals to store elastic energy to increase locomotor efficiency (121, 122), their short length and large aggregate cross sectional area make the shoulder ligaments and muscle tendons ideal for returning elastic energy very rapidly. It should be noted, however, that studies of the inferior glenohumeral ligament show lower stress at failure (~5-9 MPa) than other elastic structures such as the Achilles tendon (123, 124). These low failure stresses may help to explain why, with repetitive stretching, these structures are so frequently injured in throwing athletes. Although more research is needed to determine exactly which structures store and release elastic energy in the shoulder, it is nonetheless clear

that elastic energy storage and release is an important source of power amplification in human throwing.

In short, the use of a kinetic chain to transfer power between segments combined with active muscle contraction and elastic energy storage and recoil at the shoulder to amplify that power enables humans to consistently produce an extremely rapid, whip-like throwing motion. This overhand throwing motion can both affect and be affected by underlying soft tissue and skeletal anatomy. For example, morphological variations that effect range of motion (ROM) at critical joints could reduce throwing performance. Similarly, high muscular forces generated during the throwing motion can lead to identifiable damage or remodeling of muscle attachment sites on bone. Therefore, variations in these morphological features evident in both humans and in the hominin fossil record can be used to test hypotheses regarding how throwing performance changed over time and when high-speed throwing first arose.

5.5 Who threw first?

Two types of evidence exist that can shed light on when hominins first began to throw with high-speed and accuracy: First, the presence of projectiles in the archaeological record, and second, morphological signatures of throwing capacity or usage. Both lines of evidence are addressed here.

Archaeological evidence - The archaeological evidence for the presence or use of projectiles is the most direct way to address the antiquity of high-speed throwing behavior. However, the earliest appearance of projectile points in the archaeological

record is a subject of ongoing debate (20, 21). Levallois points first appear in east Africa at the beginning of the Middle Stone Age at approximately 275 ka (21, 125). These points were likely hafted (21, 126) and some may have been used as projectiles (21). Other researchers have suggested that early Levallois points were not used for throwing but instead for thrusting and cutting and that the earliest lithic tipped projectiles may have been significantly more recent (~90-45 ka) (20, 127, 128). Aside from hafted spear/dart points, there have been claims that older, Early Stone Age lithic tools such as handaxes (129), spheroids (130), and manuports (131) may have also been used as projectiles, although such hypotheses are difficult to assess and have not been supported by experiments (132, 133). It is also possible and in fact likely that the earliest projectiles that were be thrown with considerable force were minimally modified stones, sticks, or untipped wooden spears which could be difficult to identify or fail to preserve in the archaeological record. The only archaeological evidence of such projectiles are three, 400 ka asymmetrically weighted spears from Schöningen, Germany which have been interpreted as throwing spears (134). However, the size of these spears and the range over which could have been thrown have been used to call into question their use as thrown projectiles (20, 135).

Other corollary evidence of throwing behavior from the archaeological record comes from signs of projectile damage in faunal remains. Although evidence for damage from projectiles is common in recent assemblages (136-138), very few bones with hunting lesions exists for the Middle Stone Age/Middle Paleolithic or earlier. A single equid scapula from the site of Boxgrove in the United Kingdom,

dated to ~500 ka, shows a rounded lesion that has been interpreted as an projectile impact wound from an untipped spear (139). The only other known hunting lesion of any antiquity is an imbedded, partial Levallois point in an equid cervical vertebrae from the site of Um el Tlel in Syria (dated to >50 ka), which has also been cautiously suggested as a possible projectile lesion (140). Although these limited and controversial specimens are intriguing, they do not provide a clear record for thrown projectiles.

In short, while throwing projectiles probably predates 45ka, the archaeological record does not provide enough information to evaluate how often high-speed throws were produced, nor the context in which such throws occurred. In this light, examination of functional morphological signatures of throwing behavior in hominin fossils remains the only avenue for addressing the antiquity of high-speed throwing.

Fossil evidence - Although interpreting the archaeological record for throwing is straightforward, evaluating morphological evidence of this behavior is less clear and bears further explanation. Two approaches can be used to identify signatures of throwing capacity or behavior in skeletal material. The first approach relies on identifying derived morphological features in humans and hominins that enable high-speed, accurate throwing. Such features should have important and testable performance effects on the throwing motion. Further, determining whether a given feature is an adaptation or exaptation for high-speed throwing requires knowing when the feature arose, its role in other mechanical actions, and whether the feature

leads to trade-offs in the performance of other tasks, such as climbing or stone tool manufacture/usage, exist. The second approach involves the identification of osseous markers of throwing usage in the form of skeletal modifications or damage from forces generated during the throwing action. For such epigenetic markers to be useful, they must be both consistently present in modern human throwers and unambiguously related to throwing behavior.

Here, I review both types of morphological data for the upper body and evaluate how useful these data are for addressing the evolution of high-speed throwing. For clarity, I discuss throwing mechanics and functional hypotheses regarding each major segment of the upper body separately. I then review the fossil evidence for each segment for morphological indications of high-speed throwing.

The torso

Mechanics - The torso is highly mobile during the human overhand throwing motion (52, 53). During the windup, the torso rotates the throwing arm away from the target. This rotation is followed by lateral flexion towards the throwing side as the contralateral leg strides forward. During the following arm-cocking phase, the torso begins to rotate the throwing side arm rapidly towards the target while also laterally extending to its neutral, upright posture. The rapid rotation of the torso during this phase peaks in the last quarter of the cocking phase and can exceed 1000°/s (54, 100, 102, 141). The angular velocity of torso rotation drops during the late cocking phase and through the brief acceleration phase. Even so, an analysis of the angular velocity contributions of each upper body joint motion to projectile

velocity shows that this reduced torso rotation velocity is still the 3rd largest contributor to projectile speed at release (99).

Chapter 4 hypothesizes that this rapid, rotational acceleration of the torso is critical for loading an elastic energy storage mechanism at the shoulder. We suggest that by positioning the mass of the forelimb away from the rotational axis of the torso, the inertial mass of the forelimb is increased, causing the throwing side forelimb to lag behind the accelerating torso. The lagging forelimb thus stretches the ligaments, muscles, and tendons crossing the shoulder and stores some of the energy generated by the torso in these elastic elements. Only when the torso begins to decelerate at the end of the cocking phase and the elbow begins to extend does the inertial mass of the forelimb drop, and elastic energy is recovered. When we tested the effect of torso rotation on the proposed mechanism by restricting ROM using a therapeutic back brace, we found that complete restriction of intervertebral rotation caused a greater than 5% drop in negative work at the shoulder during the cocking phase (a proxy for elastic energy storage) (54). This resulted in an equivalent reduction in projectile speed, which we interpreted as support for the role of torso rotation in powering elastic energy storage at the shoulder.

It is worth noting that the mechanics of torso rotation and pelvic rotation during throwing are not entirely independent. Previous studies have noted that the initiation of pelvic rotation at the hips immediately precedes the initiation of torso rotation (52, 53, 95). However, variation in pelvic rotation onset does not affect maximum torso rotation angular velocity achieved nor projectile speed (141).

Chapter 4 also showed that even when intervertebral torso rotation ROM was completely removed using a back brace, that torso rotation angular velocity remained unchanged (54). This finding suggests that the rapid torso rotation motion is primarily powered by the hip rotator muscles and not the intrinsic spinal rotators. Given the important role that these lower body, hip rotator muscles play in generating angular velocity in the upper body, it is worth discussing their morphology as well.

Functional anatomy – Although most evolutionary studies of throwing focus on morphological shifts in the shoulder and forelimb, Fifer (10) has suggested an important role for the torso. Fifer proposes that humans' tall, mobile waists are inefficient during bipedal locomotion and are therefore best explained by the role of torso rotation in the throwing motion. Although there are numerous studies that dispute Fifer's assertion that torso rotation was detrimental to locomotor efficiency (142-144), assessing the importance of the human waist during throwing bears further consideration. The expansion of the human waist results from a shift in the positional identity of the last thoracic/first lumbar vertebrae (*Pan* T13 becomes Humans L1, increasing lumbar number from 4 (*Pan*) to 5 (*Homo*))(145), an increase in lumbar centrum size(142, 146), and shift in the orientation of pelvic ilia (from a coronal orientation that entrapped the lower lumbar vertebrae (*Pan*) to a para-sagittal orientation (*Homo*))(144, 147). However, this expanded lumbar region probably had little effect on torso rotation ROM as very little axial rotation occurs in this region(148). It is more likely that a narrowing of the pelvis and inferior rib cage

(142) and the reduction in size of the thoracolumbar fascia are responsible for the increased rotational ROM.

Torso restriction data confirm that increased torso rotational mobility does significantly increase throwing performance (54). By limiting torso rotation ROM, Chapter 4 showed significant reductions in projectile speed and in kinetic performances measures in the forelimb. Such data support the hypothesis that morphological shifts that increase torso rotation ROM would benefit throwing performance. There is good evidence for the expansion of the lumbar region of the spine in the hominin fossil record dating back to the australopiths (*A. africanus* - Stw H8/H41, Sts 14, Stw 431; *A. afarensis* – AL 288-1; *A./P. robustus* – Skw 14002) (143, 146), however, evidence for the potentially more important narrowing of the waist does not appear until the emergence of *Homo* (142, 149). Although many adaptive explanations for these modifications to the lower back do not include throwing (142, 144, 150), these morphological changes would clearly affect throwing performance.

The *Gluteus maximus*, especially its cranial portions are expanded in the modern humans, probably as an adaptation for trunk stabilization during running (142, 151, 152). Fifer also suggested that humans' expanded *Gluteus maximus* would have been very useful in generating power at the hips during the throwing motion (10). The cranial portion of the *G. maximus* (which externally rotates and extends the hip) is significantly expanded in humans relative to chimpanzees (151, 153). Electromyography on the human *G. maximus* during throwing shows that this muscle is highly active and that the activation intensity in the throwing side *Gluteus*

is positively correlated with pelvic rotation velocity (154, 155). Chapter 4 has further suggested that the pelvic rotator muscles at the hips (such as the *G. maximus*) are primarily responsible for powering the rapid rotation of the torso (54). Such data provide strong, albeit indirect support for modifications to the *G. maximus* having significant effects on throwing performance. Fossil evidence of expanded gluteal muscles is thought to be definitively present in *H. erectus* pelvic fossils (KNM WT 15000, KNM ER 3228, BSN49/P27), which have very human-like pelves (142, 151, 156-158). However, it has been suggested that expanded gluteals were also present in *Australopithecus* (AL 288-1, Sts 14, MH1, MH2) (144, 159, 160), although this remains the subject of ongoing debate (151, 161).

The shoulder

Mechanics – Shoulder mechanics during the throwing motion are complex, involving both small movements of the scapula and larger actions at the glenohumeral joint. Patterned motion at the shoulder begins at the end of the stride phase, when the humerus is abducted approximately 90° (52, 53) and the scapula has already been rotated slightly upward (cranially) (162). As the arm-cocking phase begins, the humerus is horizontally extended fully and externally rotated to its passive ROM maxima. During the arm-cocking phase the scapula slightly retracts, externally rotates approximately 20°, cranially rotates ~30°, and posteriorly tilts ~10°, with each motion reaching its maxima with the maximum external rotation of the humerus (162). In the brief acceleration phase that follows, the humerus is horizontally flexed and rapidly internally rotated, reaching angular velocities of up

to 9000°/s (53). During acceleration, the scapula internally rotates ~10° and tilts anteriorly ~5° (162). Larger scapular movements (major protraction, caudal rotation, anterior tilt) occur during the deceleration and follow-through phases after projectile release.

Analysis of angular velocity contributions to projectile speed show that internal rotation of the humerus is the single largest contributor, accounting for 25-45% of projectile linear velocity at release (99). The power generated around this rotational joint axis during acceleration is very high and exceeds even generous estimates of muscle power production capacity (50). Chapter 3 and 4 hypothesized that this power discrepancy is evidence of power amplification at the shoulder via elastically stored energy (50). I propose that evolutionary shifts that enable increased torso rotational mobility and the "relaxation", or caudal rotation, of the shoulder complex allow humans to take advantage of large torques generated around the spinal axis of the body. By positioning the mass of the forelimb away from this rotational axis, passive motion at the shoulder, caused by the forelimb's inertial lag, can stretch the elastic ligaments, tendons, and muscles crossing the shoulder and store elastic energy. The implications of this hypothesis are that some of the derived features of the shoulder are likely adaptations for EES. Most importantly, the relaxation of the shoulder complex would result in two critical changes. First, such a reorganization of the shoulder would reorient the major line of action of the *Pectoralis major* muscle, enabling action by this muscle to contribute to elastic energy storage (54). Secondly, this shoulder relaxation would prevent a

significant performance tradeoff between internal rotation of the humerus and extension of the elbow, the two largest contributors to projectile velocity.

To experimentally test this hypothesis, chapter 4 used braces to alter the *Pectoralis major's* line of action in throwers. These experiments showed significant performance reductions in projectile speed and shoulder rotational power (54). Consequently, it seems likely that the *P. major* powers the rapid internal rotation of the humerus both actively through it own muscular action and passively by helping to load the elastic elements crossing the shoulder. Interestingly, while the *P. major's* large horizontal flexion torque at the shoulder helps to load the elastic storage mechanism, horizontal flexion of the shoulder does not contribute to the upper limb's angular velocity at release (99). Further experimental data limiting the external rotational ROM at the shoulder also showed reductions in ball speed and shoulder rotational power (50, 54). The data suggest anatomical modifications at the shoulder that would alter rotation ROM, for example changes in humeral torsion, would likely have significant performance effects during throwing.

Scapula – Chapter 4 proposes that a laterally oriented glenoid fossa, indicative of a relaxed, caudally rotated scapula would enable effective use of an elastic storage mechanism at the shoulder. Brace restriction data confirm that scapular orientation affects throwing performance (54). The most informative scapular measure, vertebral-glenoid angle, shows that chimpanzees have significantly more cranially oriented glenoid fossa (*P. troglodytes* – 32.6°) than humans (*H. sapiens* – 3.4°)(163). However, measuring this angle in fossil scapulae is

often impossible as the thin scapular body typically does not preserve. The bar-glenoid and axillo-glenoid angles have been used as better-preserved proxy measures for glenoid orientation in fossil taxa and show a moderately cranially oriented glenoid in the Australopithecines (*A. afarensis* - AL 288-1l, KSD-VP-1/1g, DIK-1-1; *A. africanus* – Sts 7; *A. sediba* – MH 2) (143, 164-168) and more caudally directed, human-like glenoid angle in *Homo* (*H. erectus* - KNM WT 15000; *H. floresiensis* – LB 6/4; *H. heidelbergensis* – AT-320, AT-801; *H. neanderthalensis* – see (169)) (164, 169-171). Interestingly, a fragmentary *H. erectus* scapula from Dmanisi (D4166) appears to show a more cranially oriented glenoid, although no angular measures have been published yet (172). These data, with the potential exception of Dmanisi, suggest a more human-like scapula is first consistently present in *H. erectus* indicating a shift in shoulder girdle morphology from a "shrugged" cranially oriented posture to a more "relaxed" laterally oriented shoulder. As the shoulder orientation brace restriction data indicate, such a shift likely had significant effects on throwing performance. It is worth noting, however, that Larson (164) proposes an alternate reconstruction of shoulder position in *H. erectus* based on clavicular length (discussed below).

One potentially important signature of throwing may be the shape of the glenoid fossa, which Churchill and Rhodes (22) have suggested may be an adaptation for withstanding high forces generated at the shoulder during throwing. They note that both anterior/posterior as well as compressive forces at the glenohumeral joint are quite high (102, 103, 119) during throwing and that an expanded glenoid may help to distribute these forces and prevent injury. Using

index measurements of glenoid breadth/height, they further suggest that significant differences between Neandertals (lower indices) and modern humans (higher indices) may be evidence that Neandertals did not habitually throw. An expansion of this hypothesis to look at earlier fossil hominins finds low glenoid indices in all non-human taxa (22, 171, 173), suggesting that if Churchill and Rhodes are correct about the relationship between glenoid index and throwing, that habitual throwing is relatively recent. However, it is worth noting that although the shallow glenoid will experience large compressive forces during the throwing motion, its flat shape precludes any significant application of force in the anterior/posterior plane. These forces are instead borne by the soft tissues surrounding the joint. Further, although expanded glenoid fossae would be useful in distributing large compressional forces, Neandertals actually have absolutely larger glenoid surfaces than do modern humans (171, 173). What drives the increased glenoid index in humans is thus a reduction in glenoid height compared to Neandertals and not an expansion in breadth.

Another potential osteological indicator of habitual throwing suggested by Knusel (174) is the pronounced dorsally oriented sulcus on the axillary border of the Neandertal scapula (169, 175, 176). This sulcus, or groove in the bone, is present at the attachment site of individuals with enlarged *Teres minor* muscles (177, 178). However, given *T. minor* is a lateral rotator of the shoulder, its role in producing high-speed throws is unclear. It is possible that such an expanded *T. minor* is important in decelerating the humerus after projectile release. Such sulci have been noted to occur in high frequency in *H. heidelbergensis* (171), *H. neanderthalensis*

(175, 177), and moderate frequency in Upper Paleolithic *H. sapiens* (177). However, the absence/low prevalence of pronounced sulci in modern humans (177) suggest this trait is more a marker of upper body robusticity than throwing behavior.

Clavicle – Morphological variation in clavicle length has been proposed to have significant effects on shoulder position and throwing ability. Larson (164) has proposed that despite a "relaxation" or more caudal orientation of the scapula in *H. erectus,* that the presence of a short clavicle has resulted in an a novel, intermediate morphology in which the glenoid is very anteriorly oriented. According to her model, this anterior glenoid orientation would result in a detrimental shift to the rotational ROM at the shoulder and thus reduced throwing ability. This hypothesis is based on a low claviculohumeral ratio (clavicle length/humeral length *100) calculated for the reconstructed KNM WT 15000 skeleton (40.9) (164, 179). However, although the claviculohumeral value for KNM WT 15000 is low for humans, it does fall within the measured range of variation for modern East Africans (164), in whom no deficit in throwing ability has been reported. Furthermore, estimates of claviculohumeral ratios from the contemporaneous, reconstructed Dmanisi fossils fall squarely within the human range (Adult male – 46.5L, 46R; juvenile – 43.7) (172). Although the accuracy of the reconstructed Dmanisi values is unknown (no length estimation methods are reported), these values call into question this intermediate morphology. Further, a number of complete/nearly complete *Homo* clavicles that do not have associated postcrania for size standardization have long absolute lengths that fall within the human range (*H. habilis* - OH 48; *H. antecessor* - ATD6-50; *H. neanderthalensis* - see (180), also long relative lengths) (180-182). The *H.*

floresiensis (LB1) clavicles are an exception, with very low claviculohumeral ratios (164, 170). However, whether the claviculohumeral ratio of this species provides support for an anteriorly positioned shoulder (164) is complicated by unusual limb scaling associated with dwarfing that may result in a relatively longer humerus (183, 184).

A related issue to consider is whether humeral length is a useful scalar for clavicle length when trying to reconstruct the position of the scapula. Jungers has shown that humeral length scales isometrically with body mass among primates(185), but it is not clear that a body mass correction is necessarily appropriate for reconstructing shoulder position. It is thought that size and shape changes in both the clavicle and the superior portion of the rib cage affect scapular position (50, 164, 186). However, size and shape changes in the upper torso are likely only partially explained by changes in body mass. Accordingly, mass independent changes in the superior torso will affect shoulder position, but not the claviclohumeral ratio. For example, chimpanzees have low claviculohumeral ratios (164) and yet their scapulae are dorsally positioned due to their small superior rib cage volume. For this reason, it remains to be seen whether claviculohumeral ratio alone can be used to reconstruct shoulder position. In the fossil record, there is evidence for an expansion of the superior rib cage in *H. erectus* (142, 149) which has been suggested to predate *Homo* (163). In addition to affecting shoulder position, this lateral broadening of the superior rib cage in *Homo* will result in increased linear velocity of the shoulder and thus projectile speed.

Humerus - Many arguments about the evolution of throwing have focused on the humerus, especially humeral torsion, defined as the highly variable angle between the orientation of the humeral head and the distal condyle in the elbow (Figure 5.5). Humeral torsion has been shown to be 10-20° lower in the throwing arm of pain-free athletes than both their own non-preferred arms and the arms of non-throwing controls (187-190). Studies have shown that this reduced throwing arm torsion is significantly correlated with an increased external rotational ROM at the shoulder (188-192). Chapter 2 also found that individuals with lower throwing arm torsion achieved higher maximum throwing speeds (50). They suggest that this performance enhancement occurs because reduced torsion both increases the amount of elastic energy storage at the shoulder and allows for more internal rotation acceleration prior to projectile release.

Applying these performance data to the fossil record is complex because multiple factors affect humeral torsion. Chimpanzees have human-like levels of humeral torsion (164, 193), likely resulting from the need to position the hands near the midline of the body during quadrupedal locomotion. However, both australopiths (*A. afarensis* – AL 288-1r; *A. africanus* – Sts 7; *A. sp. indet.* – Omo 119-73-2718; *A./P. boisei* – KNM ER 739; *A. sediba* – MH1, MH2)(164, 168, 193) and early *Homo* (*H. erectus* – KNM WT 15000, D4507)(164, 172, 194) show moderately low to very low torsion respectively, consistent with the moderately low torsion seen in throwing athletes dominant arms (50, 187). Low torsion in earlier hominins is thought to represent a relaxation of functional demands on the humerus at this point during human evolution (164). However, since such low torsion provides a

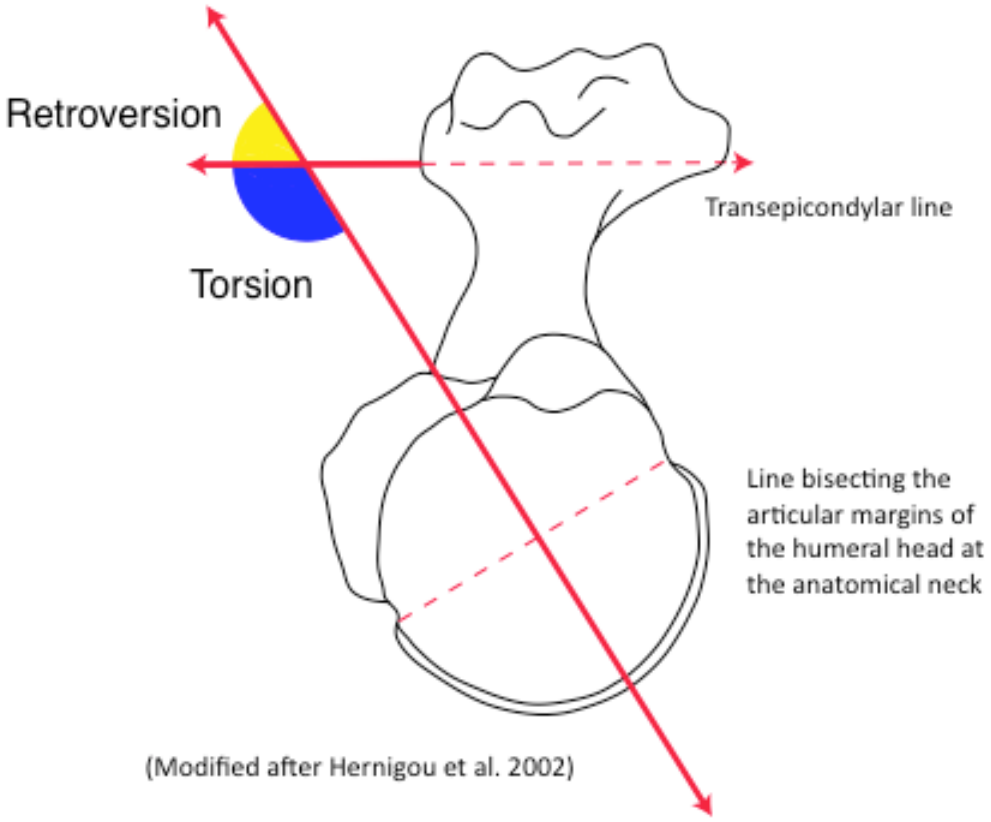


Figure 5.5. Humeral torsion (blue) is measured as the angle between the orientation of the humeral head and the distal condyle of the humerus. In the clinical literature, the same angle is referred to as humeral retroversion (yellow) and is measured in the opposite direction.

performance benefit during throwing, it could also be an exaptation for this behavior. Moderately higher torsion and asymmetry in torsion appear in later *Homo* (*H. heidelbergensis* – AT - Hum II; *H. neanderthalensis* – see (180); *H. sapiens* – see (195)) (164, 171, 180, 195), with the notable exception of *H. floresiensis* (164, 194). One possibility is that this increase in torsion may be related to changes in torso shape and scapular position (195, 196). This model suggests that as the torso broadens, higher torsion angles are required to maintain anterior ROM useful for

manipulative tasks. However, such shape changes cannot explain the pattern of lower torsion values found in modern human throwing athletes. Furthermore, although humeral torsion is highly plastic, early ontogenetic differences in torsion between human populations suggests a heritable component (197, 198).

Several studies have noted that side asymmetries in the upper body (199-202) and in humeral torsion specifically (198, 203, 204) may be related to throwing ability. However, the results from studies attempting to link asymmetry levels and throwing activity have been equivocal (198, 204). Furthermore, it is worth noting that asymmetries in torsion develop when moderately low, juvenile levels of humeral torsion are maintained in the dominant arm although non-dominant arm torsion increases over ontogeny (197). Whether this lower dominant arm torsion is the result of selective pressures and/or activity patterns, it is not the presence of asymmetries in torsion but the maintenance of lower torsion into adulthood that provides a performance advantage during throwing (50, 187). Accordingly, the absence of humeral torsion asymmetry in individuals or species with low humeral torsion is unlikely to provide insight into throwing performance or behavior.

The humerus is also a likely site for the presence of osseous markers of throwing behavior. Knusel (174) has suggested that the presence of enthesopathies (osseous lesions) at muscle/ligament attachment sites that experience high stress during the throwing motion may provide useful indicators of throwing behavior. Unilateral enthesopathies on the medial epicondyle of the distal humerus have proven to be useful markers of throwing behavior (205-210). However, although

these entheses are useful for evaluating recent material (210), older fossils are often too poorly preserved to determine their presence.

Churchill and Rhodes (211) find that relative deltoid tuberosity size in Neandertals and early Upper Paleolithic humans is smaller than later Paleolithic and modern human populations. They use this data to again infer that these Neandertals and early humans did not throw (198, 211). However, although the deltoid is important in positioning the arm during the early cocking phase, electromyography data on the deltoid during this phase and the following acceleration phase show only moderate to low activity (106, 107, 212-214). Furthermore, the abduction motion, for which the deltoids are primarily responsible, provides no angular velocity contribution to projectile speed at release (99), nor does it induce accelerations in any other joint (100). Accordingly, the performance effects this reduction in deltoid size would cause during throwing are likely minimal.

The cross sectional geometry of the humeral shaft also has been argued to provide insight into habitual throwing behavior. Churchill and colleagues (195, 200) note that the cross sectional shape of the humeral shaft in early Upper Paleolithic *H. sapiens* were less well suited to resisting torsional loads than later Upper Paleolithic *H. sapiens*. This observation is inferred to suggest that early Upper Paleolithic humans likely did not throw (195, 198, 200). They further note that the early Upper Paleolithic humeri were similar in cross section to modern humans. However, given that modern human throw very well, this performance inference is not supported. Furthermore, the size standardization used in this analysis (polar moment

standardized to body size) obscures what is likely a higher actual torsional resistance in humeri of the robust, large bodied Paleolithic humans (215-218) compared to modern throwers.

Trinkaus and colleagues point out that there is considerable bilateral asymmetry in humeral cross sectional strength measures in Neandertals and Upper Paelolithic humans (199, 219). In modern humans, similar levels of humeral strength asymmetry are typically only found in overarm athletes (199, 202, 220). Churchill and colleagues (200) have hypothesized that such strength asymmetry (with the right arm typically more robust) results from habitual use of thrusting spears. However, a recent electromyography study by Shaw and colleagues (221) show that right handed subjects produced higher activation in the muscles of their left arm during the spear thrusting motion. They argue that given that right-handedness predominates and has probably done so for a long time, spear thrusting is likely not the source of Neandertal and Upper Paleolithic humeral strength asymmetry. Although the presence of such bilateral strength asymmetry is potentially useful is recognizing throwing behavior, determining what activities caused the asymmetry is difficult. Furthermore, the preservation of both of an individuals humeri is exceedingly rare before the advent of burial and therefore of limited utility before the European Middle Paleolithic.

The elbow

Mechanics – Another highly active region during the throwing motion is the elbow. Early in the arm-cocking phase, the elbow is typically flexed just less than 90°,

where it stays until the last quarter of the cocking phase (52, 53). At this time the *Biceps* are briefly deactivated (98) and the forearm begins to extend rapidly at angular velocities up 6000°/s (53). This flexion acceleration continues through the first half of the following acceleration phase and slows as release approaches (53, 54, 102). Elbow extension is the second largest angular velocity contributor to projectile speed at release (99). However, kinetic analyses of the elbow show that this rapid extension is largely powered by centrifugal forces generated in the trunk and shoulder and not by action in the *Triceps* (50, 54, 100, 101, 104). Electromyography data showing highly variable activation of the triceps during this rapid acceleration, as well as performance data from an individual with a paralyzed *Triceps,* support these findings (106, 108).

During both the cocking and early acceleration phases the forearm is slightly pronated (52, 53). At the end of the acceleration phase (and into the following deceleration phase), the forearm hyperpronates, providing spin to the projectile. The angular velocity of hyperpronation during acceleration is low and the peak torque produced is very small (222-224). Pronation provides no angular velocity contribution to projectile velocity at release (99) and has been suggested to be a passive byproduct of more proximal joint actions (52). However, a recent study of pronation and throwing performance has noted a weak relationship between pronation acceleration and vertical projectile movement (225).

Functional anatomy – Studies have noted that the length and mass of the forearm will affect projectile speed (198, 226). For a given elbow extension angular

velocity a longer forearm will increase the linear velocity of the hand. Similarly, a reduction in forearm mass will reduce the moment of inertia around the elbow, thus requiring less power to achieve higher angular velocities. However, some consideration of scaling effects is required when comparing across taxa as overall body size will affect both the absolute length of the forearm as well as the inertial mass of the forearm and the ability to generate torque to overcome that inertia. Brachial index (radius length/humerus length *100) measures in chimpanzees (92) show they have relatively longer forearms than humans do (78) (147). Chimpanzee forearm mass also represents a significantly larger percentage of overall body mass compared to humans (142, 227). Brachial indices in *Australopithecus* fossils show relatively elongated forearms, in some cases exceeding chimpanzee values (*A. garhi* – BOU-VP-12/1; *A. afarensis* – AL 288-1, AL 438-1; *A. sediba* – MH2) (168, 228-230). Estimates of *A./H. habilis* show a similarly high brachial index, although caution is advised given the fragmentary nature of this fossil (OH 62) (231). All other members of the genus *Homo* exhibit modern human-like brachial indices (*H. erectus* – KNM WT 15000; *H. neanderthalensis* – see (232); *H. floresiensis* – LB1) (230, 232-235).

In considering the effects of these differences on throwing performance, it is worth noting that although humans, and most fossil specimens attributed to *Homo*, have relatively shorter forearms compared to chimpanzees and australopiths, this relative reduction in forearm length is accompanied by a significant decrease in forearm mass. For example, while the body size corrected chimpanzee forearm is ~18% longer than the human forearm (aiding in the production of projectile linear

velocity), the relative mass of the forearm is 50% higher in the chimpanzees (142, 147, 227). Thus, the laws of scaling dictate that any beneficial increase in forearm length will be offset by a much larger detrimental increase in the forearm's inertial mass. Furthermore, chapter 4 suggests that even minor increases in relative forearm mass may have large effects on elastic energy storage, resulting in significantly lower throwing speeds. Churchill and Rhodes have commented that the robust Neandertal forearm may have limited forearm acceleration during throwing (22). Given similar robusticity is observed in Neandertal humeri (199, 236) and that Neandertals have a low, human-like brachial index (232), this seems unlikely. Although an absolutely larger forearm necessitates more power to accelerate the larger mass, the large Neandertal body was likely capable of providing such power.

Churchill and Rhodes (22) propose that hypertrophy of the ulnar supinator crest may also provide a useful osseous indicator of throwing behavior. Although the supinators are not involved in generating propulsive power during the throw, they propose that this muscle may be highly active during the deceleration of the arm. However, electromyography data from the single published study which quantifies supinator activity shows very low activity in this muscle through all phases of the throw (237). Churchill and Rhodes analysis of ulnar supinator crest size and asymmetry in Neanderthals, Upper Paleolithic, and modern humans typically found relatively larger supinator crests on the left ulna and no statistical difference between sides in any group (22). They do find significant differences in supinator index between Neandertals and a number of *H. sapiens* populations as well as within *H. sapiens.* The authors interpreted these results as support for a

Middle Paleolithic origin of habitual throwing. However, there are several reasons to question this interpretation. Firstly, the most significant difference in supinator index reported is between Neandertals and early Upper Paleolithic *H. sapiens*, both of whom the authors suggest do not habitually throw. Secondly, no significant differences are found in either asymmetry nor between males and females, both of which would be expected if this morphology was an accurate osseous indicator of habitual throwing. The lack of related performance data for the supinator muscle further calls into question the functional importance of this character in the throwing motion. Finally, it is worth noting that the variable presence of a prominent supinator crest in males across a number of early hominin taxa (*A. afarensis* – AL 438-1; *A./P. boisei* – OH 36; *H. erectus* – KNM WT 15000; *H. sp. indet.* – KNM BK 66) (238-240) suggests that this trait is a signature of skeletal robusticity and not necessarily throwing behavior.

Churchill and Rhodes (211) also point out that Neandertals have significantly longer olecranon processes relative to ulnar length than humans. They note that although these longer processes would increase the mechanical efficiency of the *Triceps*, this increased efficiency could result in costly reductions in elbow extension velocity. They suggest that these elongated olecranon processes would have negatively impacted Neandertal throwing ability. However, given that rapid elbow extension during throwing is driven largely by passive forces (50, 54, 100, 101, 104), a small increase in ulnar olecranon process length is not likely to affect throwing performance.

The wrist & hand

Mechanics – The final region of the upper body that is involved in throwing is the wrist and hand. Action at the wrist begins during the cocking phase, when the wrist slowly hyperextends from its neutral position (53, 54, 241). As the acceleration phase begins, the wrist is rapidly flexed reaching angular velocities in excess of 1000°/sec (54, 241), making this motion the fourth largest contributor to projectile velocity at release (99). During the acceleration phase, this rapid wrist flexion action is accompanied by a small, low velocity (>30°/s) ulnar deviation motion (241). Similar to the elbow extension motion, kinetic analyses of wrist flexion show that this rapid motion is largely powered by passive forces generated in more proximal joints and not by action in the wrist flexors (50, 54, 100, 101, 104).

It is assumed that at release, the pollical adductors and digital flexors relax (potentially coupled with antagonistic contractions), loosening the grip, and allowing the projectile to come free (242). The neural control of this release timing and its role in achieving accurate throws is a subject of considerable study and debate (18, 57, 243-250). It should be noted that precision and accuracy in rapid mechanical tasks is strongly correlated with practice and familiarity (251-254). Although these complex neurological mechanics are beyond the scope of this study, it is useful to discuss how proposed functional morphological signatures of the precision grip are thought to be vital to achieving accurate projectile release.

Functional anatomy – Wrist – Marzke has suggested that humans' derived ability to hyperextend the wrist would have been critical to throwing ability (255).

Chapter 4 has further hypothesized that during throwing the ability to hyperextend the wrist allows for the point of release to be delayed while still maintaining an accurate release trajectory. They further propose that such a delay would enable additional time for angular motions at the shoulder and elbow to accelerate. However, a test of this performance hypothesis using a wrist brace restricting hyperextension showed equivocal results. Although limiting wrist hyperextension had significant performance effects at the shoulder and elbow, these effects do not appear to be related to timing differences. Furthermore, the added mass of the brace at the wrist led to unexpected complications during these trials. Accordingly, further experimental data are needed to assess the validity of this hypothesis and test the performance effects of morphological shifts at the wrist.

Cadaveric studies of human and chimpanzee wrist mobility have shown significant differences between these two species in wrist extension ROM (*Pan* ~30°; *H. sapiens* ~70°) (256, 257). A number of researchers have hypothesized that wrist hyperextension in chimpanzees may be limited by a dorsal ridge on the distal radius (257-262). Richmond and colleagues (261, 262) note that a pronounced dorsal ridge on the distal radius has been found in a number of early australopiths (*A. anamensis* – KNM ER 20419; *A. afarensis* – AL 288-1), but is absent in later australopiths (*A. africanus* - Stw46; *A./P. robustus* – SKX 3602) and *Homo*. However, a recent geometric morphometrics study by Tallman suggests that this dorsal ridge is present to varying degrees in all australopiths (263). Adding to the uncertainty, the presence and morphology of a dorsal ridge has not been assessed for recent *Australopithus* (168) and *Ardipithecus* (264) radial finds and no distal radii exist for

early *Homo*. While it may still be reasonable to assert a more extendable wrist was present in the later australopiths and *Homo,* more fossils are needed to better address this hypothesis.

Functional anatomy – Hand - The ability of the hand to produce a precision grip has been hypothesized to be vital to the accurate release of projectiles (242, 265, 266). The precision grip requires both digit lengths that allow thumb opposition and strong pollical flexors (267-270). Chimpanzees' elongated fingers, metacarpals, and carpals coupled with a short, weakly muscled pollex make the production of a precision grip impossible (242, 267-270). Humans, on the other hand, have elongated, muscular thumbs and shorter digits. Furthermore, humans' expanded fleshy, palmar finger pads may provide additional sensory feedback vital to the fine motor control required for projectile release (242).

Fossil evidence for the emergence of precision gripping comes from relative digit lengths, the size of the apical tufts of the distal phalanges, the presence of a fossa for the attachment of the *Flexor pollicis* muscle. The earliest hominin fossil evidence, a well-preserved *Ardipithecus ramidus* (ARA-VP-6/500) hand, shows very ape-like digit lengths (264). *A. afarensis* (AL 333-x) phalangeal and metacarpal fossils show an intermediate morphology with a relatively elongated thumb and slightly reduced non-pollical digit lengths when compared to chimpanzees, but not quite human-like proportions (265, 271). Marzke (265) argues that *A. afarensis* was capable of producing a three-jaw chuck precision grip that could have enabled throwing ability. A slight expansion of the apical tufts is also reported for *A*.

afarensis (272). An *A. africanus* distal phalanx of the thumb (Stw 294) is reported to show an expanded apical tuft and a prominent *Flexor pollicis* fossa (273). Ricklan (273) interprets these data, and additional measures of a number of metacarpals, as consistent with throwing ability. Well developed apical tufts and prominent *Flexor pollicis* fossae are also reported for *A./P. robustus* (Skx 5016, Skx 8963) (274). A nearly complete *A. sediba* hand shows an elongated thumb and shortened fingers consistent with the production of a precision grip (275). In *Homo,* all available fossils are consistent with human hand proportions, strength, and expanded fingertips and indicate the ability to produce precision grips (170, 172, 175, 242, 274, 276-279).

Summary of evidence

The archaeological and morphological evidence for the evolution of high-speed throwing is complex, and often incomplete. However, much can be gleaned from integrating the information currently available. Archaeological evidence of the presence and use of projectiles remains the best way to positively confirm the capacity and usage of high-speed throwing. However, although there is wide agreement on recent evidence of projectiles associated with *H. sapiens* in Europe and the Levant, there is still no consensus on whether projectiles were made by earlier *H. sapiens* let alone in other hominin taxa. The lack of unequivocal material evidence of projectiles has been used to suggest that high-speed throwing behavior dates back to only the later Middle Paleolithic/Middle Stone Age (20, 22, 198). However, absence of evidence is not always evidence of absence, and the poor

preservation of organic material and the inability to identify minimally modified tools likely obscures the presence of the earliest thrown implements, such as untipped spears, rocks, and throwing sticks. Accordingly, although archaeological evidence provides excellent data on the minimum earliest appearance of throwing behavior it yields very poor information on the maximum or true first appearance of high-speed throwing.

The best evidence for the evolution of high-speed throwing thus falls to the functional interpretation of hominin fossils. Taken as a whole, the morphological evidence for high-speed throwing does not accord with the archaeological evidence and suggests that the capacity to produce high-speed throws is considerably older. First, morphological shifts in the torso that enable increased rotational motion have been shown to significantly affect throwing performance. Modern human-like torso rotation mobility appears to date back at least to *Homo erectus* and possibly earlier. Second, a lateral shoulder positioning has also been shown to have significant performance effects on throwing velocity. Fossil scapular glenoid orientation data show a more "relaxed" caudally rotated morphology is present in *Homo*. However, it has been suggested that *H. erectus* may have had short clavicles resulting in an anteriorly oriented shoulder thought to be detrimental to throwing behavior. Other *H. erectus* fossil material has been used to call this reconstruction into question. Further fossils and analyses of *H. erectus* clavicles, humeri, and superior rib cage size and shape are needed to address this hypothesis more fully. Third, low humeral torsion is found in both the australopiths and early *Homo* and has been linked to throwing performance. In fact, higher torsion only appears in later *Homo,* although

lower torsion is maintained in the dominant arm, resulting in side asymmetries. Side asymmetries in humeral bone strength also appear in later *Homo,* although the cause of such strength asymmetries is non-specific. Fourth, reductions in forearm length also appear with *H. erectus,* and when coupled with even larger reductions in forearm mass are inferred to result in improved throwing performance. Shifts in wrist morphology enabling increased wrist extension are thought to occur in the later australopiths, although the timing of this shift as well as its effect on throwing performance remain subjects of debate. Finally, changes in digit proportions and evidence of expanded fleshy fingertips also suggest that the ability to produce a precision grip, thought to be vital for accurate projectile release, dates back well into the australopiths.

With the exception of inconclusive evidence regarding relative clavicle length, all of these morphological data suggest the capacity to produce high-speed throws was present dating back to *Homo erectus*. Additionally, morphological shifts in the *H. erectus* lower body (increased *Gluteus maximus,* longer legs (142, 147)) are also consistent with increase throwing ability. Furthermore, data on upper body asymmetries and entheses that have been used to assert a much later origin for high-speed throwing are not well correlated with throwing performance measures and show no consistent morphological shifts.

5.6 Why do we throw?

Skeletal evidence (264, 280, 281) and parsimony reconstructions (45) suggest that the earliest hominins were quite chimpanzee-like in many ways. Given

that neither chimpanzees nor early hominins show morphological adaptations to throwing, it is unlikely that the human/chimpanzee LCA threw well. However, even low velocity chimpanzee throws are sufficient to scatter their compatriots during aggressive displays. Throws by early hominins likely were used in similar contexts and to similar effect.

The most likely evolutionary pressures driving the emergence of high-speed throwing behavior relate to its role in hunting. The timing of the emergence of high-speed throwing behavior in *Homo erectus* suggests that the evolutionary origins of this behavior may be related to early hunting and possibly also scavenging. The paleoanthropological record shows hominins had access to meat dating back at least 2 million years (282-284) and potentially significantly earlier (285, 286). Analyses of lithic cutmarks suggest that by 1.5-2 million years ago hominins enjoyed early access to medium to large animal carcasses (282, 287-289). Such data suggest that hunting or power scavenging (in which predators are driven from the own fresh kills) dates back to *H. erectus.* These lithic and faunal cutmark data accord well with significant increases in brain and body size in *H. erectus* consistent with an increase in dietary quality (3, 142, 147, 290). How *H. erectus* was hunting or driving predators from their kills has been a subject of debate (2, 8, 142, 291). Evidence for the emergence of endurance running capabilities in *H. erectus* suggests that persistence hunting may have played an important role in early meat procurement (142). Strong morphological evidence for high-speed throwing capabilities at this time indicates an important role for throwing as well. Although these dual signatures of throwing and endurance running suggest a complex behavioral

strategy for early hunting, throwing may provide a number of adaptive advantages. First, while early thrown projectiles, such as untipped spears, were unlikely to result in the instantaneous death of prey, they would have resulted in substantial injury. These injured animals would have been easier to track and incapable of moving over long distances therefore greatly reducing the energetic cost of their capture. Furthermore, injuring a prey animal would greatly increase the chance of success during a persistence hunt. Secondly, the ability to kill or injure animals from a distance significantly reduces the risk to a hunter. Evidence of persistence hunting data among !Kung foragers show that persistence hunts frequently ended with a hand thrown spear killing an exhausted, but still unpredictable animal (292, 293). Although ethnographic data on hand thrown spears suggests short effective ranges for these projectiles (294), even these short distances would have greatly reduced danger to the hunter. Finally, throwing would also provide a significant safety advantage in driving scavengers away from hominin kills as well as scavenging kills from other predators.

Throwing ability, in addition to being an advantage to the earliest hunters, would also have provided significant advantages to later hunters as well. Throwing was likely an important component of the flexible hunting strategies required of hominins as they migrated out of Africa as early as 1.85 million years ago (295). High-speed throwing would have been increasingly important as hominins dispersed to more varied and seasonal environments in which persistence hunting was not possible for much of the year. Increased reliance on throwing ability later in human evolution is further supported by the accumulation of technological

improvements in throwing armament in the form of lithic spear points and atlatls/spear throwers.

It is worth noting that although early hunting provides a strong adaptive context for the emergence of throwing behavior, throwing may also provide additional (exapted) benefits in other contexts including social enforcement and reducing the costs of aggression. Furthermore, although the functionally relevant morphologies discussed here all provide significant performance enhancements during throwing, it is always difficult to identify the specific selective pressures driving morphological shifts. The fact that some of the traits identified here as vital to throwing performance predate the emergence of *H. erectus* suggests that these novel morphologies were originally selected for other functions and later were useful for high-speed throwing. In this way, improvement in hominin throwing ability was likely somewhat gradual. For example, expansion of the waist first began in the australopiths, likely related to locomotor demands and was exapted for high-speed throwing. Similarly, evolutionary changes in the wrist and hand may have originally been driven by increased tool use and the manufacture of stone tools, only to be co-opted for improved throwing performance. However, the lower (and wider) shoulders in *H. erectus* are a different story. As chapters 3 and 4 argued, this change in shoulder position likely had the largest effect on throwing performance by enabling large amounts of elastic energy to be stored and released (50). I have hypothesized that low, wide shoulders likely reduced climbing efficiency, probably had little effect on stone tool use or manufacture, and are only adaptive for high-speed throwing. Altogether, the accumulated presence of functional important

morphologies in *H. erectus* provides a novel, adaptive suite that when combined would enable high-speed throwing.

5.7 What questions remain?

Despite strong evidence for high-speed throwing ability dating back to *Homo erectus,* a number of important questions remain. Morphologically, the length of the *H. erectus* clavicle and its effect on shoulder positioning and throwing performance are still unclear. Although additional fossil material will always be the best way to address this question, further analyses of existing material are still needed. For example, little is known about how superior rib cage shape and size affect shoulder position or whether a low claviculohumeral ratio accurately reflects a shortened clavicle and anteriorly oriented shoulder. In terms of the throwing performance, more data are needed on the effects of wrist extension in order to accurately assess whether morphological shifts at this joint are relevant to throwing performance. Archaeologically, little is known about the penetration and wounding potential of the untipped wooden spears that likely played an important role in early throwing behavior.

More biomechanical studies using similar analytical methods are needed to address the competing functional requirements of the upper body. For example, while much is known about the mechanics of primate climbing, very little is known about how power is generated during human climbing and what the actual performance costs of changes in the hominin shoulder are. Even less is known about the mechanics of human stick digging. Digging up energy rich roots and tubers using

a minimally modified stick has been proposed to be an important dietary and behavior shift early in human evolution (296). Mechanically, the digging motion probably requires significant force and can occupy several hours of work a day for hunter-gatherer women (297). However, how this force is generated likely differs from the requirements of high-speed throwing. I would hypothesize that significant force is generated by the adductor and extensor muscles of the shoulder, neither of which contributes significantly to throwing. Biomechanical data are needed to test this hypothesis. Finally, and potentially most importantly, how power is generated during stone tool manufacture and usage is still poorly understood. The intensified use of tools and the novel incorporation of modified lithic tools especially, were likely hallmark events in hominin evolution. While knapping bears some similarities to the throwing motion, including a whip-like production of power involving internal rotation of the humerus, these motions are much less rapid in knapping and likely require significantly less power. Inverse dynamics and induced acceleration data on knapping will be invaluable in comparing the two motions and determining the mechanical similarities and differences between these tasks.

Finally, Larson notes the evolutionary importance of the use and manufacture of tools in describing a problem *Homo erectus* may have faced as a result of having very low humeral torsion (164). She hypothesizes that when combined with a laterally oriented shoulder, low humeral torsion would result in a restricted range of motion for manipulative tasks and infers that the ability to use and manufacture tools could suffer as a result. She further proposes this problem is overcome in *H. erectus* via an anteriorly directed shoulder, resulting from a

relatively shorter clavicle. While I have questioned the reconstruction of the *H. erectus* clavicle as relatively short (Chapters 2 and 5), this does raise interesting questions regarding how *H. erectus* both threw well and knapped stone tools. To address this question, further data are needed on the costs to knapping performance imposed by very low torsion, as well as on whether simple postural shifts at the shoulder (shoulder flexion, scapular protraction) are capable of recovering any performance loss due to low torsion. Addressing these remaining questions will allow us to better refine our understanding of the evolutionary history of high-speed throwing and of the unique human behaviors that throwing ability enables.

5.8 Acknowledgements

Many thanks are due to Dan Lieberman for his help in developing and refining the ideas presented in this paper. I would also like to thank Amanda Lobell for her helpful comments on the manuscript and many members of the Harvard HEB department for interesting discussions of throwing over my time there.

5.9 Literature Cited

1. Darwin C (1874) *The descent of man, and selection in relation to sex* (A.L. Burt, New York,) Reprinted from 2d English Ed pp vii, 797 p.

2. DeVore I & Lee RB eds (1968) *Man the Hunter* (Aldine de Gruyter, New York).

3. Aiello LC & Wheeler P (1995) The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. *Current Anthropology* 36(2):199-221.

4. Stanford CB & Bunn HT (1999) Meat Eating and Hominid Evolution. *Curr Anthropol* 40(5):726-728.

5. Milton K (1999) A Hypothesis to explain the Role of Meat-Eating in Human Evolution. *Evolutionary Anthropology* 8(1):11-21.

6. Darwin C (1871) *Descent of Man* (John Murray, London).

7. Isaac B (1987) Throwing and human evolution. *The African Archaeological Review* 5:3-17.

8. O'Connell JF, Hawkes K, & Blurton Jones NG (1988) Hadza Scavenging: Implication for Plio/Pleistocene hominid subsistance. *Curr Anthropol* 29(2):356-363.

9. Bingham PM (1999) Human uniqueness: A general theory. *Q Rev Biol* 74(2):133-169.

10. Fifer F (1987) The adoption of bipedalism by the hominids: A new hypothesis. *Human Evolution* 2(2):135-147.

11. Carrier DR (2011) The advantage of standing up to fight and the evolution of habitual bipedalism in hominins. *PLoS One* 6(5):e19630.

12. Dunsworth H, Challis JH, & Walker A (2003) Throwing and bipedalism: a new look at an old idea. *Upright Walking*, eds Franzen JL, Dohler M, & Moya-Sola S (Senckenberg Institute, Frankfurt), pp 105-110.

13. Darlington PJ (1975) Group Selection, Altruism, Reinforcement, and Throwing in Human Evolution. *Proceedings of the National Academy of Sciences of the United States of America* 72(9):3748-3752.

14. Chapais B (2011) The evolutionary history of pair-bonding and parental collaboration. *The Oxford Handbook of Evolutionary Family Psychology*, eds Salmon CA & Shackelford TK (Oxford University Press, Oxford, UK), pp 33-50.

15. Bingham PM (2000) Human evolution and human history: A complete theory. *Evol Anthropol* 9(6):248-257.

16. Bingham PM & Souza J (2009) *Death from a distance and the birth of a humane universe* (BookSurge, Charleston, SC).

17. Calvin WH (1982) Did Throwing Stones Shape Hominid Brain Evolution. *Ethol Sociobiol* 3(3):115-124.

18. Calvin WH (1983) A stone's throw and its launch window: timing precision and its implications for language and hominid brains. *J Theor Biol* 104(1):121-135.

19. Calvin WH (1983) *The Throwing Madonna: Essays on the Brain* (Bantam, New York).

20. Shea JJ (2006) The origins of lithic projectile point technology: evidence from Africa, the Levant, and Europe. *Journal of Archaeological Science* 33:823-846.

21. McBrearty S & Brooks AS (2000) The revolution that wasn't: a new interpretation of the origin of modern human behavior. *J Hum Evol* 39(5):453-563.

22. Churchill SE & Rhodes JA (2009) The evolution of the human capacity for "killing at a distance": The human fossil evidence for the evolution of projectile weaponry. *The evolution of hominin diets: Integrating approaches to the study of Paleolithic subsistence*, eds Hublin JJ & Richards MP (Springer, New York).

23. Coss RG & Biardi JE (1997) Individual variation in the antisnake behavior of California Ground Squirrels (*Spermophilus beecheyi)*. *J Mammology* 78(2):294-310.

24. Cooke JAL, Roth VD, & Miller FH (1972) The urticating hairs of the Theraphosid spiders. *Am Museum Novitates* 2498:1-43.

25. Rossel S, Corlija J, & Schuster S (2002) Predicting three-dimensional target motion: how archer fish determine where to catch their dislodged prey. *J Exp Biol* 205(Pt 21):3321-3326.

26. de Groot JH & van Leeuwen JL (2004) Evidence for an elastic projection mechanism in the chameleon tongue. *Proc Biol Sci* 271(1540):761-770.

27. Heimlich S & Boran J (2001) *Killer Whales* (Voyageur Press, Stillwater, MN).

28. Meyer-Rochow VB & Gal J (2003) Pressures produces when penguins pooh - calculations of avian defaecation. *Polar Biol* 27:56-58.

29. Wickler W & Seibt U (1997) Aimed object-throwing by a wild African elephant in an interspecific encounter. *Ethology* 103(5):365-368.

30. Cleveland A, Rocca AR, Wendt EL, & Westergaard GC (2003) Throwing behavior and mass distribution of stone selection in tufted capuchin monkeys (Cebus apella). *Am J Primatol* 61(4):159-172.

31. Westergaard GC & Suomi SJ (1997) Transfer of tools and food between groups of tufted capuchins (Cebus apella). *Am J Primatol* 43(1):33-41.

32. Leca JB, Nahallage CA, Gunst N, & Huffman MA (2008) Stone-throwing by Japanese macaques: form and functional aspects of a group-specific behavioral tradition. *J Hum Evol*.

33. Goodall J (1986) *The Chimpanzees of Gombe: Patterns of Behavior* (Harvard University Press, Cambridge).

34. Goodall J (1964) Tool-Using and Aimed Throwing in a Community of Free-Living Chimpanzees. *Nature* 201:1264-1266.

35. Hopkins WD, Russell JL, & Schaeffer JA (2012) The neural and cognitive correlates of aimed throwing in chimpanzees: a magnetic resonance image and behavioural study on a unique form of social tool use. *Philos Trans R Soc Lond B Biol Sci* 367(1585):37-47.

36. Kohler W (1925) *The Mentality of Apes* (Harcourt and Brace, New York).

37. Sugiyama Y & Koman J (1979) Tool-using and making behavior in wild chimpanzees at Bossou, Guinea. *Primates* 20:513-524.

38. Galdikas BMF (1982) Orang-utan tool-use at Tanjung Puting Reserve, Central Indonesian Borneo (Kalimantan Tengah). *J Hum Evol* 10:19-33.

39. Jordan C (1982) Object manipulation and tool-use in captive pygmy chimpanzees (*Pan paniscus*). *J Hum Evol* 11:35-39.

40. Nakamichi M (1999) Spontaneous use of sticks as tools by captive gorillas (*Gorilla gorilla gorilla)*. *Primates* 40(3):487-498.

41. Sibley CG & Ahlquist JE (1987) DNA hybridization evidence of hominoid phylogeny: results from an expanded data set. *J Mol Evol* 26(1-2):99-121.

42. Caccone A & Powell JR (1989) DNA divergence among hominoids. *Evolution* 43(5):925-942.

43. Ruvolo M (1997) Molecular phylogeny of the hominoids: inferences from multiple independent DNA sequence data sets. *Mol Biol Evol* 14(3):248-265.

44. Anonymous (2005) Initial sequence of the chimpanzee genome and comparison with the human genome. *Nature* 437(7055):69-87.

45. Wrangham R & Pilbeam D (2001) African Apes as Time Machines. *All Great Apes Great and Small, Volume I : African Apes,* African Apes, ed Galdikas BMF, Briggs, N.E., Sheeran, L.K., Shapiro, G.L. and Goodall, J. (Kluwer Academics/Plenum Publishers, New York), Vol I, pp ch. 1, pg. 5-17.

46. Hopkins WD, Russell JL, Cantalupo C, Freeman H, & Schapiro SJ (2005) Factors influencing the prevalence and handedness for throwing in captive chimpanzees (Pan troglodytes). *J Comp Psychol* 119(4):363-370.

47. Bauman JE (1923) The strength of the chimpanzee and orang. *The Sci Monthly* 16:432-439.

48. Finch G (1943) The bodily strength of chimpanzees. *J Mammal* 24:224-228.

49. Walker A (2009) The strength of great apes and the speed of humans. *Curr Anthropol* 50(2):229-234.

50. Roach NT (2012) Chapter 3 - Elastic energy storage in the shoulder and the evolution of high-speed throwing in *Homo;* in The Biomechanics and Evolution of High-Speed Throwing *PhD dissertation* (Harvard University, Cambridge, MA).

51. Axe MJ, Snyder-Mackler L, Konin JG, & Strube MJ (1996) Development of a distance-based interval throwing program for Little League-aged athletes. *Am J Sports Med* 24(5):594-602.

52. Dillman CJ, Fleisig GS, & Andrews JR (1993) Biomechanics of pitching with emphasis upon shoulder kinematics. *J Orthop Sports Phys Ther* 18(2):402-408.

53. Pappas AM, Zawacki RM, & Sullivan TJ (1985) Biomechanics of baseball pitching. A preliminary report. *Am J Sports Med* 13(4):216-222.

54. Roach NT (2012) Chapter 4 - The biomechanics of power generation during rapid, overhand throwing in humans; in The Biomechanics and Evolution of High-Speed Throwing *PhD dissertation* (Harvard University, Cambridge, MA).

55. Westergaard GC, Liv C, Haynie MK, & Suomi SJ (2000) A comparative study of aimed throwing by monkeys and humans. *Neuropsychologia* 38(11):1511-1517.

56. Watson NV & Kimura D (1991) Nontrivial sex differences in throwing and intercepting: relation to psychometrically-defined spatial function. *Person. Individ. Diff.* 12(5):375-385.

57. Jardine R & Martin NG (1983) Spatial Ability and Throwing Accuracy. *Behav Genet* 13(4):331-340.

58. van den Tillaar R & Ettema G (2004) Effect of body size and gender in overarm throwing performance. *Eur J Appl Physiol* 91(4):413-418.

59. Hall JA & Kimura D (1995) Sexual orientation and performance on sexually dimorphic motor tasks. *Archives of sexual behavior* 24(4):395-407.

60. Thomas JR & French KE (1985) Gender differences across age in motor performance a meta-analysis. *Psychological bulletin* 98(2):260-282.

61. Maccoby EE & Jacklin CN (1974) *The psychology of sex differences* (Stanford University Press, Palo Alto, CA).

62. Lorson KM & Goodway JD (2008) Gender differences in throwing form of children ages 6-8 years during a throwing game. *Res Q Exerc Sport* 79(2):174-182.

63. Thomas JR, Alderson JA, Thomas KT, Campbell AC, & Elliott BC (2010) Developmental gender differences for overhand throwing in Aboriginal Australian children. *Res Q Exerc Sport* 81(4):432-441.

64. Barton RF (1922) *Ifugao economics* (Unviersity of California Press, Berkeley).

65. Conzemius E (1932) Ethnographical survey of the Mishkito and Sumu Indians of Honduras and Nicaragua. (Washington, DC).

66. Dieterlen G (1951) Essai sur la religion bambara. (Paris).

67. Hart CWM, Pilling AR, & Goodale JC (1987) *The Tiwi of North Australia* (Holt Rinehart and Winston, New York).

68. Merker M (1910) *Die Masai: Ethnographische Monographie eines ostrafrikanischen Semitenvolkes* (Dietrich Reimer (Ernst Vohsen), Berlin).

69. Nimuendaju C (1952) *The Tukuna* (University of California Press, Berkeley).

70. Puccioni N (1936) *Anthropologia e etnografia delle genti della Somalia* (Nicola Zanichelli, Bologna).

71. Titiev M (1971) *Old Oraibi: a study of the Hopi Indians of the Third Mesa* (Kraus Reprint Company, New York).

72. Parmentier RJ (1987) *The sacred remains: myth, history, and polity in Belau* (University of Chicago Press, Chicago).

73. Pollard S (1921) *In unknown China: a record of the observartions, adventures and experiences of a pioneer missionary during a prolonged sojourn amongst the wild and unknown Nosu tribe of western China* (J. B. Lippincott, Philadelphia).

74. Clark WF (1975) *Population, agriculture and urbanization in the Kingdom of Tonga* (Michigan State University, Ann Arbor, MI).

75. Edgerton RB (1988) *Like lions they fought: the Zulu war and the last Black empire in South Africa* (Collier MacMillan, New York).

76. Foster GM (1944) *A summary of Yuki culture* (University of California Press, Berkeley).

77. Gulliver PH (1951) A preliminary survey of the Turkana: a report complied for the government of Kenya. (Rondebosch, Cape Town).

78. Homer (1961) *The Iliad* (University of Chicago Press, Chicago, IL).

79. Lang C ed (1869) *Epitoma Rei Militaris* (Teubner, Leipzig).

80. Chagnon NA (1968) *Yanomamo: the fierce people* (Holt, Rinehart and Winston, New York).

81. Murphy RF (1959) Intergroup hostility and social cohesion. *American Anthropologist* 59:1018-1035.

82. Uberoi JP (1971) *Politics of the kula ring: an analysis of the findings of Bronislaw Malinowski* (Manchester University Press, Manchester, UK).

83. Hambly WD (1934) The Ovimbundu of Angola. in *Museum Ethnological Expedition to West Africa 1929-30*, ed Laufer B (Field Museum of Natural History, Chicago, IL).

84. Griaule M (1938) *Masques Dogon* (Institut d'Ethnologie, Paris).

85. Glatzer B (1977) *Nomaden von Gharjistan: Aspekte der wirtschaftlichen, sozialen und politischen Organisation nomadischer Durrani-Paschtunen in Nordwestafghanistan* (Franz Steiner Verlag, Wiesbaden).

86. Routledge WS (1910) *With a prehistoric people: the Akikuyu of British East Africa, being some account of the method of life and mode of thought found existent amongst a nation on its first contact with European civilisation* (Ebward Arnold, London).

87. Hill WW (1938) *The agricultural and hunting methods of the Navaho Indians* (Yale University Press, New Haven).

88. Grinnell GB (1962) *Blackfoot lodge tales: the story of a prairie people* (University of Nebraska Press, Lincoln, NE).

89. Handy ES, Handy EG, & Pukui MK (1972) *Native planters in old Hawaii: their life, lore, and environment* (Bishop Museum Press, Honolulu).

90. Sutlive VH (1973) *From longhouse to pasar: urbanization in Sarawak, East Malaysia* (University Microfilms, Ann Arbor, MI).

91. Tooby J & DeVore I (1987) The reconstruction of hominid behavioral evolution through strategic modeling. *The evolution of human behavior: Primate models*, ed Kinzey WG (SUNY Press, Albany, NY).

92. Wrangham R, Jones JH, Laden G, Pilbeam D, & Conklin-Brittain N (1999) The Raw and the Stolen : Cooking and the Ecology of Human Origins. *Current Anthropology* 40(5):567-594.

93. Dahlberg F ed (1983) *Woman the Gatherer* (Yale University Press, New Haven, CT).

94. Kuhn SL & Stiner MC (2006) What's a Mother to Do? A Hypothesis about the Division of Labor among Neandertals and Modern Humans. *Current Anthropology* 47(6):953-980.

95. Hong DA, Cheung TK, & Roberts EM (2001) A three-dimensional, six-segment chain analysis of forceful overarm throwing. *J Electromyogr Kinesiol* 11(2):95-112.

96. Debicki DB, Gribble PL, Watts S, & Hore J (2011) Wrist muscle activation, interaction torque and mechanical properties in unskilled throws of different speeds. *Exp Brain Res* 208(1):115-125.

97. Hore J, Debicki DB, Gribble PL, & Watts S (2011) Deliberate utilization of interaction torques brakes elbow extension in a fast throwing motion. *Exp Brain Res* 211(1):63-72.

98. Hirashima M, Kadota H, Sakurai S, Kudo K, & Ohtsuki T (2002) Sequential muscle activity and its functional role in the upper extremity and trunk during overarm throwing. *J Sports Sci* 20(4):301-310.

99. Hirashima M, Kudo K, Watarai K, & Ohtsuki T (2007) Control of 3D limb dynamics in unconstrained overarm throws of different speeds performed by skilled baseball players. *J Neurophysiol* 97(1):680-691.

100. Hirashima M, Yamane K, Nakamura Y, & Ohtsuki T (2008) Kinetic chain of overarm throwing in terms of joint rotations revealed by induced acceleration analysis. *J Biomech* 41(13):2874-2883.

101. Putnam CA (1993) Sequential motions of body segments in striking and throwing skills: descriptions and explanations. *J Biomech* 26 Suppl 1:125-135.

102. Fleisig GS, Andrews JR, Dillman CJ, & Escamilla RF (1995) Kinetics of baseball pitching with implications about injury mechanisms. *Am J Sports Med* 23(2):233-239.

103. Fleisig GS, Barrentine SW, Escamilla RF, & Andrews JR (1996) Biomechanics of overhand throwing with implications for injuries. *Sports Med* 21(6):421-437.

104. Feltner ME (1989) 3-Dimensional Interactions in a 2-Segment Kinetic Chain .2. Application to the Throwing Arm in Baseball Pitching. *Int J Sport Biomech* 5(4):420-450.

105. Atwater AE (1979) Biomechanics of overarm throwing movements and of throwing injuries. *Exerc Sport Sci Rev* 7:43-85.

106. DiGiovine NM, Jobe FW, Pink M, & Perry J (1992) An electromyography analysis of the upper extremity in pitching. *J Shoulder Elbow Surg* 1:15-25.

107. Gowan ID, Jobe FW, Tibone JE, Perry J, & Moynes DR (1987) A comparative electromyographic analysis of the shoulder during pitching. Professional versus amateur pitchers. *Am J Sports Med* 15(6):586-590.

108. Roberts EM (1971) Cinematography in biomedical investigation. *Selected Topics in Biomedical Invesitgation. Proceedings of the C.I.C. Symposium on Biomechanics*, ed Cooper JM (The Athletic Institute, Chicago), pp 71-81.

109. Higgins JR (1977) *Human Movement: an integrated approach* (The C.V. Mosby Company, Saint Louis).

110. Ishikawa M, Komi PV, Grey MJ, Lepola V, & Bruggemann GP (2005) Muscle-tendon interaction and elastic energy usage in human walking. *J Appl Physiol* 99(2):603-608.

111. Anderson FC & Pandy MG (1993) Storage and utilization of elastic strain energy during jumping. *J Biomech* 26(12):1413-1427.

112. Biewener AA, Farley CT, Roberts TJ, & Temaner M (2004) Muscle mechanical advantage of human walking and running: implications for energy cost. *Journal of Applied Physiology* 97:2266-2274.

113. Komi PV & Bosco C (1978) Utilization of stored elastic energy in leg extensor muscles by men and women. *Medicine and science in sports* 10(4):261-265.

114. Kubo K, Kawakami Y, & Fukunaga T (1999) Influence of elastic properties of tendon structures on jump performance in humans. *J Appl Physiol* 87(6):2090-2096.

115. Patek SN, Nowroozi BN, Baio JE, Caldwell RL, & Summers AP (2007) Linkage mechanics and power amplification of the mantis shrimp's strike. *J Exp Biol* 210(Pt 20):3677-3688.

116. Peplowski MM & Marsh RL (1997) Work and power output in the hindlimb muscles of Cuban tree frogs Osteopilus septentrionalis during jumping. *J Exp Biol* 200(Pt 22):2861-2870.

117. Roberts TJ & Azizi E (2011) Flexible mechanisms: the diverse roles of biological springs in vertebrate movement. *J Exp Biol* 214(Pt 3):353-361.

118. Altchek DW & Dines DM (1995) Shoulder Injuries in the Throwing Athlete. *J Am Acad Orthop Surg* 3(3):159-165.

119. Meister K (2000) Injuries to the shoulder in the throwing athlete. Part one: Biomechanics/pathophysiology/classification of injury. *Am J Sports Med* 28(2):265-275.

120. Rodeo SA, Suzuki K, Yamauchi M, Bhargava M, & Warren RF (1998) Analysis of collagen and elastic fibers in shoulder capsule in patients with shoulder instability. *Am J Sports Med* 26(5):634-643.

121. Biewener AA, Konieczynski DD, & Baudinette RV (1998) In vivo muscle force-length behavior during steady-speed hopping in tammar wallabies. *J Exp Biol* 201(Pt 11):1681-1694.

122. Astley HC & Roberts TJ (2012) Evidence for a vertebrate catapult: elastic energy storage in the plantaris tendon during frog jumping. *Biol Lett* 8(3):386-389.

123. Bigliani LU*, et al.* (1992) Tensile properties of the inferior glenohumeral ligament. *J Orthop Res* 10(2):187-197.

124. McMahon PJ, Dettling J, Sandusky MD, Tibone JE, & Lee TQ (1999) The anterior band of the inferior glenohumeral ligament. Assessment of its permanent deformation and the anatomy of its glenoid attachment. *J Bone Joint Surg Br* 81(3):406-413.

125. Brooks AS, Yellen JE, Nevell L, & Hartman G (2005) Projectile technologies of the African MSA: implications for modern human origins. *Transitions before the transition: Evolution and stability in the Middle Paleolithic and Middle Stone Age*, eds Hovers E & Kuhn S (Kluwer, Nerw York), pp 233-255.

126. Wendt WE (1975) 'Art mobilier' aus der Apollo 11 - Grotte in Sudwest-Afrika: die altesten datierten Kunstwerke Afrikas. *Acta Praehist Archaeol* 5:1-42.

127. Volman RP (1984) Early prehistory of Southern Africa. *Southern African Prehistory and Paleoenvironments*, ed Klein RG (Balkema, Rotterdam), pp 169-220.

128. Debenath A, Raynal JP, Roche J, Texier JP, & Ferembach D (1986) Stratigraphie, habitat, typologie et devinir de l'Aterien Marocain: donnees recentes. *L'Anthropologie* 90:233-246.

129. O'Brien EM (1981) The projectile capabilities of an Acheulian handaxe fro Olorgesailie. *Curr Anthropol* 22(1):76-79.

130. Clark JD (1955) The stone ball: its associations and use by prehistoric man in Africa. *Congres Panafricain de Prehistorie: Actes de la IIe Session (Alger 1952)*, ed Balout L (Arts et Metiers Graphiques, Paris).

131. Cannell A (2002) Throwing behaviour and the mass distribution of geological hand samples, hand grenades and Olduvian manuports. *Journal of Archaeological Science* 29(4):335-339.

132. Schick KD & Toth N (1994) Early Stone Age technology in Africa: a review and case study into the nature and function of spheroids and subspheroids. *Integrative Paths to the Past: Paleoanthropological Advances in Honor of F. Clark Howell*, eds Robert SC & Ciochon RL (Prentice Hall, Englewood Cliffs, NJ), pp 429-449.

133. Whittaker JC & McCall G (2001) Handaxe-hurling Hominids: an unlikely story. *Curr Anthropol* 42:566-572.

134. Thieme H (1997) Lower Palaeolithic hunting spears from Germany. *Nature* 385(6619):807-810.

135. Schmitt D, Churchill SE, & Hylander WL (2003) Experimental evidence concerning spear use in Neandertals and early modern humans. *Journal of Archaeological Science* 30(1):103-114.

136. Rust A (1937) *Das altsteinzeitliche Rentierjagerlager Meiendorf* (Karl Wachholtz Verlag, Neumunster).

137. Bratlund B (1991) A study of hunting lesions containing flint fragments on reindeer bones at Stellmoor, Schleswig-Holstein, Germany. *The Late Glacial in north-west Europe: human adaptation and environmental change at the end of the Pleistocene*, eds Barton N, Roberts AJ, & Roe DA (Alden Press, Oxford), pp 193-207.

138. Letourneux C & Petillon JM (2008) Hunting lesions caused by osseous projectile points: experimental results and archaeological implications. *Journal of Archaeological Science* 35(10):2849-2862.

139. Roberts MB & Parfitt SA (1999) *Boxgrove: A Middle Pleistocene Hominid Site at Eartham Quarry, Boxgrove, West Sussex* (English Heritage, London).

140. Boeda E*, et al.* (1999) A Levallois point embedded in the vertebra of a wild ass (Equus africanus): Hafting, projectiles and Mousterian hunting weapons. *Antiquity* 73(280):394-402.

141. Wight J, Richards J, & Hall S (2004) Influence of pelvis rotation styles on baseball pitching mechanics. *Sports Biomech* 3(1):67-83.

142. Bramble DM & Lieberman DE (2004) Endurance Running and the Evolution of Homo. *Nature* 432:345-352.

143. Robinson JT (1972) *Early hominid posture and locomotion* (University of Chicago Press, Chicago).

144. Lovejoy CO (1988) Evolution of human walking. *Sci Am* 259(5):118-125.

145. Pilbeam D (2004) The anthropoid postcranial axial skeleton: comments on development, variation, and evolution. *J Exp Zoolog B Mol Dev Evol* 302(3):241-267.

146. Sanders WJ (1998) Comparative morphometric study of the australopithecine vertebral series Stw-H8/H41. *Journal of Human Evolution* 34:249-302.

147. Aiello LC & Dean C (1990) *An Introduction to Human Evolutionary Anatomy* (Academic Press, New York) p 596.

148. Gregersen GG & Lucas DB (1967) An in vivo study of the axial rotation of the human thoracolumbar spine. *J Bone Joint Surg Am* 49(2):247-262.

149. Jellema LM, Latimer B, & Walker A (1993) The Rib Cage. *The Nariokotome Homo erectus Skeleton*, eds Walker A & Leakey REF (Harvard University Press, Cambridge), pp 294-325.

150. Whitcome KK, Shapiro LJ, & Lieberman DE (2007) Fetal load and the evolution of lumbar lordosis in bipedal hominins. *Nature* 450(7172):1075-1078.

151. Lieberman DE, Raichlen D, Pontzer H, Bramble D, & Cutright-Smith E (2006) The Human Gluteus Maximus and its Role in Running. *J Exp Biol* 209:2143-2155.

152. Marzke MW, Longhill JM, & Rasmussen SA (1988) Gluteus maximus muscle function and the origin of hominid bipedality. *Am J Phys Anthropol* 77:519-528.

153. Stern JT, Jr. (1972) Anatomical and functional specializations of the human gluteus maximus. *Am J Phys Anthropol* 36(3):315-339.

154. Oliver GD & Keeley DW (2010) Pelvis and torso kinematics and their relationship to shoulder kinematics in high-school baseball pitchers. *J Strength Cond Res* 24(12):3241-3246.

155. Oliver GD & Keeley DW (2010) Gluteal muscle group activation and its relationship with pelvic and trunk kinematics in high school baseball pitchers. *J Strength Cond Res* 24(11):3015-3022.

156. Rose MD (1984) A hominine hip bone, KNM-ER 3228, from East Lake Turkana, Kenya. *Am J Phys Anthropol* 63(4):371-378.

157. Ruff CB (1995) Biomechanics of the hip and birth in early Homo. *Am J Phys Anthropol* 98(4):527-574.

158. Simpson SW*, et al.* (2008) A female Homo erectus pelvis from Gona, Ethiopia. *Science* 322(5904):1089-1092.

159. Haeusler M (2002) New insights into the locomotion of *Australopithecus africanus* based on the pelvis. *Evol Anthropol* 11:53-57.

160. Kibii JM, *et al.* (2011) A partial pelvis of Australopithecus sediba. *Science* 333(6048):1407-1411.

161. Toussaint M, Macho GA, Tobias PV, Partridge TC, & Hughes AR (2003) The third partial skeleton of a late Pliocene hominin (Stw 431) from Sterkfontein, South Africa. *S Afr J Sci* 99:215-233.

162. Meyer KE, *et al.* (2008) Three-dimensional scapular kinematics during the throwing motion. *J Appl Biomech* 24(1):24-34.

163. Haile-Selassie Y, *et al.* (2010) An early Australopithecus afarensis postcranium from Woranso-Mille, Ethiopia. *Proc Natl Acad Sci U S A* 107(27):12121-12126.

164. Larson SG (2007) Evolutionary Transformation of the Hominin Shoulder. *Evolutionary Anthropology* 16:172-187.

165. Campbell BG (1966) *Human Evolution* (Heinemann, London).

166. Oxnard CE (1968) A note on the fragmentary Sterkfontein scapula. *American Journal of Physical Anthropology* 28(213-217).

167. Vrba E (1979) A new study of the scapula of *Australopithecus africanus* from Sterkfontein. *American Journal of Physical Anthropology* 51:117-130.

168. Berger LR, *et al.* (2010) Australopithecus sediba: a new species of Homo-like australopith from South Africa. *Science* 328(5975):195-204.

169. Trinkaus E (1983) Neandertal postcrania and the adaptive shift to modern humans. in *The Mousterian Legacy: Human biocultural change in the Upper Pleistocene*, ed Trinkaus E (Oxford, UK).

170. Larson SG, *et al.* (2008) Descriptions of the upper limb skeleton of Homo floresiensis. *J Hum Evol*.

171. Carretero JM, Arsuaga JL, & Lorenzo C (1997) Clavicles, scapulae and humeri from the Sima de los Huesos site (Sierra de Atapuerca, Spain). *J Hum Evol* 33(2-3):357-408.

172. Lordkipanidze D, *et al.* (2007) Postcranial evidence from early Homo from Dmanisi, Georgia. *Nature* 449(7160):305-310.

173. Churchill SE & Trinkaus E (1990) Neandertal scapular glenoid morphology. *Am J Phys Anthropol* 83(2):147-160.

174. Knusel C (1992) The throwing hypothesis and hominid origins. *Human Evolution* 7(1):1-7.

175. Trinkaus E (1983) *The Shanidar Neandertals* (Academic Press, New York).

176. Trinkaus E (1977) A functional interpretation of the axillary border of the Neandertal scapula. *J Hum Evol* 6(3):231-234.

177. Trinkaus E (2008) Kiik-Koba 2 and Neandertal axillary border ontogeny. *Anthropol Sci* 116(3):231-236.

178. Schwalbe G (1914) Kritische Besprechung von Boule's Werk: "L'homme fossile de La Chapelle-aux-Saints" mit eigenen Untersuchungen. *Zeitschrift für Morphologie und Anthropologie* 16:527-610.

179. Larson SG (2009) Evolution of the hominin shoulder: Early Homo. *The first humans: Origins of the genus Homo,* Vertebrate Paleobiology and Paleoanthropology Series, eds Grine FE & Leakey RE (Springer, New York).

180. Vandermeesch B & Trinkaus E (1995) The postcranial remains of the Regourdou 1 Neandertal: the shoulder and arm remains. *Journal of Human Evolution* 28:439-476.

181. Napier JR (1965) Comment on "New discoveries in Tanganyika: their bearing on hominid evolution by PV Tobias. *Curr Anthropol* 5:402-403.

182. Carretero JM, Lorenzo C, & Arsuaga JL (1999) Axial and appendicular skeleton of Homo antecessor. *J Hum Evol* 37(3-4):459-499.

183. Jungers WL*, et al.* (2008) Descriptions of the lower limb skeleton of Homo floresiensis. *J Hum Evol*.

184. Jungers WL*, et al.* (2009) The foot of Homo floresiensis. *Nature* 459(7243):81-84.

185. Jungers WL (1994) Ape and hominid limb length. *Nature* 369:194.

186. Kagaya M, Ogihara N, & Nakatsukasa M (2010) Is the clavicle of apes long? An investigation of clavicular length in relation to body mass and upper thoracic width. *Int J Primatol* 31:209-217.

187. Pieper HG (1998) Humeral torsion in the throwing arm of handball players. *Am J Sports Med* 26(2):247-253.

188. Crockett HC, *et al.* (2002) Osseous adaptation and range of motion at the glenohumeral joint in professional baseball pitchers. *Am J Sports Med* 30(1):20-26.

189. Reagan KM, *et al.* (2002) Humeral retroversion and its relationship to glenohumeral rotation in the shoulder of college baseball players. *Am J Sports Med* 30(3):354-360.

190. Osbahr DC, Cannon DL, & Speer KP (2002) Retroversion of the humerus in the throwing shoulder of college baseball pitchers. *Am J Sports Med* 30(3):347-353.

191. Chant CB, Litchfield R, Griffin S, & Thain LM (2007) Humeral head retroversion in competitive baseball players and its relationship to glenohumeral rotation range of motion. *J Orthop Sports Phys Ther* 37(9):514-520.

192. Roach NT, Lieberman DE, Gill TJ, IV, Palmer WE, & Gill TJ, III (2012) The effect of humeral torsion on rotational range of motion in the shoulder and throwing performance. *J Anat* 220:293-301.

193. Larson SG (1996) Estimating humeral torsion on incomplete fossil anthropoid humeri. *Journal of Human Evolution* 31:239-257.

194. Larson SG, *et al.* (2007) Homo floresiensis and the evolution of the hominin shoulder. *J Hum Evol*.

195. Churchill SE (1994) Human upper body evolution in the Eurasian Late Pleistocene. PhD (University of New Mexico, Albequerque).

196. Churchill SE (1996) Particulate versus integrated evolution of the upper body of Late Pleistocene hominids: a test of two models. *American Journal of Physical Anthropology* 100(559-583).

197. Cowgill LW (2007) Humeral torsion revisited: a functional and ontogenetic model for populational variation. *Am J Phys Anthropol* 134(4):472-480.

198. Rhodes JA & Churchill SE (2009) Throwing in the Middle and Upper Paleolithic: inferences from an analysis of humeral retroversion. *J Hum Evol* 56(1):1-10.

199. Trinkaus E, Churchill SE, & Ruff CB (1994) Postcranial robusticity in Homo. II: Humeral bilateral asymmetry and bone plasticity. *Am J Phys Anthropol* 93(1):1-34.

200. Churchill SE, Weaver AH, & Niewoehner WA (1996) Late Pleistocene human technological and subsistence behavior: Functional interpretations of upper limb morphology. *Reduction Processes ("Chaines Operatoires") in the European Mousterian*, eds Bietti A & Grimaldi S (Quaternaria Nova), pp 18-51.

201. Churchill SE & Formicola V (1997) A case of marked bilateral asymmetry in the upper limbs of an Upper Paleolithic male from Barma Grande (Liguria), Italy. *Int J Osteoarchaeol* 7:18-38.

202. Shaw CN & Stock JT (2009) Habitual throwing and swimming correspond with upper limb diaphyseal strength and shape in modern human athletes. *Am J Phys Anthropol* 140(1):160-172.

203. Rhodes JA & Knusel CJ (2005) Activity-related skeletal change in medieval humeri: cross-sectional and architectural alterations. *Am J Phys Anthropol* 128(3):536-546.

204. Rhodes JA (2006) Adaptations to humeral torsion in medieval Britain. *Am J Phys Anthropol* 130(2):160-166.

205. Commandre F (1977) *Pathologie Abarticulaire* (Cetrane, Maurecourt).

206. Dutour O (1986) Enthesopathies (lesions of muscular insertions) as indicators of the activities of neolithic Saharan populations. *Am J Phys Anthropol* 71(2):221-224.

207. Dutour O (1992) Activities physiques et squelette humain: le difficile passge de l'actuel au fossile. *Bull Mem Soc Anthropol Paris* 4:233-241.

208. Dutour O (2000) Chasse et activites physiques dans la Prehistorie: les marqueurs osseux d'activites chez l'homme fossile. *Anthropologie et Prehistorie* 111:156-165.

209. Ouellette H, Bredella M, Labis J, Palmer WE, & Torriani M (2008) MR imaging of the elbow in baseball pitchers. *Skeletal radiology* 37(2):115-121.

210. Villotte S, Churchill SE, Dutour OJ, & Henry-Gambier D (2010) Subsistence activities and the sexual division of labor in the European Upper Paleolithic and Mesolithic: evidence from upper limb enthesopathies. *J Hum Evol* 59(1):35-43.

211. Churchill SE & Rhodes JA (2006) How strong were the Neandertals? Leverage and muscularity at the shoulder and elbow in Mousterian foragers. *Periodicum Biologorum* 108(4):457-470.

212. Jobe FW, Tibone JE, Perry J, & Moynes D (1983) An EMG analysis of the shoulder in throwing and pitching. A preliminary report. *Am J Sports Med* 11(1):3-5.

213. Kelly BT, Backus SI, Warren RF, & Williams RJ (2002) Electromyographic analysis and phase definition of the overhead football throw. *Am J Sports Med* 30(6):837-844.

214. Glousman R*, et al.* (1988) Dynamic electromyographic analysis of the throwing shoulder with glenohumeral instability. *J Bone Joint Surg Am* 70(2):220-226.

215. Shackelford LL (2007) Regional variation in the postcranial robusticity of late Upper Paleolithic humans. *Am J Phys Anthropol* 133(1):655-668.

216. Duarte C*, et al.* (1999) The early Upper Paleolithic human skeleton from the Abrigo do Lagar Velho (Portugal) and modern human emergence in Iberia. *Proc Natl Acad Sci U S A* 96(13):7604-7609.

217. Holliday TW (2002) Body size and postcranial robusticity of European Upper Paleolithic hominins. *J Hum Evol* 43(4):513-528.

218. Ruff CB, Trinkaus E, & Holliday TW (1997) Body Mass and Encephalization in Pleistocene Homo. *Nature* 387:173-176.

219. Trinkaus E (2010) The Tianyuan 1 upper limb remains. *The early modern human from Tianyuan Cave, China*, eds Shang H & Trinkaus E (Texas A&M University Anthropology Series, College Station, TX), pp 96-131.

220. Warden SJ, Bogenschutz ED, Smith HD, & Gutierrez AR (2009) Throwing induces substantial torsional adaptation within the midshaft humerus of male baseball players. *Bone* 45(5):931-941.

221. Shaw CN, Hofmann CL, Petraglia MD, Stock JT, & Gottschall JS (2012) Neandertal humeri may reflect adaptation to scraping tasks, but not spear thrusting. *PLoS One* 7(7):e40349.

222. Feltner M & Dapena J (1986) Dynamics of the Shoulder and Elbow Joints of the Throwing Arm during a Baseball Pitch. *Int J Sport Biomech* 2(4):235-259.

223. Sakurai S, Ikegami Y, Okamoto A, Yabe K, & Toyoshima S (1993) A 3-Dimensional Cinematographic Analysis of Upper Limb Movement during Fastball and Curveball Baseball Pitches. *Journal of Applied Biomechanics* 9(1):47-65.

224. Fleisig GS*, et al.* (1996) Kinematic and kinetic comparison between baseball pitching and football passing. *Journal of Applied Biomechanics* 12(2):207-224.

225. Keeley DW, Wicke J, Alford K, & Oliver GD (2010) Biomechanical Analysis of Forearm Pronation and Its Relationship to Ball Movement for the Two-Seam and Four-Seam Fastball Pitches. *Journal of Strength and Conditioning Research* 24(9):2366-2371.

226. Tullos HS & King JW (1973) Throwing mechanism in sports. *The Orthopedic clinics of North America* 4(3):709-720.

227. Zihlman AL & Brunker L (1979) Hominid bipedalism: then and now. *Yb Physical Anthropol* 22:132-162.

228. Asfaw B*, et al.* (1999) Australopithecus garhi: a new species of early hominid from Ethiopia. *Science* 284(5414):629-635.

229. Drapeau MS (2001) Functional analysis of the associated partial forelimb skeleton from Hadar, Ethiopia (AL 438-1). Ph. D (University of Missouri - Columbia, Columbia, MO).

230. Richmond BG, Aiello LC, & Wood BA (2002) Early hominin limb proportions. *J Hum Evol* 43(4):529-548.

231. Johanson DC*, et al.* (1987) New partial skeleton of Homo habilis from Olduvai Gorge, Tanzania. *Nature* 327(21):205-209.

232. Trinkaus E (1981) Neanderthal limb proportions and cold adaptation. *Aspects of human evolution*, ed Stringer CB (Taylor and Francis, London), pp 187-224.

233. Walker A & Leakey RE eds (1993) *The Nariokotome Homo Erectus skeleton* (Harvard University Press, Cambridge, MA).

234. Holliday TW (1997) Body proportions in Late Pleistocene Europe and modern human origins. *J Hum Evol* 32(5):423-448.

235. Brown P*, et al.* (2004) A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia. *Nature* 431(7012):1055-1061.

236. Trinkaus E, Churchill SE, Ruff CB, & Vandermeesch B (1999) Long Bone Shaft Robusticity and Body Proportions of the Saint-Cesaire 1 Chatelperronian Neanderthal. *J Archaeol Sci* 26:753-773.

237. Sisto DJ, Jobe FW, Moynes DR, & Antonelli DJ (1987) An electromyographic analysis of the elbow in pitching. *Am J Sports Med* 15(3):260-263.

238. Drapeau MS, Ward CV, Kimbel WH, Johanson DC, & Rak Y (2005) Associated cranial and forelimb remains attributed to Australopithecus afarensis from Hadar, Ethiopia. *J Hum Evol* 48(6):593-642.

239. Aiello LC, Wood B, Key C, & Lewis M (1999) Morphological and taxonomic affinities of the Olduvai ulna (OH 36). *Am J Phys Anthropol* 109(1):89-110.

240. Anton SC (2003) Natural history of Homo erectus. *Am J Phys Anthropol* Suppl 37:126-170.

241. Pappas AM, Morgan WJ, Schulz LA, & Diana R (1995) Wrist kinematics during pitching. A preliminary report. *Am J Sports Med* 23(3):312-315.

242. Young RW (2003) Evolution of the human hand: the role of throwing and clubbing. *Journal of Anatomy* 202:165-174.

243. Chowdhary AG & Challis JH (1999) Timing accuracy in human throwing. *J Theor Biol* 201(4):219-229.

244. Hore J (1996) Motor control, excitement, and overarm throwing. *Can J Physiol Pharmacol* 74(4):385-389.

245. Hore J, Ritchie R, & Watts S (1999) Finger opening in an overarm throw is not triggered by proprioceptive feedback from elbow extension or wrist flexion. *Exp Brain Res* 125(3):302-312.

246. Hore J, Watts S, & Tweed D (1996) Errors in the control of joint rotations associated with inaccuracies in overarm throws. *J Neurophysiol* 75(3):1013-1025.

247. Hore J, Watts S, Tweed D, & Miller B (1996) Overarm throws with the nondominant arm: kinematics of accuracy. *J Neurophysiol* 76(6):3693-3704.

248. Jardine R & Martin NG (1983) Throwing Accuracy and the Genetics of Spatial Ability. *Behav Genet* 13(5):538-538.

249. Cordo P, Carlton L, Bevan L, Carlton M, & Kerr GK (1994) Proprioceptive coordination of movement sequences: role of velocity and position information. *J Neurophysiol* 71(5):1848-1861.

250. Cordo PJ (1990) Kinesthetic control of a multijoint movement sequence. *J Neurophysiol* 63(1):161-172.

251. Karni A (1996) The acquisition of perceptual and motor skills: a memory system in the adult human cortex. *Brain research. Cognitive brain research* 5(1-2):39-48.

252. Karni A*, et al.* (1995) Functional MRI evidence for adult motor cortex plasticity during motor skill learning. *Nature* 377(6545):155-158.

253. Karni A & Sagi D (1993) The time course of learning a visual skill. *Nature* 365(6443):250-252.

254. Sanes JN & Donoghue JP (2000) Plasticity and primary motor cortex. *Annual review of neuroscience* 23:393-415.

255. Marzke MW (1971) Origin of the human hand. *American Journal of Physical Anthropology* 34:61-84.

256. Schreibner H (1936) Die extrembewegungen der schimpsenhand. *Gegnbauers Morph. Jahr.* 77:22-60.

257. Tuttle RH (1967) Knuckle-walking and the Evolution of Hominoid Hands. *American Journal of Physical Anthropology* 26:171-206.

258. Corruccini RS (1978) Comparative Osteometrics of the hominoid wrist joint, with special reference to knuckle-walking. *Journal of Human Evolution* 7:307-321.

259. Jenkins FA, Jr. & Fleagle JG (1975) Knuckle-walking and the functional antomy of the wrists in living apes. *Primate functional morphology and evolution*, ed Tuttle RH (Mouton, The Hague), pp 213-231.

260. Napier JR (1960) Studies of the hands of living primates. *Proceedings of the Zoological Society of London* 134:647-657.

261. Richmond BG & Strait DS (2000) Evidence that Humans Evolved from a Knuckle-Walking Ancestor. *Nature* 404:382-385.

262. Richmond BG, Begun DR, & Strait DS (2001) Origin of Human Bipedalism: The Knuckle-Walking Hypothesis Revisited. *Yearbook of Physical Anthropology* 44:70-105.

263. Tallman M (2012) Morphology of the distal radius in extant hominoids and fossil hominins: implications for the evolution of bipedalism. *Anat Rec (Hoboken)* 295(3):454-464.

264. White TD*, et al.* (2009) Ardipithecus ramidus and the paleobiology of early hominids. *Science* 326(5949):75-86.

265. Marzke MW (1983) Joint Functions and Grips of the Australopithecus-Afarensis Hand, with Special Reference to the Region of the Capitate. *Journal of Human Evolution* 12(2):197-211.

266. Kirschmann E (1999) *Das Zeitalter der Werfer* (Eduard Kirschmann Grunlinde 4, 30459, Hannover, Germany).

267. Napier JR (1956) The Prehensile Movements of the Human Hand. *Journal of Bone and Joint Surgery-British Volume* 38(4):902-913.

268. Napier JR (1980) *Hands* (George Allen & Unwin, London).

269. Marzke MW (1992) Evolutionary development of the human thumb. *Hand Clin* 8(1):1-8.

270. Marzke MW (1997) Precision grips, hand morphology, and tools. *Am J Phys Anthropol* 102(1):91-110.

271. Stern JT, Jr. & Susman RL (1983) The locomotor anatomy of Australopithecus afarensis. *American Journal of Physical Anthropology* 60:279-317.

272. Bush ME, Lovejoy CO, Johanson DC, & Coppens Y (1982) Hominid Carpal, Metacarpal, and Phalangeal Bones Recovered from the Hadar Formation - 1974-1977 Collections. *American Journal of Physical Anthropology* 57(4):651-677.

273. Ricklan DE (1988) Functional anatomy of the hand of *Australopithecus africanus*. *J Hum Evol* 16:643-664.

274. Susman RL (1989) New hominid fossils from the Swartkrans formation (1979-1986 excavations): postcranial specimens. *Am J Phys Anthropol* 79(4):451-474.

275. Kivell TL, Kibii JM, Churchill SE, Schmid P, & Berger LR (2011) Australopithecus sediba hand demonstrates mosaic evolution of locomotor and manipulative abilities. *Science* 333(6048):1411-1417.

276. Napier J (1962) Fossil Hand Bones from Olduvai Gorge. *Nature* 196(4853):409-&.

277. Susman RL (1979) Comparative and functional morphology of hominoid fingers. *Am J Phys Anthropol* 50(2):215-236.

278. Lorenzo C, Arsuaga JL, & Carretero JM (1998) Hand and foot remains from the Gran Dolina Early Pleistocene site (Sierra de Atapuerca, Spain). *J Hum Evol* 37:501-522.

279. Arsuaga JL*, et al.* (1997) Sima de los Huesos (Sierra de Atapuerca, Spain). The site. *J Hum Evol* 33(2-3):109-127.

280. Guy F, *et al.* (2005) Morphological affinities of the Sahelanthropus tchadensis (Late Miocene hominid from Chad) cranium. *Proc Natl Acad Sci U S A* 102(52):18836-18841.

281. Haile-Selassie Y, Suwa G, & White TD (2004) Late Miocene teeth from Middle Awash, Ethiopia, and early hominid dental evolution. *Science* 303(5663):1503-1505.

282. Braun DR, *et al.* (2010) Early hominin diet included diverse terrestrial and aquatic animals 1.95 Ma in East Turkana, Kenya. *Proc Natl Acad Sci U S A* 107(22):10002-10007.

283. de Heinzelin J, *et al.* (1999) Environment and behavior of 2.5-million-year-old Bouri hominids. *Science* 284(5414):625-629.

284. Dominguez- Rodrigo M & Barba R (2005) A study of cut marks on small-sized carcasses and its application to the study of cut-marked bones from small mammals at the FLK Zinj site. *J Taphon* 3:121-134.

285. McPherron SP, *et al.* (2010) Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* 466(7308):857-860.

286. Semaw S, *et al.* (2003) 2.6-million-year-old stone tools and associated bones from OGS-6 and OGS-7, Gona, Afar, Ethiopia. *Journal of Human Evolution* 45(2):169-177.

287. Pobiner BL, Rogers MJ, Monahan CM, & Harris JWK (2008) New evidence for hominin carcass processing strategies at 1.5 Ma, Koobi Fora, Kenya. *Journal of Human Evolution* 55(1):103-130.

288. Dominguez-Rodrigo M & Barba R (2006) New estimates of tooth mark and percussion mark frequencies at the FLK Zinj site: The carnivore-hominid-carnivore hypothesis falsified. *Journal of Human Evolution* 50(2):170-194.

289. Bunn HT (1981) Archaeological Evidence for Meat-Eating by Plio-Pleistocene Hominids from Koobi Fora and Olduvai Gorge. *Nature* 291(5816):574-577.

290. Aiello LC & Key C (2002) Energetic Consequences of Being a Homo erectus Female. *American Journal of Human Biology* 14:551-565.

291. Pickering TR & Bunn HT (2007) The endurance running hypothesis and hunting and scavenging in savanna-woodlands. *J Hum Evol*.

292. Attenborough D (2002) Food for thought. in *The Life of Mammals*, ed Attenborough D (BBC).

293. Farbman N (1947) Bushman throwing his spear at a winded gemsbok. in *Life Magazine* (Life digital archive (images.google.com/hosted/life), New York).

294. Churchill S (1993) Weapon technology, Prey Size Selection, and Hunting Methods in Modern Hunter Gatherers: Implications for hunting in the Palaeolithic and Mesolithic. *Hunting and Animal Exploitation in the Later Palaeolithic and Mesolithic of Eurasia*, eds Peterkin GL, Bricker HM, & Mellars P (Archaeological Papers of the American Anthropological Association Washington, DC), Vol 4.

295. Ferring R, *et al.* (2011) Earliest human occupations at Dmanisi (Georgian Caucasus) dated to 1.85-1.78 Ma. *Proceedings of the National Academy of Sciences of the United States of America* 108(26):10432-10436.

296. Laden G & Wrangham R (2005) The Rise of the Hominids as an Adaptive Shift in Fallback Foods: Plant Underground Storgae Organs (USOs) and Australopith Origins. *Journal of Human Evolution* 49:482-498.

297. Marlowe FW (2010) *The Hadza: Hunter-Gatherers of Tanzania* (University of California Press, Berkeley, CA).

Appendix 1 – Supplemental data for Chapter 2

Supplemental table 2.1. Measurement reliability using Intra-class correlation coefficients (ICC)

	Average Measures ICC	*Single Measures ICC*	*Significance*
Goniometric ROM			
External ROM maxima	0.918	0.848	0.000
Internal ROM maxima	0.947	0.899	0.000
Kinematic ROM			
External ROM maxima	0.932	0.872	0.000
Internal ROM maxima	0.965	0.933	0.000
CT scan measures			
Superior scans	0.973	0.922	0.000
Inferior scans	0.999	0.996	0.000

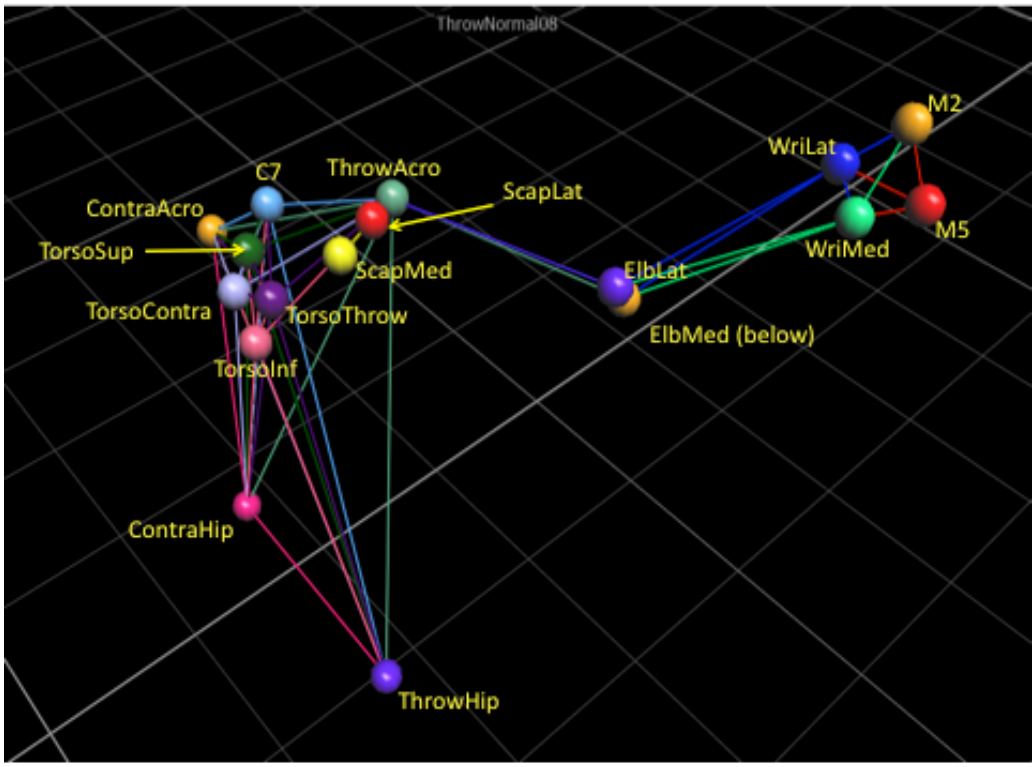
All intra-class correlations were calculated using a two-way random model for absolute agreement

Supplemental Table 2.1. Measurement reliability data for humeral torsion and range of motion data.

Appendix 2 – Supplemental Material for Chapter 3

Pre-enrollment performance task & data exclusion criteria – All subjects were required to pass an initial performance task prior to enrollment in the study. Each potential subject was given 5 tries to hit a 1m x 1m target with a baseball from 10 meters away at a minimum speed of 22.35 m/sec (50 mph). Twenty-five subjects successfully completed the task and were enrolled in the study (one subject subsequently removed himself prior to data collection). Of the 24 total subjects, 3 failed to achieve any throw of at least 22.35 m/sec during the full data collection and were excluded from the study. One further subject was removed from normal vs. restricted analysis due to an abnormal response to the shoulder restricted condition, rendering him an outlier in all analyzed data. The final sample size for all conditions is 20 subjects.

Kinematics – Twenty-one 25mm passive reflective markers were used to define the torso, arm, forearm and hand (Sup. Figure 3.1). The markers were placed on bony landmarks using both double-sided toupee tape and cloth medical tape. The torso was defined with 5 markers (C7, C7 prominens; ThrowAcro, throwing side acromion; ContraAcro, contralateral side acromion; ThrowHip, throwing side greater trochanter of the femur; and ContraHip, contralateral side greater trochanter of the femur). A rigid cluster containing 4 markers was also placed on the back between the scapula on trials were no brace restricted its application (TorsoSup, superior; TorsoInf, inferior; TorsoThrow, throwing side; and TorsoContra, contralateral side). Two markers were placed on the scapular spine



Supplemental Figure 3.1. Reflective markers on a subject at ball release. Note: there is no arm cluster in this trial.

(ScapLat, lateral; and ScapMed, medial). The arm was defined using a functionally defined shoulder joint (see Supplemental text below) and two distal markers (ElbLat, lateral humeral epicondyle; and ElbMed, medial humeral epicondyle). On some trials a second rigid cluster was applied to the dorsal side of the arm (ArmProx, proximal; ArmDist, distal; ArmMed, medial; and ArmLat, lateral). The forearm was defined using the calculated midpoint between ElbLat and ElbMed proximally and two markers distally (WriLat, radial styloid; and WriMed, ulnar styloid). The hand was defined again using the calculated midpoint of the wrist markers as well as two distal markers (MC2, distal end of the 2nd metacarpal; and

MC5, distal end of the 5th metacarpal). All markers were identified using Vicon Nexus v. 1.7.1 software.

Experimental conditions – All subjects performed both "slow" and "fast" throws in each of 5 conditions. During slow throws the subject was instructed to make a comfortable throw with no consideration of speed. During fast throws the subject was tasked to throw as fast as he felt comfortable throwing. The conditions were normal unrestricted kinematics and four brace restricted conditions (clavicular elevation, torso immobilization, shoulder rotation, and wrist extension). Condition order was randomized across subjects. The brace restrictions used commercially available therapeutic braces to limit range of motion at a specific joint. All brace conditions (except for torso immobilization) also included an intermediate sub-condition in which the brace was worn but no restriction was applied. During loaded brace conditions, subjects were instructed to attempt their normal throwing motion. In this paper, only data from the normal unrestricted and shoulder rotation restricts are used.

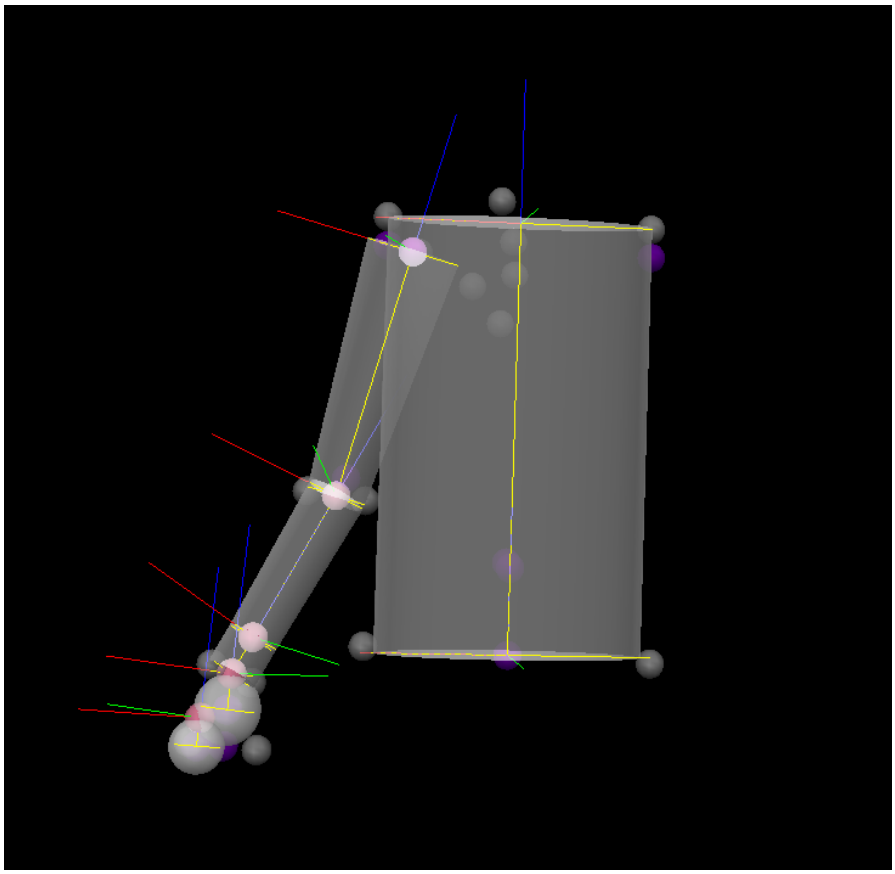
Kinetics – The kinetic model was created using C-Motion Visual3D software. Segment definitions and rotational axes are described in Sup. Table 3.1. All segment masses, centers of mass, and radii of gyration are taken directly from Dempster (1). A number of the markers used to define and track segments are virtual calculated markers. The markers midHip and midWrist represent the calculated midpoint between the hip and wrist markers respectively. The FuncSho marker is calculated as a functional joint from a movement trial. In this movement trial, the subject keeps

Supplemental Table 3.1 - Segment Definitions				
Segment	**Geometry**	**Defining Markers**	**Tracking Markers**	**Axes**
Thorax/Pelvis	Cylinder	Proximal: ThrowHip, ContraHip Distal: ThrowAcro, ContraAcro	midHip (calc) ThrowAcro ContraAcro	X: axial flex/extension Y: lateral flex/extension Z: axial rotation
Arm	Cone	Proximal: FuncSho (calc), ThrowAcro Distal: ElbMed, ElbLat	FuncSho (calc) ElbMed EldLat	X: flex/extension Y: ab/adduction Z: int/external rotation
ForearmUpper	Cone	Proximal: ElbMed, ElbLat Distal: RFA80 (calc)	ElbMed ElbLat RFA80 (calc)	X: flex/extension
ForearmLower	Cone	Proximal: RFA80 (calc) Distal: WriMed, WriLat	RFA80 (calc) WriMed WriLat	Z: pro/supination
Hand	Sphere	Proximal: WriMed, WriLat Distal: MC5, MC2	midWrist (calc) MC5 MC2	X: flex/extension Y: ulnar/radial deviation
Ball	Sphere	Single marker: Ball Prox (calc)	midWrist (calc) MC5 MC2	No independent motion

Supplemental Table 3.1. Segment parameters using in the kinetic model. Segment length and diameter is obtained using the defining markers sets. Segmental movements are recorded using the tracking markers around the defined axes.

his torso still, the arm is abducted 90 degrees and the elbow is fully extended. The subject then proceeds to slowly circumduct the arm keeping the elbow straight. The motion is tracked as two temporary segments (torso – ThrowAcro, ContraAcro, C7; arm – ThrowAcro, ElbMed, ElbLat). An optimization is performed to find the functional joint center between the two segments with the lowest residual.

The final calculated marker (RFA80) bears further explanation. RFA80 is both a marker and a joint (Sup. Figure 3.2). This marker is calculated as lying 80% of the distance towards the wrist along the chord from the calculated midElbow and midWrist markers. The marker was created to establish a virtual, independent segment in the forearm that allows for accurate measures of pro/supination and solves a tracking problem in the elbow. Because the humeroulnar and humeroradial joints have different joint centers, defining a single forearm segment requires choosing a joint center that accurately represents one forearm motion but the other poorly or represents both poorly. This is evident when a single forearm segment model is loaded into the data as the forearm tracks very poorly at the elbow. To solve this problem, we have created a two-segment forearm using the RFA80 marker. The proximal segment, ForearmUpper, contains 80% of the mass and length of the forearm, while the distal segment, ForearmLower, contains 20% of the mass and length. Due to the way both segments are defined, the motion at the joint between these two segments should be confined to movement around the Z axis.



Supplemental Figure 3.2. Visual3D kinetic model showing the segments used in the inverse dynamics analysis. Note the distal ball segment as well as the location of the RFA80 and functional shoulder joints.

Joint angle data from ForearmLower shows that this is largely the case, although there are minor angular changes around the X and Y axes (<6 degrees, approximately 4% of total angular motion at the joint). These minor movements likely represent slight deviations in the axis of pro/supination away from our estimated axis. The definition of these segments also prevents any problems with calculated moments as the lack of flex/extension motion at the ForearmPS joint (Sup. Table 3.2) and pro/supination motion at the elbow joint create non-

Supplemental Table 3.2 - Joint Definitions				
Joint	**Segment**	**Reference Segment**	**Resolution Coordinate System**	**Cardan Sequence for Joint Angles**
Torso	Thorax/Pelvis	Lab	Lab	X,Y,Z
Shoulder	Arm	Thorax/Pelvis	Arm	X,Y,Z
Elbow	ForearmUpper	Arm	Arm	X,Y,Z
ForearmPS	ForearmLower	ForearmUpper	ForearmUpper	X,Y,Z
Wrist	Hand	ForearmLower	ForearmLower	X,Y,Z

Supplemental Table 3.2. Joint parameters used in the kinetic model. The cardan sequence is the series of rotations used to define both the joint Euler angles and the joint velocity, which is calculated using the instantaneous axis of rotation and not the first derivative of the Euler angles.

independent masses for the entire forearm. The use of a two-segment forearm also resolves the model-tracking problem in the elbow.

The most distal segment in our kinetic model is the ball. The ball segment is defined as a calculated marker, Ball, which is placed 130% of the distance along the chord from the WriLat to MC2 marker and 20% of the distance along the chord between the MC2 and MC5 markers. This places the ball between and slightly distal to the 2nd and 3rd metacarpal heads (a common placement for a standard split finger

throw). The ball was given the appropriate mass (144g) and radius (3.68cm) of a standard baseball. The ball segment was tracked using the same markers as the hand segment and therefore is non-independent. In all kinetic data from after the moment of release, the mass of the Ball segment is dropped to zero.

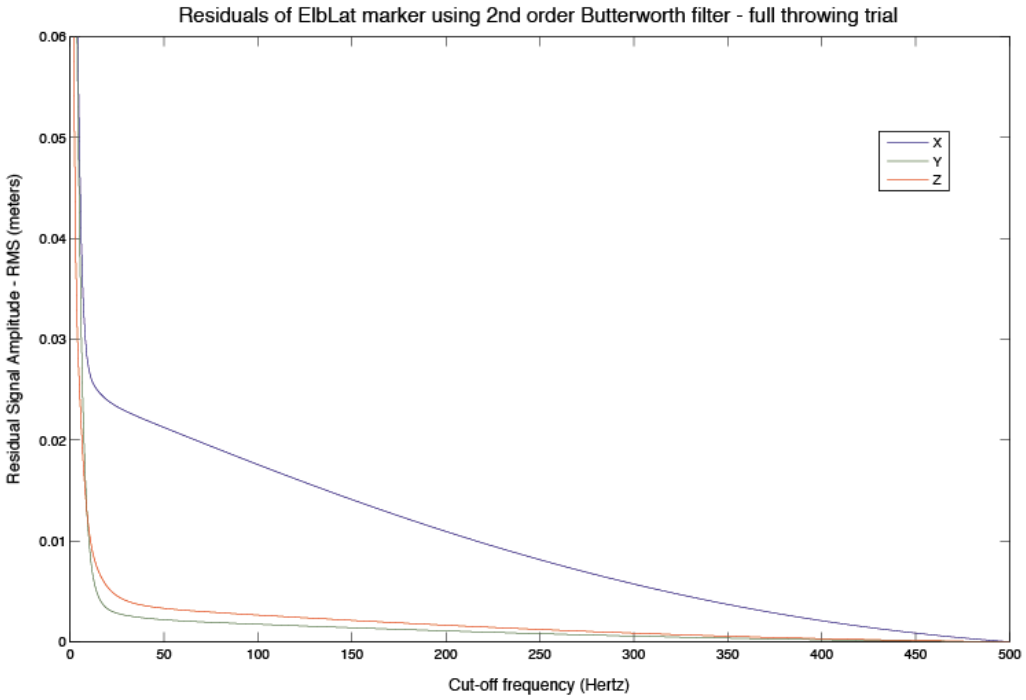
All defined joints in the kinetic model are described in Sup. Table 3.2. It should be noted that all joint angles and velocities are defined using a X,Y,Z Cardan sequence of rotations and all joint measures are resolved relative to the proximal segment with the exception of the torso/pelvis, which is necessarily resolved relative to the lab global coordinate system, and the shoulder, which is resolved relative to its own axis to bring angular velocities and related measures in line with previously published data (2, 3).

Filtering – Residual analysis, as described in Winter (4), was conducted on throwing trials from 5 randomly chosen subjects using a custom MATLAB script. The residual was calculated for 2nd, 4th and 6th order Butterworth lowpass filters with the cutoff frequency iterated between 1Hz and the Nyquist frequency of the data (500Hz). The residual was calculated for the ThrowHip, ThrowAcro, ElbLat, WristLat and MC2 markers using the formula;

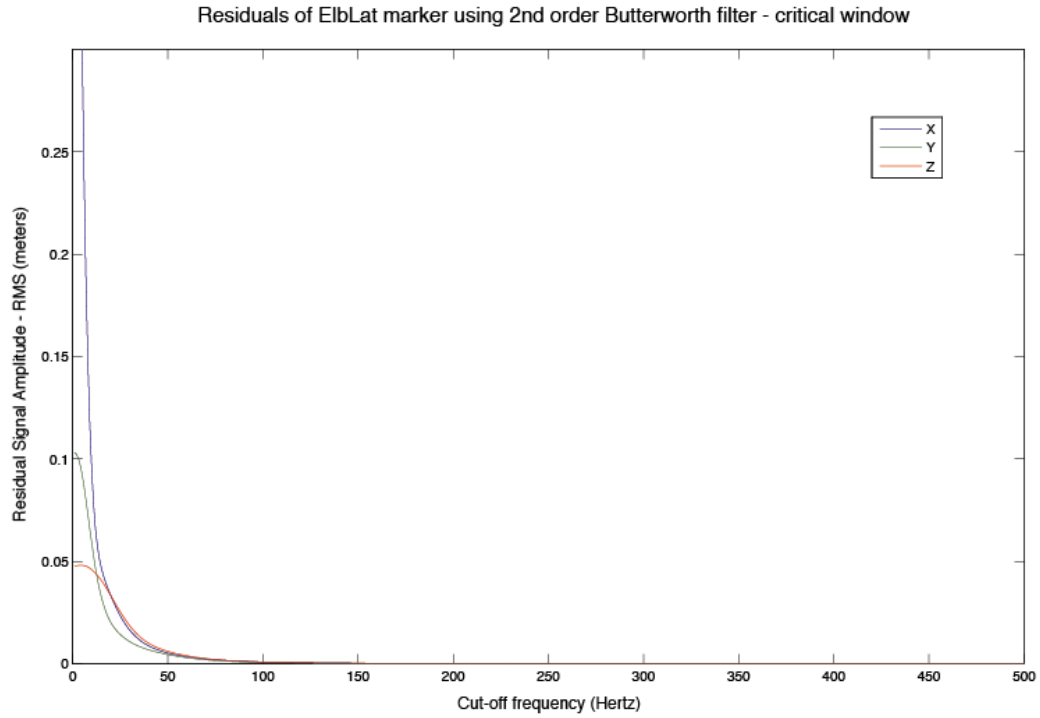
Equation S1:

$$R(f_c) = \sqrt{\frac{1}{N}\sum_{i=1}^{N}(X_i - \hat{X}_i)^2} \qquad \text{(Eq. S1)}$$

where *R* is the residual in meters, f_c is the cutoff frequency, X_i is the raw data of the *i*th sample, and $\hat{X}_i$ is the filtered data of the *i*th sample. The full residual analysis was



Supplemental Figure 3.3. Sample residual analysis data from the full trial ElbLat marker data using a 2nd order Butterworth filter (Subject 006, trial 8).



Supplemental Figure 3.4. Sample residual analysis data from the critical period ElbLat marker data using a 2nd order Butterworth filter (Subject 006, trial 8).

conducted twice; once with the full throwing trial (Sup. Figure 3.3) and once using only the critical period from the initiation of internal rotation of the humerus to ball release (Sup. Figure 3.4). Cutoff frequencies were manually chosen following Winter (4).

A 2nd order filter was chosen as the best fit for the data as it consistently returned the lowest actual residuals across all markers. Full trial and critical period cutoff frequency means were statistically different ($p < 0.05$) using a matched pairs t-test (Sup. Table 3.3). The mean was calculated from the X, Y, and Z residuals from each marker and then again from all markers (all marker XYZ mean: 17.3 Hz – full data set; 36.7 Hz – critical period). For data processing, we split the difference between the full data period and the critical period frequencies by using a 25 Hz cutoff frequency. As a final check on the sensitivity of our analyses, we added random noise (2mm width, zero mean) to all markers from a single subject's raw, unfiltered data. After filtering, no significant differences were detected in any kinetic measures.

Throwing phase standardization – Differences in timing between throws are controlled for in the kinematic and kinetic data by assigning portions of the motion to 5 standardized phases (5). The windup and stride phases are collapsed into a single phase as we are unable to differentiate these two phases with our marker setup. The two phases reported here are defined as: Arm Cocking – from the moment of leading foot contact with the ground at the end of stride (STR) to the maximum external rotation (MER) of the shoulder, & Acceleration – from MER to

Supplemental Table 3.3 - Cutoff frequency data (Hz) - 2nd order Butterworth filter					
Marker	***Data set***	***X***	***Y***	***Z***	***Mean XYZ***
ThrowHip	*full*	14.8(4.8)	12.2(3)	10.2(3.2)	12.4(3.7)
	critical	41(11.5)	35(7.8)	37.4(6.8)	37.8(8.7)
ThrowAcro	*full*	21(12.9)	12.8(4.4)	18(11.3)	17.3(9.5)
	critical	67.8(46.5)	58.4(45.7)	26.6(9.7)	50.4(34)
ElbLat	*full*	18.8(8.9)	15.2(3)	14.8(4.8)	16.3(5.6)
	critical	35.6(8.4)	34.2(8.5)	36.8(7.3)	35.5(8.1)
WristLat	*full*	30.2(15.7)	15.8(5)	13.2(1.6)	19.7(7.4)
	critical	41.8(11.9)	25(4.7)	25.2(4.3)	30.7(7)
MC2	*full*	34.4(10.9)	16(4.4)	12.4(1.8)	17.1(5.7)
	critical	25.2(9.4)	24.8(8.4)	24.2(7.5)	25.3(8.4)

Supplemental Table 3.3. Mean cutoff frequencies (and standard deviations) from 5 subjects using a 2nd order Butterworth filter.

the moment of release (REL). STR was defined using the minimum point of mid-pelvis linear velocity. MER was defined as the shoulder rotation angular velocity zero point following STR. Data from the entire internal rotation motion (including

the full acceleration and deceleration phases) were further calculated from MER to DECEL, defined as the shoulder rotation angular velocity zero point following REL.

Given that these phases often differ in duration between throws, further standardization is required in order to calculate mean values and variances for all parameters. Accordingly, all joint angles, angular velocities, torques and power values were processed in MATLAB by interpolating each phase 1000 fold and subsequently down sampling each throw to a set length. The acceleration phase was down sampled to 100 data points and the arm-cocking phase to 894 points (in keeping with the mean arm cocking/acceleration duration ratio). It should be noted that the different throwing conditions did vary in this ratio (see Supplemental Data below), but that in order to achieve comparable data between conditions the mean 8.94:1 ratio was used for all conditions.

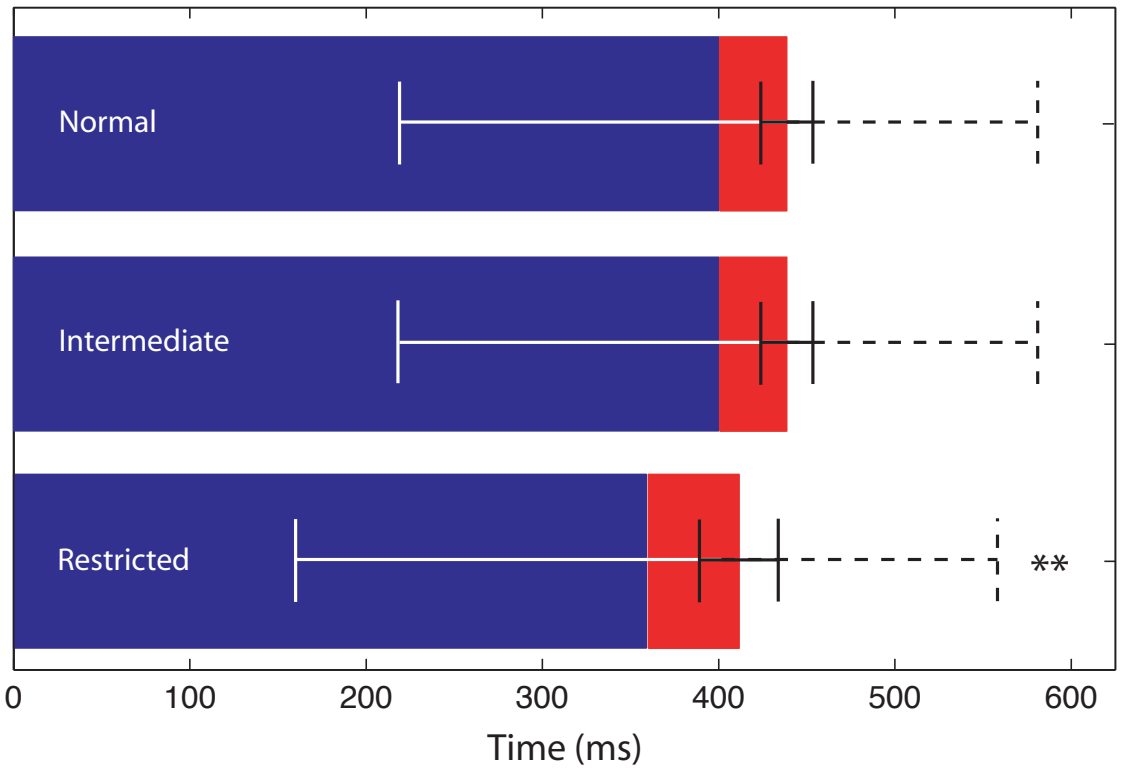
Effects of projectile type – For practical reasons, we chose to collect data on individuals throwing standard baseballs. However, given that hominin throwers were likely throwing objects such as rocks and untipped spears, it is worth noting how throwing kinematics differ between projectile types. While the throwing literature largely focuses on baseball throwing, there are a number of studies addressing the throwing kinematics of footballs (6-9), handballs (10-12), and javelins (13-15). These projectiles differ from baseballs in both mass and shape. Results from these studies show that a standard sequence and timing of motions is conserved across all throw types (6, 16). Importantly, these standard kinematic patterns include consistent external rotation of the arm into the passive ROM during

the arm-cocking phase, when we propose that elastic energy is stored (6, 17, 18). Modeling research by Alexander (19) suggests that projectile mass may be important in dictating arm position differences during the arm-cocking phase. These positioning differences, where heavier projectiles are positioned closer to the shoulder joint by reducing arm abduction angle and increasing elbow flexion, may help to reduce the arm's moment of inertia during cocking to prevent damage to the ligaments and tendons crossing the shoulder. Data on arm positioning during the cocking phase suggest that this may be the case for a number of heavier projectiles (handball ~ 450g; shot put - 7260g) (18, 20). Such a constraint may have compromised hominin throwing performance when throwing heavy projectiles or affected the choice of how heavy a projectile was thrown. Scarce ethnographic data on hand-thrown spears suggests that human hunter-gatherers choose lighter spears (averaging 184g), potentially to avoid injury or compromised throwing mechanics (21). Projectile shape likely also has effects on throwing kinematics, especially in the positioning of the hand.

Elongated projectiles (such as footballs, javelins, or spears) require that the palm of the hand is positioned alongside the elongated axis the projectile, as opposed to spherical projectiles (such as baseballs, handballs, etc…) where the palm is typically positioned behind the projectile (22, 23). When throwing elongated projectiles, this is accomplished through a more supinated position of the forearm. While this more supinated forearm position is required of both football quarterbacks and javelin throwers, the kinematics of hominin spear throwing were likely more similar to those of football passing than javelin throwing. This is because

spear throwing for hunting as well as football passing require both power and accuracy in order to be effective, while javelin throwing requires only power, as the marker of performance is simply the distance the javelin has travelled from the thrower. For this reason, the differences between baseball pitching and javelin throwing (including the run up and unstable release) will not be discussed here. Detailed comparisons of the football passing and baseball throwing motions show that while these motions are largely similar, football quarterbacks tend to achieve slower torso rotational velocities and faster shoulder flexion velocities (6). Quarterbacks also externally rotate their arm ~9° less than baseball pitchers during the cocking phase (6). It has been suggested that these differences in football passing kinematics may be accommodations to the increased mass of the football (~ 415g), in order to reduce the risk of injury to the shoulder and elbow (6). Similar kinematic accommodations may have been employed by spear throwing hominins for the same purpose. Finally, it is worth noting that throwing athletes from all sports show reduced humeral torsion in their dominant arm versus non-dominant arm (24-28).

Timing differences between experimental conditions – Experimental conditions involving the brace showed significantly different timing in both the duration and relative duration of the arm-cocking (repeated measures ANOVA, $p = 0.0255$, Mauchly's sphericity = 0.2404) and acceleration phases (MANOVA, $p = 0.0024$, Mauchly's sphericity < 0.0001) (Sup. Figure 3.5). Post-hoc pairwise testing shows these differences are due to reduction of the arm-cocking phase and elongation of the acceleration phase in the restricted condition. The reason for the



Supplemental Figure 3.5. Duration of the arm cocking phase (blue) and acceleration phase (red) for the normal and shoulder brace conditions. Restricted throw timing differed significantly from both normal and intermediate throws.

change in cocking duration is not clear, but the elongated acceleration seems to represent a slowdown associated with reduced acceleration of the arm due to the lack of elastic energy storage in this condition. Such reduced acceleration could delay the moment of release and elongate the acceleration phase.

Muscle data – Muscle volumes used for muscle modeling are taken from the Visible Human Project data set (29). These volumes are calculated from a single male subject and are the largest available in the literature (which contains other males in the 95th percentile in height and the 90th percentile in weight) (30). Muscle volumes for forelimb muscle (Sup. Table 3.4) were calculated from MR images by

Garner and Pandy (31). The values used for the anterior deltoid were calculated by dividing the entire deltoid volume by three. These volumes were then converted to masses by multiplying by an empirically derived measure of mammalian muscle density from the literature (32). The summed muscle mass of all internal rotators of the humerus was then used to normalize our power data by potentially contributing muscle mass. Our use of these very large muscle volumes in our analysis, as well as the assumption that all fibers are contributing at 100% of their capacity and solely to humeral internal rotation, intentionally overestimate the potential muscular contribution to joint power at the shoulder. This significant overestimation is designed to reduce the effects of error within the inverse dynamics torque estimates.

Modeled vs. actual power output - One way to test the hypothesis that elastic energy provides most of the rotational power for throwing is to compare estimates of the maximum power production capacity of all the muscles potentially responsible for internally rotating the humerus with the actual calculated power. The maximum power production of all internal rotators of the humerus is calculated using the average actual power during the acceleration phase, thus minimizing the effects of instantaneous changes in angular acceleration. This average actual power value is then adjusted by a mass estimate for all potentially contributing muscles (see Supplemental Methods above). This mass specific power estimate (in W/kg^{-1}) is then compared to published maximum mass specific power values from the literature, which range from ~250-500 W/kg^{-1} (33-35). This conservative model

Supplemental Table 3.4 – Shoulder Internal Rotator Muscle Volumes (cm^3)	
Muscle (Garner & Pandy 2003)	
Pectoralis major	676.40
Latissimus dorsi	549.69
Anterior deltoid	792.87/3 = (264.29)
Teres major	231.40
Subscapularis	318.52
Total internal rotator volume (cm^3)	***2040.30***
Muscle Density (Mendez & Keys, 1960)	*1.06 g/cm^3*
Total internal rotator muscle mass (kg)	***2.16***

Supplemental Table 3.4. Calculated total muscle volume and mass for internal rotators of the shoulder. The largest volumes for each are taken from the literature.

shows that the average actual power at the shoulder exceeds the maximum isotonic power production capacity for muscle by at least 3-7 fold (Sup. Table 3.5). However, it is well known that when muscle is actively stretched during or just prior to concentric contraction there is a notable increase in force production (36-39). Plyometric models propose that the pre-stretching of the shoulder internal rotator muscles during arm-cocking augment force enhancement during the subsequent acceleration phase of the throw (40). Accordingly, we also compared our average actual power values to force enhancement adjusted (1.75x - (38)) values of

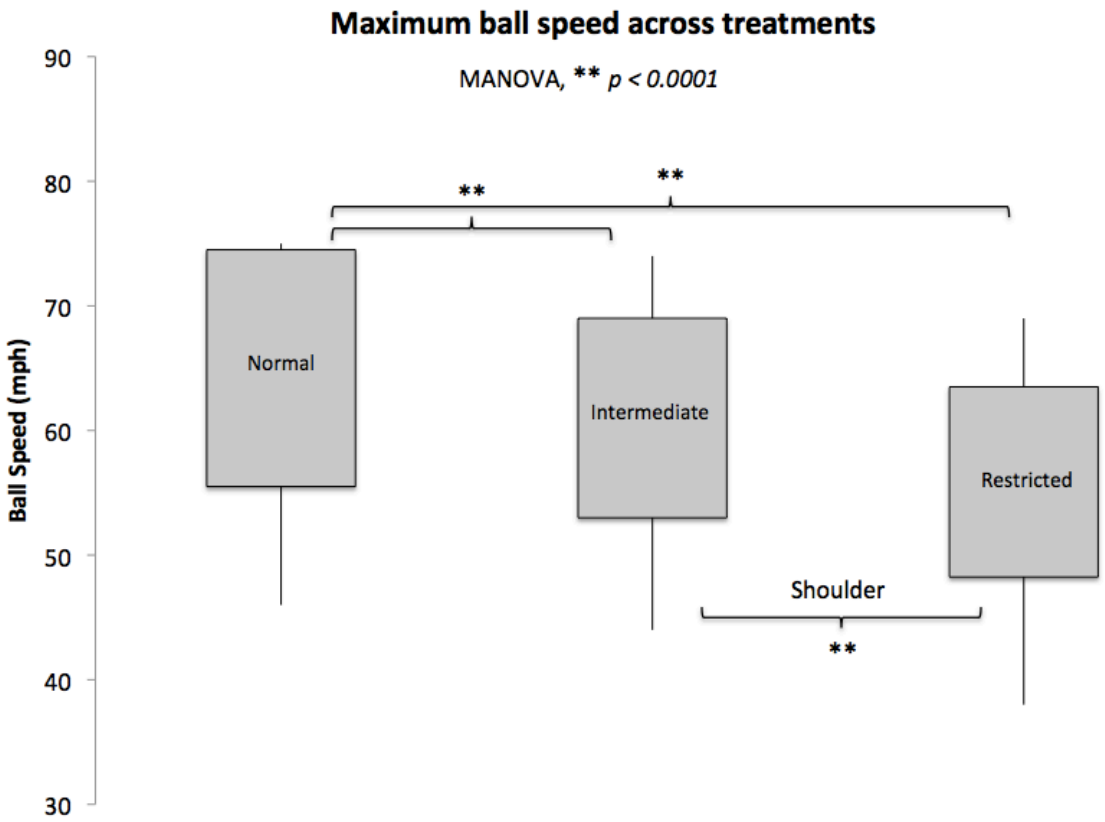
Supplemental Table 3.5 – Modeled Power Comparison	
Maximum isotonic power - skeletal muscle (*W kg $^{-1}$*)	**250-500**
Adjustment for force enhancement due to stretching	1.75x
Maximum modeled muscle power - skeletal muscle (*W kg $^{-1}$*)	**438-800**
_____	
Predicted values	
Shoulder rotation work during acceleration (*J*)	132 ± 52
Time of acceleration (sec)	0.034 ± 0.013
Average joint power (*W*)	3,847 ± 1967
Estimated total muscle mass (*kg*)	2.16
Adjusted average kinetic power - acceleration (*W kg $^{-1}$*)	**1,781 ± 911**
Average kinetic power > Maximum muscle power	

Supplemental Table 3.5. Average kinetic power (shoulder rotation) adjusted by modeled total internal rotator muscle mass compared to known maximum power values for skeletal muscle.

maximum muscle force, ranging from ~438-875 W/kg^{-1}. Even with this significant force enhancement, our measured average rotational power in the shoulder exceeds the maximum muscle values by 2-4 times. Thus, in order to achieve this joint power using muscular power alone, the individuals in this analysis would require internal rotator muscles at least 2-4 times larger than those used here. Given that the muscle masses used are the largest published (31), this is highly unlikely and suggests that

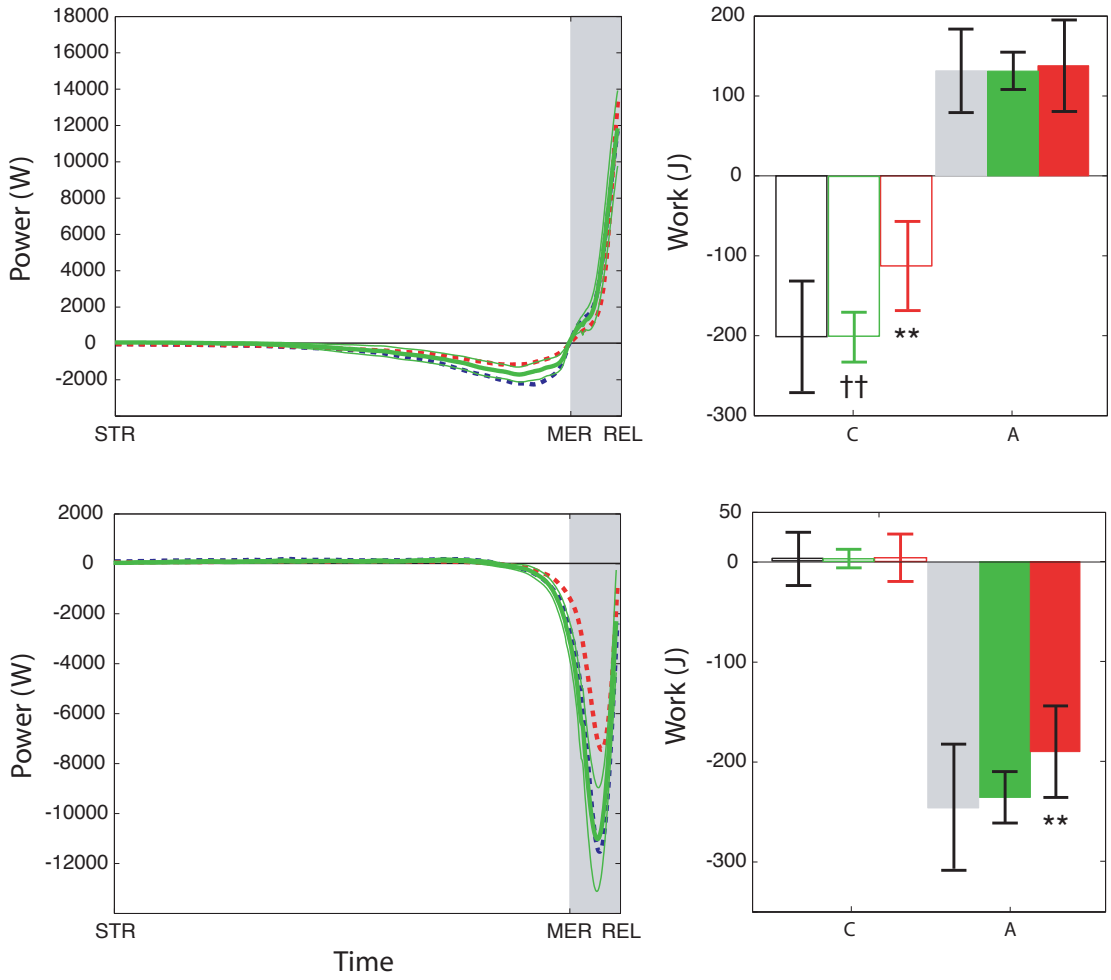
elastic energy stored in the shoulder is used to enhance the internal rotation power output.

Location of elastic energy storage – Exactly where elastic energy is being stored at the shoulder is currently unknown. While further *in vivo* soft tissue imaging of the ligaments, tendons, and muscles crossing this joint are needed to resolve this question, clinical data on repetitive injuries in the shoulder do provide some insight. Throwing athletes show an increased prevalence of shoulder instability and stretching related tears and laxity in the glenohumeral ligaments and at the origin of the biceps tendon on the superior glenoid labrum (41-43). Over-stretching injuries to these elastic structures suggest they may be involved in storing elastic energy. For example, by actively positioning the arm during the early cocking phase a number of shoulder ligaments are pulled taut (anterior band of the inferior glenohumeral ligament, the middle glenohumeral ligament, and the coracohumeral ligament) (44). It is quite likely that during following late cocking phase, when the humerus is further passively rotated, these already taut ligaments would stretch considerably. Furthermore, microscopic analyses of the glenohumeral ligaments in those suffering from shoulder instability show higher amounts of elastin present in these ligaments and an increase in the number of large diameter collagen fibrils (45), effectively making these ligaments more tendon-like. Although these elastic structures are not typical of those used by many animals to store elastic energy to increase locomotor efficiency (46, 47), their short length and large aggregate cross sectional area make the shoulder ligaments and muscle tendons ideal for returning elastic energy very rapidly.



Supplemental Figure 3.6. Maximum ball speed across treatment conditions showed significant differences between all conditions as expected.

Ball speed & accuracy – Mean maximum ball speed was compared across experimental conditions (Sup. Figure 3.6). Significant differences were found between condition means (MANOVA – $p < 0.0001$), but not between condition variances (Levene's - $p = 0.94$). Post-hoc pairwise comparisons showed significant differences between all three conditions. As expected, the intermediate condition in which the brace was worn but not tightened showed an intermediate reduction in ball speed, while the full restricted showed a greater reduction. Mean accuracy was also compared across conditions. No significant differences were found between conditions for mean accuracy (repeated measures ANOVA - $p = 0.1485$) or variance



Supplemental Figure 3.7. Mean joint power (green dashed) and work (green) for the sham condition. The mean values for the normal condition (blue dashed, grey) and restricted condition (red dashed, red) are shown for comparison. A 95% confidence interval (± 2 st. error) bounds the mean sham values in the power curve and all work values. Significant reductions ($p < 0.05$) from both the normal and intermediate conditions are indicated by **, while the †† indicates significant differences from both the normal and restricted conditions.

(Levene's – $p = 0.4574$). Within all conditions, no condition order effects were found in either speed or accuracy.

Intermediate/sham condition – Data were collected for an intermediate condition in which the shoulder brace was applied, but the restriction mechanism

was not loaded. This intermediate condition allows for the analysis of the effect of the brace itself somewhat independently of the restriction. In this condition, the shoulder brace acted like a tight-fitting jacket and reduced external rotational range of motion at the shoulder approximately -11° (compared to the restricted condition which limited external rotational ROM -28.3°). This intermediate level of restriction resulted in a small but significant reduction in maximum projectile velocity from the normal trials. However, the intermediate condition showed significantly higher projectile velocity than the restricted condition. Kinetic data show this intermediate condition is largely indistinguishable from the normal condition (Sup. Figure 3.7), with the exception of the shoulder rotation work done during the arm cocking phase which drops -9±13% ($p < 0.05$) from the normal condition.

Chimpanzee throwing performance – Although data exist on the frequency of chimpanzee throwing behavior (48-51), all published descriptions of throwing performance have been qualitative. We collected preliminary throwing velocity data (Table S6) from 3 chimpanzees with previous overhand throwing training at a sanctuary in Auburn, CA. While not directly comparable to human throwing data due to limited practice and training, these data further illustrate the lack of projectile velocity, corroborating previous published accounts.

Although chimpanzees are facultative rather than skilled throwers, chimpanzee throwing behavior and anatomy can provide insight into the

Supplemental Table 3.6 – Chimpanzee throwing velocity (mph)			
	Juvenile Male (3 years)	***Juvenile Male (9 years)***	***Adult female (~30 years)***
Mean velocity	12.4	12.5	19*
N	17	18	12*
Maximum velocity	14.3	15.5	22.4*
Standard Deviation	1.4	1.7	2.4*

Supplemental Table 3.6. Throwing velocity data from 3 chimpanzees. Note: while the adult female had previously been trained to throw overhand, during data collection she chose to throw underhand (while standing bipedally). Her data has been asterisked accordingly.

performance effects of morphological differences between these two species. I use a model that compares human and chimpanzee throwing performance because I am interested in assessing how differences in skeletal morphology affect throwing ability. Furthermore, because many aspects of early hominin upper body anatomy more closely resembles that of chimpanzees (52-54), they are a useful comparator for humans and are helpful in assessing throwing performance in the fossil record. Regardless of whether the human-chimpanzee last common ancestor was behaviorally chimpanzee-like (53-55) or not (56, 57), comparisons of human throwing mechanics and performance to that of chimpanzees can provide valuable

insights for interpreting how throwing performance and skeletal anatomy are related.

Clavicle length in Homo erectus - Previous research reconstructing the hominin shoulder has suggested that early *H. erectus* fossils have relatively short clavicles when standardized by humeral length (58). Given that the clavicle is the only bony attachment of the shoulder girdle to the torso, clavicle length is inferred to affect scapular positioning and thus range of motion at the shoulder (58). Using the claviculohumeral ratio (clavicle length/humeral length) from the KNM WT 15000 and LB1 fossils, Larson (58) reconstructs early *H. erectus* as having novel, intermediate shoulder morphology with low, very anteriorly positioned scapula and suggests that as a result early *H. erectus* may have had compromising throwing ability.

However, while the KNM WT 15000 claviculohumeral ratio (40.9) is low for modern humans, it does fall within the measured range of normal variation seen in East African populations today (58), in whom no deficit in throwing performance has been reported. Additionally, reconstructed fossil clavicles from the early *H. erectus* site of Dmanisi show claviculohumeral ratios squarely within the modern human range (Adult male – 46.5L, 46R; juvenile – 43.7) (59). Given that both the Dmanisi and Nariokotome clavicle fossils are incomplete, assessing the accuracy of the length reconstruction methods used is important to resolve this discrepancy. However, these methods are not reported in the Dmanisi analysis. Further research is required to address this interesting discrepancy.

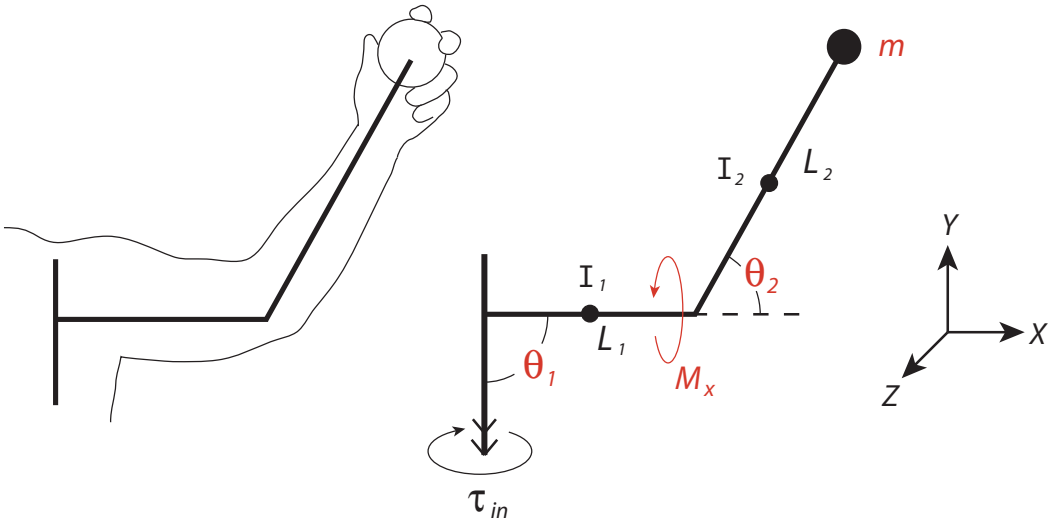
Finally, while standardizing clavicle length using the humerus has been shown to be a reasonable proxy for body mass interspecifically (58, 60), the high variability in this relationship intraspecifically suggests that this standardization method may not be very useful within a species. Furthermore, the claviculohumeral ratio may not be very useful for reconstructing shoulder position. To illustrate the problem with this metric, we look to chimpanzees, who have low claviculohumeral ratios and yet have *dorsally* positioned, cranially oriented scapula. This dorsal shoulder position is driven not by the length of the clavicle relative to body mass, but by the length of the clavicle relative to the breadth of the superior portion of the ribcage, which is evolving independently of body mass (61). Recent work investigating clavicular length in apes suggests that when chimpanzee clavicles are normalized to thorax width they fall closer to the rest of the apes in having a relatively elongated clavicle relative to monkeys (62). Such a thorax width standardization better accounts for the shoulder positioning seen in chimpanzees and humans. In sum, better data is needed to determine how clavicle length and shape, as well as thorax width and shape, relate to shoulder positioning in hominins. However, at the moment equivocal data about *H. erectus* clavicle length do not preclude high-speed throwing.

Glenoid orientation as a throwing adaptation – The "relaxation" or caudal rotation of the scapula in *H. erectus* likely had significant effects on many behaviors. We have proposed that this modification to shoulder position may be an adaptation for throwing. The logic behind this hypothesis is simply that shifts in shoulder position would result in large increases in throwing performance, while having

relatively minor or even negative effects on the performance of other important behaviors. For instance, laterally oriented shoulders likely positioned the glenohumeral joint further inferiorly on the thorax, resulting in a wider shoulder breadth that would reduce the mechanical advantage of the shoulder muscles during climbing. In addition, a more relaxed shoulder would result in a lateral reorientation of the *P. major* muscle, removing any useful flexion contribution of this muscle during stick digging. The effects that shoulder position had on knapping are more difficult to address. Given that power requirements of stone tool manufacture are probably much lower than during high-speed throwing and that the muscle most significantly affected by a change in shoulder positioning, *P. major*, is likely minimally active during knapping, little direct effect of this shoulder position shift is expected. However, Larson (58) notes that a laterally oriented glenoid in combination with very low torsion in *H. erectus* (below most modern human values, including most throwing athletes) could result in reduced range of motion for manipulative tasks such as knapping or tool use. This problem, in combination with potentially short clavicles relative to humerus length, have led Larson to propose that the shoulder in *H. erectus* was more anteriorly positioned. Given that any deficit in manipulative range of motion could be overcome by movements at the highly mobile shoulder (shoulder flexion, scapular protraction), we expect the negative effects of shoulder positioning on stone tool knapping and use were minimal. The only other context in which a low laterally oriented shoulder has been suggested to improve performance is during running (61). Bramble and Lieberman suggest that shifts in shoulder position represent a decoupling of the head and shoulders and

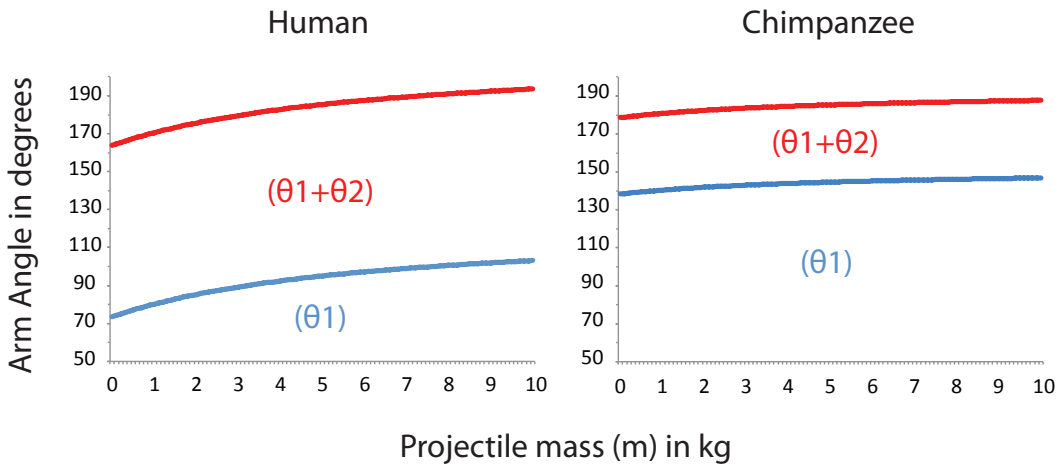
help to increase gaze stability during running. Although this decoupling would clearly insulate the head from jarring motions that would perturb the vestibule-ocular reflex, such impacts are partly damped elsewhere in the body (63, 64) reducing the performance effects of decoupled shoulders. In sum, much additional research is needed to further quantify the performance effects of a laterally oriented shoulder on many diverse activities, but there is reason to hypothesize that shifts in shoulder position have the important performance effects during throwing and may represent an adaptation for this behavior.

Static optimization of arm positioning – We have proposed that throwers store elastic energy at the shoulder by maximizing the arm's moment of inertia, causing the arm to lag behind the accelerating torso, stretching the shoulder ligaments and tendons. We have further proposed that the arm's moment of inertia is maximized by abducting the humerus in line with the torso rotation and *P. major* torques lines of action and by flexing the elbow. To test these assumptions, a static optimization of the shoulder abduction and elbow flexion angles, maximizing the arm's moment of inertia, was performed (Sup. Figure 3.8). This optimization was conducted using both chimpanzee and human morphologies (1, 65-68) and varied projectile mass. A cosine cost function was applied at the shoulder to penalize deviations in humeral abduction away from alignment with the two sources of torque, which the arm's inertial mass is proposed to resist. Results show that, as predicted, humans maximize the arm's moment of inertia by positioning the arm at a lower shoulder abduction angle and a higher elbow flexion angle than chimpanzees do (for low mass projectiles: human shoulder abduction ~80°, elbow



Supplemental Figure 3.8. Free body diagram of the parameters used in the static optimization of arm position. The optimization was tasked to maximize the arm's moment of inertia (M_x) by varying the shoulder abduction angle (θ_1) and the elbow flexion angle (θ_2). The effect of projectile mass (m) was also tested.

flexion ~90°; chimpanzee shoulder abduction ~140°, elbow flexion ~40°)(Sup. Figure 3.9). While this static optimization broadly approximates differences in human and chimpanzee throwing kinematics, it is worth noting that many human throwers abduct their humeri more than 80° during throwing (5, 69, 70). This difference may represent non-optimality in these throwers' motions or may simple result from the dynamic complexity of the throwing motion, which may be poorly captured by this simple static optimization.



Supplemental Figure 3.9. The results of a static optimization maximizing the arm's moment of inertia (M_x) by varying the shoulder abduction angle (θ_1) and the elbow flexion angle (θ_2). Results for low mass projectiles correspond to known differences in human and chimpanzee arm position during the arm-cocking phase, when elastic energy storage is proposed to occur.

1. Dempster WT (1955) *Space requirements for the seated operator* (Wright Air Development Center, Wright-Patterson Air Force Base, OH).

2. Hirashima M, Kudo K, Watarai K, & Ohtsuki T (2007) Control of 3D limb dynamics in unconstrained overarm throws of different speeds performed by skilled baseball players. *J Neurophysiol* 97(1):680-691.

3. Hong DA, Cheung TK, & Roberts EM (2001) A three-dimensional, six-segment chain analysis of forceful overarm throwing. *J Electromyogr Kinesiol* 11(2):95-112.

4. Winter DA (1990) *Biomechanics and motor control of human movement* (Wiley-Interscience, New York) 2nd Ed.

5. Dillman CJ, Fleisig GS, & Andrews JR (1993) Biomechanics of pitching with emphasis upon shoulder kinematics. *J Orthop Sports Phys Ther* 18(2):402-408.

6. Fleisig GS, *et al.* (1996) Kinematic and kinetic comparison between baseball pitching and football passing. *Journal of Applied Biomechanics* 12(2):207-224.

7. Escamilla RF & Andrews JR (2009) Shoulder muscle recruitment patterns and related biomechanics during upper extremity sports. *Sports Med* 39(7):569-590.

8. Kelly BT, Barnes RP, Powell JW, & Warren RF (2004) Shoulder injuries to quarterbacks in the national football league. *Am J Sports Med* 32(2):328-331.

9. Kelly BT, Backus SI, Warren RF, & Williams RJ (2002) Electromyographic analysis and phase definition of the overhead football throw. *Am J Sports Med* 30(6):837-844.

10. Wagner H, Buchecker M, von Duvillard SP, & Muller E (2010) Kinematic comparison of team handball throwing with two different arm positions. *International journal of sports physiology and performance* 5(4):469-483.

11. van den Tillaar R & Ettema G (2009) Is there a proximal-to-distal sequence in overarm throwing in team handball? *J Sports Sci* 27(9):949-955.

12. van den Tillaar R & Ettema G (2007) A three-dimensional analysis of overarm throwing in experienced handball players. *J Appl Biomech* 23(1):12-19.

13. Liu H, Leigh S, & Yu B (2010) Sequences of upper and lower extremity motions in javelin throwing. *J Sports Sci* 28(13):1459-1467.

14. Best RJ, Bartlett RM, & Morriss CJ (1993) A three-dimensional analysis of javelin throwing technique. *J Sports Sci* 11(4):315-328.

15. Morriss C & Bartlett R (1996) Biomechanical factors critical for performance in the men's javelin throw. *Sports Med* 21(6):438-446.

16. Atwater AE (1979) Biomechanics of overarm throwing movements and of throwing injuries. *Exerc Sport Sci Rev* 7:43-85.

17. Chagneau F, Delamarche P, & Levasseur M (1992) Stroboscopic computerized determination of humeral rotation in overarm throwing. *Br J Sports Med* 26(1):59-62.

18. Fradet L, Kulpa R, Multon F, & Delamarche P (2002) Kinematic analysis of handball throwing. *International Symposium on Biomechanics in Sports*, ed Gianikellis KE (ISBS), pp 119-122.

19. Alexander RM (1991) Optimum timing of muscle activation for simple models of throwing. *J Theor Biol* 150(3):349-372.

20. Coh M, Stuhec S, & Supej M (2008) Comparative biomechanical analysis of the rotational shot put technique. *Collegium antropologicum* 32(1):249-256.

21. Hughes SS (1998) Getting to the Point: Evolutionary Change in Prehistoric Weaponry. *Journal of Archaeological Method and Theory* 5(4):345-408.

22. Young RW (2003) Evolution of the human hand: the role of throwing and clubbing. *Journal of Anatomy* 202:165-174.

23. Wolfe SW, Crisco JJ, Orr CM, & Marzke MW (2006) The dart-throwing motion of the wrist: is it unique to humans? *J Hand Surg Am* 31(9):1429-1437.

24. Pieper HG (1998) Humeral torsion in the throwing arm of handball players. *Am J Sports Med* 26(2):247-253.

25. Reagan KM*, et al.* (2002) Humeral retroversion and its relationship to glenohumeral rotation in the shoulder of college baseball players. *Am J Sports Med* 30(3):354-360.

26. Osbahr DC, Cannon DL, & Speer KP (2002) Retroversion of the humerus in the throwing shoulder of college baseball pitchers. *Am J Sports Med* 30(3):347-353.

27. Herrington L (1998) Glenohumeral joint: internal and external rotation range of motion in javelin throwers. *Br J Sports Med* 32(3):226-228.

28. Crockett HC*, et al.* (2002) Osseous adaptation and range of motion at the glenohumeral joint in professional baseball pitchers. *Am J Sports Med* 30(1):20-26.

29. Spitzer V, Ackerman MJ, Scherzinger AL, & Whitlock D (1996) The visible human male: a technical report. *J Am Med Inform Assoc* 3(2):118-130.

30. Holzbaur KR, Murray WM, Gold GE, & Delp SL (2007) Upper limb muscle volumes in adult subjects. *J Biomech* 40(4):742-749.

31. Garner BA & Pandy MG (2003) Estimation of musculotendon properties in the human upper limb. *Ann Biomed Eng* 31(2):207-220.

32. Mendez J & Keys A (1960) Density and composition of mammalian muscle. *Metabolism* 9:184-188.

33. McGowan CP, Baudinette RV, Usherwood JR, & Biewener AA (2005) The mechanics of jumping versus steady hopping in yellow-footed rock wallabies. *J Exp Biol* 208(Pt 14):2741-2751.

34. Lutz GJ & Rome LC (1994) Built for jumping: the design of the frog muscular system. *Science* 263(5145):370-372.

35. Peplowski MM & Marsh RL (1997) Work and power output in the hindlimb muscles of Cuban tree frogs Osteopilus septentrionalis during jumping. *J Exp Biol* 200(Pt 22):2861-2870.

36. Katz B (1939) The relation between force and speed in muscular contraction. *J Physiol* 96(1):45-64.

37. Harry JD, Ward AW, Heglund NC, Morgan DL, & McMahon TA (1990) Cross-bridge cycling theories cannot explain high-speed lengthening behavior in frog muscle. *Biophys J* 57(2):201-208.

38. Biewener AA & Blickhan R (1988) Kangaroo rat locomotion: design for elastic energy storage or acceleration? *J Exp Biol* 140:243-255.

39. McMahon TA (1984) *Muscles, Reflexes, and Locomotion* (Princeton University Press, Princeton, NJ).

40. Wilk KE, *et al.* (1993) Stretch-shortening drills for the upper extremities: theory and clinical application. *J Orthop Sports Phys Ther* 17(5):225-239.

41. Fleisig GS, Barrentine SW, Escamilla RF, & Andrews JR (1996) Biomechanics of overhand throwing with implications for injuries. *Sports Med* 21(6):421-437.

42. Altchek DW & Dines DM (1995) Shoulder Injuries in the Throwing Athlete. *J Am Acad Orthop Surg* 3(3):159-165.

43. Meister K (2000) Injuries to the shoulder in the throwing athlete. Part two: evaluation/treatment. *Am J Sports Med* 28(4):587-601.

44. Clemente C (1985) *Gray's Anatomy of the Human Body* (Lea & Febiger, Philadelphia) 30th American Ed.

45. Rodeo SA, Suzuki K, Yamauchi M, Bhargava M, & Warren RF (1998) Analysis of collagen and elastic fibers in shoulder capsule in patients with shoulder instability. *Am J Sports Med* 26(5):634-643.

46. Biewener AA, Konieczynski DD, & Baudinette RV (1998) In vivo muscle force-length behavior during steady-speed hopping in tammar wallabies. *J Exp Biol* 201(Pt 11):1681-1694.

47. Astley HC & Roberts TJ (2012) Evidence for a vertebrate catapult: elastic energy storage in the plantaris tendon during frog jumping. *Biol Lett* 8(3):386-389.

48. Goodall J (1986) *The Chimpanzees of Gombe: Patterns of Behavior* (Harvard University Press, Cambridge).

49. Goodall J (1964) Tool-Using and Aimed Throwing in a Community of Free-Living Chimpanzees. *Nature* 201:1264-1266.

50. Kohler W (1925) *The Mentality of Apes* (Harcourt and Brace, New York).

51. Sugiyama Y & Koman J (1979) Tool-using and making behavior in wild chimpanzees at Bossou, Guinea. *Primates* 20:513-524.

52. White TD*, et al.* (2009) Ardipithecus ramidus and the paleobiology of early hominids. *Science* 326(5949):75-86.

53. Brunet M*, et al.* (2002) A new hominid from the Upper Miocene of Chad, Central Africa. *Nature* 418(6894):145-151.

54. Pickford M, Senut B, Gommery D, & Treil J (2002) Bipedalism in *Orrorin tugenensis* revealed by its femora. *C.R. Paleovol* 1:1-13.

55. Wrangham R & Pilbeam D (2001) African Apes as Time Machines. *All Great Apes Great and Small, Volume I : African Apes,* African Apes, ed Galdikas BMF, Briggs, N.E., Sheeran, L.K., Shapiro, G.L. and Goodall, J. (Kluwer Academics/Plenum Publishers, New York), Vol I, pp ch. 1, pg. 5-17.

56. Sayers K & Lovejoy CO (2008) The chimpanzee has no clothes: A critical examination of Pan troglodytes in models of human evolution. *Current Anthropology* 49(1):87-114.

57. Zihlmann A (1996) Reconstructions reconsidered: chimpanzee models and human evolution. *Great Ape Societies*, ed McGrew WC, Marchant, L.F., and Nishida, T. (Cambridge University Press, Cambridge), pp ch. 21, pg. 293-304.

58. Larson SG (2007) Evolutionary Transformation of the Hominin Shoulder. *Evolutionary Anthropology* 16:172-187.

59. Lordkipanidze D*, et al.* (2007) Postcranial evidence from early Homo from Dmanisi, Georgia. *Nature* 449(7160):305-310.

60. Jungers WL (1994) Ape and hominid limb length. *Nature* 369:194.

61. Bramble DM & Lieberman DE (2004) Endurance Running and the Evolution of Homo. *Nature* 432:345-352.

62. Kagaya M, Ogihara N, & Nakatsukasa M (2010) Is the clavicle of apes long? An investigation of clavicular length in relation to body mass and upper thoracic width. *Int J Primatol* 31:209-217.

63. Lieberman DE*, et al.* (2010) Foot strike patterns and collision forces in habitually barefoot versus shod runners. *Nature* 463(7280):531-535.

64. Pontzer H, Holloway JH, 3rd, Raichlen DA, & Lieberman DE (2009) Control and function of arm swing in human walking and running. *J Exp Biol* 212(Pt 4):523-534.

65. Zihlman AL (1984) Body Build and tissue composition in *Pan paniscus* and *Pan troglodytes*, with comparisons to other hominoids. *The Pygmy Chimpanzee*, ed Susman RL (Plenum Press, New York), pp 179-200.

66. Aiello LC & Dean C (1990) *An Introduction to Human Evolutionary Anatomy* (Academic Press, New York) p 596.

67. Schultz AH (1930) The skeleton of the trunk and limbs of higher primates. *Human Biology* 2:303-438.

68. Schultz AH (1937) Proportions, variability and asymmetries of the long bones of the limbs and the clavicles in man and apes. *Hum Biol* 9(3):281-328.

69. Fleisig GS, Andrews JR, Dillman CJ, & Escamilla RF (1995) Kinetics of baseball pitching with implications about injury mechanisms. *Am J Sports Med* 23(2):233-239.

70. Pappas AM, Zawacki RM, & Sullivan TJ (1985) Biomechanics of baseball pitching. A preliminary report. *Am J Sports Med* 13(4):216-222.