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The Biomechanics of Spear Throwing: An Analysis of the Effects of Anatomical Variation on
Throwing Performance, with Implications for the Fossil Record

by

Julia Marie Maki

A dissertation presented to the
Graduate School of Arts and Sciences
of Washington University in
partial fulfillment of the
requirements for degree
of Doctor of Philosophy

May 2013

St. Louis, Missouri

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LIST OF ABBREVIATIONS

Biomechanical Terms:

		F_m	muscle force
α	joint angular acceleration	f	sampling frequency
θ	pennation angle	$g_{x, y, z}$	x, y or z component of gravity vector
ω	joint angular velocity	$I_{px, py, pz}$	x, y or z axis for pelvis local reference system
$a_{x,y,z}$	acceleration with respect to x, y or z axis	$I_{sx, sy, sz}$	x, y or z axis for shoulder local reference system
A	acceleration	$I_{uax, uay, uaz}$	x, y or z axis for upper arm local reference system
A-P	anterior-posterior	$I_{wx, wy, wz}$	x, y or z axis for wrist local reference system
B1, 2, 3	ball 1, 2 or 3	i	frame number
COR	center of rotation	K_e	kinetic energy
cross	cross product	L_s	segment length (where $_s$ is thigh, shank, upper arm, forearm or hand)
$d_{ex, ey, ez}$	x, y or z component of the moment arm for Rf_e	l	fascicle length
$d_{sx, sy, sz}$	x, y or z component of the moment arm for Rf_s	LOA	line of action
$d_{wx, wy, wz}$	x, y or z component of the moment arm for Rf_w	M_b	body mass
d	moment arm (for MATLAB calculations)	M_s	segment mass (where $_s$ is thigh, shank, upper arm, forearm or hand)
dot	dot product	MER	Maximum external (shoulder) rotation
Dynamic R	Load arm measured during throwing	$M_{f_{w,e,s}}$	moment of force/torque for the wrist, elbow or shoulder
EMA	effective mechanical advantage	MOI	moment of inertia
EMG	electromyography	MRI	magnetic resonance imaging
F_{A-P}/M_b	anterior-posterior force plate trace scaled to body mass		
F_e	external force		

MVC	maximal voluntary contraction	IK	Indian Knoll
O	origin	IUP	initial Upper Paleolithic
$p_{x,y,z}$	marker position with respect to x, y or z axis	kya	thousand years ago
pCSA	physiological cross sectional area	LSA	Later Stone Age
r	moment arm	LUP	Late Upper Paleolithic
R	load arm	MP	Middle Paleolithic
$R_{f_{w,e,s}}$	reaction/resultant force for the wrist, elbow or shoulder	MPEMH	Middle Paleolithic early modern human
S1, 2, 3	spear 1, 2 or 3	MSA	Middle Stone Age
$S_{x,y,z}$	x, y or z component of segment mass or MOI constant	MUP	Mid Upper Paleolithic
ST	specific tension	mya	million years ago
Static R	Load arm measured from skeletal dimensions	Nean	Neandertal
Stride	stride length	OIS	oxygen isotope stage
T	torque	TCSA	tip cross sectional area
V_m	muscle volume	UP	Upper Paleolithic
$v_{x,y,z}$	velocity with respect to x, y or z axis	UPEMH	Upper Paleolithic early modern human
V	velocity	Anatomical Terms:	
Archaeological/Geological Terms:		1MC	first metacarpal length
BP	before present	2MC	second metacarpal length
EH	early <i>Homo</i>	5MC	fifth metacarpal length
EUP	Early Upper Paleolithic	aCSA	anatomical cross sectional area
HP	Howiesons Poort	Ankle	marker located on lateral malleolus of fibula
HTH	Hamann-Todd humans	B	brachialis
		BB	biceps brachii

Biacromion	breadth from the left to right acromion processes of the scapulae	LAsis	marker located on left anterior superior iliac spine
Biasis	breadth from left to right anterior superior iliac spines	LShoulder	marker located on the left acromion process of the scapula
ECR	extensor carpi radialis (longus and brevis)	Leg	leg length
ECU	extensor carpi ulnaris	Radius	marker located on the styloid process of the radius
Elbow	marker located on medial epicondyle of the humerus	RAsis	marker located on the right anterior superior iliac spine
FCR	flexor carpi radialis	rHam	moment arm for flexor carpi ulnaris measured from the hamate
FCU	flexor carpi ulnaris	rPis	moment arm for flexor carpi ulnaris measured from the pisiform
Fifthmc	marker located on the head of the fifth metacarpal	RShoulder	marker located on the right acromion process of the scapula
Firstmc	marker located on the head of the first metacarpal	TB	triceps brachii
Forearm	forearm length	Torso	torso length
Hand	hand length	Ulna	marker located on the styloid process of the ulna
Hip	marker located on greater trochanter of femur	Upper arm	upper arm length
Knee	marker located on lateral epicondyle of femur		

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ABSTRACT OF THE DISSERTATION

The Biomechanics of Spear Throwing: An Analysis of the Effects of Anatomical Variation on Throwing Performance, with Implications for the Fossil Record

by

Julia Marie Maki

Doctor of Philosophy in Anthropology

Washington University in Saint Louis, 2013

Professor Erik Trinkaus, Chairperson

Accurate, high velocity throwing is a skill unique to humans among living species. It likely provided an adaptive advantage for our hominin ancestors, either in the context of hunting, or protection from predators. Thus, understanding how variation in body form and anatomy influences throwing ability may provide insight into the evolution of human morphology. Research has been done on various forms of ball and javelin throwing, yet the biomechanics of spear throwing were completely unknown. Moreover, it has been suggested that early modern humans had lesser effective mechanical advantage (EMA, the ratio of moment arm to load arm) than Neandertals, as a result of selection for throwing, as this could provide increased joint angular velocity at the cost of strength. However the biomechanical principles underpinning this assertion had not been tested empirically. Thus, the purpose of this dissertation is to establish the patterns of kinetics and kinematics used during spear throwing, to examine the morphological correlates of throwing performance and strength in living humans, and to consider the implications of the patterns observed for Paleolithic fossil hominins.

Throwing performance, measured as the energy imparted to a thrown object (kinetic energy, K_e), was assessed in 41 experienced throwers throwing balls and spear-like objects.

Joint linear and angular velocities, torques, and kinetic energies were calculated using high-speed infrared cameras. Subject anthropometrics, including body mass, height, and segment lengths, were measured externally, and arm muscle cross-sectional areas and EMA of the elbow and wrist were measured from magnetic resonance images. The maximum isometric strength of the elbow and wrist were measured using a load cell. Additionally, EMA of the elbow and wrist were estimated skeletally for available early *Homo*, Neandertal, Middle Paleolithic, Upper Paleolithic, and recent human specimens.

It was demonstrated that the shoulder experiences very low angular velocities and torques, and the elbow is relatively less mobile during spear as compared with ball throwing. Thus, the literature on the arm in ball throwing will be of less relevance to the evolution of throwing. Furthermore, there is no direct correlation between spear K_e and any morphological or anatomical variable of the arm (including EMA). Instead, spear K_e is primarily produced by the legs and torso, where musculature, leg length, and shoulder breadth are correlated with greater K_e . This implies that research on throwing should focus on the legs and torso, and variation in the morphology of the arm should not be used to infer differential selection for throwing in Paleolithic hominins.

No correlation was found between the EMA of the elbow or wrist and joint strength independent of muscle cross-sectional area. This is likely due to variation in muscle recruitment and activation, and because r is correlated with muscle size independent of body size. Furthermore, it was demonstrated that EMA cannot be measured reliably in the fossil record, as load arms are highly variable within and between individuals, even performing a highly trained activity like throwing. Consequently, they cannot be predicted from skeletal dimensions available in the fossil record. Furthermore, although there is a trend towards greater EMA of the

elbow in Neandertals as compared with other fossil hominin samples, this variation is not functionally or adaptively relevant. No significant differences exist for moment arms between groups; rather, the difference in EMA is due to variation in load arms (ulna length). However, load arms measured skeletally are not relevant to living behaviors, and variation in load arms between these groups is due to known differences in brachial indices, which reflect climatic adaptations. Thus, EMA of the arm is not a useful measure of performance in Paleolithic fossil hominins.

Chapter 1

Introduction

Accurate high velocity throwing is a skill unique to humans among living species. Chimpanzees and other primates occasionally throw objects (Van Lawick-Goodall, 1970), but these throws are not of high velocity or accuracy (Roach, 2012). The origin of high velocity throwing appears to have evolved in a mosaic fashion, and the purported anatomical adaptations are all present in the earliest members of *Homo erectus* (Roach, 2012). Evidence from the archaeological record indicates that thrown tools for hunting were certainly present by the Upper Paleolithic, and likely much earlier (Thieme, 1997, 2007). Throwing likely played an important role in food procurement and defense from predators in hominin hunter-gatherers. Research using modern hunter-gatherers as analogs suggests that hunting ability is correlated with reproductive success (Smith, 2004), suggesting a direct fitness advantage for anatomical or morphological variation that increases hunting performance. Thus, understanding how variation in body form and anatomy influences throwing ability may provide insight into the evolution of human adaptations.

In this dissertation, I examine the anatomical and morphological correlates of throwing performance in living humans, and consider the implications of the patterns observed for fossil hominins. For these purposes, throwing ability will be defined in terms of the energy imparted to a thrown object. Admittedly this addresses only a portion of the variation in throwing skill, as accuracy, and the neurological control and coordination underlying it, certainly play a very large role. However these complex neural mechanisms are difficult to identify in the fossil record, and

it is fair to assume that the basic neural mechanisms were in place at the point when manufactured thrown objects appear in the archaeological record.

Throwing performance was assessed in a sample of modern humans throwing baseballs and spear-like objects, and correlations between body size and proportions and joint anatomy were examined. Existing literature addresses several potential anatomical correlates of throwing velocity, but this literature has not addressed variables such as joint mechanical advantage, nor adequately examined the interrelation between variables, and the biomechanics of *spear* throwing has not been investigated at all. I will establish which variables best predict throwing velocity during spear and ball throwing, after which patterns of variation in the fossil record can be assessed in context. Some relevant traits have been discussed in the literature previously, and these will be supplemented with data collected from casts and photographs.

Based on the material available, examination of the fossil record will primarily focus on comparisons of early modern humans and Neandertals. Relevant fossil material is rare prior to the Middle Paleolithic, and does not provide sufficient sample sizes for robust comparisons. The Neandertal/early modern human comparison is also of central importance due to assumed technological differences between the populations. Neandertals have been described as having increased strength, both in terms of joint leverage and muscle volume (Trinkaus, 1983a, 1986, 2006; Trinkaus and Villemeur, 1991; Hambucken, 1993, Villemeur, 1994; Churchill and Rhodes, 2006, 2009; Maki and Trinkaus 2011), to wield brute force style tools, whereas early modern humans are described as having had advanced technology (including throwing technology) allowing decreased bodily strength (Trinkaus, 1986; Churchill and Rhodes, 2006). These assertions assume the modern human body form would have been advantageous for throwing, an

as yet untested hypothesis. Thus, it will be examined whether morphological differences exist between Neandertals and early modern humans that may have influenced throwing performance.

An important component of this research will be to address the degree to which the observed predictors of throwing ability are actually measurable with confidence in the fossil record. Body proportions and size have been described well for the samples in question, and these assessments are likely reliable. However, factors such as mechanical advantage may not provide sufficient information to be valuable when applied to the fossil record. Estimation of mechanical advantage from a skeleton requires a number of as yet untested assumptions. Thus it will be important to assess whether mechanical advantage as estimated from skeletons provides sufficient information about real behaviors in living individuals to be useful.

Research Questions and Hypotheses.

The goal of this dissertation is to address the following interrelated research questions and test the following hypotheses:

1. *How do the kinetics and kinematics of spear throwing differ from that of ball throwing?*

Prior to the appearance of more advanced projectile weaponry such as spear-throwers or bows and arrows, humans would have thrown hand-held spears for hunting or predator defense. However, the literature to date on the biomechanics of throwing is almost exclusively limited to ball or javelin throwing. Given differences in the manual manipulation of the object, it's reasonable to assume that there are significant differences in kinematics (patterns of motion) and kinetics (forces that produce motion) between ball and spear throwing. With respect to javelin throwing, the purpose of the throw is to maximize distance, and so the trajectory of the throw is quite different from a spear throw. Furthermore, javelin throwing involves a very complex series of motions, including several sideways running steps prior to the throw and propelling the body

into the air after release, that are very unlikely to be used by spear hunters. Thus, despite the similarities in the shape of the thrown object, the kinematics and kinetics of javelin throwing very likely differ in important ways from throwing a spear for the purpose of hunting. Chapter 6 establishes the basic patterns of joint motion and energy transfer during spear throwing, and compares and contrasts these patterns with those during ball throwing. Relevant similarities and differences will be highlighted such that researchers interested in spear throwing will be able to use the ball throwing literature more effectively.

2. *How does variation in body size, body proportions, and joint anatomy influence throwing performance?*

If throwing ability (as it influences hunting success or predator defense) is adaptive, then hominin anatomy and morphology may reflect selection for throwing performance. Specifically, variation exists in body size, body proportions, and joint anatomy between Neandertals and early modern humans which has been interpreted as reflective of adaptation for throwing performance in the latter (Churchill and Rhodes, 2006). However, the biomechanical inferences of these assumptions have not been tested empirically. Alternately, anatomy and morphology may have evolved for other reasons, but still have important implications for throwing performance.

Research on ball throwing has suggested several anatomical and morphological measures that may influence throwing velocity (Pedegana et al., 1982; Bartlett et al., 1989; Lachowetz et al., 1998; Fleisig et al., 1999; Clements et al., 2001; Escamilla et al., 2001; Matsuo et al., 2001; Stodden et al., 2001, 2005; Vila et al., 2009, 2011). In chapter 7, the effects of variation in height, body mass, limb segment lengths, and joint mechanical advantage on throwing velocity during ball and spear throwing are examined. This analysis is designed to determine which

morphological and anatomical measures are predictive of throwing performance, providing the necessary biomechanical context for comparisons of fossil hominins. The following hypothesis will be tested:

H1: Throwing ability, as measured by the kinetic energy (K_e) of the thrown object, will be correlated with body form and joint anatomy.

- a. Greater limb segment lengths, height, body breadth and body mass will be positively correlated with K_e .
- b. Muscle cross-sectional area at the elbow and wrist will be positively correlated with K_e .
- c. Effective mechanical advantage (EMA) will be inversely correlated with maximum joint angular velocity of the wrist and elbow during throwing.
- d. Maximum joint angular velocity of the wrist and elbow will be positively correlated with K_e .

3. *Can joint mechanical advantage be measured meaningfully in the fossil record?*

Joint effective mechanical advantage (EMA) is a measure of the leverage of a joint (Biewener, 1989). It is assumed to be predictive of the maximum external force production and angular velocity of the joint (Levangie and Norkin, 2005), and consequently throwing performance (Churchill and Rhodes, 2006). However, the relationship between EMA and joint kinetics and kinematics has not been demonstrated empirically. Chapter 8 examines the relationship between EMA, external force production and angular velocity of the elbow and wrist in living subjects in order to establish whether EMA is correlated with external force production and angular velocity independent of other relevant measures (primarily muscle size).

Furthermore, in order to apply these principles to fossil samples, it is also necessary to demonstrate that EMA can be measured accurately from skeletal specimens, and that skeletal measures of EMA are relevant to living subjects. Thus, measures of EMA taken from skeletal landmarks will be compared with measures of EMA observed in the soft tissue. Then, the static soft tissue measures of EMA will be compared with EMA measured during activity. Together, these will provide empirical support for the hypothesis that variation in EMA between hominin samples is biomechanically relevant to performance. The following hypothesis will be tested:

H2: EMA as measured from fossil skeletons will be correlated with joint strength and velocity measured experimentally.

- a. Skeletal EMA will be correlated with maximum external force production after accounting for variation in muscle volume.
- b. Skeletal EMA will be correlated with EMA measured from tendinous muscle insertions.
- c. Skeletal/tendinous EMA will be correlated with EMA observed during throwing.

4. *Does relevant variation in EMA exist between hominin samples?*

EMA has generally been estimated in skeletal specimens by comparing skeletal features that would affect the muscle's moment arm (reflecting the leverage of the muscle). Such estimations have suggested greater EMA for the deltoid and triceps, and pronators, supinators, and flexors of the forearm in Neandertals as compared with early modern humans (Trinkaus, 1983a, b; Trinkaus and Churchill, 1988; Hambucken, 1993; Villemeur, 1994; Churchill and Rhodes, 2006; Galtés et al., 2008a). However, many of these comparisons have failed to account for variation in the load arm (reflecting the leverage of the external force). In chapter 9, EMA of

the elbow and wrist is measured in a way that more closely represents the living functional anatomy, and patterns of variation between hominin samples are compared. In conjunction with the results of the prior chapters, this will provide evidence for the argument that reduced EMA in early modern humans as compared with Neandertals is an adaptation for high velocity throwing. The following hypothesis will be tested:

H3: Based on the predictors determined in H1 (including EMA), early modern humans will be able to impart more K_e to a thrown object.

- a. EMA at the elbow and wrist will be higher in the Neandertal sample than the early and recent modern human samples.

Taken together, the results of the above analyses will establish the kinetic and kinematic patterns used during spear throwing, which aspects of anatomy and morphology produce these kinetic and kinematic patterns, and whether morphological variation exists in hominin samples that would affect spear throwing performance. This research thus provides valuable insight into a uniquely human trait that likely had important adaptive implications for our Paleolithic hominin ancestors.

Chapter 2

Throwing in Context

Prior to an examination of throwing ability, it is necessary to place the behavior in context, and to consider how it may have influenced life in the Paleolithic. Research using modern hunter-gatherers as analogs may provide valuable insight into the use and importance of throwing to survival and reproduction (fitness) in our ancestors. The following is an attempt to summarize the available information regarding throwing in modern hunter-gatherer societies. Throwing is used during hunting, so the focus will be on the function and import of hunting to hunter-gatherer life. Encroachment of modern civilization has severely limited the extent and number of these groups and many groups considered to be hunter-gatherers are increasingly making use of non-traditional lifestyles (Barnard, 2004). However, available literature may be used to qualitatively describe hunting activities and investigate the presence and import of throwing behaviors. In addition, technologies are present today that would not have been available (or not until late) in the Paleolithic. Thus, evidence presented here is considered relevant to, not indicative of, Paleolithic hominin behaviors.

In a large sample of 478 modern hunter-gatherer groups, defined by having less than 10% of their diet from domesticated foods, hunting has been estimated to make up an average of between 24 and 36% of hunter-gatherer diet, with a range from 0 to 90% (Marlowe, 2005). Gathering of non-animal resources makes up on average 30 to 55% of the diet, also with a range from 0 to 90%. In locations where fishing and marine resources are available, these are also exploited, making up on average 22 to 31% of the diet, with a range from 0 to 95%. Climatic differences are present, where significantly more dietary resources come from gathering in a

warm climate and significantly more from hunting in a cold climate, due to greater availability of plant resources in warm climates (Marlowe, 2007). Relevant here is the sexual division of labor, where a far greater percentage of hunting resources are provided by males, although by no means exclusively so. Although only a quarter to a third of the diet is from hunting, males provide on average between 47 and 65% of the overall diet (Marlowe, 2001, 2005), indicating the importance of male foraging. Here climatic differences also exist, where males provide a significantly larger percentage of the diet in a cold climate, reflecting an increase in meat in the diet, which becomes greater the colder the climate (Marlowe, 2001). In extreme conditions such as the arctic, male provided calories can be as much as 90%, as the majority of the diet comes from hunting of large bodied marine animals (Marlowe, 2001, 2007). There may be important implications of this climatic variation in the Paleolithic, given the very different climates of populations from equatorial Africa to last glacial maximum Europe. These will be discussed in later chapters.

Among the Hadza of Tanzania, for whom detailed data are available, 40% of calories men contribute are from game, and only 1% of female contributed calories are from game (Marlowe, 2003). Animals hunted include a wide range of sizes, from small birds to giraffes. The primary sources of gathered calories from Hadza males are from honey and baobab fruit (Marlowe, 2003). Although a large part of the foods provided by males are non-meat, and a large part of the foods eaten are not provided by males, there is a strong indication that male provided foods are highly desirable (Marlowe and Berbesque, 2009). Honey, meat, and baobab rank most desirable for males, and the same is true with the inclusion of berries for females. Meat is preferred to everything but honey for males, but is least preferred with the exception of tubers for women. Yet, despite their apparent lack of preference for meat, female percent body fat is

significantly higher in regions where meat is a larger percentage of the diet (Marlowe and Berbesque, 2009). Given that a deficient body fat percentage, at least as it represents a negative energy balance, can result in decreased fertility in women (Frisch, 1984; Ellison, 1990), the contribution of meat to the female diet may have a significant effect on reproduction.

Although Hadza males provide on average 42% of total calories, married males and males with offspring contribute significantly more, with the fathers of infants contributing up to 70% of calories. This is presumably due to the need for increased provisioning of mothers, particularly those with small children, who experience decreased foraging efficiency during this period (Marlowe, 2003). Males of children under 8 years of age have significantly greater caloric contributions, but the increase is largely due to increased gathering returns, rather than hunting returns (Marlowe, 2003). This may be because men are already hunting as effectively as they are capable, or because of the inherent unpredictability of hunting. Variability in hunting success from day to day is high, such that attempting to increase food returns by devoting more time to hunting may be too risky for fathers of young children. Success in gathering is likely far less variable from day to day, and thus a less risky endeavor. However, given the variation in availability of gathered resources across environments, this option is not available to all hunter-gatherer fathers. Provisioning of mothers with young offspring may be common cross-culturally (as it relates to the biological necessities of caring for young offspring), but there is significant variation in the type of calories fathers provide. Where climatic or other environmental conditions are such that hunting is a larger component of the diet, or where males provide fewer non meat calories overall, meat tends to be the primary source of increased provisioned calories (Marlowe, 2007).

Greater body fat percentage in regions where more meat is eaten, as well as increased provisioning by fathers with young children, would suggest a reproductive benefit to hunting success. In fact, reproductive success as measured by fertility and number of surviving offspring correlates with hunting success in a number of hunter-gatherer groups (Smith, 2004). The most obvious explanation is that good hunters provide more food to their wives and offspring, and this greater investment allows for higher fertility and survivorship of offspring. However, most hunter-gatherer groups (and all those included in the above study) exhibit high levels of food sharing, such that the hunter's family does not necessarily receive a larger portion of hunting returns than other group members (Smith, 2004). Although the degree and extent of food sharing has not been measured widely across hunter-gatherer groups, this suggests direct provisioning of one's own offspring may be limited. Thus, the increased reproductive success of good hunters has been suggested to result from sexual selection, where women use hunting ability as an honest signal of quality (Smith, 2004). In this way they acquire better mates and improve their fitness. This is a plausible explanation, as hunting returns are correlated with gathering returns, which are not as widely shared, and females rank 'good hunter' as a highly desirable quality in a mate (Smith, 2004). In light of the fact that males with young children increase their foraging returns, another plausible and non-mutually exclusive explanation is that males increase their fitness by direct provisioning during this 'critical period' for offspring survivorship (Marlowe, 2003). Hunting ability is correlated with gathering ability, and by increasing gathering returns, which do not need to be shared, a male can increase the calories he provides to his young children at a point when the mother is unable to provide sufficient calories herself.

These two hypotheses differ in the direct benefit that hunting would provide to fitness. If hunting is primarily a signal of quality, hunting ability itself (and throwing, to the extent it is

used), would be directly implicated in fitness. If hunting is merely a correlate of foraging success, either due to physiological or behavioral factors, the tie to throwing ability is less direct. In reality both, either, or altogether different factors may direct the relationship between hunting ability and reproductive success. The variation in the contribution of hunting to the overall diet discussed above is again relevant here. Where gathering is an option because plant resources are widely available, fathers that increase gathering output may be selected for. Where plant material is limited and hunting becomes a larger percentage of the diet, benefits of hunting success may be more in terms of mate competition than direct provisioning.

Alternatively, offspring of good hunters may benefit from more often getting a share of the hunt. Even when food is widely shared, not all individuals will necessarily benefit. The offspring of the successful hunter will almost definitely receive a share, so the offspring of a successful hunter will more often be in the position of receiving shares of food. Furthermore, there is likely variation geographically and historically in the amount of food sharing exhibited by a group. The groups discussed above are all relatively hot climate inhabitants where hunting is a smaller percentage of the diet. These patterns may differ such that under different conditions, offspring retain a greater share than the shares given out. Whatever the reasons, it seems likely, both empirically and logically, that hunting success is a selective force for modern hunter-gatherers, and would have been so for our ancestors as well.

Hunting success is therefore probably selectively advantageous, but to what degree might throwing ability affect hunting ability? To address this question, hunting technologies of modern hunter gatherers will be examined. Throwing is observed in terms of hand thrown spears and atlatls (spear throwers). Atlatls significantly improve throwing ability (Howard, 1974), and likely overwhelm any effect of anatomy on throwing velocity and distance. Thus, the discussion here

will be in terms of hand thrown spears. The following is from Churchill (1993), a broad ethnographic survey of modern hunter-gatherer hunting technologies. Modern hunter gatherers use thrown spears for hunting (including marine resources), in addition to defense from predators and warfare. When used for hunting, spears are thrown rather than thrust approximately a third of the time. As a thrusting weapon, the spear is used most often to disadvantage prey (i.e. game drives, chasing an animal into a tree). Hunting techniques which involve disadvantaging prey include additional tools or technologies, such as dogs or boats, approximately 80% of the time, suggesting that this type of technique would be less common where such tools are not available. Spear hunting (thrusting) by disadvantaging prey most often involves large bodied animals. Pursuit hunting also tends to make use of domesticated animals such as horses or dogs, with the exception of endurance hunting. Ambush hunting often involves cooperation, where one or more hunters direct the prey towards other hidden hunters. Both ambush and pursuit hunting are associated with smaller bodied prey.

Incidences of the use of spears for throwing are less common than thrusting, and are often associated with incidences of thrusting. Spears are likely used as a dual purpose weapon, and thrown when advantageous. Incidences of spear throwing are approximately equal across types of hunting techniques, with a slight trend towards disadvantaging and ambushing prey. Among the San of the Kalahari, spear hunting is the preferred technique for taking big game (Hitchcock and Bleed, 1997). Hunters pursue large animals, such as elephants, giraffes, or rhinoceroses, and both throw and thrust spears once at close range. San hunters state that spears are better for hunting large game than poison arrows (which are used in other contexts) because they kill or disable the animal more quickly, although this may be specific to the conditions and type of

poison. Spears are also thrown from blinds at night, or used in conjunction with domesticated animals (Hitchcock and Bleed, 1997).

Given the concurrence of disadvantaging and pursuit techniques with additional tools and technologies, Churchill (1993) argues that prior to the use of domesticated animals or advances in technology, hominins would have been limited to areas of the landscape with features advantageous to these types of hunting techniques. An alternative hypothesis is that hominins would have made use of other, less restrictive techniques when landscape features were not available. There are notable examples of game drives in the archaeological record (Villa and Lenoir, 2006), but these do not explain the majority of faunal assemblages, suggesting hominins were successfully employing other means of hunting. These likely included ambushing and approach hunting (stalking to effective weapon range). Spear throwing is observed in approximately equal proportion to thrusting in ambush hunting, and exclusive of thrusting in approach hunting (Churchill, 1993). Thus, there is reason to believe that prior to the advent of more advanced technologies and domesticated animals, spear throwing may have been a more prominent feature of hunting than that seen in modern hunter-gatherers, and used at least as much as thrusting. Although the exact antiquity of the domestication of dogs is unknown, dogs may have been present and participating in hunting activities as early as the Aurignacian in Europe (Germonpré et al., 2009; Ovodov et al., 2011), and would have been highly valuable in aiding the effectiveness of hunting with spears.

Taken in total, the above evidence suggests the potential importance of throwing ability to hunting success in the past, particularly given the absence of domesticated animals and advanced technology. Furthermore, hunting success is clearly tied to reproductive success, implying a fitness advantage to throwing ability, although the causal relationships are not yet

clear. This would be especially true of cold or highly seasonal climate inhabitants, where hunting makes up a larger part of the diet overall.

Chapter 3

Throwing in the Paleolithic

Indications of the onset of throwing may be gleaned from the fossil record and the archaeological record. The following summarizes the available evidence for throwing behaviors in the Paleolithic, as indicated through hominin anatomy, archaeological evidence for projectile technology, and evidence regarding the presence and extent of meat in the diet (through isotopic analyses and faunal assemblages). This will provide insight into when and where throwing was present and could have been selectively advantageous.

The relevant archaeological periods under consideration are the Middle and Upper Paleolithic (MP, UP) in Eurasia, and the Middle and Later Stone Age in Africa (MSA, LSA). The MP originates ≈ 300 thousand years ago (kya) and ends between 43 and 30 kya in Europe, when it gradually and sporadically transitions into the Early Upper Paleolithic (EUP) (Holt and Formicola, 2008; Roebroeks, 2008). This transition appears to have occurred earlier in Western Asia, between 43 and 47 kya (Bar-Yosef et al., 1996). The MP is often equated with Neandertal technology (Roebroeks, 2008), but anatomically modern humans are also associated with MP tools (Shea, 1989), and Neandertals appear to have been associated with EUP tools as well in several instances (d'Errico et al., 1998; Trinkaus 2005). The MSA spans an approximately equivalent time period in Africa, beginning around 280 kya and gradually transitioning to the LSA between 50 and 20 kya (Ambrose, 1998; McBrearty and Brooks, 2000). The EUP persists until ≈ 28 kya, and is generally associated with early modern humans, despite the lack of clearly associated hominin remains at many sites (Holt and Formicola, 2008). The Middle and Late Upper Paleolithic (MUP, LUP) are exclusively associated with early modern humans, and span

from ≈ 28 kya to ≈ 20 kya, and ≈ 20 to ≈ 10 kya consecutively (Holt and Formicola, 2008). The LSA of Africa is exclusively associated with early modern humans, and spans from ≈ 40 to ≈ 10 kya (Wadley, 1993).

I. Evidence for projectile weaponry.

The earliest possible archaeological indication of spear throwing is several spear-like objects from Schöningen, Germany, from approximately 400 kya (Thieme, 1997, 2007). These are heavy wooden implements that are sharpened at both ends and tapered. The implements are found in association with a very large faunal assemblage, primarily of horse, many specimens of which show cut marks and fracturing. The objects are 0.78 and 2.30 m in length and 29 to 47 mm in diameter, and appear to follow a common design pattern in terms of weight distribution. Oakley (1977) noted that similarly sized modern implements are used as either throwing or thrusting spears, or as game stakes (implements placed into the ground on which animals will inadvertently impale themselves). Based on measurements taken from a range of available such tools, measured game stakes are generally about 2 m long, and between 60 and 100 mm in diameter (Oakley, 1977). Spears used for thrusting range from 283 to 1358 g in mass, 21.8 to 30 mm in diameter, and 1.85 to 2.72 m in length (Oakley, 1977; Hughes, 1998). Spears primarily used for throwing range from 113 to 453 g in mass, 12 to 23 mm in diameter, and 1.6 to 4.0 m in length (Oakley, 1977; Hughes, 1998). Thieme (1997) argued that the overall shape and balance of the spears are similar to modern javelins, and suggested their use as projectiles. Furthermore, reconstructions of these objects have been demonstrated to function as handheld throwing spears under experimental conditions (Steguweit, 1999). However, it has also been argued that the length and width of these objects are more similar to modern thrusting spears than throwing spears, and based on the length and width, would have been far heavier than any known throwing

spear (Schmitt et al., 2003, Shea, 2006). Thus, the use of these objects for throwing rather than thrusting remains controversial.

A similar wooden implement from the Mid Pleistocene site of Clacton-on-Sea, England, has been described, based on its overall shape and size, as the broken end of a thrusting spear (Oakley et al., 1977). The implement was clearly artificially sharpened, but not hardened with fire. Additionally, a more complete wooden spear is known from Lehringen, Germany (Movius, 1950). This artifact dates to approximately 125 kya, and was found embedded in the ribs of an extinct elephant. It was sharpened with stone tools and hardened with fire (Movius, 1950). As it was found embedded in its prey, this object was certainly a hunting tool, and likely a spear, but whether it was thrust or thrown is unknown. By analogy with modern elephant-hunting pygmies, Movius (1950) suggested thrusting as the method of kill. However, as noted previously, the distinction between thrusting and throwing spears in modern hunter gatherers is likely unnecessary. Spears are almost always used as both thrusting and throwing implements, based on the particular conditions (Churchill, 1993). Given the upper limb robusticity of pre-recent modern human hominins (Ruff et al., 1993; Trinkaus, 1997), it is possible that the makers of these heavier spears were capable of throwing them, and did so under certain conditions. Conservatively, the presence of wooden implements for hunting at approximately 400 kya indicates that hominins were capable of manufacturing functional spears prior to the MP, and prior to the emergence of *Homo sapiens*.

Although a wooden spear alone is capable of penetrating and killing prey (Smith, 2003), the addition of a stone tip to a spear significantly increases its penetrating ability (Hughes, 1998). The spears discussed above are sharpened at one or both ends, but the first indication of the hafting of lithics onto spears is in the MP of Europe and the MSA of Africa, as inferred from

several lines of evidence, including particular tip fracture patterns, wear on the proximal edges of the lithic where it would have been bound, wear on the dorsal or ventral surface from abrasion against the haft, and the presence and pattern of organic materials used as binding agents (Fischer, 1984; Shea, 1988; Lombard, 2004, 2005; Villa et al., 2009a,b).

Patination patterns in a lithic from Blombos Cave, South Africa, and a Mousterian lithic from Quneitra, Israel have been used to infer that they were hafted (Friedman et al., 1994-1995; Villa et al., 2009b). Patination is created when the lithic is exposed to atmospheric conditions, and a lack of patina in a distinct pattern can indicate the former presence of a haft, a result that has been replicated experimentally (Villa et al., 2009b). One of the Blombos lithics also has a resharpening pattern that was most likely produced by working the tool while in a haft (Villa et al., 2009b).

The presence and patterns of particular organic substances, such as plant materials, resins, and ochre can indicate hafting. The oldest known lithics with organic substances for hafting are from a Middle to Late Pleistocene site in central Italy, where they are associated with elephant remains (Mazza et al., 2006; Modugno et al., 2006). Birch-bark pitch with imprints from hafting has been found at the MP site of Königsau, Germany (Grünberg, 2002). MSA lithics from Sibudu, South Africa, demonstrate the presence of such materials at or near the proximal end of the lithic more often than the medial or distal end, where they would have been of use to the hafting process (Lombard, 2005). At the MSA site of Rose Cottage, South Africa, a number of plant residues are found significantly more often on the backed (blunted) edge of the tool (Gibson et al., 2004). Vegetal substances indicative of hafting were found on approximately half of the tools analyzed at the MP sites of Buran Kaya and Starosele, Ukraine (Hardy et al., 2001), and are present at the MP sites of Biache-St-Vaast, France and El Kowm Basin, Syria,

and the MSA sites of Africa, GwJill, Kenya and Apollo 11, Namibia (Wendt, 1976; Beyries, 1987; Boëda, et al., 2002; Gibson et al., 2004).

When a stone tool is hafted, particular wear patterns may develop on the lithic as a result of bindings or abrasion against the haft itself. These include edge-rounding, edge damage, polish, and striations (Odell and Cowan, 1986; Lombard, 2005). Lithics from Buran Kaya and Starosele demonstrate these distinctive wear patterns, and a few have impact fractures as well (Hardy et al., 2001). At the Levantine MP sites of Kebara and Qafzeh, Israel, approximately 12% of employed tools bear these wear patterns (Shea, 1988, 1989). At Sibudu, edge-rounding, polish, and striations are all present, and the distribution of these are concentrated at the proximal ends of the lithics, where such effects would be expected if they were due to hafting (Lombard, 2005).

Levallois points from MP assemblages at Oscurusciuto and Asolo in Italy, and Bouheben, France, have burin-like, step-terminating, and crushing impact fractures (Mussi and Villa, 2008; Villa et al., 2009a). Several Mousterian points from La Cotte de St Brelade, France, and approximately 7% of employed lithics from Kebara and Qafzeh demonstrate such impact fractures (Shea, 1988, 1989; Villa and d'Errico, 2001). Similar fractures have been also observed in the MSA, at Blombos Cave, Rose Cottage Cave, and Sibudu, South Africa (Harper, 1997; Lombard, 2005; Mussi and Villa, 2009, Villa et al., 2009b). Experimental studies have re-created these types of fractures by throwing and thrusting hafted lithics (Fischer, 1984; Odell and Cowan, 1986; Lombard, 2004), and thus they are generally considered to be diagnostic of use as a weapon (Fischer, 1984; Lombard, 2004, 2005; Mussi and Villa, 2008, 2009; Villa et al., 2009a; 2009b). However, Shea (2006) suggests that such fractures may be produced on hafted lithics used as chisels or carving tools, or may result from production failures.

The final, and probably strongest, argument for hafting in the MP of Europe and MSA of Africa is the presence of stone tools lodged into the remains of prey. In South West Asia, a fragment of a levallois point embedded in the vertebra of a wild ass is known from a Mousterian assemblage at Umm el Tlel, Syria (Boëda et al., 1999). The authors indicate that for the point to become deeply embedded (having passed through the vertebral pedicle) it must have been firmly hafted. Similarly, a lithic fragment embedded in the vertebra of a buffalo is known from the MSA site of Klasies River Mouth, South Africa (Milo, 1998). The faunal remains include a total of 18 bones with broken fragments of tools embedded in them, the majority of which were left behind during butchering. One embedded lithic fragment in particular is distinct in being larger than any known butchering tool, and the size and shape of the puncture wound are unique. An additional vertebra with a puncture wound is present, and despite the lack of a lithic in the wound, the shape and size are highly indicative of an injury produced by a hafted tool. Thus, it is clear that hafting of lithics is present in both Europe and Africa prior to the UP, and at least some of these hafted tools were used as hunting weapons (spears), either thrust or thrown (Milo, 1998; Boëda et al., 1999; Lombard, 2004).

Although in many ways similar, the MP and MSA are not equivalent (Brooks et al., 2006), and may vary in the relative frequency of hafting. Several authors argue that, in contrast to its occasional occurrence in the MP, hafting was probably routine throughout the MSA (McBrearty and Brooks, 2000; Brooks et al., 2006; Mohapi, 2009). African MSA assemblages include points in a variety of regional styles (McBrearty and Brooks, 2000; Brooks et al., 2006). These authors argue that the shape and size of MSA points suggest both hafting, and use as projectile weapons, possibly even arrow tips. The Howiesons Poort (HP) industry from the late MSA in particular includes a number of microliths, which have generally been considered to

have been projectile points or spearheads (Singer and Wymer, 1982; Deacon, 1989; Wadley and Mohapi, 2008). The presence of notches in approximately 19% of such tools at Klasies River Mouth, South Africa, strongly suggests that they were at least hafted (Singer and Wymer, 1982; Wurz, 1999), and the very small size and balanced shape around the midline of these points have been used to argue for their use as arrow tips (McBrearty and Brooks, 2000; Brooks et al., 2006; Wadley and Mohapi, 2008). Detailed morphological analyses of the Howiesons Poort assemblages from Sibudu and Umhlatuzana have concluded that both spearheads and arrowheads are present (Wadley and Mohapi, 2008; Mohapi, 2009). Furthermore, experiments demonstrate that these lithics are capable of killing prey when used as a hafted projectile (Pargeter, 2007). However, Villa and Lenoir (2010) argue against HP microliths as arrowheads due to their relative rarity in HP and absence from later MSA and LSA assemblages, and the lack of any other evidence for bows and arrows until the Holocene in Africa. Rather, they argue that the HP backed microliths were an innovative way of hafting spear points.

In addition to stone points and microliths, several bone objects are known from the MSA (McBrearty and Brooks, 2000). These include polished bone tools from Grotte d'el Mnasra, Morocco, a bone point of questionable association from Kabwe, Zambia, two warthog tusk 'daggers' from Border Cave, South Africa, a cylindrical bone point from Klasies River Mouth, South Africa, several barbed bone points from Katanda, D.R. Congo, two cylindrical bone points from Blombos, South Africa, and bone points from White Paintings Shelter, Botswana, and Peers Cave and Sibudu, South Africa (Singer and Wymer, 1982; Hajraoui, 1994; Yellen et al., 2005; McBrearty and Brooks, 2000; d'Errico and Henshilwood, 2007; Backwell et al., 2008). The Katanda barbed points would have been ineffective as harpoons, and McBrearty and Brooks (2000) have suggested they were spear points. Morphometric analyses place the Blombos and

Peers Cave points in the range of modern spear points, but the bone points from Sibudu and Klasies River fall in the range of modern arrow heads (d’Errico and Henshilwood, 2007; Backwell et al., 2008). As with the HP microliths, despite the shape and size similarity, designating these objects as arrow heads is questionable, given the lack of other evidence for bows and arrows until the Holocene in Africa (Villa and Lenoir, 2010). Function of the remaining artifacts has not been determined, and it is difficult to ascertain the significance of this group of artifacts. At minimum it can be said that bone points were present, but not common or widespread in the MSA.

Although several bone and antler objects have been found at LP and MP sites in Europe, there is currently only a single known bone point from the MP of Europe, from Großen Grotte, Germany (Wagner, 1983). McBrearty and Brooks (2000) suggest that the presence of bone points in MSA but not (or extremely rarely) in MP contexts is associated with more advanced projectile technology in the MSA. Alternately, Villa and d’Errico (2001) suggest that differences in organic tool use in the MP versus the MSA reflect differences in game choice and hunting method rather than technological skill. Specifically, they note that ethnographic evidence indicates that bone and antler points tend to be used against smaller game, and used with longer range projectile weapons. Stone points from the MP tend to be larger and were likely used with larger hafts, a technique which is more effective for hunting larger animals at close range. Lithic points are sharper and draw more blood, and as such would have been better in certain contexts. In the UP, there is evidence for hunting of smaller bodied prey, and small lithic or bone points on longer range weapons would have been more effective for this type of hunting.

If hafting of projectiles was present in the MP, the frequency and complexity of these objects likely increased dramatically in the UP. The MP to UP transition is defined by an

increase in blade-based assemblages (Mellars, 1989; Bar-Yosef, 2002). Although blades were present at sites across Eurasia prior to the UP (Brose and Wolpoff, 1971; Bar-Yosef and Kuhn, 1999), blades from the UP were more often manufactured using soft hammer or indirect percussion techniques, which results in a more standardized product (Mellars, 1989; Bar-Yosef and Kuhn, 1999). These types of highly standardized lithics would have been ideal for composite tools, as they could be removed from a haft and replaced, resulting in an almost identical tool (Mellars, 1989; Bar-Yosef and Kuhn, 1999). Furthermore, the production of bladelets is present in the EUP and becomes common in the later UP (Bar-Yosef, 2002). Blades are also highly standardized in size and shape, and are generally too small to have been used independently, suggesting their use in composite tools (Bar-Yosef and Kuhn, 1999). The increased reliance on composite tools in the UP has been argued to indicate a shift from quickly made and easily replaced tools to higher investment (curated) toolkits. The latter would require more time and effort to produce, but would allow easy replacement of component parts, and as such increase reliability (Mellars, 1989; Bar-Yosef and Kuhn, 1999). Teyssandier et al. (2008) suggest that several types of EUP transitional point forms may have been local variations of the common goal of arming spear tips. A variety of types of points that were clearly hafted based on the presence of backing or tangs attests to continued importance of hafting of projectiles through the MUP and LUP (Peterkin, 1993).

In addition to lithic technologies, bone and antler weaponry becomes common in Europe beginning in the EUP (Knecht, 1997). Morphological and temporal classification systems have been created to describe the various EUP organic points (Peyrony, 1933; Knecht, 1991, 1993), and all have been demonstrated experimentally to function as long range weapons (tested with a crossbow) (Knecht, 1997). Bone and antler projectile points are significantly more labor

intensive to make than similar lithic points, but are less likely to fracture during use and are more repairable (Knecht, 1997). As such, they signify a shift towards increased investment in long-lasting tools, consistent with the shift from flakes to blades in the UP.

In contrast to the MP/UP transition, the MSA/LSA transition represents a shift from point dominated to backed microlith dominated assemblages (Ambrose, 2002). The transition is not abrupt, as Howiesons Poort assemblages contain backed microliths and the earliest LSA assemblages contain few backed microliths, and are defined as LSA by size alone (Wadley, 1993; Ambrose, 2002). Bone points were present in the MSA, and do not greatly increase in frequency in the LSA (Wadley, 1993). Since hafting was clearly present and possibly routine in the MSA, the transition to microliths is likely not a result of increased hafting in general, as in the UP (Ambrose, 2002), but instead may represent an increased reliance on hafting for effective projectiles (Shea, 2006).

Shea (2006) and Hughes (1998) suggest an increase in hafting for darts or arrow heads in both the UP and LSA, based on an analysis of lithic tip cross sectional areas (TCSA), as TCSA will influence flight and penetration. Using modern projectile points as analogs, Shea (2006) compared TCSAs of MP/MSA and UP/LSA lithics, and found that MP/MSA lithics are significantly larger in TCSA than known projectile points, and more closely resemble thrusting spear points. In the initial Upper Paleolithic (IUP), lithic TCSAs begin to resemble TCSAs of known dart tips. However, Shea (2009) later notes that the current sample of MP points is inadequate to conclusively reject that Neandertals used long-range weaponry. In a separate analysis, it was found that TCSAs of the Howiesons Poort MSA microliths are consistent with TCSAs of modern arrowheads or dart tips (Pargeter, 2007, Mohabi, 2009), potentially indicating the presence of projectile technologies in Africa at least sporadically prior to the LSA.

In the above study, Shea compares MP/MSA TCSAs to modern dart tips, arrows and thrusting spears, but not throwing spears. Little evidence for darts or arrows exists in the MP/MSA (excluding the HP material) thus if these were used as projectiles, they were likely used as spear points, not dart or arrow tips. Although the hypothesis was not tested, given that spears tend to be dual purpose weapons (see chapter 2), it would not be surprising if throwing spear points were indistinguishable in TCSA from thrusting spear points, and the similarity between MP/MSA lithics and thrusting spear points would also apply to throwing spear points. This would imply that the important contrast between the MP/MSA (excluding HP) and the UP/LSA is instead a transition from larger spear tips, to smaller spear tips that were designed specifically for their projectile properties. This is still an important distinction, as better projectile aerodynamics may have had a significant effect on hunting ability, but does not imply the absence of thrown weapons in the MP/MSA.

Incontrovertible evidence of long range projectile weaponry in the form of actual spear throwers or bows is first found in the late Mid Upper Paleolithic (MUP), with a small spear thrower made of antler from Combe-Saunière cave, France, dated to 17,000 – 19,000 BP (Cattelain, 1989). By the Late Upper Paleolithic (LUP), these objects are quite common in Europe, particularly in the Magdalenian of France (Garrod, 1955; Cattelain, 2005). Spear throwers are highly effective long distance throwing weapons, capable of reaching distances up to 100 m or more, although throwing distances with high accuracy are likely closer to 30 m (Cattelain, 1997; Hutchings and Brüchert, 1997). Spear throwers were originally thought to function as a ‘catapult’, whereby the arm was effectively lengthened and greater rotational velocity was achieved (Raymond, 1986). However, when thrown correctly, the spear is not catapulted but travels in a straight line. Rather, the increased lengthening of the throwing arm

functions to maintain contact with the spear for a longer time, including the downward thrust at the end of the throw, and thus transfer more energy to the spear (Howard, 1974; Raymond, 1986). At the point in the throw when a hand thrown spear is released, the spear thrower maintains contact with the spear, and the downward thrust of the arm which follows is converted into forward thrust for the spear (Howard, 1974; Raymond, 1986). Additionally, it appears that the spear thrower provides a better grip, which seems to improve accuracy (Howard, 1974), and may also have biomechanical effects. These weapons have been demonstrated experimentally to be capable of fatally wounding animals as large as deer from up to 20 m (Cattelain, 1997; Callahan, 1994).

Bows do not appear in the archaeological record of Europe until the final part of the LUP (Cattelain, 1997), but since bows are made entirely of wood and have no bone, antler, or stone components (besides projectile points), they would be less likely to preserve than spear throwers. Bows are also highly effective long distance weapons, achieving maximum shooting distances potentially as far as 185 m (Cattelain, 1997), depending on the size of the bow. Accurate shooting distances are much shorter, but still farther than spear throwers at up to 45 m (Cattelain, 1997).

Both spear throwers and bows would have provided a significant improvement in hunting success over thrown or thrust spears, and reduced the hunter's risk of injury. In fact, spear throwers have been demonstrated to increase throwing distance by around 58% compared with hand thrown spears in amateur throwers (Howard, 1974). Thus these tools provide a great improvement over the hand thrown spear, and likely overwhelm the effect of anatomical variation on throwing velocity. Furthermore, although using a spear thrower could potentially be similar biomechanically to throwing a spear by hand, the specific physical and biomechanical

requirements are not yet known. Thus the spear thrower will not be considered ‘throwing’ a spear for these purposes.

Summary.

Large wooden artifacts potentially used as throwing spears first appear in the archaeological record around 400 kya in Europe. Beginning in the MP of Europe and the MSA of Africa, lithics are found with wear on the proximal edges from binding, wear on the dorsal or ventral surface from abrasion against a haft, and evidence of organic materials used as binding agents, all indicative of hafting. During the UP/LSA, lithics become smaller and more consistent in size and shape, a trend suggesting increased curation of hafted tools. Bone points are present in both the MSA and LSA, and become frequent in the UP. Thus, overall it appears that hafting was present prior to the UP and LSA, but likely increased in frequency around the MP/UP and MSA/LSA transitions. The presence of particular tip fracture patterns and lithics embedded in prey suggest the use of hafted objects as thrown or thrust spear tips starting in the MP/MSA, and the frequency of bone/lithic points and curated tools in the UP suggest increased use of hafted lithics as projectiles starting in the EUP. The size and shape of MP/MSA lithics indicate that they were not regularly used for dart or arrow tips until the IUP and LSA at the earliest, and actual spear throwers show up in the archaeological record at the end of the MUP. Even assuming spear throwers were used prior to their first occurrence in the archaeological record, they were probably not common or widespread prior to the end of the MUP. Thus, the archaeological record indicates that the throwing of hand-delivered spears potentially began prior to the MP, was present if not ubiquitous in the MP/MSA, and became very common in the UP/LSA. From the late MUP, highly effective long range throwing weapons were in use, although it remains unclear to what degree this would have replaced the use of hand thrown spears.

II. Anatomical evidence for throwing.

The modern human glenoid fossa is shallow and laterally oriented, allowing a great range of humeral mobility. This allows for the large external rotation, abduction, and extension (horizontal abduction) angles used during throwing (see figures 5.7-8 for motion descriptions). Patterns of change in shoulder anatomy in fossil hominins may therefore be indicative of selection for or increased ability to throw. The earliest hominins for which such data are available, the gracile australopithecines, have cranially oriented glenoid fossae reminiscent of the great ape configuration, and likely reflecting a continued adaptation for climbing (Stern, 2000; Alemseged et al., 2006; Green and Alemseged, 2012; Larson, 2012). Humeral torsion, the angle between the orientations of the proximal and distal ends of the humerus, is also lower in early hominins than in modern humans (Larson, 1996).

Specimens with preserved shoulder elements attributed to the genus *Homo* include KNM-WT 15000 (*H. erectus*), and several individuals from Dmanisi variously attributed to *H. erectus* or *H. habilis* (Meyer, 2005; Lordkipanidze et al., 2007). Measurements of the orientation of the Dmanisi scapulae by different researchers are divergent, resulting in scapular orientations either within the modern human range or below it (a more cranially facing glenoid fossa) (Lordkipanidze et al., 2007; Larson et al., 2009). However, the scapular orientation of the nearly complete KNW-WT 15000 specimen indicates a fully modern configuration in *H. erectus*. In contrast, humeral torsion values continue to fall below the modern human range of variation in these early *Homo* specimens, and clavicular length appears to be small relative to humeral length, both traits likely retaining the primitive condition (Larson et al., 2009). Humeral torsion allows the elbow to function parasagittally despite a medially oriented humeral head, and the low torsion angles observed in australopithecine and early *Homo* species suggests an elbow

flexion/extension orientation that would have been less than ideal for throwing. Larson et al. (2009) instead suggests a configuration of the shoulder in early *Homo* where the scapulae are positioned laterally with an anterior facing glenoid, which would retain parasagittal function of the elbow despite low torsion angles and short clavicles. However, it is argued that this position is also poorly configured for throwing, as the humerus would likely have very narrow range of motion in horizontal abduction (extension of the arm while in abduction). Thus, in either case, the shoulder anatomy of early *Homo* likely did not allow for a modern throwing action.

The earliest indication of a modern shoulder configuration is with absolutely long clavicles from Atapuerca, attributed to *H. antecessor* (Carretero et al., 1999), however no humeri are known from this site to confirm the relative length of the clavicles. MP and UP early modern humans display relative clavicle lengths comparable to recent modern humans (Voisin, 2006; Larson et al., 2009), indicating modern clavicular proportions from the origin of the species. Neandertals, both European and Near Eastern, display even greater clavicle lengths (relative to humeral length) than recent modern humans (Vandermeersch and Trinkaus, 1995; Voisin, 2004, 2006; Larson et al., 2009), which may be associated with a scapula positioned higher on the thorax (Voisin, 2004, 2006). One author has even suggested that a greater clavicle length may have allowed Neandertals greater throwing ability than early modern humans (Voisin, 2004). Neandertal clavicular length is not large relative to estimates of body mass, however (E. Trinkaus, personal communication), and thus this difference may simply be due to body size variation.

Humeral torsion angles decrease in *H. heidelbergensis* and Neandertals compared with earlier hominins, however remain slightly high compared with recent modern humans (Vandermeersch and Trinkaus, 1995; Carretero et al., 1997). This is potentially explained by

scapular position, where a more anterior orientation of the glenoid may have necessitated lower torsion angles to maintain optimal positioning of the elbow (Vandermeersch and Trinkaus, 1995; Rhodes and Churchill, 2009). It has also been suggested that patterns of variation in humeral torsion may be related to throwing (Rhodes and Churchill, 2009), as repetitive behaviors such as throwing prior to developmental maturity result in lower torsion angles in modern humans (Cowgill, 2007). Indeed, throwing athletes such as baseball and handball players tend to have a high degree of bilateral asymmetry in humeral torsion angle, and lower torsion angles than non throwing athletes (Crockett, 2002; Osbahr et al., 2002; Rhodes and Churchill, 2009). Decreased humeral torsion is associated with external rotation range of motion, and this difference may have performance effects during throwing (Roach et al., 2012).

It is unlikely that low torsion angles are reflecting throwing behaviors in Neandertals, as between limb and between sex comparisons are opposite of what would be expected, assuming handedness and sexual division of labor were present (Rhodes and Churchill, 2009). Rhodes and Churchill (2009) conclude that this result indicates that Neandertals were not throwing habitually. However, patterns of humeral torsion in the early modern human and modern human samples do not follow predictions based on throwing either (between sex comparisons, comparisons between likely throwing and non-throwing samples). In fact, the only predictable pattern in humeral torsion among modern human samples is that dominant limbs tend to have lower torsion angles, even in samples for whom throwing was not habitual (European and African Americans). Thus, it is more likely that humeral torsion angles do not track throwing in any consistent manner, and thus do not provide information about any of the samples examined. More importantly, Neandertal humeral torsion values fall within the range of variation of modern humans, indicating that they were not functionally limited by this feature. Rather, independent of

the cause of the torsion angles, Rhodes and Churchill (2009) point out that decreased torsion angles (within a functional range) may in fact be beneficial, as they allow for greater external rotation (Roach et al., 2012), providing more distance over which to accelerate a thrown object. Thus, patterns in torsion angles across Late Pleistocene samples should probably not be considered reflective of throwing behavior, but may be relevant to biomechanical comparisons of throwing ability.

Besides scapular orientation, which appears largely in its modern form by *H. erectus*, the shape of the glenoid fossa varies between groups (Churchill and Trinkaus, 1990; Trinkaus, 2008; Churchill and Rhodes, 2009). When considered relative to its superior-inferior dimension and relative to humeral articular dimensions (proximal and distal), the Neandertal glenoid fossa is dorso-ventrally narrow, a pattern which appears to be primitive based on the condition in KNM-WT 15000, Dmanisi, and several specimens from Atapuerca (Churchill and Trinkaus, 1990; Di Vincenzo et al., 2011). Furthermore, this pattern appears to be shared by the MP specimens Qafzeh 8 and 9, although these are too incomplete to be conclusive (Trinkaus, 2008; Churchill and Rhodes, 2009). The shape of the glenoid fossa does not appear to correlate with thoracic shape, robusticity, or body size within samples of archaic and modern humans, and asymmetry between sides is very low (Trinkaus et al., 1994; Churchill, 1996).

Churchill and Rhodes (2009) argue glenoid fossa shape primarily reflects the selective history of the population. The wider glenoid of the UP and later humans would have been better configured to withstand the large joint reaction forces experienced at the shoulder during throwing, which can be as large as 400 Newtons (N) posteriorly, and 75 N anteriorly during a baseball throw (Meister, 2000). It is suggested that this anatomy may have reduced the likelihood of developing degenerative osteoarthritis of the shoulder (Churchill and Rhodes, 2009), while the

narrower breadth of the pre-UP hominins may reflect absence of selection on the shoulder for throwing (Churchill and Trinkaus, 1990; Trinkaus, 2008). Alternatively, Di Vincenzo et al. (2011) claim that the onset of projectile weaponry is not sufficient to explain the pattern of change in glenoid shape over hominin evolution. Instead, these authors argue that delayed maturity and a longer developmental period over hominin evolution would have resulted in increased bone deposition at the secondary center of ossification, and consequent dorso-ventral expansion of the glenoid fossa.

Muscle size, as indicated by muscle insertion area (but see Chapter 4 for a critique of this technique), for several muscles which are known to be important in throwing are significantly different between MP and UP hominins, potentially indicating habitual throwing. As indicated by research on baseball pitching, the supinator muscle is used to control pronation of the forearm as the arm decelerates after ball release (Fleisig and Escamilla, 1996). Its attachment on the proximal ulna has been used to infer habitual spear throwing in populations of modern humans (Peterson, 1998; Kennedy, 2004). Churchill and Rhodes (2009) found that the supinator crest is significantly smaller in Neandertals and MP early modern humans, versus UP and recent modern humans. However, the supinator crest was also larger in females versus males, and on the left versus the right, in a number of samples, including a sample known to use spear throwers. This casts doubt on the premise that the size of the supinator crest is reflective of habitual throwing.

Fibers of the deltoid are active in all phases of overhand throwing to obtain and maintain the arm in an abducted position (DiGiovine et al., 1992). The relative size of the insertion for the deltoid is significantly narrower in Neandertals than any early or recent modern human sample, and it is smaller in MP early modern humans than any other human sample, although the difference is not significant (Endo, 1971; Churchill and Smith, 2000; Churchill and Rhodes,

2006). This feature appears to be primitive, based on several early *Homo* specimens (Carretero et al., 1997). Furthermore, deltoid tuberosity width is larger for males than females in all samples, and smaller in relatively less active samples, lending weight to the conclusion that these differences track a habitual behavior, potentially throwing. However, Carretero et al. (1997) argue that greater deltoid tuberosity width is related to greater humeral retroversion angles. Thus, the higher retroversion angles of all samples prior to early modern humans would explain the narrowness of the deltoid tuberosity in Neandertals, and it may not be a useful indicator of behavior inter-specifically.

Another potentially relevant area of the anatomy to consider are the vertebrae, as these may provide information about the relative size of the spinal cord and its branches into the upper limb. The brachial plexus of nerves, which control the upper limb musculature, exit the spinal cord through the intervertebral foramina of the the fifth through eight cervical vertebrae and the first thoracic vertebra. The relative size of the skeletal structure surrounding the spinal cord in this region should be indicative of the relative size of the nerves themselves, which in turn, should be indicative of the level of neuro-muscular complexity of the upper limb (MacLarnon, 1995). Given that the upper limb was most certainly involved in a great number of manipulative behaviors, spinal cord dimensions cannot be tied directly to throwing behaviors, but coordinated high speed throwing is unlikely to have preceded increases in brachial plexus size.

The size of the vertebral foramen for C7 in KNM-WT 15000 is somewhat small relative to vertebral body size (MacLarnon, 1993). However, Carretero et al. (1999) point out that it is well within the recent human range of variation, and vertebral foramina sizes are highly variable across species and time. A *H. antecessor* specimen from Atapuerca has a relatively large vertebral foramen, while a later specimen from the same region assigned to *H. heidelbergensis*

has a relatively small vertebral foramen (Carretero et al., 1999). The fossil specimens from Dmanisi also retain measureable vertebrae, and these specimens all show modern-sized vertebral foramina (Meyer, 2005). The dimensions of the spinal canal in available Near Eastern Neandertals are all comparable to that of early modern and recent human samples (Trinkaus, 1995). Thus, there does not appear to be a consistent pattern of change in spinal canal size over time, but seems to take a consistently modern form by at least the MP.

Summary.

The orientation of the glenoid fossa, the relative length of the clavicle and the angle of torsion of the humeral head are relevant to humeral positioning and thus throwing ability. In pre-*Homo* hominins, glenoid fossa orientation and humeral torsion values retain the primitive condition. Glenoid fossa orientation appears to be modern by *H. erectus*, but in the earliest hominins from the genus *Homo* for which such data are available, relative clavicle lengths and humeral torsion angles continue to be primitive. Possibly by *H. antecessor*, but certainly by *H. neanderthalensis*, clavicle lengths reach the modern human range. Humeral torsion angles are slightly lower in pre-recent modern humans, but these values would not have impaired throwing ability, and may in fact have improved it. Furthermore, the size of the spinal canal, which is likely indicative of the neuro-muscular complexity of the upper limb, is modern by *H. neanderthalensis*. The shape of the glenoid fossa and the insertion for the deltoid muscle are narrow prior to the UP, and these have been considered counter-indicative of habitual throwing. However, alternative explanations have also been presented. Thus, the anatomical evidence suggests that most features required for throwing were modern by the MP, and there is no conclusive evidence that throwing was not present or habitual prior to the UP.

III. Evidence for hunting.

The presence of hunting implements in the archaeological record indicates the ability of the makers to hunt, but additional detail may be gained by considering evidence for the relative amount of meat in the diet. As discussed in chapter 2, environmental and climatic variation may reflect the relative amount of meat in a hunter-gatherer's diet, and thus provide information about the importance of hunting (as a function of the importance of hunting in general) to fossil populations. Furthermore, diet can be examined directly in several ways, including analyzing faunal assemblages at hominin sites, and from chemical analyses of surviving tissues in the fossil specimens themselves. The following is a brief overview of the available evidence concerning hunting ability and meat in the diet during the MP/MSA and UP/LSA.

The Middle to Upper Pleistocene in Europe saw a gradual climatic shift towards colder, drier glacial cycles (Gamble, 1986). The European Upper Pleistocene is characterized by a short interglacial followed by increasingly glacial conditions, peaking around 18 kya. During this period, ice sheets covered much of northern Europe, with permafrost extending down almost to the Mediterranean (Gamble, 1986). During warmer phases, plant resources would have been available seasonally in the form of deciduous forests. During the coldest phases, polar desert would have covered most of northern Europe, and plant resources would have been available only in southern portions of the continent, particularly areas of Spain (Gamble, 1986). Thus, European Middle and Upper Pleistocene hominins are expected to have made increasing use of animal resources as the climate worsened towards the last glacial maximum.

Evidence from faunal assemblages indicates a heavy reliance on animal resources obtained by hunting during the Middle and Upper Pleistocene of Europe (Marean and Assefa, 1999; Patou-Mathis, 2000; Richards et al., 2000; Stiner, 2002). Despite some researchers' early

claims that Neandertals were not capable hunters (Binford, 1985; Mellars, 1989), many sites across Europe, including sites as far west as France and as far east as Russia have faunal assemblages indicative of skilled hunting as far back as the late Middle Pleistocene (Marean and Assefa, 1999; Patou-Mathis, 2000; Stiner, 2002). These sites have faunal assemblages that are often dominated by a single species, prime aged adult animals, and more desirable skeletal elements. Some Neandertal sites in the Mediterranean, where the climate would have been more favorable, also show use of marine resources (Stringer et al., 2008). Although the frequency is difficult to demonstrate due to poor preservation, there is clear evidence that Neandertals consumed plant foods as well, including charred seeds, fruit, and other plant remains at sites from the Near East (Hardy, 2010), and starch grains in dental calculus from Europe (Hardy and Moncel, 2011; Hardy et al., 2012). With the emergence of the Upper Paleolithic, skilled hunting remained highly important (Grayson and Delpech, 2002), but there may have been a shift towards a broader diet (Grayson and Delpech, 1998; Stiner et al., 1999; Hoffercker et al., 2009). This includes both a wider variety of the same large bodied ungulates hunted by Neandertals (Grayson and Delpech, 1998), but also includes more small bodied prey species (Stiner et al., 1999; Stiner, 2002; Stiner and Munro, 2002; Hoffercker et al., 2009). This shift was likely a response to increasing population density through the UP (Stiner et al., 1999; Stiner, 2002; Stiner and Munro, 2002).

Chemical analyses of the ratio of stable isotopes of carbon and nitrogen from bone collagen confirm the abundance of meat in the Neandertal diet (Fizet et al., 1995; Richards et al. 2000, 2008; Bocherens et al., 1999, 2005). The ratios of nitrogen isotopes in bone collagen reflect the source of dietary protein consumed by the individual over several years prior to death (Richards et al., 2000). By comparing these values with values from other animals from the same

site, the trophic level of the individual can be determined. Stable isotope values from specimens from Croatia, France, Germany and Belgium indicate Neandertals were top level carnivores (Fizet et al., 1995; Bocherens et al., 1999, 2005; Richards et al., 2000, 2008; Richards and Trinkaus, 2009). Consistent with the zooarchaeological evidence, stable isotope values for European early modern humans reflect a broadening of the diet to include a wider range of food resources, including freshwater fish and fowl and marine mammals beginning in the MUP (Richards et al., 2001, 2005; Pettitt et al., 2003; Richards and Trinkaus, 2009).

Climate change also occurred in Africa over the Middle to Upper Pleistocene, where the climate was warmer and wetter than current conditions until around 115 kya, followed by a gradual cooling and drying (Carto et al., 2009). This resulted in a reduction of rainforests, and an expansion of grasslands (Carto et al., 2009). Much of northern, western and eastern Africa would have been too dry for occupation, and hominins would have been confined to the grasslands and coasts (or expanding out of Africa), making use of animal and plant resources abundant in this climate (Carto et al., 2009).

Like MP hominins, MSA hominins were capable hunters, and exploited large-bodied ungulate prey as effectively as LSA hominins (Faith, 2008). The use of marine resources had an earlier origin in Africa, as assemblages from southern coastal MSA sites dating as far back as ≈ 164 kya have numerous shellfish and seal remains (Marean et al., 2007; Steele and Klein, 2008). The use of marine resources on the Southern coast of Africa may be related to lesser availability of terrestrial foods in this region (Klein et al., 2004). There are differences in diet breadth and marine resource exploitation across the MSA/LSA divide, where LSA sites have greater diet breadth and more intensive exploitation of marine resources (Klein et al., 2004;

Faith, 2008; Steele and Klein, 2008). This is explained as a response to increased population density, comparable to the change in diet breadth from the MP to the UP (Steele et al., 2009).

From the above evidence, it would seem that selective pressures regarding throwing ability would have been different between Neandertals and early modern humans occupying Europe in the Middle and Upper Pleistocene, and between these and MSA/LSA early modern humans. The increasingly cold climate would have theoretically increased the importance of animal resources to the diet for European hominins, and thus the importance of hunting to survival. However both European and African early modern humans appear to have also experienced increasing population densities, and responded by increasing diet breadth. Although some of the new food resources could have been spear hunted (rabbits, etc.), evidence from modern hunter-gatherers suggests that spear hunting is more commonly used for larger-bodied prey (see chapter 2). The coincident increase in more aerodynamic projectiles in the EUP/LSA and long range projectile technology that began in the MUP may be well explained by this change in diet breadth, and the need to hunt animals not easily caught with large throwing or thrusting spears (Churchill, 1993).

Summary.

Neandertal and early modern human populations from the MP, UP, MSA and LSA were all capable hunters, and their diets contained a large proportion of meat. However, hunting patterns changed slightly at the MP/UP and MSA/LSA boundaries, with a greater range of prey species hunted in the UP/LSA. This change was likely a result of increased population density, and is consistent with dietary evidence for increased diet breadth around this time. Increased use of small prey species and marine resources would likely be associated with a decrease in the use of thrown spears, as spears are most effective hunting large bodied animals. Thus, this pattern is

consistent with the contemporaneous onset of smaller more aerodynamic spears and later spear throwers, which would have been ideal for hunting smaller bodied prey.

Chapter 4

Biomechanics of Throwing

The goal of spear throwing is to hit and penetrate the skin of animal prey. Thus, one must transfer as much energy as possible to the spear prior to its release (also taking into account aim). Doing so requires the coordinated actions of the whole body, in a particular order and pattern, to generate energy and maximally transfer it to the hand and spear. The kinetic energy (K_e) of the spear as it leaves the hand can be measured as $\frac{1}{2} MV^2$, where M is the mass of the spear and V is its velocity. Thus, for a spear of a given mass, K_e will be a function of the velocity of the hand at release. Velocity of the hand will be a function of both linear and angular motions. Linear velocity can be generated by the legs pushing off the ground, and the muscular actions of the torso, propelling the body forward (and bringing the arm along) (Stodden et al., 2006). Angular velocity can be generated by torques in the pelvis, torso, shoulder, elbow, and wrist, as well as stretching and release of tendons, and centripetal forces, causing angular movements around the joint centers. These motions should be coordinated such that they are additive and velocity is maximal at the hand just before spear release. The following is a discussion of how maximal throwing velocity is achieved in modern athletes, how variation in anatomy may affect this pattern, and how these principles may be applied to fossil hominins.

I. Biomechanics of throwing in modern humans.

The research to date on the biomechanics of throwing has shown that the kinetics and kinematics of throwing are qualitatively similar in baseball, football and handball (Fleisig and Escamilla, 1996; Loftice et al., 2004), indicating that there is a basic pattern for over-arm throwing used by most competitive athletes. Although throwing a spear may be more similar to

throwing a javelin or even a football than a baseball, javelins are thrown to optimize distance rather than force and aim at close range, and there is not a great deal of research on the relationship between anatomy and throwing performance for javelin or football throwing (Best et al., 1993; Morriss and Bartlett, 1996). Thus this discussion will focus on baseball throwing (the most thoroughly researched throwing behavior), with additions from other throwing sports where available. Furthermore, it has been shown that baseball pitching and regular overhand throwing of a baseball are not qualitatively different, and thus they will be discussed interchangeably here.

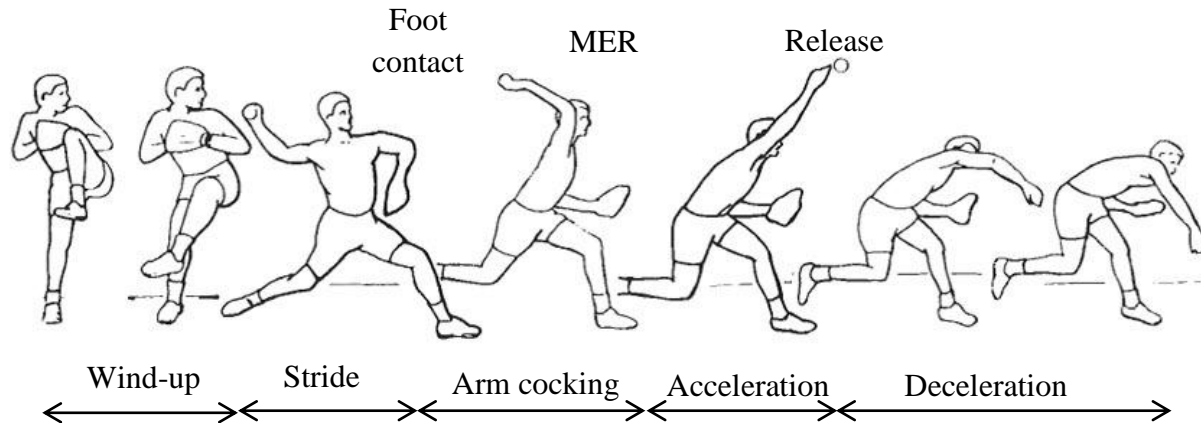


Figure 4.1 Phases of a baseball throw. Wind-up phase: beginning of throw until initiation of stride. Stride phase: initiation of stride to foot contact. Arm cocking: foot contact to maximum external rotation (MER). Acceleration: MER to ball release. Deceleration: release to end of throw. Modified from Dillman et al. (1993).

An over-arm throw is typically described as having six phases: windup, stride, arm cocking, arm acceleration, arm deceleration, and follow-through (figure 4.1). For the following descriptions, angles and joint positions are defined as in figures 5.7-9 for a right handed individual. The following description of the phases is after Dillman et al. (1993). The wind-up phase begins the throw, as the thrower raises the left leg and prepares to step forward. The left

leg is flexed and the body is rotated 90° so that the left shoulder is facing forward. The throwing arm is also brought backward in preparation. The stride phase follows, as the left leg steps forward. The supporting leg (the right) flexes slightly, lowering the body. The torso is tilted backwards, to provide as much room for forward movement as possible in the following phases. The thrower places the stride foot directly in front of the supporting foot, in order to allow room for the hips to rotate fully forward. As the left leg moves forward, the pelvis and torso follow, and the pelvis reaches maximum velocity during the arm cocking phase, followed by a quick deceleration from the braking of foot contact. The torso continues to move forward until after ball release. The stride phase ends when the stride foot contacts the ground (foot contact). At this point, the arm is beginning to externally rotate in preparation for the cocking phase. The elbow ends this phase at about 85° of flexion.

After stride foot contact the arm continues to externally rotate (cocking phase). The pelvis and torso continue to accelerate and rotate, bringing the cocked arm forward into the direction of the throw. Once the arm reaches maximum external shoulder rotation (MER), it accelerates until ball release (acceleration phase). Most of the acceleration of the arm occurs during this phase, as powerful shoulder internal rotation is combined with energy transferred from the trunk (Feltner and Dapena, 1986; Fleisig and Escamilla, 1996; Loftice et al., 2004). The upper arm begins in an abducted, horizontally adducted and externally rotated position, then it is internally rotated, slightly adducted, and horizontally abducted until ball release (Jobe et al., 1984; Feltner and Dapena, 1986; DiGiovine et al., 1992). Internal rotation is probably accomplished by a combination of passive stretching of the tendons for the internal rotators during MER (Feltner and Dapena, 1986), and by activation of the pectoralis major and latissimus

dorsi (Jobe et al., 1984; DiGiovine et al., 1992). Maximum internal rotation angular velocities of approximately 6100 °/s are reached just before ball release (Feltner and Dapena, 1986).

After foot contact, the shoulders rotate to face forward, and it is thought that centripetal force, in concert with the elbow extensors (triceps), acts to swing the forearm away from the body through extension of the elbow (Werner et al., 1993; Loftice et al., 2004). The elbow flexors restrict extension of the elbow until just before MER, such that the elbow can be extended at high velocity during the acceleration phase (Werner et al., 1993). The elbow begins in slight flexion and then rapidly extends to approximately 160°, reaching maximum angular velocities of approximately 2100 °/s to 2700 °/s shortly before ball release (Feltner and Dapena, 1986; Fleisig and Escamilla, 1996). Correspondingly, electromyography (EMG) shows modest biceps activity just after MER, followed by some triceps activity (Jobe et al., 1984; DiGiovine et al., 1992).

The wrist begins in maximal extension (approximately 32°), and rotates approximately 90° over the course of the acceleration phase (Feltner and Dapena, 1986; Pappas et al., 2009). The wrist reaches a maximum angular velocity of approximately 1080 °/s (Pappas et al., 2009). Forearm pronators activate during the acceleration phase, beginning in slight supination and pronating to 7° at ball release, but maximum pronation velocity is not achieved until after ball release (DiGiovine et al., 1992; Nissen et al., 2007). Forearm pronation is thought to function primarily to stabilize and prevent injury at the elbow and wrist, rather than contributing to ball velocity (Elliott et al., 1986). Actions after ball release have no bearing on ball velocity, and thus are not considered here.

Throwing ability is a function of both anatomical factors and technique. Good throwing technique will maximize both ball velocity and accuracy, and is likely a result of the interaction

of several broad factors such as coordination, training, and experience. Although these factors are invisible in the fossil record, it is still valuable to examine the available literature on how technique influences throwing performance.

Optimizing throwing technique involves performing movements with ideal timing and placement, for example timing and placement of the stride, or position of the arm at the beginning of the acceleration phase. A study of within-pitcher variation indicates that the timing of horizontal adduction and rotation of the arm, angle of trunk tilt, and angle of shoulder abduction and horizontal adduction significantly affect ball velocity (Stodden et al., 2005). A study of children of varying levels of throwing skill found several correlates of throwing velocity that children develop as they learn proper throwing technique (Stodden et al., 2006). These include increasing stride length, correct stride foot positioning, and timing of trunk rotations. Ideally, the pelvis should begin its rotations prior to stride foot contact, and prior to shoulder rotation. This creates a lag between hip rotation and shoulder rotation that pre-stretches the muscles and tendons of the upper body, allowing them to generate maximal forward velocity (Stodden et al., 2006). Furthermore, these authors found that as much as 40% of the increase in ball velocity from the least to most skilled throwers was a result of decreasing the time from stride foot contact to ball release; essentially increasing the pace of the post-stride portion of the throw. However, it is unclear exactly how this pace increase was achieved.

The ability to time motions from proximal to distal has long been suspected to be an important aspect of throwing technique (Jöris et al., 1985; Herring and Chapman, 1992; Mero et al., 1994; Tuma and Zahalka, 1997). Maximizing segment velocities in a proximal to distal sequence would seem the best way to transfer energy additively to the distal segment, the hand. However, recent research indicates that joint velocities do not follow a strict proximal to distal

sequence (Hong et al., 2001; Fradet, 2004; van den Tillar and Ettema, 2004a, 2009). Van den Tillar and Ettema (2009) found that maximal velocities of joint segments were reached in a largely sporadic fashion, but with the exception of knee extension and shoulder horizontal adduction, the actions were *initiated* in sequence. This finding suggests either that even the most skilled throwers are not capable of coordinating movements perfectly (but attempt to by initiating actions in sequence), or that a proximal to distal sequence is not the ideal throwing technique. For example, van den Tillar and Ettema (2009) note that the flexors of the wrist may contribute more to aim than to ball velocity, and must therefore activate earlier than would be predicted by the proximal to distal sequence.

It should be noted that even though there is a clear effect of technique on throwing ability as described above, among individuals who are experienced throwers, variation is very low for positional and temporal throwing variables (Fleisig et al., 1999; Escamilla et al., 2001). Thus, even though technique is not indicated in the fossil record, it seems likely that hominins experienced with throwing would have adopted a consistent and successful, if not necessarily optimized, throwing technique.

Summary.

Optimal overhand throwing to maximize velocity involves activation of all the segments of the body in a coordinated manner, such that energy is additively transferred to the thrown object. The standard overhand throwing motion involves six phases, wind up, stride, arm cocking, arm acceleration, arm deceleration, and follow through, during which the thrower prepares to throw, strides forward, pulls the arm back into maximum external rotation, and whips the arm forward at maximal velocity. The majority of the acceleration of the object is generated during the acceleration phase, during which extremely large shoulder internal rotation angular

velocities and elbow angular velocities are achieved. Proper technique is required to achieve high throwing velocity, including proper timing of pelvis rotation, and shoulder horizontal adduction and internal rotation, as well as proper placement of the stride foot, and angle of abduction and horizontal adduction of the arm. Yet, for skilled throwers, variation is low for positional and temporal variables (Fleisig et al., 1999; Escamilla et al., 2001), indicating a consistency in technique that likely would have been found in experienced Paleolithic spear throwers as well.

II. Relevant anatomical variation between hominin populations.

The available throwing literature suggests several potential anatomical correlates of throwing velocity that are observable in, and may vary between, hominin populations. The following will present the evidence for these suggested anatomical variables, and discuss how they vary between fossil samples. This will begin to organize the available data for the purpose of generating predictions about variation in throwing ability between the samples.

Body mass is primarily a function of muscle volume and fat volume, both of which are related to body proportions. Body strength is a function of muscle volume and joint leverage. Body size, body strength and body proportions are thus all interrelated, but may affect throwing velocity independently.

1. Muscle volume.

Several researchers have found significant correlations between body mass and ball velocity for handball and water polo players (Van den Tillar and Ettema, 2004; Vila et al, 2009; Ferragut et al., 2011). The correlation was stronger when considering fat free mass versus absolute mass or height (Van den Tillar and Ettema, 2004), indicating the primary cause is body strength. This was further supported by a strong correlation between specific isometric strength (strength during the exact throwing motion) and fat free mass (Van den Tillar and Ettema, 2004).

Ferragut et al. (2011) also found a significant correlation between throwing velocity and muscle mass as a percentage of total body composition. A number of other studies have found correlations between strength, either measured directly or inferred from segment circumference, and throwing velocity (Jöris et al., 1985; Lachowetz et al., 1998; Fleisig et al., 1999; Vila et al., 2009; Ferragut et al., 2011) and specifically strength of the shoulder in adduction, internal and external rotation, horizontal adduction and abduction, elbow extension, and wrist extension (Pedegana et al., 1982; Bartlett et al., 1989; Clements et al., 2001; Stodden et al., 2005). These results point to the importance of strength in generating ball velocity, however strength across the various muscles of the body is likely to be highly correlated (assuming muscle volume is a primary predictor of strength, see below) (Clauser et al., 1969), and no study to date has examined the effect of strength on throwing velocity in all the muscles concurrently. Thus, it is not yet clear which muscles, if not all, are causally related to throwing velocity. This is further complicated by the fact that muscles do not act in isolation, and the strength of relevant antagonists also influences muscle performance. Improving antagonist strength can improve agonist performance (Jarić et al., 1995). However, agonist and antagonist strength is generally correlated, because imbalances can lead to greater injury risk (Cook et al., 1987; Hughes, 1999), thus there is likely to be a predictable relationship between agonist and antagonist strength.

Variation in strength is due to several factors, including muscle size and joint leverage. Joint leverage will be discussed in section II.2. The maximum force a muscle can produce (F_m) during an isometric (static) contraction can be calculated as:

$$F_m = V_m \cdot l^{-1} \cdot \cos \theta$$

where V_m is muscle volume, l is fascicle length, and θ is pennation angle (Fukunaga et al., 2001). The ratio of muscle volume to fiber length ($V_m \cdot l^{-1}$) is often referred to as physiological cross

sectional area (pCSA), and provides a quantification of the force potential of the muscle (Zajac, 1992). If the muscle fibers are not aligned in parallel however, F_m will also be affected by the pennation angle, such that $pCSA \cdot \cos \theta$ is a more accurate representation of F_m (Zajac, 1992). Although pennation angle varies between muscle types, it is generally conserved within humans for a particular muscle (Yamaguchi et al., 1990; Narici et al., 1992; Albracht et al., 2008), and pennation angle only affects muscle force greatly at $\theta > 20^\circ$ (since $\cos \theta$ approaches 1 at decreasing θ) (Zajac, 1992). Pennation angles for the main muscles of the elbow and wrist are between 0 and 15° (Lieber et al., 1992; Murray et al., 2000), indicating that for the elbow and wrist, muscle force is primarily a function of pCSA. This is supported by experimental evidence, as pCSA estimated from magnetic resonance imaging (MRI) is highly correlated with measured F_m in human subjects (Fukunaga et al., 2001). Furthermore, if fiber length scales proportionately with muscle volume, then the largest absolute cross section of a muscle (anatomical cross sectional area, aCSA) will be correlated with pCSA, and consequently F_m . Fukunaga et al. (2001) found a strong correlation between both aCSA and pCSA of arm muscles and their F_m (aCSA: $r = .89$, pCSA: $r = .91$), indicating that muscles of different sizes are generally similar in shape. Thus, in comparing the force producing potential of muscles between individuals of the same species, muscle volume, pCSA, and aCSA are all appropriate measures of strength.

The above equation for F_m assumes that muscles of the same volume have the same force per unit cross-sectional area, or specific tension (ST). In fact, the proportion of fast-twitch and slow-twitch fibers present in a muscle will affect contractile velocity and to some degree, specific tension (Howald, 1982; Maganaris et al., 2001), such that the equation above could be modified to:

$$F_m = V_m \cdot ST \cdot l^{-1} \cdot \cos \theta$$

Fiber type composition varies across muscle types within an individual (i.e. postural versus phasic muscles), and to a lesser degree, for the same muscle type between individuals (Howald, 1982). Fiber type composition varies genetically, and changes can be induced through rigorous training (Howald, 1982; Simoneau et al., 1985). However, similar patterns of fiber-type composition have been found amongst athletes of a given sport (Tesch and Karlsson, 1985), indicating a general similarity in persons who habitually engage in the same activities, and differences in specific tension due to variation in fiber type composition do not seem to produce significant differences in torque production between human subjects in vivo (Schantz et al., 1983).

The above discussion of F_m applies to isometric muscle contractions at a specific joint angle. However, when muscles act dynamically, or joint angle varies, fascicle length and contraction velocity greatly affect F_m (Biewener, 2003). There is an optimal muscle length (joint angle) at which maximal tension is created. When the muscle is lengthened or compressed away from this optimum, as it is over the range of motion of the joint, the isometric force generated will decrease in relation to the amount of lengthening or contraction that occurs (Herzog and ter Keurs, 1988; Hoy et al., 1990; Lieber et al., 1994). Contraction velocity also affects force, such that muscle forces produced during eccentric contraction (lengthening of the muscle fibers under load) will be larger than muscle forces produced during isometric contraction, and will decrease during concentric contraction (shortening under load) with increased shortening velocity (Hill, 1938; Doss and Karpovich, 1965; Perrine and Edgerton, 1978; Griffin, 1987). Although these are important sources of variation within an individual, theoretically highly skilled individuals should perform an optimal throw in a similar manner, minimizing variation in muscle length and contraction velocity.

As discussed, force potential for a given muscle is primarily a function of muscle cross sectional area, and comparisons of muscularity in fossil hominins have been performed using relative muscle insertion sizes and/or rugosity (e.g. Trinkaus, 1983a, 2006; Hambucken, 1993, Villemeur, 1994; Churchill and Rhodes, 2006, 2009). Although their reliability has been questioned (Stirland, 1998; Wilczak, 1998; Weiss, 2003; Zumwalt, 2006), the size and rugosity of muscle markings have been used to describe muscle hypertrophy (e.g. Churchill and Morris, 1998; Hawkey, 1998; Steen and Lane, 1998), since the amount of force generated by the muscle will be applied to the bone at its insertion (Galtés et al., 2006). Potential problems with the use of muscle markings to infer muscularity include difficulty in scoring sizes and rugosity objectively, non-discrete insertion areas, potentially confounding effects of sex, age, and body size, and difficulty in tying observations to behavior (Stirland, 1998; Wilczak, 1998; Weiss, 2003). There is clear evidence that age, sex and body size have an effect on muscle markings, thus comparisons should always be scaled to body size, and within sex and side. Great caution should be taken when comparing specimens of dissimilar age, and when making inferences to behavior. However when the rugosity and size of the insertion can be adequately distinguished and the insertion is discrete and solitary, the use of muscle markings to infer hypertrophy is generally still considered informative (Peterson and Hawkey, 1998).

When discussing the effects of muscularity on throwing velocity, the primary focus should be muscles that are active just prior to, or during the acceleration phase, since this is when most of the energy is transferred to the thrown object (Feltner and Dapena, 1986; Fleisig and Escamilla, 1996; Loftice et al., 2004). Muscles may be highly active at other times, but these are likely contributing to proper placement of the body before and regaining stability after the throw.

Placement and stabilization are certainly important for proper technique and avoiding injuries, but are not of primary importance to generating ball velocity.

Several studies comparing muscle markings between hominin samples were discussed above (Chapter 3: II). Several authors have compared the relative sizes of the deltoid (from its partial distal insertion on the deltoid tuberosity) and supinator muscles between Neandertals and early modern humans (Endo, 1971; Carretero et al., 1997; Churchill and Smith, 2000; Churchill and Rhodes 2006, 2009), finding significantly smaller insertions among Neandertals compared with early and recent modern humans for both muscles. The supinator muscle is primarily active during deceleration (DiGiovine et al., 1992), and thus it is unlikely to affect ball velocity at release. The deltoid, particularly the posterior fibers, is quite active during the acceleration phase, serving to keep the arm in an abducted position through the throw (DiGiovine et al., 1992). However, it is unclear if variation in deltoid humeral insertion size in hominin samples is actually related to muscular hypertrophy (Carretero et al., 1997), and its proximal attachments on the clavicle and acromion process are quite pronounced in several Neandertals (Trinkaus, 1983a). These attachments are also modest to pronounced in the Dolní Věstonice MUP early modern humans (Trinkaus, 2006).

In conjunction, the latissimus dorsi and the pectoralis major are major contributors to ball velocity (DiGiovine et al., 1992). These muscles are extremely important in producing the large internal rotation velocities of the humerus that generate ball velocity (DiGiovine et al., 1992). Body size scaled pectoralis major insertion area size is significantly greater in Neandertal versus UP early modern humans (Trinkaus, 1982, 1983a, b, 2006; Vandermeersch and Trinkaus, 1995; Churchill and Smith, 2000; Shang et al., 2007; Walker et al., 2011). It has been noted that the insertion for latissimus dorsi is robust in a number of Neandertal specimens and less pronounced

in early modern humans (Trinkaus, 1983a, b, 1986, 2006), although quantitative analyses have not been performed.

Also highly active during the acceleration phase are the scapular muscles, including the trapezius, serratus anterior, rhomboids, and levator scapulae (DiGiovine et al., 1992). The scapular muscles keep the scapula stable during the large joint angular velocities and torques of the humerus (DiGiovine et al., 1992). The clavicular attachment for the trapezius is pronounced in Shanidar 1 and 3 (Trinkaus, 1982, 1983a), and Neandertal ribs tend to be robust, likely as a result of robusticity of the muscles that insert there, including serratus anterior (Trinkaus, 1983b; Franciscus and Churchill, 2002). In fact, the serratus anterior attachments are very rugose in several Neandertals as compared with recent modern humans (Franciscus and Churchill, 2002). Unfortunately, little else can be said about these muscles from insertion sites.

The Kebara 2 Neandertal scapula was found to have larger scapular area for insertion of the supraspinatus, infraspinatus, and subscapularis than all early and recent modern human samples (Churchill and Rhodes, 2006). Relatively large area for insertion of these muscles in Neandertals has also been observed elsewhere (Trinkaus 1982, 1983a, b). This is highly relevant as the glenohumeral muscles are all very active during the acceleration phase to keep the humerus precisely positioned in the glenoid fossa, and resist dislocation of the humerus (DiGiovine et al., 1992). Variation also exists in the modern human sample, where scapular area in MP and UP early modern human males is significantly lower than the recent modern human male samples (Churchill and Rhodes, 2006). The other rotator cuff muscle, teres minor, was originally thought to be hypertrophied in Neandertals based on a more frequent occurrence of the dorsal sulcus pattern on the axillary border of the scapula (Trinkaus, 1977), but this hypothesis has since been retracted (Churchill and Trinkaus, 1990). In fact, multiple studies have failed to

find a correlation between axillary border shape and glenohumeral hypertrophy as evidenced by the humerus (Churchill, 1996; Franciscus and Schoenebaum, 2000; Odwak, 2006).

The radial tuberosity serves as the insertion for the biceps brachii muscle, a flexor and supinator of the forearm. Relative radial tuberosity size is larger in Neandertal males and females, as compared with all early and recent modern human samples, although not all comparisons are significant (Trinkaus, 1982, 1983a, b; Vandermeersch and Trinkaus, 1995; Churchill and Rhodes, 2006). This dimension is smaller in UP versus recent modern humans, and around the middle of the human range of variation in MP early modern humans (Churchill and Rhodes, 2006). Given that the biceps is hypertrophied in Neandertals, the relative weakness of the supinator muscle discussed above may not be functionally important. However, the biceps is only minimally active until the deceleration phase of the throw (DiGiovine et al., 1992), suggesting this muscle is not of great importance in generating ball velocity.

Relative humeral epicondylar area is larger in Neandertals than any early or recent modern human sample, although the difference is not significant in all cases (Churchill and Rhodes, 2006). The humeral epicondyles serve as insertions for the common flexor and extensor tendons, and as such should reflect forearm muscularity. The UP sample is quite variable for this measure, with male EUP/MUP epicondylar area lower than any other sample, and male LUP epicondylar area near the upper end of the human range (Churchill and Rhodes, 2006). Additionally, the lateral supracondylar ridge is quite large in Shanidar 1, 3, 4, and 6, implying a robust extensor carpi radialis longus (Trinkaus, 1983a). Neandertals also have large palmar tuberosities on the scaphoid, trapezium and hamate, which may indicate hypertrophy of the wrist flexors (Trinkaus, 1983a, b, 2006; Villemeur, 1994). The pronator teres does not have a clear discrete marking for its distal insertion (Trinkaus, 1983b), but the pronator quadratus insertion is

quite pronounced in Neandertals as compared with EUP and recent modern humans (Trinkaus 1982, 1983a, b; Vandermeersch and Trinkaus, 1995). Of the forearm musculature, the pronator teres, flexor carpi radialis, flexor digitorum superficialis, and flexor carpi ulnaris, are highly active during the acceleration phase of the throw to resist valgus stress (DiGiovine et al., 1992). The forearm extensors are only moderately active during the acceleration phase (DiGiovine et al., 1992). It is unclear how relevant the size of the humeral epicondyle and carpal palmar tuberosities are to throwing velocity, since the function of the flexors is primarily stability of the joint, and the extensors are relatively inactive.

With the possible exception of the deltoid and supinator muscles, Neandertals had muscular hypertrophy for all shoulder and upper limb muscles for which such information is available. The muscles that appear to be the most important to generating throwing velocity are the scapular muscles, the glenohumeral muscles, and the triceps. Of these, Neandertals appear to have had larger pectoralis, latissimus dorsi, subscapularis, supraspinatus, and infraspinatus muscles. Even if the deltoid was in fact smaller in Neandertals, relative weakness in one muscle could be easily compensated for by the hypertrophy of the other shoulder muscles, and should not have been functionally important. Furthermore, there is evidence that the elbow flexors and forearm muscles were hypertrophied in Neandertals. Although these muscles are not highly active during the acceleration phase in baseball pitching, hand and arm position will necessarily be different throwing a spear versus a baseball. Thus, it remains to be seen if the hypertrophied elbow flexors and forearm muscles in Neandertals are of importance to spear throwing.

It should be noted that this is in no way a thorough or complete assessment of muscularity, as sample sizes are very small, there is much missing information, and given the complications of using muscle insertion sites as indicators of hypertrophy discussed above.

However, all indications seem to be that the complex of muscles involved in throwing was stronger in Neandertals than early and recent modern humans. The pattern within the UP remains unclear. The scapular muscles are significantly smaller in MP and UP than recent modern humans, but little can be said conclusively about the remaining throwing muscles.

In addition to specific muscle hypertrophy, total body mass has been estimated in hominin samples. Neandertal body mass, estimated from femoral head size or stature and body breadth, tends to be larger than early modern humans, likely as a result of climatic adaptation (Ruff, 1994; Holliday, 1997a; Weaver, 2003; Ruff et al., 2005). European UP hominins are similar in body mass to modern Europeans, and there are no known differences in body mass within the UP (Holliday, 2002). Body mass in early *Homo* is smaller than that seen in archaic *Homo*, and including the very small female from Gona (BSN49/P27) it is much smaller (Ruff, 2010). Although muscularity is likely the causal factor when considering the relationship between body mass and throwing velocity (van den Tillar and Ettema, 2004b), body mass may prove a useful measure of ‘whole body’ muscularity, at least for within-sex comparisons of lean individuals. The larger body masses of Neandertals are likely an indicator of greater ‘whole-body’ muscularity that would correlate with greater throwing velocity (van den Tillar and Ettema, 2004b; Ferragut et al., 2011).

2. *Effective mechanical advantage.*

As discussed above, muscles of a given size exert a force F_m , and the resulting torque (T), or rotational force, is a function of F_m and the joint’s leverage. Torque is calculated as $F_m \cdot r$, where r (the muscle moment arm) is the perpendicular distance between the center of rotation (COR) of the joint and the line of action (LOA) of the muscle force. Under static conditions, $F_m \cdot r$ must be equal to $F_e \cdot R$, where F_e is the external force and R is the lever arm for the external

force (called the load arm). The load arm is calculated as the perpendicular distance between the COR of the joint and the LOA of the external force. EMA, calculated as r/R , provides a ratio of the external force to the muscle force, such that high EMA describes a joint where low F_m is required for a given F_e . In a dynamic situation, when EMA is high, the F_e that can be exerted with a given F_m should be high. EMA also has a relationship with the velocity of rotation of the joint, where increased shortening of the muscle is required to produce a given angular displacement of the distal portion of the segment (Levangie and Norkin, 2005). Specifically, muscles with large moment arms maximize initial acceleration, producing overall greater average angular velocity of the joint (Stern, 1974). Muscles with relatively smaller moment arms produce lesser initial accelerations, but eventually reach higher instantaneous velocities (Stern, 1974). Thus, a trade-off should exist in limb design such that greater EMA would allow for greater maximum joint torque and greater average joint angular velocity, but lesser instantaneous velocity. Conversely, lower EMA of the arm joints should generate greater instantaneous linear velocities of the distal arm (the hand and ball), producing a faster throw. These principles are applied theoretically in sports and physical therapy contexts (Levangie and Norkin, 2005), and the effect of differences in EMA within subjects over different joint angles has been documented (Smidt, 1973; Delp et al., 1996; Gonzalez et al., 1997; Murray et al., 2000). Yet, the effect of variation in EMA *between* subjects has been inconclusive in non-humans (Lieber and Boakes, 1988), and has not been documented in humans.

The theoretical relationships between EMA, joint torque, and joint velocity have been applied to fossil hominins to compare joint strength and speed (Trinkaus, 1983a, b; Trinkaus and Villemeur, 1991; Miller and Gross, 1998; Trinkaus and Rhoads, 1999; Niewoehner, 2001; Trinkaus et al., 2001; Churchill and Rhodes, 2006; Sockol et al., 2007; Galtés et al., 2008a; De

Groote, 2011; Maki and Trinkaus, 2011; Raichlen et al., 2011), and even used to infer adaptation for throwing velocity (Churchill and Rhodes, 2006). EMA has been estimated in fossil skeletons by comparing skeletal features that would affect r , sometimes in conjunction with limb segment length as a proxy for R (assuming an F_e perpendicular to the segment applied at the distal end of the segment). The following summarizes the available information regarding EMA in Paleolithic hominins, as it applies to throwing velocity. Effects of limb segment lengths and proportions will be discussed separately, in section II.3.

In the shoulder, the scapular spine tends to be more dorsally projecting in Neandertals versus early modern humans, which places the acromion process further from the COR of the joint (Trinkaus, 1983a, b). This effectively increases r for the posterior fibers of the deltoid. Additionally, the proximo-distal distance of the deltoid tuberosity on the humerus may affect deltoid EMA slightly at increasing degrees of flexion and abduction. Churchill and Rhodes (2006) found no difference between Neandertals and any early or recent human sample for this measure.

The triceps brachii muscle is the primary extensor of the elbow, and inserts on the olecranon process of the ulna. Churchill and Rhodes (2006) estimated triceps EMA at 90° of flexion as the length of the olecranon process relative to ulna length. Neandertals and one recent modern human sample (Aleutian Islanders) were found to have significantly greater EMA for the triceps than MP, UP, or recent modern humans. All modern human samples with the exception of the Aleutian Islanders were very homogenous. Moment and load arm values were not provided to determine if this pattern is a result of variation the moment arm, the load arm (possibly as a function of variation in brachial indices) or both.

Flexion of the forearm is accomplished by the brachialis and biceps brachii muscles. The moment arm for these muscles at 90° of flexion can be estimated as the distance from their insertions on the radius and ulna to the COR of the elbow (Churchill and Rhodes, 2006), which passes through the medial and lateral epicondyles of the humerus (Ericson et al., 2003). Using ulna and radius length as R, the mechanical advantage for both the elbow flexors is greater in Neandertal than any early or recent modern human sample (Churchill and Rhodes, 2006). Differences in Neandertal brachialis EMA were significant with respect to EUP and LUP, but not MP early modern humans, and no other significant differences were found.

Early modern humans tend to have more antero-medially oriented radial tuberosities as compared with Neandertals, whose radial tuberosities tend to be more medially oriented (Trinkaus, 1983b; Trinkaus and Churchill, 1988; Hambucken, 1993; Churchill and Rhodes, 2006). The radial tuberosity marks the insertion for biceps brachii, and the more medial orientation in Neandertals has been argued to provide a more advantageous arrangement for the biceps in supination (Trinkaus and Churchill, 1988). Neandertal radii also tend to have a higher degree of diaphyseal curvature, which serves to increase the maximum distance of the pronator muscle bellies to the axis of rotation for pronation (a line that runs through the middle of the radial and ulnar heads) (Trinkaus, 1983a,b). This has been shown through simulations to provide a better moment arm for the pronator quadratus and pronator teres (Galtés et al., 2008a).

The large palmar tuberosities found in Neandertal wrists discussed above not only provide increased surface area for the attachment of the wrist flexor complex, but should also increase the distance of the insertions of the wrist flexor tendons from the COR in the wrist, thereby increasing the moment arms for these muscles (Trinkaus 1983a, b; Villemeur, 1994).

Increased EMA has also been observed for the opponens pollicis (Maki and Trinkaus, 2011) and pollical flexors (Trinkaus and Villemeur, 1991; Villemeur 1994).

The primary muscles involved in throwing are the scapular and gleno-humeral muscles, as well as the triceps. Of these, the deltoid and triceps appear to have had better mechanical advantage in Neandertals versus early and recent modern humans. Unfortunately, little can be said about the remaining scapular and gleno-humeral muscles from the available literature. The biceps brachii, forearm muscles, and several hand muscles also appear to have had increased EMA in the Neandertal sample. The greater EMA in Neandertals may have allowed them to produce greater forces (i.e., increased their strength), but the effect of greater EMA of these muscles on throwing velocity is less straightforward. Lower EMA should produce larger instantaneous joint angular velocities (Stern, 1974), which should lead to greater instantaneous linear velocity of the object at release. In fact, ball velocity is correlated with maximum angular velocity of shoulder internal rotation and elbow extension (Jöris et al., 1985; Fleisig et al., 1999; Jegede et al., 2005), as well as with torque production for elbow flexion (Stodden et al., 2005), concentric elbow extension (Pedegana et al., 1982; Clements et al., 2001), concentric wrist extension (Pedegana et al., 1982), shoulder internal rotation (Clements et al., 2001), shoulder adduction (Bartlett et al., 1989) and shoulder external rotation, flexion, and extension (Pedegana et al., 1982). However, the kinetic energy of the object is determined by its velocity, not its acceleration (as is torque), so it should be more strongly correlated with the maximum instantaneous angular velocity of the joint than joint torque. Therefore, object kinetic energy at release should be inversely predicted by joint EMA, and the lower EMA of early and recent modern humans would suggest the ability to throw a spear with greater kinetic energy.

3. *Body proportions.*

Several authors have suggested that stature and limb lengths might influence ball velocity in throwing (Escamilla et al., 2001; Matsuo et al., 2001; Derbyshire, 2007), but studies correlating arm length and height with throwing velocity have found mixed results. Matsuo et al. (2001) found significant differences in height and arm length between high and low velocity throwing groups. In an analysis of 1996 Olympic pitchers, the tallest pitchers with the longest arms had the fastest throwing velocities, but the difference was not significant (Escamilla et al., 2001). Furthermore, correlations were not found between arm length and/or height and throwing velocity in cricket players (Derbyshire, 2007), handball players (Jöris et al., 1985), or water polo players (Vila et al., 2009). Arm length could affect throwing velocity in terms of its effect on EMA, but even for a joint with the same EMA rotating at the same angular velocity, the distal end of a longer limb will cover more distance in the same time; i.e., it will have greater linear velocity. Depending on the joint angles used during the throw, total arm length or individual segment lengths may be relevant.

Ball velocity will increase when forces are applied over a greater distance (Matsuo et al., 2001). Greater leg length will increase stride length, thereby propelling the body forward a greater distance. Increasing ball velocity has been shown to correlate with stride length as children develop (Stodden et al., 2006). Similarly, a taller individual can cover more distance during the throw with greater forward trunk tilt. Matsuo et al. (2001) found significantly greater maximum trunk tilt at the moment of ball release as well as greater height, in a high velocity versus a low velocity throwing group; presumably these are related.

Stature estimations for European and West Asian Neandertals are consistently lower than all early modern human samples (Trinkaus, 1983a; Feldesman et al., 1990; Ruff, 1994; Ruff et

al., 2005). Stature has important consequences for thermoregulation, and Neandertals are cold-adapted as compared with the tall linear body proportions of early modern humans (Ruff, 1994; Holliday, 1997a, b; Weaver, 2003), reflecting African ancestry (Holliday, 1997b). *H. erectus* also appear to be taller than Neandertals and similar to UP early modern humans (although the sample is small and highly variable) (Feldesman et al., 1990).

Also important to thermoregulation are limb proportions, and Neandertals had shorter limbs (Holliday, 1997a, b). Upper and lower limb segments are shorter in Neandertals compared with MP and UP early modern humans (Ruff, 1994; Holliday, 1997a, b), but the pattern is more extreme with distal limb segments (Holliday, 1997a, b, 1999). There are also differences in limb proportions within the UP, where EUP early modern humans tend to have longer proximal and distal limb segments than LUP early modern humans (Holliday, 1997a). Middle Paleolithic early modern humans and *Homo erectus* (KNM-WT 15000) are at the extreme of the modern African range of variation, with very long upper and lower limb segment lengths (Ruff and Walker, 1993; Ruff, 1994), whereas other archaic *Homo* from higher latitudes follow the expected arctic pattern (Ruff, 2002).

Body breadth, as measured by pelvis and shoulder width, may also have important biomechanical consequences for throwing velocity. From just prior to foot contact until ball release, the pelvis and torso forcefully rotate, generating centripetal force in the arm, which may be important in generating high elbow angular velocities (Werner et al., 1993; Loftice et al., 2004). Bi-asis breadth (between the anterior superior iliac spines of the pelvis) and biacromial breadth (between the acromion processes of the scapulae) may have consequences for how fast the hips and torso can rotate. Vila et al. (2009) and Ferragut et al. (2011) found significant correlations between bi-acromial and bi-asis breadth and throwing velocity. Stodden et al. (2001)

found significant correlations between average pelvis and shoulder angular velocities and ball velocity.

As measured by bi-iliac breadth (maximum distance between iliac crests), Neandertals have relatively wide bodies, falling at the upper end of the range of modern human variation (Ruff, 1994; Trinkaus, 2011). As with height and relative limb lengths, the relatively wide pelves of Neandertals appear to be shared with other higher-latitude archaic *Homo* specimens (Arsuaga et al., 1999; Ruff, 2002; Ruff, 2010). MP and UP Early modern humans are intermediate with respect to the modern human range of variation (Ruff, 1991, 1994). Ruff (2010) describes early *Homo* bi-iliac breadth as somewhat narrower than MP *Homo*, although not so narrow as would be expected based on the modern African climatic pattern. Clavicle length was discussed above (Chapter 3: II), and has been shown to correlate with bi-acromial breadth in living humans, providing an estimate of shoulder breadth (Piontek, 1979). Clavicle length is relatively large in Neandertals compared with MP and UP early modern humans (Trinkaus, 1983a, 2007; Vandermeersch and Trinkaus, 1995; Voisin, 2004, 2006). Clavicle length appears to be large in *H. antecessor* as well (Carretero et al., 1999), but estimated clavicle lengths for several other early *Homo* specimens are short (*H. erectus* from Zhoukoudian, OH48 *H. habilis*, Dmansi D2724). Thus, based on shoulder and hip width, Neandertals and other archaic *Homo* from higher latitudes likely had broad bodies as compared early *Homo*, early modern humans and recent modern humans from low latitudes.

Summary.

Throwing velocity between subjects is likely affected by strength and body proportions. Muscular strength is primarily a function of muscle size and the leverage of the joint system. Comparisons of muscle insertion size have found hypertrophy of the pectoralis major, latissimus

dorsi, subscapularis, supraspinatus, infraspinatus, biceps brachii, pronator quadratus, and the forearm flexors and extensors, in Neandertals as compared with early and recent modern humans. Estimation of joint mechanical advantage, based on the ratio of moment arm length to segment length, indicates greater EMA in Neandertals versus early and recent modern humans for the deltoid, triceps, and pronators, supinators, and flexors of the forearm. Of these, the pectoralis major, latissimus dorsi, subscapularis, supraspinatus, infraspinatus and triceps brachii have been shown to be highly active during the acceleration phase of baseball pitching, suggesting their importance in generating ball velocity. It has also been suggested that greater height, segment lengths, and body breadth may have a significant effect on throwing velocity. Estimated stature and limb lengths are significantly lower in Neandertals versus early modern humans, while body breadth is significantly greater, reflecting differential climatic adaptation. Thus, based on strength (as a function of torque production) and body breadth, one would expect Neandertals to have been superior throwers. However, based on EMA, height, and limb lengths, one would expect early modern humans to have been the superior throwers. Experimental data is thus necessary to establish which of these factors is primary in determining throwing velocity, and to delineate which hominin sample would have been better suited for throwing.

Chapter 5

Materials and Methods

This chapter discusses the samples and methods used to test the research hypotheses. The data collection included two parts, experimental data for a sample of modern humans, and skeletal measurements of fossil samples. Experimental data collection included anthropometrics, strength testing, kinematics and kinetics during throwing, and anatomical data from magnetic resonance imaging (MRI), for a sample of experienced throwers. Skeletal data collection involved measurements of effective mechanical advantage (EMA) from a sample of Paleolithic fossil hominins, and two recent human samples. Skeletal measurements taken personally were supplemented with published data where available.

Materials

I. Human Subjects.

Forty one human subjects (20 male, 21 female) participated in the experimental portion of the research protocol. Approval for all recruitment and study procedures was obtained from the Washington University in Saint Louis Human Research Protection Office (HRPO# 09-088). Thirty participants were recruited from the Washington University in St. Louis (Division III) and University of Missouri St. Louis (Division II) baseball and softball teams (Competitive sample), and 11 additional participants were members of college intramural softball teams (Non-Competitive sample). MR images were only collected for the Competitive sample. Subjects were screened for previous injuries to the throwing arm, which could alter throwing kinetics or kinematics, and for pregnancy or presence of metal in the body, which are counter-indicated for

MR imaging. Subjects were informed of the study protocol verbally and in writing before signing the approved consent document. Compensation was provided for participation, \$25 after completion of the throwing session, and \$25 after completion of the MRI session. Sessions were completed on different days, with no more than two months interval between sessions.

All subjects were healthy, experienced throwers. The competitive players were engaged in training and/or competing at the time of the data collection. Non-competitive players were generally not engaged in training or competition at the time of the data collection, but had played softball or baseball on an intramural team within the prior six months. In order to observe the effects of anatomy and body proportions on throwing performance, sufficient variation in body size and proportions was necessary. The subjects selected display a wide range of variation in height, body mass, and limb lengths (see appendix I).

II. Skeletal Materials.

Skeletal specimens fall into five categories: Early *Homo* (EH, N = 1), Neandertals (Neand, N = 11), Middle Paleolithic early modern humans (MPEMH, N = 5), Upper Paleolithic early modern humans (UPEMH, N = 6), and recent modern humans (N = 122). Due to limitations of sample availability, the UPEMH sample represents only the Mid Upper Paleolithic (MUP). Although there are potentially relevant differences in behavior and technology within the UP, these must be investigated in future analyses with expanded sample sizes. However, this MUP sample represents an important contrast with the MP samples, as throwing was clearly more frequent than in the MP, but occurs prior to the use of the spear-thrower.

Fossil specimens are summarized in table 5.1, and were chosen based on access to original skeletal material or availability of a high quality cast, radiograph, or photograph. With one exception (Skhul photographs), all casts, photographs of original fossil material, and

radiographs belong to E. Trinkaus, and were used with permission. These were supplemented with published data for limb segment lengths where available, which increases the sample size for certain analyses. Sample sizes of known Nean and EMH specimens are modest to begin with, and the number of specimens measured for this analysis was exceptionally small. For certain comparisons, the sample size available will not provide sufficient evidence to accept or reject the hypotheses. Instead, any patterns observed will be discussed in the context of known patterns of variation in the fossil record to reinforce the results. Future analyses will expand the sample studied to confirm any observed patterns.

The purpose of the fossil analysis was to establish whether differences exist in EMA at the elbow and wrist between Paleolithic hominin samples. To do so ideally requires sufficiently complete articulated joints. Due to the fragmentary nature of fossil specimens, many represent a single element of the joint. To maximize sample size, isolated elements were used (see below for discussion of how isolated elements were treated). If both left and right elements were available, limb dominance was assessed, and both sides were measured, allowing a comparison of EMA between limbs for a sub-sample of the fossil specimens. Dominance was assessed using the maximum diameter of the midshaft of the humerus and ulna. Where only one side was available, limb dominance could not be assessed, and whatever material was available was used.

Sex determinations from previous research were used (where available), and comparisons were made within sexes when patterns in the comparative samples indicated significant differences between sexes. Pooling sexes and sides could potentially lead to type II errors as it might reduce the magnitude of differences between samples, but it is necessary given the meager samples available. Comparison of sexes (where known) and dominant versus non-dominant sides in fossils and recent samples can provide insight into how much effect pooling is likely to have

had on the results. All available adults were included. Since the non-plastic aspects of EMA primarily reflect evolutionary history, and those that are plastic primarily reflect conditions during development (Pearson and Lieberman, 2004), mature age variation should not bias results. Specimens that were obviously pathological were excluded if the pathology affected the joint or limb element in question.

Two recent human samples were selected to contextualize the fossil samples, the Indian Knoll (IK) Native Americans from the Webb Osteology and Archaeology Collection, and the Hamann-Todd (HTH) documented collection from the Cleveland Museum of Natural History. The former is an Archaic Period burial site from near the Green River in Kentucky (Webb, 1946). The site dates from approximately 6415 to 4143 BP (before present), and represents occupation by a semi-sedentary population of hunter-gatherers (Winters, 1974). Winters (1974) describes the Indian Knoll subsistence pattern as a harvesting economy based around a triumvirate of food resources: deer, mussels, and nuts. These resources were exploited with highly developed plant processing, hunting, and fishing technologies. Hunting technologies included the use of spear-throwers (Webb, 1946), and division of labor is assumed, such that males would have been solely responsible for hunting (Winters, 1974). Thus, this sample provides a reference for a highly active population where throwing was used for subsistence (albeit with a spear-thrower rather than hand thrown spears), and a clear division of labor. The latter is a collection of early 20th century Americans from the Cleveland, Ohio, area, obtained from medical school dissections (Cobb, 1935). It includes both ‘white’ and ‘African-American’ specimens, the former originating from across Europe. Since this is a somewhat diverse ethnic and geographical sample, any patterns observed will more likely represent lifestyle than

phylogeny. Thus, this sample represents a relatively low activity level baseline for comparison with little relevant division of labor.

Recent human samples included approximately equal sexes (IK: 33 male, 29 female; HTH: 30 male, 30 female). The dominant limb was measured for all specimens, and the non-dominant limb was also measured for a sub-sample of specimens ($N = 27$). Limb dominance for the Haman-Todd collection was determined by the maximum diameter of the midshaft of the humerus and ulna. Most specimens demonstrated a clear pattern of dominance in both humerus and ulna. Several specimens were eliminated from the sample because limb dominance could not be assessed reliably. Data on limb dominance for the Indian Knoll collection was provided by G. Thomas. Samples include only prime-age adults. For the Hamann-Todd collection, approximate age at death was included in the documentation for each specimen, and age at death for the Indian Knoll collection was obtained from the Goldman Data Set (Auerbach and Ruff, 2004; 2006).

Table 5.1 Fossil specimens.

Sample	Specimen	Side	Joint	Approximate Geological Age (kya)
Early <i>Homo</i>	KNMWT 15000 *	R, L	Elbow	1.5 mya ¹
Neandertal	Amud 1 *†	L	Wrist	50 ²
	La Chapelle 1 *	R, L	Elbow, Wrist	56 ²
	La Ferrassie 1 *	R, L	Elbow, Wrist	35 ³
	Kebara 2 *	R, L	Elbow, Wrist	60 ^{2, 4}
	Neandertal 1 *	R	Elbow	40 ⁶
	La Quina 5 *	L	Elbow	32.5 ⁷
	Regourdou 1 *	R	Elbow	OIS 4 ⁸
	Shanidar 4 *	L	Elbow, Wrist	60 ⁹
	Shanidar 5 *	R	Elbow	45 ⁹
	Shanidar 6 *	R	Elbow	60 ⁹
	Tabun 1 *	L	Elbow, Wrist	122 ¹⁰
MPEMH	Qafzeh 7 †	R	Elbow	90 -120 ^{2, 11}
	Qafzeh 9 *	R, L	Elbow	"
	Skhul 4 *	R, L	Elbow	100 – 135 ¹²
	Skhul 5 +	R, L	Elbow, Wrist	"
	Skhul 7 +	L	Elbow	"
UPEMH	Dolní Věstonice 13 +	R, L	Elbow	25 – 27 ¹³
	Dolní Věstonice 14 *	R, L	Elbow	"
	Dolní Věstonice 16 +†	R	Elbow	"
	Pavlov 1 +	R, L	Elbow	"
	Prědmostí III +	R	Elbow	26 ¹⁴
	Sunghir 1 +	R	Elbow	27.1 ¹⁵

Specimens include those for which the moment arm for at least one muscle could be measured. Abbreviations: MPEMH, Middle Paleolithic early modern human; UPEMH, Upper Paleolithic early modern human. +Specimen measured from photograph of original material; * Specimen measured from cast of original material; †Specimen measured from radiograph of original material. With the exception of Skhul photographs of original material, all photographs of original material, radiographs, and casts belong to E. Trinkaus. References for geological ages: ¹Brown and McDougall, 1993; ²Grün and Stringer, 1991; ³Bertran et al. 2008; ⁴Valladas et al., 1987; ⁵Simek and Smith, 1997; ⁶Schmitz et al., 2002; ⁷Dujardin, 2003; ⁸Vandermeersch and Trinkaus, 1995; ⁹Trinkaus and Thompson, 1987; ¹⁰Grün and Stringer, 2000; ¹¹Valladas et al., 1988; ¹²Grün et al., 2005; ¹³Svoboda, 2006; ¹⁴Matiegka, 1938; ¹⁵Dobrovolskaya et al. 2012.

Methods

I. Experimental data collection.

The experimental protocol involved two sessions, a laboratory session which took place in the Human Energetics and Biomechanics Laboratory at Washington University, and a MRI session which took place at the Center for Clinical Imaging Research (CCIR), Washington University School of Medicine. The laboratory session was prior to the MRI session, and consent and screening took place upon arrival of the subject for the first session. Time between the two sessions was limited (no more than two months) to minimize changes in strength, since subjects were engaged in training and competition during the data collection period. Several of the first sessions encountered technical difficulties, and the subject was asked to return on a different day to re-collect the data.

1. Anthropometrics.

After obtaining consent, subjects were given fitted spandex shorts and a sleeveless tank-top to wear. Body mass, height, segment lengths, age, sex, and self-reported limb dominance were recorded (appendix I). Body mass was measured with a standard bathroom scale, and height and segment lengths were measured using a flexible tape measure. The following segment lengths were measured based on palpation of standard anatomical landmarks on the dominant side: biacromial breadth (between the acromion processes of the scapulae), upper arm (acromion process to the lateral epicondyle of the humerus), forearm (lateral epicondyle of the humerus to the radial styloid process), proximal thumb (radial styloid process to first metacarpo-phalangeal joint), proximal hand (ulnar styloid process to fifth metacarpo-phalangeal joint), bi-asis (between anterior superior iliac spines), thigh (greater trochanter to lateral condyle of the femur), shank (lateral condyle of femur to lateral malleolus of fibula).

2. *Strength testing.*

Each subject's strength in flexion and extension at the elbow and wrist was assessed using a tension/compression load cell (Dillon FI-127; Fairmont, MN, USA). As discussed in Chapter 4 (II.1), muscles exert a force F_m about a joint with a given EMA, measured as r/R , and the resulting F_e is measured by the load cell. Subjects were seated in an experimental chair and the dominant arm was placed in supination against a padded wooden block (figure 5.1). The height of the chair was adjusted such that the elbow was at a 90° angle, the humerus was fully adducted, and the shoulders were level. A strap attached to the padded wooden block was tightened across the wrist (for elbow strength tests) and across the metacarpal heads (for wrist strength tests). The subjects were asked to flex or extend against the resistance of the strap (flexion) or the block (extension) at maximal effort for 3-5 seconds (an isometric maximal voluntary contraction, MVC). The padded wooden block was attached to the load cell through a non-pliable metal rod, such that compression and tension applied by the subject to the strap or block would be transferred to the load cell with as little compliance as possible. The resulting F_e applied to the load cell was transmitted in real time to a desktop computer running ComTestSerial (Microridge Systems, Sunriver, OR, USA), from which the maximum value over the trial was recorded. Subjects were asked to perform three to four MVCs, and the mean was taken.



Load Cell

Padded wooden block

Figure 5.1 Strength testing apparatus.

Subjects were seated in the chair, which was adjusted to the appropriate height. The arm was placed against the padded wooden block, in supination. The black strap was placed over the wrist (elbow strength testing) and over the hand (wrist strength testing). A non-pliable metal rod transferred the applied force to a load cell placed at the base. The magnitude of the applied force was transmitted in real time to a desktop computer running ComTestSerial (Microridge Systems, Sunriver, OR, USA).

Strength was measured under isometric conditions, such that the joint angle did not change over the course of the contraction. F_e measured during concentric and eccentric contractions will be different than that measured isometrically (Hill, 1938; Doss and Karpovich, 1965; Perrine and Edgerton, 1978; Griffin, 1987), and during throwing muscles will engage in both concentric and eccentric activity. However, there should be a predictable relationship between maximum strength produced during isometric, concentric, and eccentric contractions (Doss and Karpovich, 1965; Griffin, 1987), and isometric strength has been shown to correlate with throwing velocity (Clements et al., 2001). Furthermore, torque measured isometrically is more applicable to the torque estimations based on fossil skeletal measurements, where limb segment length is used as a proxy for R . This is only strictly true when the joint contracts isometrically with the limb segment perpendicular to the ground and the load is applied at the distal end of the limb.

3. *Kinematics and kinetics.*

Kinematic (motion) and kinetic (force) data were obtained for subjects throwing up to six objects at maximal effort into a large net. Figure 5.2 demonstrates the set-up for throwing trials. Subjects stood with the back leg on a force plate (AMTI OR-6; Watertown, MA, USA) collecting at 4000 Hz, and stepped forward with the stride leg onto a wooden platform level with the force plate. Subjects were asked to throw overhand at maximal effort into the net, and to place only the back foot on the force plate. Subjects were allowed to practice throwing until they felt warmed up and comfortable with the set up.

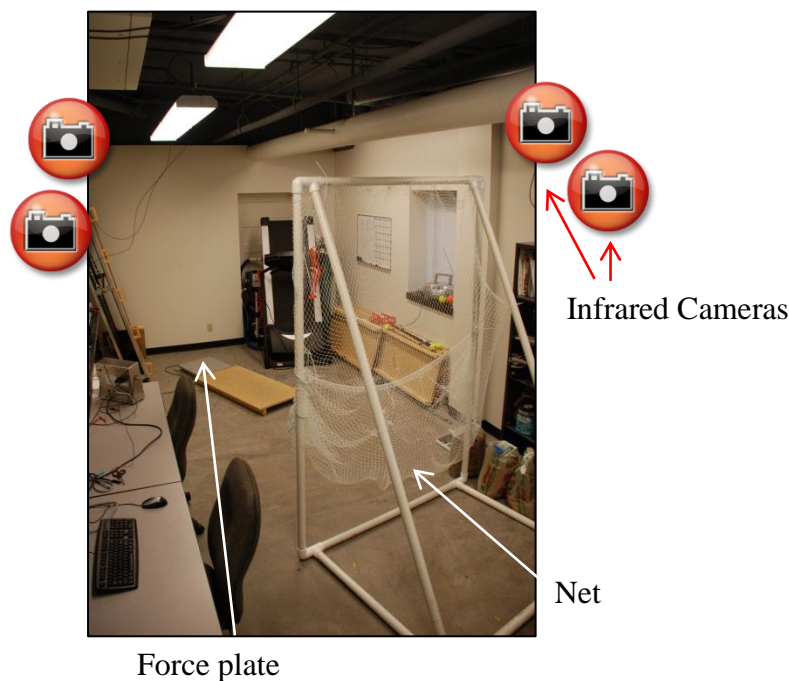
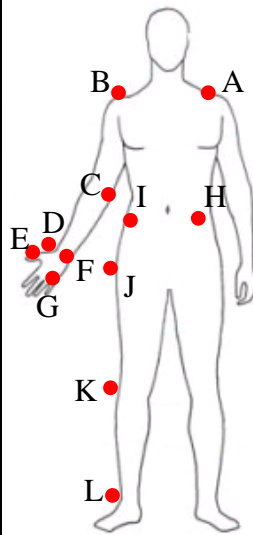
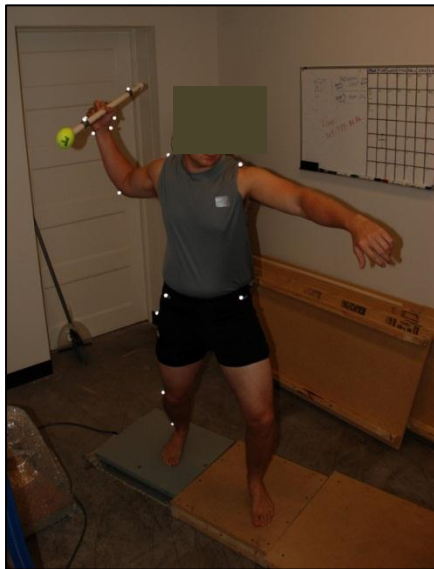


Figure 5.2 Set-up for throwing trials. Subjects stood with the back foot on the force plate and stepped forward with the stride leg onto the wooden track way. Camera icons represent approximate location of the infrared cameras. Force plate and marker position data were transmitted in real time to the Vicon Motion

Infrared reflective markers were placed on the following joint centers of the dominant limb (except where noted) (figure 5.3): left and right acromion processes of the scapulae (L and RShoulder), medial epicondyle of the humerus (Elbow), radial (Radius) and ulnar (Ulna) styloid processes, first (Firstmc) and fifth (Fifthmc) metacarpal heads, left and right anterior superior

iliac spines (L and RAsis), greater trochanter of the femur (Hip), lateral epicondyle of the femur (Knee), lateral malleolus of the fibula (Ankle), and the thrown object (Ball, Spear). Joint centers were located by palpation of bony landmarks and visualization of the COR during movement where necessary. Three dimensional coordinates of the markers were recorded with four wall-mounted high-speed infrared cameras, transmitting to a Vicon motion capture system (Vicon; Centennial, CO, USA) at 200 Hz. The global reference system was defined by the force plate, where the x and y axes were aligned with the corner of the force plate. The y axis was in the direction of the throw, the z axis was perpendicular to the ground, and the x axis was orthogonal to these.



5.3 Infrared Marker Positions and Descriptors.

A: left scapular acromion process (LShoulder), B: right scapular acromion process (RShoulder), C: medial epicondyle of the humerus (Elbow), D: radial styloid process (Radius), E: first metacarpal head (Firstmc), F: ulnar styloid process (Ulna), G: fifth metacarpal head (Fifthmc), H: left anterior superior iliac spine (LAsis), I: right anterior superior iliac spine (RAsis), J: greater trochanter of the femur (Hip), K: lateral epicondyle of the femur (Knee), L: lateral malleolus of the fibula (Ankle).

Subjects threw either four (Non-Competitive sample) or six (Competitive sample) objects. All subjects threw three spear-like objects of equal length and diameter but varying mass (0.40 kg, 0.60 kg, 1.40 kg). The lightest spear was a wooden dowel, the mid-weight spear was a

pvc pipe filled with flour, and the heaviest spear was a metal rod. All spears had a tennis ball on the front to protect the net and nearby equipment, and the center of balance was marked with tape. Each spear had a reflective marker adhered at the front and back so spear angle could be calculated. All subjects threw a standard baseball 76 mm in diameter, weighing 0.18 kg. The Competitive sample threw two additional baseballs of the same diameter, weighing 0.20 kg and 0.31 kg. Each ball had a single reflective marker adhered to it. Subjects threw each object 3-4 times at maximal effort, and data was collected starting before the initiation of the throw, and ending after the object hit the net.

Due to the size and shape of the room used for data collection, several problems were encountered during data collection. The wall-mounted cameras were placed approximately 1.55 and 2.69 m from the ground, halfway down the lab space. During a throw, subjects turn their shoulders approximately 90°, such that if subjects threw directly towards the cameras, their markers would be invisible to half the cameras prior to shoulder rotation (this could have been avoided if the cameras were placed higher, but ceiling height would not allow this). To accommodate the turning of the body, subjects threw at a 45° angle to the cameras. This allowed improved visualization of the markers by the cameras, however, there were still points during the throw when only two or three cameras could see a particular marker. To accurately determine its 3-D coordinates, the camera system requires the marker to be visible to at least 3 and ideally all 4 cameras, and the error increases the fewer cameras are recording the location of the marker. Even with the best possible placement of the cameras and the subject, it was not possible to have all markers in view of all cameras during the whole trial, resulting in greater positional error and loss of some markers at certain points in the throw. The problem was aggravated with larger throwers, since the camera angle was lower relative to the thrower. Furthermore, with the tallest

throwers, the cameras could not view the throwing hand (when it was lifted up during the throw) and the feet with the same camera set-up. Given the purpose of the study, and the necessity to include throwers of a wide range of heights, the foot marker was sacrificed for these subjects. The handling of marker location error and missing markers will be discussed at more length below.

4. *Electromyography.*

To measure muscle activation during the throw, electromyographic (EMG) signals were collected simultaneously with kinematic and force-plate data. Self-adhering bi-polar surface electrodes were placed over the major muscle bellies of the arm and forearm, based on recommendations in Hermens et al. (2000). Electrodes were placed over the largest part of each muscle belly approximately 2 cm apart, parallel to the muscle fibers. Sensors were placed over the biceps and triceps at their largest bulge, approximately two thirds of way down the upper arm. Sensors were placed over the forearm flexors and extensors, on the antero-medial and postero-lateral surfaces of the proximal forearm respectively. A reference electrode was placed low on the back of the hand, as a relatively electrically inactive location. Sensors were connected by fiber optic cable to an amplifier unit, worn around the waist. The cables were adhered to the skin using fabric tape to assure that they did not put tension on the electrodes during motion. The amplifier unit transmitted conditioned EMG signals along a fiber optic cable to a receiver, and analog signals were passed through the Vicon MX Control A/D board and recorded at 4000 Hz. After placing and securing the electrodes, subjects performed several throws to assure the cables and amplifier unit did not interfere with the throwing motion.

During several data collection sessions, problems with the EMG equipment were encountered, including failure of the amplifier unit to turn on, electrodes refusing to remain

attached, and other, non-diagnosable, problems leading to poor quality signals. Given the secondary nature of the EMG data compared with the kinematics and kinetics, and the unpredictability of the EMG data collection equipment, sessions were continued without EMG in these instances. EMG was collected successfully for 27 subjects, which is a useful subsample for examination.

5. *Magnetic resonance imaging.*

To assess muscle size and joint mechanical advantage, MR images were taken using a 1.5T whole body scanner (Avanto; Siemens, Erlangen, Germany) at the Center for Clinical Imaging Research. Scans were taken of the dominant limb from the level of the humeral head proximally to beyond the metacarpal heads distally, in the Competitive throwing sample. Subjects were allowed to flex their fingers, so most scans included the whole hand. In order to make EMA measurements relevant to strength tests and fossil skeletal measurements, scans were performed with the elbow at 90° of flexion, the forearm fully supinated, and the wrist at 0° of flexion. To accommodate the flexed elbow in the small space of the scanner, the subject laid on the bed of the scanner prone, with the arm raised above the head. Pillows were placed under the subject's chest, head, and arm for comfort and to assure that they did not move during the scan. Images were acquired in two overlapping sections using a 3D spoiled gradient echo sequence with 1.2 mm isometric sections, which allowed visualization in all three orientations. The scanning protocol was chosen to optimize visualization of bone, muscle, and tendon, while minimizing scanning time (and therefore costs). While the protocol did not result in ideal scans, they were determined to be sufficient for visualizing the necessary muscle boundaries and bony landmarks.

II. Skeletal data collection.

Skeletal measurements to assess body size and proportions and moment arms were taken for each available fossil or recent human specimen. Skeletal measurements include long bone lengths (humerus, radius, ulna, femur, tibia, 1st and 2nd metacarpal), bi-iliac breadth, and femoral head diameter. Humerus, radius, ulna, femur, and tibia biomechanical lengths were measured using an osteometric board. Femoral head diameter was measured as the maximum diameter using standard calipers. To measure bi-iliac breadth, the innominates and sacrum were held together using rubber-bands or by hand (depending on the size of the specimen), and the maximum breadth of the iliac crests was measured using a tape measure. Many elements were missing or damaged, so not all measurements were possible for each specimen.

Moment arms (r) at the elbow and wrist were measured from a set of scaled and oriented photographs. Photos were used because they can increase precision and accuracy in taking measurements on bones by allowing the researcher to take measurements in a highly consistent manner with very low within observer error. The main source of error with this method is distance perspective, where objects closer to the lens appear proportionally larger (Spencer and Spencer, 1995). However, this can be minimized by increasing the distance of the object to the lens (thereby reducing the relative depth of points on the object), and by aligning the elements to be measured (including the scale bar) in the same plane. Moment arms have been estimated elsewhere as the distance from the proximal or distal end of the segment, or the joint articulation, to the muscle insertion (Trinkaus, 1983; Trinkaus and Churchill, 1988; Trinkaus and Rhoads, 1999; Churchill and Rhodes, 2006; Galtés et al., 2008a; De Groote, 2011; Maki and Trinkaus, 2011; Raichlen et al., 2011). However, the most accurate representation of r requires visualization of the line of action (LOA) of the muscle and the center of rotation (COR) of the

joint concurrently. Photographs reduce these three dimensional lines into the relevant two dimensions, and allow exact measurement of the perpendicular distance between them. Thus, as long as care is taken in the placement of the skeletal elements and the scale bar, photography allows measurement of a skeletal dimension that would be otherwise impossible.

Photos were taken with a Nikon D80 SLR camera, with an 18-135mm zoom lens. Joints were articulated using plasticine clay or museum wax and positioned in a sandbox. Black aquarium sand was used to increase contrast between bone and sand. The elbow was photographed in medial and lateral view (figure 5.4), with the joint COR aligned with the photographic plane, determined visually. The lateral photograph of the elbow was taken with the humerus, radius, and ulna articulated (to measure r for biceps brachii), and the medial photograph was taken with the humerus and ulna articulated (to measure r for brachialis and triceps brachii). Three dimensional bony landmarks that are difficult to view in two dimensions were marked with chalk or drafting tape. The wrist was photographed in radial and ulnar views (figure 5.5), with the COR aligned perpendicular to the photographic plane, determined visually. The radial view of the wrist included the articulated capitate, hamate, triquetral, and pisiform. The ulnar view included the capitate, scaphoid, trapezium, and trapezoid. Moment arms for flexion and extension were measured in both views.

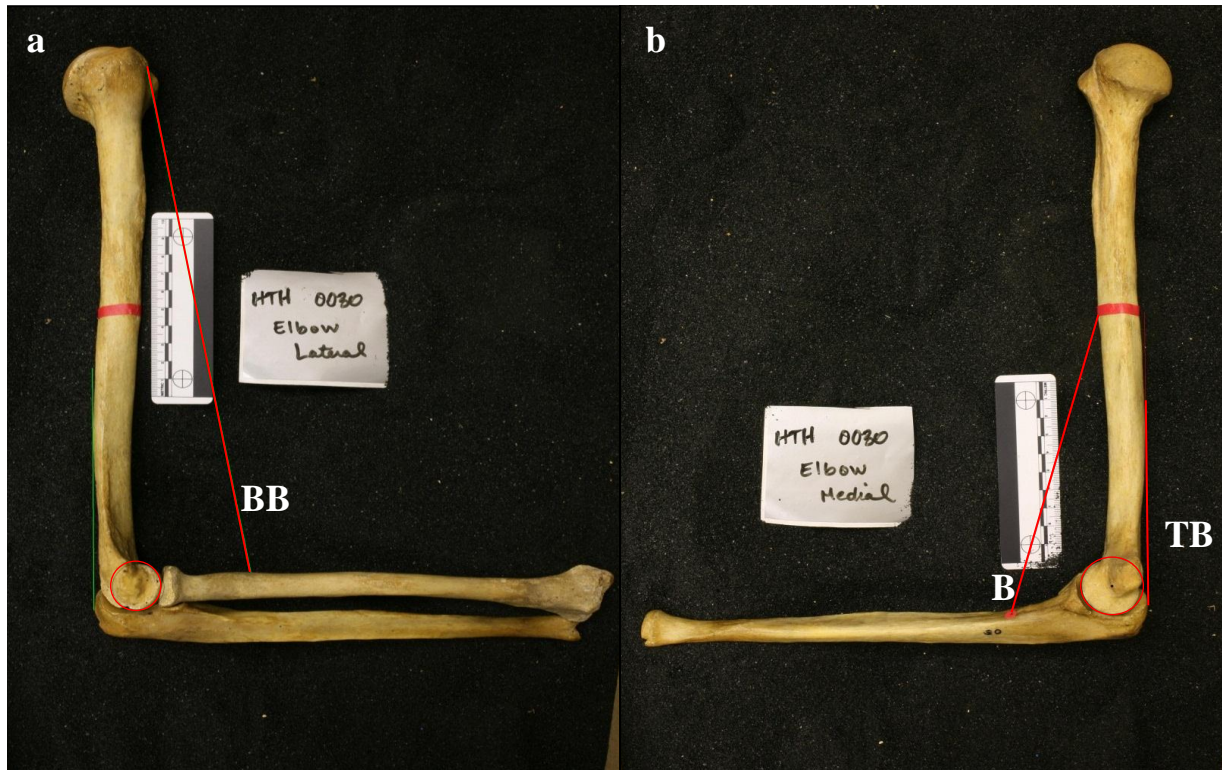


Figure 5.4 Skeletal measurement of moment arms at the elbow. (a) lateral view, (b) medial view. The elbow was photographed with the joint COR perpendicular to the photographic plane. Red lines represent lines of action for biceps brachii (BB), triceps brachii (TB), and brachialis (B). Red circle is the surface about which rotation occurs, the center of this circle is the COR. Moment arms were measured as the perpendicular distance between the COR and each line of action.

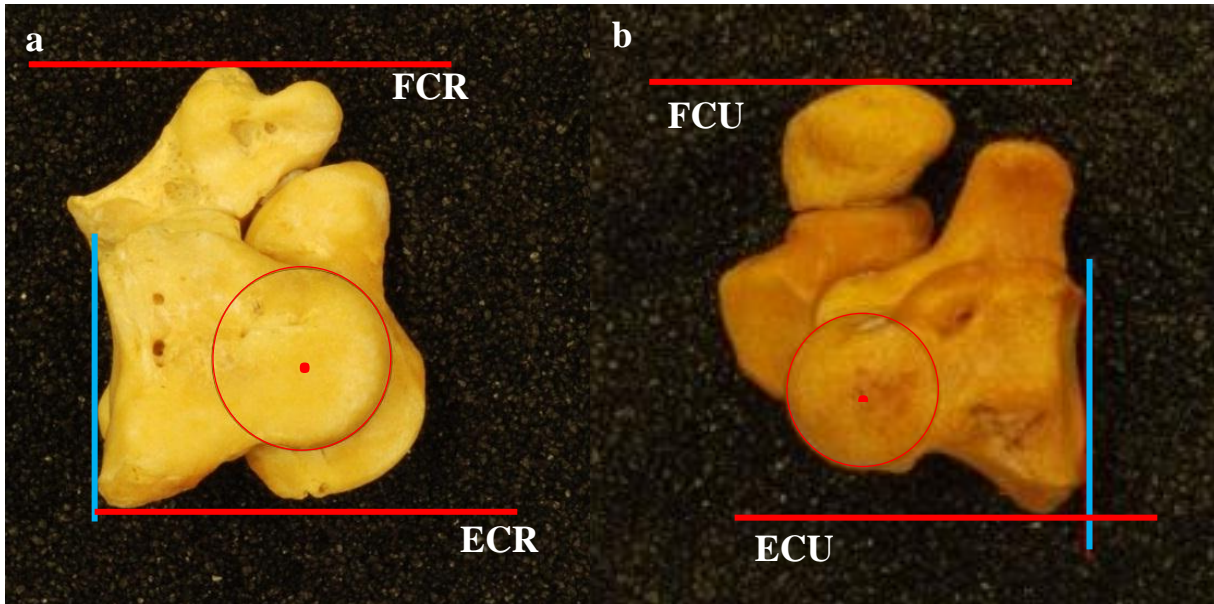


Figure 5.5 Skeletal measurement of moment arms at the wrist. (a) ulnar view, (b) radial view. Photos were taken with the plane of the 2nd and 3rd metacarpal surfaces of the capitate perpendicular to the photographic plane. Photos were then oriented using the distal-most projections of the metacarpal surface of the capitate to define the superior-inferior plane (blue lines). The COR was drawn around the head of the capitate (red circle). The lines of action for flexor carpi ulnaris (FCU), flexor carpi radialis (FCR), extensor carpi ulnaris (ECU), and extensor carpi radialis (longus and brevis, ECR) were drawn perpendicular to the blue lines at the dorsal or palmar-most point on relevant carpals. The moment arms for the flexors and extensors were measured as the perpendicular distance between the COR and each red line.

III. Experimental data processing.

1. Kinematics and kinetics.

Data collected during the throwing trials was visualized in three dimensions in Vicon Nexus 1.3 software. Each reflective marker was identified and labeled. Once a marker is labeled in a single frame, Vicon software automatically labels the marker forward and backward, semi-automating the process. Automated marker identification was checked in each frame, and corrected where necessary. As discussed in section I.3, markers were often missing from a given frame or series of frames. Vicon software allows the user to fill missing markers using either a polynomial spline fill function or the movement of a nearby marker. The former method makes use of the location and trajectory of the previous marker positions and those after the marker

reappears, and generally works well for gaps of no more than 60 frames (gaps here were generally less than 10 frames). A spline function interpolates missing data by piecing together a series of low order polynomials (Robertson et al., 2004). However, the larger the gap, the more unpredictable the motion, and the lower the quality of the data, the less likely the spline fill function will interpolate correctly. Visual assessment was used to evaluate the accuracy of the spline fill function, and it was determined to be sufficient for most gaps. For gaps that the spline function could not adequately fill, the pattern fill function was used. A nearby marker with a similar pattern of motion was chosen, and Vicon generated coordinates based on the trajectory of motion. This function worked well for markers on the hand, since these were close in space and traveling a similar trajectory. The amount of filling required was highly variable between subjects, but very similar within subjects between trials, indicating that the cause was likely the pattern of motion employed by a given subject, or their size relative to the equipment.

Most gaps were able to be filled sufficiently, however in certain cases the gaps could not be filled. The kinematic and kinetic calculations could not be performed on data with missing frames, so where gaps could not be filled, segments of data before or after the gap were removed (if the remaining portion was valuable), or the marker was discarded. If the right or left shoulder, elbow, or RAsis markers were missing, none of the necessary calculations could be performed, so the trial was discarded. On average, each subject had 2.47 trials per object once unusable trials were removed. Several subjects did not have any sufficient trials for a given object, resulting in a loss of approximately 4-5 subjects per object. If non-vital markers were discarded the trial was used, but certain calculations could not be performed, resulting in reduced sample sizes for certain calculations.

Once the markers were labeled and filled, the 3-D coordinates were exported to an excel spreadsheet. All further processing was done using a custom written routine for MATLAB v.7.6 (MathWorks Inc., Natick, MA, USA). Excel spreadsheets containing 3-D marker coordinates, force plate data, EMG data, and the subject's body mass were loaded into MATLAB. Force plate data included the x, y, and z force vectors applied by the subject's back leg to the force plate. EMG and force plate data were collected at 4000 Hz, while kinematic data was collected at 200 Hz, so the force plate and EMG data were resampled to obtain compatible matrices. Force plate data was smoothed using a 9th order, zero-lag butterworth filter, with the cut-off set to 100 Hz. Low pass digital filtering is designed to attenuate (selectively reject) the high frequency portion of the spectrum, which is assumed to be noise (Winter, 2005). Attenuation of noise is particularly important for movement data, because any noise will be magnified exponentially when calculating velocity and acceleration as the first and second derivative of the marker position. Butterworth filters are designed to pass the frequencies below a given cutoff, and attenuate the spectrum above this cutoff. The cutoff is chosen to maximize signal to noise ratio, as a cutoff frequency that is too low will attenuate too much of the signal, and a cutoff frequency that is too high will allow too much noise to pass. When attenuating the signal, a phase shift can occur, such that the output signal is time lagged from the original signal. To remove this time lag, the filter is performed again in the reverse direction. Marker position data was smoothed using a 4th order, zero-lag butterworth filter, with the cut-off set to 16 Hz, following Zheng et al. (2004) for similar throwing data. All further calculations were performed on filtered data.

To determine the beginning and end of the relevant portion of the trial (the actual throw), reference points were chosen. The beginning of the throw was defined as the point when the marker for the Asis on the dominant side reached its maximum linear velocity, after van den

Tillaar and Ettema (2004). This moment was chosen as an “early and clearly identifiable moment in the goal directed movement” (van den Tillaar and Ettema, 2004). Other movements at the onset of the throw are less consistent between subjects, and prior to this time several markers were not consistently visible due to the position of the subject relative to the cameras. Furthermore, this time coincided relatively well with a sudden increase in velocity of the hand and thrown object (the acceleration phase). The end of the trial was defined by the release of the ball or spear, since movements after release will not impact maximum velocity or acceleration of the object. When the object is released by the hand, the distance between them suddenly increases. Additionally, at the moment of release the object is no longer accelerated by the hand, and its velocity curve plateaus slightly, in advance of a downward acceleration due to gravity. Thus, ball/spear release was determined by visual inspection of two graphs, the distance between the hand and the ball/spear relative to time, and the velocity of the ball/spear relative to time. Figure 5.6 demonstrates these events. The ‘throw’ was thus defined as the frames occurring between these two events, and all calculations and measurements were performed on this segment of the data only. Relative timings of events were compared as a proportion of the throw.

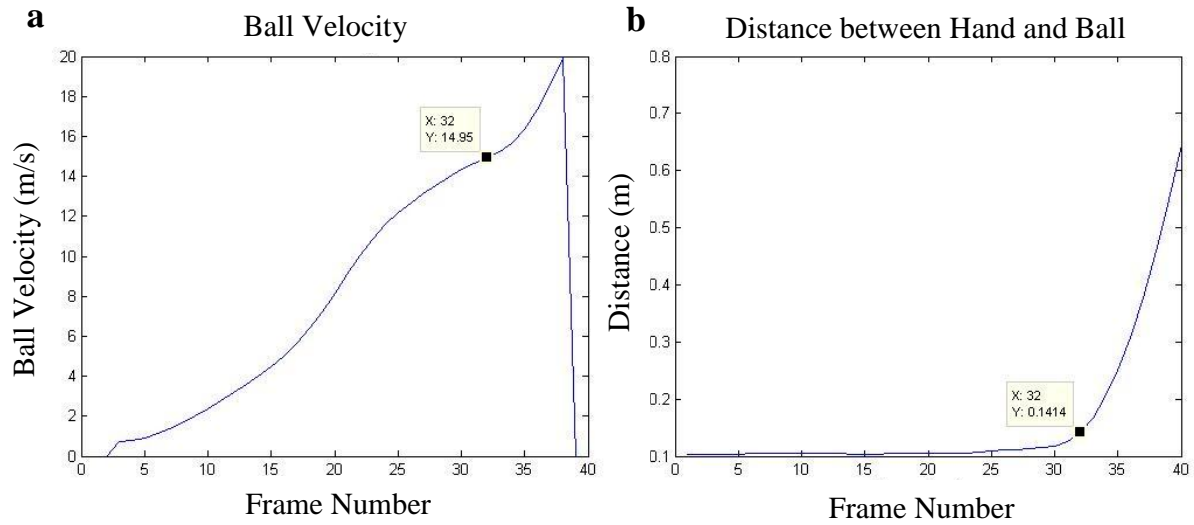


Figure 5.6 Method for determining ball/spear release frame. Ball/spear release was determined from visual inspection of the graphs for (a) ball/spear velocity over time, and (b) the distance between the hand and the ball/spear over time. The frame when ball/spear velocity dipped and the distance between the hand and the ball/spear began to increase was chosen as the release frame.

All measurements and equations calculated in MATLAB are summarized in table 5.2.

Segment lengths were measured using marker positions, to supplement and verify measurements taken externally and with MRI, and to calculate segment mass, center of mass (COM), and moment of inertia (MOI). Segment lengths (L_s) were measured as the Euclidean distance between the markers as:

$$L_s = \sqrt{((x_1 - x_2)^2 + (y_1 - y_2)^2 + (z_1 - z_2)^2)}$$

where L_s is the distance between the points (x_1, y_1, z_1) and (x_2, y_2, z_2) , averaged across the trial.

Segment mass and COM were calculated according to equations from Winter (2005) from body mass and segment lengths (see table 5.2). Segment MOI was calculated according to equations from de Leva (1996).

Linear velocity of the marker positions was calculated using a five point derivative, after Zheng et al. (2004), for similar throwing data. This method uses two frames prior and two frames after any given marker position to provide additional smoothing to the derivative calculations, and reduce the effects of noise still present after filtering. The temporally closer frames are weighted higher in the calculation. Marker and segment COM velocity (v_x), and acceleration (a_x) in the x direction were calculated as:

$$v_x = 1/12 \cdot (-p_x[i+2] + 8 \cdot p_x[i+1] - 8 \cdot p_x[i-1] + p_x[i-2]) \cdot f$$

$$a_x = 1/12 \cdot (-v_x[i+2] + 8 \cdot v_x[i+1] - 8 \cdot v_x[i-1] + v_x[i-2]) \cdot f$$

where $p_x[i]$ and $v_x[i]$ refer to the marker position and velocity with respect to the x axis in the i th frame, and f is the sampling frequency. This was repeated to calculate v_y , v_z , a_y and a_z . The magnitude of the velocity (V) and acceleration (A) vectors with these three components were calculated as:

$$V = \sqrt{(v_x)^2 + (v_y)^2 + (v_z)^2}$$

$$A = \sqrt{(a_x)^2 + (a_y)^2 + (a_z)^2}$$

Linear kinetic energy of the markers and segment COMs were calculated as $\frac{1}{2} M_s V^2$, where M_s is the relevant segment mass (see table 5.2).

To calculate angular velocities and accelerations, local reference systems were defined for the shoulder, upper arm, and wrist. This is necessary because joint motions calculated with reference to the global system will not accurately reflect motions relative to the joint center. The local reference system and motion definitions for the shoulder are illustrated in figure 5.7. The following descriptions and equations are adapted from Zheng et al. (2004). For shoulder motions, the marker on the dominant shoulder was defined as the origin (O), and the x axis (I_{sx}) was the vector from the origin to the non-dominant shoulder. The z axis (I_{sz}) was the vector from the

origin to the ASIS on the dominant side, and the y axis (I_{sy}) was orthogonal to these. Using a vector for the upper arm from the origin to the elbow marker, angles were calculated as the position of the upper arm vector rotating around the y axis (abduction/adduction) and the z axis (horizontal abduction/adduction).

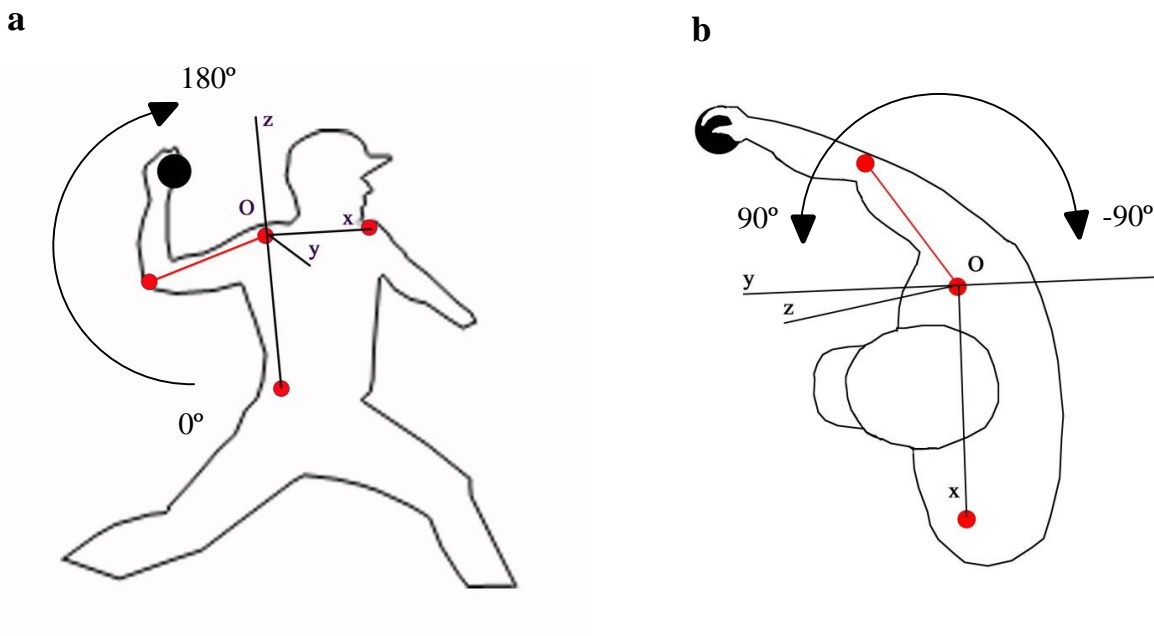


Figure 5.7 Local reference system and motion definitions for the shoulder. The origin (O) is the right shoulder marker. The x axis is defined as the vector passing through the right and left shoulder markers, the z axis passes through the right shoulder and the right ASIS, and the y axis is orthogonal to these. (a) Shoulder abduction/adduction is defined as rotation of the vector passing through O and the elbow marker (red line) around the y axis. (b) Shoulder horizontal abduction/adduction is defined as rotation of the vector passing through O and the elbow marker (red line) around the z axis. Note: horizontal abduction is defined as negative.

Shoulder rotation was defined as the rotation of the upper arm about its own long axis (figure 5.8). A separate local reference system was used, where the x axis (I_{uax}) passed through the elbow and the shoulder of the dominant side. The y axis (I_{uay}) was perpendicular to I_{uax} and a vector from the dominant shoulder to the ASIS of the dominant side, and the z axis (I_{uaz}) was

orthogonal to I_{uax} and I_{uay} . Then, shoulder rotation was defined by the vector of the forearm rotating around I_{uax} . Motions at the elbow are assumed to occur in only one plane. Thus, elbow flexion and extension were determined by the angle between the upper arm vector and the forearm vector.

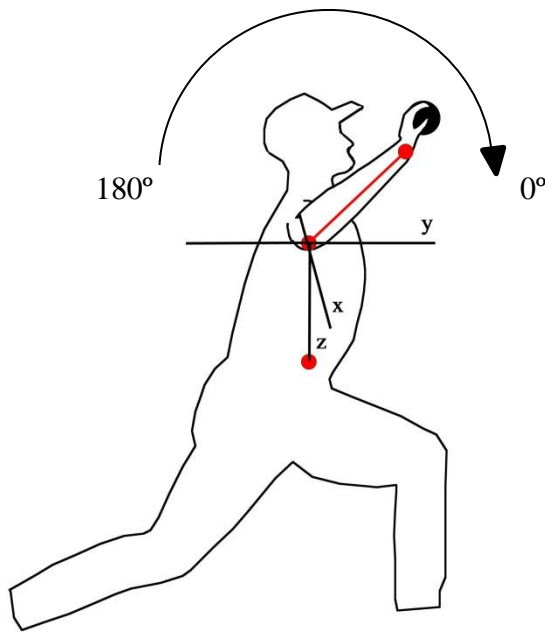


Figure 5.8 Local reference system and motion definitions for shoulder internal/external rotation. The x axis is defined as the vector passing through the right shoulder and elbow markers. The z axis is a vector passing through the right shoulder in the same plane as the right ASIS. The y axis is orthogonal to these. Shoulder internal/external rotation is defined as rotation of the vector passing through the elbow and distal ulna markers around the x axis. Note: shoulder internal rotation is defined as negative.

Wrist motion was determined in a wrist local reference system (figure 5.9), where the x axis (I_{wx}) passed through the markers on the distal ulna and radius. The y axis (I_{wy}) was the forearm vector, and the z axis (I_{wz}) was orthogonal to these. Wrist flexion was calculated as the rotation of the vector for the hand (Radius and Firstmc markers) about I_{wx} . From the joint angles, joint angular velocities (ω) and accelerations (α) were calculated using the equations for v and a above, where $p[i]$ is replaced with joint angle in the i th frame, and $v[i]$ is replaced with ω in the i th frame.

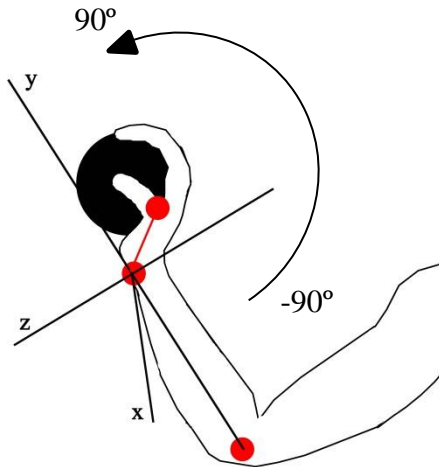


Figure 5.9 Local reference system and motion definitions for the wrist. The x axis is defined as the vector passing through the distal ulna and distal radius markers. The y axis passes through the distal ulna marker and the elbow marker. The z axis is orthogonal to these. Wrist flexion/extension is defined as rotation of the vector passing through the distal radius and the first metacarpal around the x axis

To calculate the torques produced during the throw, a link segment model approach was used, according to Robertson et al. (2004) and Winter (2005). This method infers joint reaction forces and torques from anthropometric measures and the movement of the linked segments. The limb is treated as a series of segments, each segment represented by a fixed point mass located at the COM, and connected by hinge or ball and socket joints (Winter, 2005). Segments in the system are subject to forces from gravity, muscle and ligament forces, and other external forces (Winter, 2005). During throwing, the arm moves freely through space, thus the link segment model for throwing does not involve external forces besides gravity (Robertson et al., 2004). Therefore, after accounting for the known effect of gravity (9.8 m/s in the global z axis), the movement observed will be due to muscle and ligament forces. A limitation of this approach is the inability to determine the contribution of muscle versus tendon and ligament, and tendon and ligament contributions may be significant at high movement speeds (Winter et al., 2005).

Each segment is subject to linear forces (reaction or resultant forces, R_f) and rotational forces (torques or moments of force, M_f) applied by gravity and the proximal and distal segments in the linked chain. Using the observed movement, the known gravitational forces, and

the inferred forces applied from the proximal and distal segments, the resultant joint reaction force and joint moments can be calculated. Beginning with the most distal segment, the hand, which moves freely in this model, Rf_w (resultant force at the wrist) and Mf_w (moment of force at the wrist) were calculated with respect to the x, y and z axes from Newtonian principles as:

$$Rf_{wx} = M_s a_x - M_s g_x$$

$$Mf_{wx} = I_x \alpha_x - Rf_{wx} \cdot d_{wx}$$

where M_s is the mass of the hand and object, a_x is the acceleration of the hand COM with respect to the x axis, and g is the acceleration due to gravity (note: g has only a z component in the global reference system), I_x is the MOI of the hand with respect to the x axis, α_x is the angular acceleration of the segment with respect to the x axis, and d_w is x component of the moment arm for the Rf_w applied by the hand to the wrist. Rf_w was calculated in the global reference system, then converted to the wrist local reference system. Mf_w was then calculated with respect to rotation about each local axis using the relevant x, y and z components of the Rf_w .

At the elbow, Rf_e and Mf_e were calculated with respect to the x, y and z axes as:

$$Rf_{ex} = M_s a_x - M_s g_x + Rf_{wx}$$

$$Mf_{ex} = I_x \alpha_x - Rf_{ex} \cdot d_{ex} + Rf_{wx} \cdot d_{wx} + Mf_{wx}$$

where M_s is the mass of the forearm and I_x is the MOI of the forearm with respect to the x axis.

Rf_w , g , a , Mf_w , d_e and d_w were all converted to the upper arm local coordinate system to be compatible, then Rf_e and Mf_e were calculated in the upper arm local coordinate system.

Similarly, Rf and Mf at the shoulder were calculated with respect to the x, y and z axes as:

$$Rf_{sx} = M_s a_x - M_s g_x + Rf_{ex}$$

$$Mf_{sx} = I_x \alpha_x - Rf_{sx} \cdot d_{sx} + Rf_{ex} \cdot d_{ex} + Mf_{ex}$$

where M_s is the mass of the upper arm and I_x is the MOI of the upper arm with respect to the x axis. Rf_e , g , a , Mf_e , d_e and d_s were all converted to the shoulder local coordinate system to be compatible, then Rf_s and Mf_s were calculated in the shoulder local coordinate system.

The load arm, R , for the elbow was calculated based on a vector for the force of the combined forearm and hand. The position in space of the x component of the COM for the combined hand and forearm was calculated as:

$$x[i] = (M_{s1}x_1 + M_{s2}x_2)/M$$

where $x[i]$ is the position of the COM of the multi-segment system in the i th frame, M_{s1} and M_{s2} are the mass of the hand and forearm, x_1 and x_2 are the x positions of the hand and forearm COMs, and $M = M_{s1} + M_{s2}$. This was repeated to find the y and z components. The velocity and acceleration of this COM were calculated using the equations for V and A above, and its force was calculated as $F = M_sA$, where M_s is the mass of the forearm and hand, and A is the acceleration of the forearm and hand in the plane of motion of elbow flexion and extension. Using the position of this vector in space, the perpendicular distance to the COR of the elbow was calculated as R .

Table 5.2 Summary of MATLAB equations.

Measurement	Equation	Abbreviations
Segment Length	$L_s = \sqrt{(x_1-x_2)^2 + (y_1-y_2)^2 + (z_1-z_2)^2}$	L_s : segment length (x_1, y_1, z_1): coordinates of proximal marker (x_2, y_2, z_2): coordinates of distal marker
Segment Mass	$M_s = M_b \cdot S$	M_b : body mass S: segment mass constant (thigh: 0.100, shank: 0.047, upper arm: 0.028, forearm: 0.016, hand: 0.006)
Segment COM	$COM_s = L_s \cdot S$	S: segment length constant (thigh: 0.433, shank: 0.433, upper arm: 0.436, forearm: 0.430, hand: 0.506)
Segment MOI	$I_{sx} = (L_s \cdot S_x)^2 \cdot M_s$	I_{sx} : Segment MOI with respect to x axis S_x : segment MOI constant in x (upper arm x: 0.153, upper arm y: 0.265, upper arm z: 0.282, forearm x: 0.269, forearm y: 0.108, forearm z: 0.261, hand x: 0.580, hand y: 0.368, hand z: 0.484, thigh: 0.323, shank: 0.302)
Marker Velocity	$v_x = 1/12 \cdot (-p_x[i+2] + 8 \cdot p_x[i+1] - 8 \cdot p_x[i-1] + p_x[i-2]) \cdot f$ $V = \sqrt{(v_x)^2 + (v_y)^2 + (v_z)^2}$	$v_x[i]$: velocity in x in the i^{th} frame $p_x[i]$: marker position in x in the i^{th} frame f: sampling frequency V: magnitude of velocity
Marker Acceleration	$a_x = 1/12 \cdot (-v_x[i+2] + 8 \cdot v_x[i+1] - 8 \cdot v_x[i-1] + v_x[i-2]) \cdot f$ $A = \sqrt{(a_x)^2 + (a_y)^2 + (a_z)^2}$	$a_x[i]$: acceleration with respect to the x axis in the i^{th} frame A: magnitude of acceleration
Joint Angular Velocity	$\omega = 1/12 \cdot (-\theta[i+2] + 8 \cdot \theta[i+1] - 8 \cdot \theta[i-1] + \theta[i-2]) \cdot f$	ω : joint angular velocity $\theta[i]$: joint angle in the i^{th} frame
Joint Angular Acceleration	$\alpha = 1/12 \cdot (-\omega[i+2] + 8 \cdot \omega[i+1] - 8 \cdot \omega[i-1] + \omega[i-2]) \cdot f$	α : joint angular acceleration $\omega[i]$: joint angular velocity in the i^{th} frame
Linear Kinetic Energy	$K_e = \frac{1}{2} M_s V^2$	M_s used for shoulder: arm mass + ball/spear mass; elbow: forearm mass + ball/spear mass; hand: hand mass + ball/spear mass

Measurement	Equation	Abbreviations
Resultant Force at Wrist	$Rf_{wx} = M_s a_x - M_s g_x$	Rf_{wx} : resultant of wrist with respect to x axis M_s : mass of hand and ball a_x : acceleration of hand COM in x g_x : acceleration due to gravity in x
Resultant Force at Elbow	$Rf_{ex} = M_s a_x - M_s g_x + Rf_{wx}$	Rf_{ex} : resultant of elbow with respect to x axis M_s : mass of forearm a_x : acceleration of forearm COM in x
Resultant Force at Shoulder	$Rf_{sx} = M_s a_x - M_s g_x + Rf_{ex}$	Rf_{sx} : resultant of shoulder with respect to x M_s : mass of upper arm a_x : acceleration of upper arm COM in x
Moment of Force at Wrist	$Mf_{wx} = I_x \alpha_x - Rf_{wx} \cdot d_{wx}$	Mf_{wx} : wrist moment with respect to x axis I_x : MOI of hand with respect to x axis α_x : angular acceleration of wrist in x d_{wx} : moment arm for Rf_w in x
Moment of Force at Elbow	$Mf_{ex} = I_x \alpha_x - Rf_{ex} \cdot d_{ex} + Rf_{wx} \cdot d_{wx} + Mf_{wx}$	Mf_{ex} : elbow moment with respect to x axis I_x : MOI of forearm with respect to x axis α_x : angular acceleration of elbow in x d_{ex} : moment arm for Rf_e in x
Moment of Force at Shoulder	$Mf_{sx} = I_x \alpha_x - Rf_{sx} \cdot d_{sx} + Rf_{ex} \cdot d_{ex} + Mf_{ex}$	Mf_{sx} : shoulder moment with respect to x axis I_x : MOI of upper arm with respect to x axis α_x : angular acceleration of shoulder in x d_{sx} : moment arm for Rf_s in x

Measurement	Equation	Abbreviations
Location of COM of Multi-segment System	$x[i] = (M_{s1}x_1 + M_{s2}x_2)/M$ $M = M_{s1} + M_{s2}$	$x[i]$: x position of multi-segment COM $M_{s1,2}$: masses of segments 1 and 2 $x_{1,2}$: x location of COMs of segments 1 and 2
Distance Between LOA and COR in MRIs	$A = \text{cross}(\text{LOA}_2 - \text{LOA}_1, \text{COR}_2 - \text{COR}_1)$ $B = \text{LOA}_1 + \text{dot}(\text{cross}(\text{COR}_1 - \text{LOA}_1, \text{COR}_2 - \text{COR}_1), A) / \text{dot}(A, A) \cdot (\text{LOA}_2 - \text{LOA}_1)$ $d = \text{norm}(B - A) \cdot 1.2$	d = shortest distance between COR and LOA $\text{LOA}_{1,2}$: points defining the LOA $\text{COR}_{1,2}$: points defining the COR Dot: dot product Cross: cross product

2. *EMG.*

Electromyographic signals were viewed and visually assessed in Vicon, then exported to an excel spreadsheet for further processing in MATLAB. Processing of EMG data was performed with a custom MATLAB routine written by D. Raichlen for Pontzer et al. (2009). The signals were band-pass filtered using a fourth- order, zero-lag Butterworth filter with cut-offs at 60 and 300Hz, and processed using Thexton's randomization method (Thexton, 1996). Thextonization separates the signal of muscle firing from the inherently noisy background of electrical activity detected by the EMG electrodes. Noise is by definition random with respect to time, so the method compares the original signal to a series of signals where the data has been randomized. This method has the advantage that it does not require the signal to be rhythmic or for any segment of the data to be identifiable as just noise. The signal was full-wave rectified and binned using a 0.01s reset integral. Full-wave rectification generates the absolute value of the signal, and gives a good indication of the approximate contraction level of the muscle over time (Winter, 2005).

3. *MRI.*

Magnetic resonance images were viewed and processed in Analyze 10.0 software (Biomedical Imaging Resource, Mayo Clinic, Rochester, MN, USA). Initial inspection revealed several problematic scans, including one with movement blur (subject 32, forearm scan), one with distortion due to a metal clip in the subjects clothing near the proximal humerus (subject 30, upper arm scan), and several with geometric distortion (subjects 15, 22, 29, 31, 37, 38, upper arm scans). Geometric distortion is a result of non-linearity of the gradient coil used for the scan. Corrections were applied with manufacturer supplied proprietary software. Such distortion corrections have been shown to remove geometric distortion to the level of pixel resolution (Sumanaweera et al., 1993). The scan with movement blur was removed from the sample, as no measurements could be taken accurately. The scan was not repeated because the subject was no longer available. The scan with distortion around the proximal humerus was used, but no measurements requiring total humeral length were included.

The scans were acquired in two overlapping sections, such that both scans included the elbow. Thus, all measurements could be taken within one scan, and the scans did not need to be appended. Since scans were performed isometrically they could be reconstructed and viewed in all three dimensions simultaneously (figure 5.10). Long bone lengths (humerus, radius, ulna, 1MC, and 2MC) were measured between the proximal most and distal most coordinates of the bone as $L_s \cdot 1.2$, where L_s is the Euclidian distance from the equation for segment length above, and 1.2 is the voxel size.

The relevant muscle and joint anatomy used for the moment arm calculations in MRIs and fossil photographs is summarized in table 5.3, along with descriptions of how the LOAs were modeled for each joint. To calculate muscle moment arms at the elbow, a landmark was

chosen for the origin and insertion of the muscles (biceps brachii, brachialis, triceps brachii), and the LOA was defined as the line passing through the 3-D coordinates for these points. Figure 5.10 demonstrates the selection of the 3-D coordinates for the insertion for triceps brachii on the olecranon process. The moment arm was calculated in two ways, first based on visualization of the LOA of the tendon prior to its insertion (tendon method), and second based on bony landmarks of the origin and insertion (skeletal method). For more details on the skeletal method see figure 5.3, and section IV below. The former is the most functionally accurate representation of r , while the latter allowed direct comparison with the skeletal measurements taken on the fossil specimens.

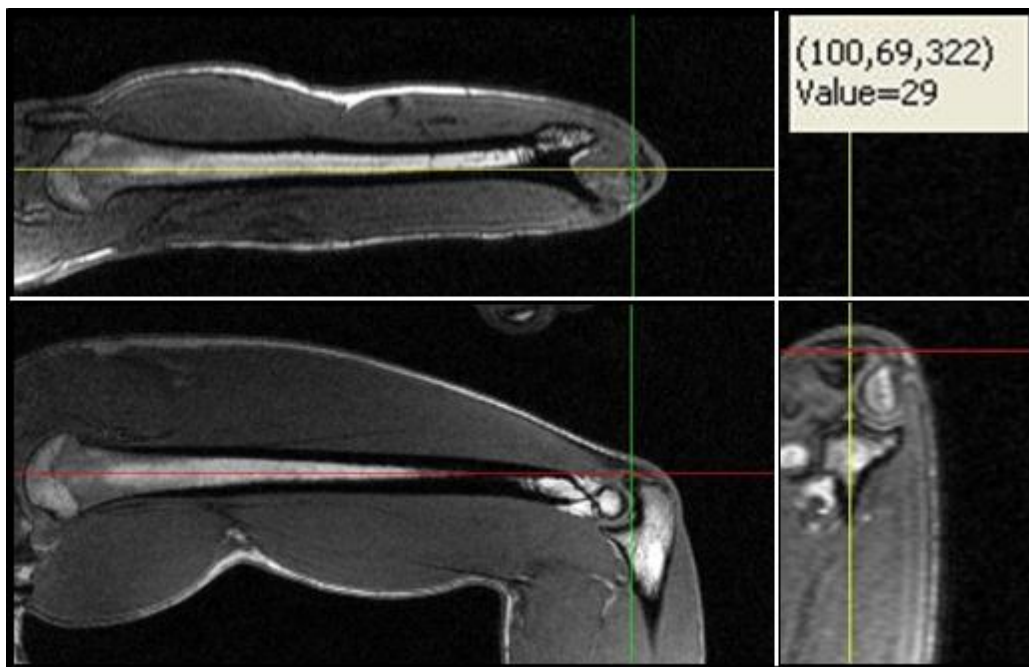


Figure 5.10 Visualization of 3-D coordinates in Analyze. Selection of the coordinates for the insertion for triceps brachii on the olecranon process of the ulna.

For the tendon method, a bony landmark was selected for the insertion, and a point in the center of the tendon proximal to its insertion on the bone was chosen as the ‘origin’. Brachialis was an exception, as this muscle remains quite broad with no clearly identifiable central tendon near the insertion. Instead, the center of the muscle near its origin on the anterior surface of the humerus was used. This muscle travels a relatively straight path from origin to insertion (when the elbow is at 90°), so this should be functionally equivalent to choosing a point near the insertion. For the skeletal method, the same insertion was used, but the bony landmark for the proximal insertion of the muscle, or other clearly observable bony landmark, was used as the origin. The line connecting the origin and insertion was defined as the LOA. The COR was defined as the line passing through the medial and lateral epicondyles of the humerus (Ericson et al., 2003; Deland et al., 1987). The shortest distance (d) between the LOA and COR in 3-D was calculated in MATLAB as:

$$A = \text{cross}(\text{LOA}_2 - \text{LOA}_1, \text{COR}_2 - \text{COR}_1)$$

$$B = \text{LOA}_1 + \text{dot}(\text{cross}(\text{COR}_1 - \text{LOA}_1, \text{COR}_2 - \text{COR}_1), A) / \text{dot}(A, A) \cdot (\text{LOA}_2 - \text{LOA}_1)$$

$$d = \text{norm}(B - A) \cdot 1.2$$

where $\text{LOA}_{1,2}$ and $\text{COR}_{1,2}$ are the two points defining the LOA and the COR respectively, dot and cross refer to the dot product and cross product, and 1.2 is the voxel size.

Measurements of r were performed using the tendon and skeletal methods for flexor carpi ulnaris (FCU), flexor carpi radialis (FCR), extensor carpi radialis longus and brevis (together ECR) and extensor carpi ulnaris (ECU) at the wrist. The COR for the wrist passes through the center of the capitate (Youm, 1978). However, the image resolution was not sufficient to define a three dimensional line through the capitate. Instead, a single point in the center of the head of the capitate was used as the COR, and the distance from this point to the LOA in sagittal view was

measured as r . This assumes that flexion and extension occurs perpendicular to the sagittal plane, and is directly comparable to how the COR was defined for the skeletal measurements. For the tendon method, LOA was defined by the direction of the tendon in sagittal view prior to inserting on or crossing the carpals, and r was the shortest distance in sagittal view between the LOA and the single point for the COR. For the skeletal method, r was the distance in sagittal view between the COR and the most distal point on the carpal where the muscle inserts or crosses the joint. This assumes that the line of pull is parallel to the long axis of the forearm, which should be approximately true when the wrist is in 0° of flexion, and is directly comparable to how measurements were taken skeletally. To measure these distances, the 'caliper tool' in Analyze 10.0 was used (figure 5.11). At one end of the tool, a circle was fit around the head of the capitate. For the tendon method, a line was fit through the center of the tendon, just proximal to its insertion (figure 5.12). For the skeletal method, the most dorsal or palmar point on the relevant carpal was chosen. The caliper tool provided the distance between the center of the circle and the second point or line parallel to the line defined by the processes on the metacarpal facets of the capitate (see figure 5.11).

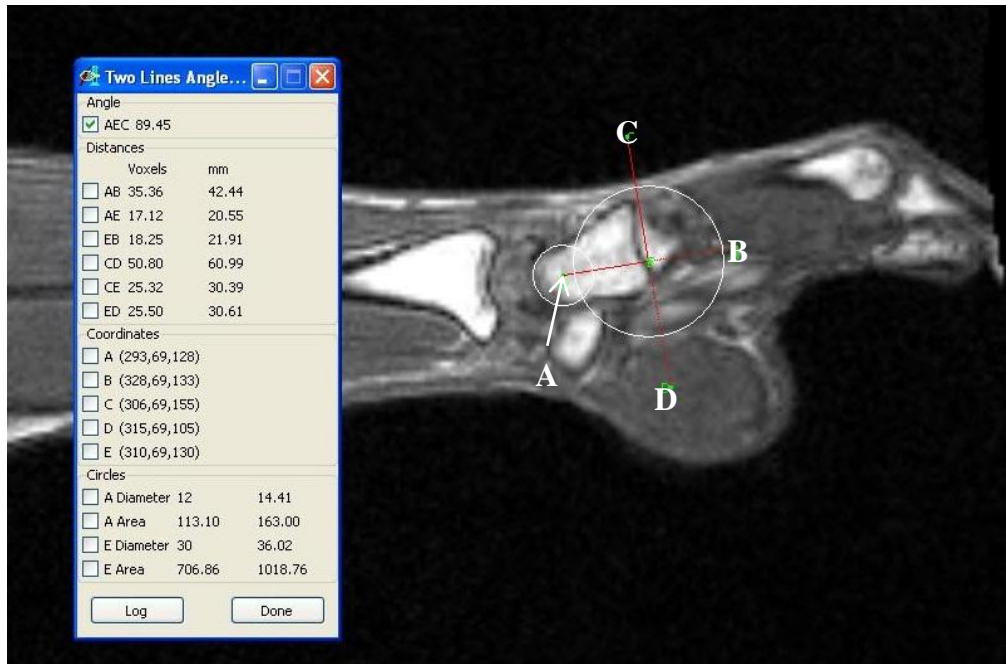


Figure 5.11 Selection of the center of rotation for the wrist. The caliper tool in Analyze was used to visualize a circle around the head of the capitate. The center of the circle (A) is the COR for the wrist. Measurements of r for flexors and extensors were taken from A to the insertion of the relevant muscles (skeletal method), in a plane perpendicular to the processes on the metacarpal facets of the capitate (line C-D).

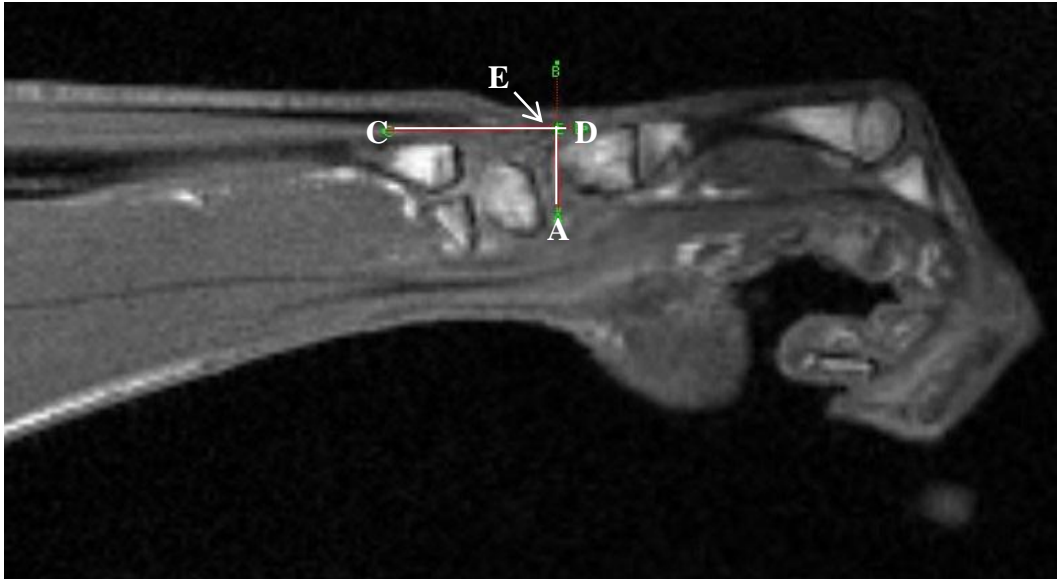


Figure 5.12 Measurement of moment arms in Analyze. Moment arms were measured as the perpendicular distance from the COR (A) to the line of action of the tendon (tendon method). Line C-D represents the line of action of the extensor carpi ulnaris, and line A-E is the moment arm. As above, A is the center of the head of the capitate, which is not visible in this slice.

Muscle cross-sectional areas were measured as the largest single cross section (aCSA) in axial (transverse) view. Muscle aCSA is highly correlated with pCSA and total muscle volume, and is considered to be an appropriate measure of strength (Fukunaga et al., 2001). For each muscle or muscle group, a series of points were drawn around the outer border of what appeared to be the largest cross-section of muscle. Using the ‘region of interest’ tool, the points were connected and smoothed to create a 2-D object, and the area of the object was noted (figure 5.13). The object was then copied to the proximal and distal slices, and the boundaries compared to determine if the muscle was getting larger or smaller. If the boundary appeared to be expanding, the shape would be adjusted to fit the new muscle boundary, and the area compared with the original value. This was repeated until the largest cross-sectional area was found. Muscle aCSA was determined for the biceps brachii, triceps brachii and brachialis individually,

and for the total flexor and extensor (minus brachioradialis) compartments in the forearm. Ideally, aCSA would have been calculated for ECRL/ECRB, ECU, FCR, and FCU individually, since these are the primary flexors and extensors of the wrist, and r was calculated for these muscles specifically. However, the resolution and range of intensities of the scans did not allow visualization of the individual muscle boundaries in the forearm, given their small size.

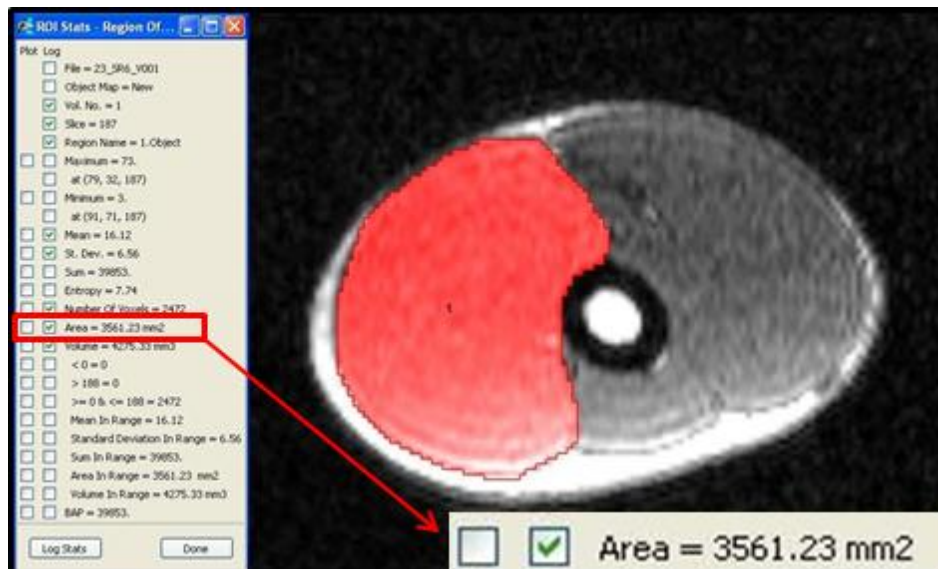


Figure 5.13 Measurement of muscle cross sectional area in Analyze. A series of points were drawn around the outer border of the muscle. Using the 'region of interest' tool, the points were connected and smoothed to create a 2-D object, and the area of the object was recorded.

Table 5.3 Muscle anatomy for moment arm calculations. (a) origins and insertions, (b) lines of action.

a.

Joint	CoR	Motion	Angle	Muscle	Origin	Insertion
Elbow	horizontal through center of trochlea and capitulum of humerus ¹	flexion	90°	B	distal half of anterior surface of humerus	ulnar tuberosity
				BB	coracoid process (short head) and supraglenoid tubercle of scapula (long head)	radial tuberosity
		extension		TB	infraglenoid tubercle of scapula (long head), proximal (lateral head) and distal (medial head) posterior surface of humerus	olecranon process of ulna
Wrist	line running through head of capitate ²	flexion	0°	FCU	medial epicondyle of humerus	palmar surface of pisiform
				FCR		palmar surface of bases of 2 nd and 3 rd MCs
		extension		ECRL/ECRB	lateral supracondylar ridge of humerus	dorsal surface of bases of 2 nd and 3 rd MCs
				ECU	lateral epicondyle of humerus	dorsal surface of base of 5 th MC

Table 5.3 cont.

b.				
Joint	Motion	Muscle	LOA (skeletal)	LOA (tendon)
Elbow	flexion	B	Line connecting ulnar tuberosity to anterior surface of humerus at 50% of humeral length	Line connecting ulnar tuberosity to center of muscle near its origin on the anterior humerus
		BB	Line connecting radial tuberosity to bicipital groove of humerus	Line connecting radial tuberosity to center of BB tendon proximal to the joint
	extension	TB	Line connecting posterior-most points of humerus and olecranon process of ulna	Line connecting posterior most point on olecranon process to center of TB tendon proximal to the joint
Wrist	flexion	FCU	Line parallel to long axis of forearm at the level of the palmar-most point on the pisiform or hamate	Line through tendon as it inserts or crosses the joint
		FCR	Line parallel to long axis of forearm at level of palmar-most point on trapezium	
	extension	ECRL/ECRB	Line parallel to long axis of forearm at the level of the dorsal-most point on capitate or scaphoid	
		ECU	Line parallel to the long axis of the forearm at the level of the dorsal-most point on the capitate, hamate or triquetral	

4. Statistical analyses.

As a result of the methodological difficulties encountered during the collection of the kinematic data, there was significant inter-trial variation in many of the kinematic and kinetic measurements. Thus, it was vital to investigate this variation and remove outliers. All kinematic and kinetic measurements were represented by results from up to 18 trials (3 trials each for up to 6 objects). Subject specific boxplots of the results for all trials were plotted, and outliers were observed and investigated. For some measurements (ex. segment lengths) the result is expected

to be the same for all trials, as they are not affected by the object thrown. Other variables are expected to demonstrate variation between objects (ex. spear kinetic energy). Thus caution was taken in interpreting results of subject-specific boxplots, as some extreme values could be due to expected differences between objects. Once outliers were removed, each subject's trials for a given object were averaged to obtain a single data point.

One assumption of many statistical tests (including regression models and t-tests) is the normality of the distribution (Zuur et al., 2010). Thus, to investigate the distribution of each variable, histograms were generated and tests for normality were performed (Kolmogorov-Smirnov, Shapiro-Wilk). Variables were considered non-normal if normality tests obtained significant results ($p < 0.05$), and there was deviation from linearity of Q-Q plots. Non-normal variables were transformed using the least extreme transformation that obtained a normal distribution, including log (base 10 or e) and square root transformations. All comparisons were performed on transformed data (for those that needed transformation), except where noted. Linear relationships between variables were examined using least squares regression (simple and multiple). Results for categorical variables such as sex and competitive versus non-competitive groups were compared using unpaired t-tests. Comparisons between object masses and object types were made using repeated measures ANOVA, with Greenhouse-Geisser correction for violations of sphericity, and Bonferroni adjustment for post-hoc comparisons. All statistical analyses were performed using SPSS 17.0.

IV. Skeletal Data Processing.

Methods for measuring moment arms from photographs are summarized in table 5.3. Moment arms were measured from skeletal photographs of the articulated elbow for flexion and extension at 90° in medial and lateral view (figure 5.4). For extension, the relevant muscle is the

triceps brachii, which originates along the posterior surface of the humerus (lateral and medial heads) and on the infraglenoid tubercle of the scapula (long head), and inserts on the olecranon process. The LOA for triceps brachii was modeled as connecting the olecranon process to the posterior-most point on the humerus which was largely a function of humeral curvature. The COR for the elbow passes through the trochlea and capitulum of the humerus (Ericson et al., 2003), and was determined by placing a circle around these visually, then finding the center of the circle. The moment arm for triceps brachii was measured as the perpendicular distance between the LOA and the COR in medial view.

Two muscles are involved in elbow flexion, biceps brachii and brachialis. Biceps brachii originates on the corocoid process (short head) and supraglenoid tubercle (long head) of the scapula, and inserts on the radial tuberosity. The LOA for biceps brachii was modeled as connecting the most distal point of the radial tuberosity to the bicipital groove of the humerus. This LOA is directly relevant for the long head, and will be similar to the LOA for the short head in the relevant plane of action. The moment arm was measured as the perpendicular distance between this LOA and the COR in lateral view. Brachialis originates along the distal half of the anterior surface of the humerus, and inserts on the ulnar tuberosity. Thus the LOA for brachialis was modeled as connecting the distal most point of the ulnar tuberosity to a line marking 50% of total humeral length. The moment arm was measured as the perpendicular distance between the LOA and the COR in medial view.

The load arm for the elbow was calculated by subtracting r for TB, which is essentially the length of the olecranon process from the center of rotation posterior, from ulna length. This provides an approximation of the length of the ulna without the olecranon process. Mechanically, this is the relevant load arm assuming a load perpendicular to the long axis of the forearm

applied at the wrist (as is the case for the strength testing). EMA for the flexors and extensors was measured as the relevant moment arm divided by R.

Moment arms at the wrist were measured for flexion and extension at 0°, in medial and lateral views (figure 5.5). Flexion at the wrist is accomplished primarily by the flexor carpi ulnaris (FCU) and flexor carpi radialis (FCR). Both originate via the common flexor tendon on the medial epicondyle of the humerus. The FCU inserts on the pisiform and hook of the hamate. The LOA for FCU was modeled as parallel to the long axis of the forearm at the level of the palmar most point on the pisiform or hamate (generally the pisiform, as this bone projects farther from the COR in most individuals). To determine the orientation of the long axis of the forearm and hand (assuming 0° of flexion), the metacarpal facets of the capitate were used. A line was drawn connecting the processes of the metacarpal facets of the capitate, and this was assumed to be perpendicular to the long axis of the forearm. The moment arm for FCU was measured as the perpendicular distance from the COR to the LOA in radial view.

The FCR inserts on the bases of the 2nd and 3rd metacarpals, and its tendon passes through a groove in the palmar surface of the trapezium. The relevant LOA should be where the tendon crosses the joint, however the groove for the FCR on the trapezium is a continuous surface, making it difficult to choose a single point on this surface consistently. Furthermore, this groove was not visible in MRIs. Instead, the LOA for FCR was modeled as parallel to the long axis of the forearm at the level of the palmar-most point on the trapezium. This assumes that there is a predictable relationship between the distance from the COR to the groove for the FCR, and the palmar most point of the trapezium, an assumption which can be easily tested in the same photos.

Extension of the wrist is accomplished primarily by the extensor carpi radialis longus and brevis (together ECR), and the extensor carpi ulnaris (ECU). These originate via the common

extensor tendon on the lateral supracondylar ridge and lateral epicondyle of the humerus. ECR inserts on the dorsal surfaces of the bases of the 2nd and 3rd metacarpals. The LOA for ECR was modeled as parallel to the long axis of the forearm, at the level of the dorsal most point on the capitate, or scaphoid, since the tendon must cross the carpals before inserting distally. The moment arm was measured as the perpendicular distance from the COR to the LOA in ulnar view. The ECU inserts on the base of the 5th metacarpal. The LOA for ECU was modeled as parallel to the long axis of the forearm at the level of the dorsal most point on the capitate, hamate, or triquetral (usually the capitate was dorsal most). The moment arm was measured as the perpendicular distance from the COR to the LOA in radial view. The load arm for the wrist was 2nd metacarpal (2MC) length, which is approximately the relevant R given a load perpendicular to the long axis of the forearm applied at the metacarpo-phalangeal joint (as was the case for strength testing). EMA was calculated as the relevant moment arm divided by R.

Most of the fossil specimens were missing one or more skeletal elements, requiring adjustment of these methods. If the humerus was missing, the curvature of the trochlear notch was used to find the center of rotation of the joint. To find the origin for brachialis and biceps brachii, an estimate of humeral length was used, either from the length of the humerus of the opposite side, or from prediction equations for humeral length from ulna length in the HTH sample. Variation exists in brachial indices making these predictions less than ideal, however small errors in estimation of humeral length will have minimal effects on the LOA and ultimately r. A line representing the anterior surface of the humerus was drawn perpendicular to the long axis of the ulna at the level of the coronoid process, and the origin for brachialis was marked at half of this length (since brachialis is modeled as originating at half of humerus length). The moment arm for triceps brachii was measured as the distance from the COR to a line

perpendicular to the long axis of the ulna, at the level of the posterior-most point on the olecranon process. This method assumes minimal humeral curvature, but small differences in the LOA due to humeral curvature should have a minimal effect on the moment arm measurement.

No measurements were taken if only a humerus was present, as the variation in the moment arm measurement was primarily a function of the location of the insertion. Similarly, no measurements were taken if only a radius was present, as it would be impossible to define a COR without the distal humerus or proximal ulna. For several specimens, neither side preserved a complete ulna. In these instances, ulna length (for R) was estimated based on predictive equations from radius length in the HTH sample, or from previous estimations of ulna length from radius length provided by E. Trinkaus.

Due to the difficulty of articulating and orienting carpals when elements are missing, measurements were only taken when most of the elements needed for each photo (see above) were present. The capitate was required in all circumstances to estimate the COR and orient the joint. Many fossil specimens retain a capitate and hamate, but not a pisiform. The pisiform generally projects farther from the COR than the hamate, so it would bias the results to measure r from the pisiform for some specimens and from the hamate for others. Instead, r was measured for the hamate and pisiform separately, and the correlation between the two was investigated in the modern human samples. Assuming a strong correlation, r for FCU measured based on the hamate can be used to compare samples. This will not indicate the maximum possible moment arm for FCU, but the pattern of variation should be consistent.

Due to the small sample sizes of fossil samples, inter-group variation was examined using non-parametric tests (Kruskal-Wallis, Mann-Whitney U) with Bonferroni adjustments for multiple comparisons. These tests do not assume a normal distribution, and are more

conservative, making them preferable for small sample sizes. Comparisons within or between modern human samples were made using unpaired student's t-tests for independent samples. All statistical analyses were performed using SPSS v. 17.0.

Chapter 6

Kinetics and Kinematics of Throwing

This chapter will explore the kinematics (motion) and kinetics (forces that produce motion) of throwing. Data were collected on six objects of increasing mass: three baseballs (0.18 kg, 0.20 kg, 0.31 kg) and three spears (0.40 kg, 0.60 kg, 1.40 kg). There is a significant literature on the kinetics and kinematics of baseball throwing, but these data have not been published for spear throwing. Thus, the goal of this chapter is to present the patterns of joint motion and energy used in spear throwing, and to explore the kinetic and kinematic differences between the thrown objects, which will be a result of differences in object mass, object type, or both. The comparison of ball and spear throws will be valuable, as most inferences about hominin spear throwing have relied on patterns of kinetics and kinematics from ball throwing. Differences may exist between the two behaviors that change the assumptions about the adaptation (or lack thereof) of hominins to throwing. The comparison of object masses will be valuable for understanding the implications of average projectile mass in the Paleolithic, which appears to change with time (see chapter 3:I). Most importantly, the data presented on the kinetics and kinematics of throwing will establish a framework for the subsequent chapter, which will discuss how anthropometrics influence the patterns of joint motion and energy observed here.

The discussion will follow the transfer of energy through the kinetic chain, beginning with the legs and torso, followed by the shoulder, elbow and wrist. Kinematics (linear velocities and kinetic energies (K_e)) were calculated for each joint. Torques were only calculated for the shoulder, elbow and wrist, and EMG was only collected for the elbow and wrist, but the force plate data provides insight into the kinetics of the legs during the throw. The energy of a thrown

object at release should be a function of the contributions of each of the segments in the linked chain. In a perfectly efficient system, the contributions would be additive such that the energy of the object would be the sum of the energy generated at each segment through linear and rotational movements. Of course, biological systems will never be perfectly efficient, and there may be many reasons for inefficiencies in the system. However, in a general sense the observed K_e of each of the linked segments should contribute to the K_e of the next link in the chain, and ultimately the K_e of the thrown object. Thus the K_e of a segment should reflect the total energy input to the system up to that point in the chain.

Comparisons will be made of the maximum K_e and velocity of a segment to determine if differences exist between object types (ball versus spear) and object masses. The mass of the object is expected to affect the kinetics and kinematics of the throw by reducing the acceleration and velocity of the joint segments. Muscles achieve lesser shortening velocities when contracting against greater loads (load-velocity relationship, see chapter 4: II.1). Thus, with larger objects, some or all joints may accelerate less and reach lesser maximum velocities. Maximum linear velocity of each segment will be compared to determine if the greater object mass had such kinematic effects.

However, since the K_e of each segment is also a function of the mass of the object (the object is essentially part of the segment until it is released), the reduced velocity may or may not outweigh the effects of greater object mass, depending on the magnitude of the kinematic effects. Thus, maximum K_e of each segment will be compared to determine the ultimate effect of object mass on the energy imparted by the segment to the throw. Where there is an absolute difference in maximum segment or object K_e , this will have a meaningful effect on the outcome of the throw (greater or lesser energy imparted to the throw), and this may be useful in understanding

the potential motivations a thrower has for choosing a larger or smaller object. Although the implications are less clear, it is also possible that differences in kinematics and kinetics exist between object types, presumably due to their different shapes. Thus, similar comparisons will be made between object types to determine if shape affects velocity and K_e (independent of mass). These comparisons will be made with repeated measures ANOVA with Bonferroni adjustments for multiple comparisons, and Greenhouse-Geisser adjustments for violation of sphericity (where necessary).

However, an additional complication exists, in that with the exception of the first link in the chain, each segment's motion will be a function of actions at that joint and actions proximal in the chain. Thus, to determine whether differences in velocity exist independent of variation occurring proximal in the chain (i.e., due to the kinematics and/or kinetics of that joint), a linear mixed effects model will be employed. This technique has the advantage of allowing missing data points, and taking repeated measures into account as random effects. The velocity of the distal segment will be predicted using subject ID and the velocity of the proximal segment as random effects, and object type and object mass as fixed effects. Significant effects of object type (between types) or object mass (within types) will indicate variation in velocity that is independent of variation proximal in the chain.

Where differences exist in the linear velocity of a given segment, the potential causes will be examined. The contribution of each joint to the throw should be measurable by its joint angular velocity (ω), since the maximum linear velocity of the distal end of the segment (and thus its K_e) should be a direct function of the maximum absolute rotational velocity of the segment (and between individuals, its length). If the rotational motion is produced by muscular forces (F_m), the torques measured will be valuable in indicating the magnitude of F_m required for

producing a given ω . Muscle activation patterns from EMG will be presented for the elbow and wrist to determine if patterns of activation correspond with measured torques. Due to the nature of these data, comparisons will be visual, not statistical. If the angular velocities and/or torques observed are not primarily due to F_m , the torques will provide little useful information regarding the contribution of the joint to the throw.

I. Kinetics and kinematics of the legs and torso.

Assuming the K_e of the anterior superior iliac spine (ASIS) on the dominant side (abbreviated as RASIS, since most subjects are right dominant) represents the total energy generated by the legs, comparisons were made of RASIS K_e within subjects across object masses and types. Figure 6.1a presents a boxplot for RASIS K_e for all objects. No significant differences were observed between ball masses (Ball 1 (B1):B2, $p = 0.078$, B2:B3, $p > 0.999$, B1:B3, $p = 0.140$), and the only significant difference for the spears was between S1 and S2 (S1:S2, $p = 0.003$, S2:S3, $p > 0.999$, S1:S3, $p = 0.175$). This indicates that despite differences in object mass, there is a general similarity in the total K_e achieved by the legs. Furthermore, figure 6.1b presents the results of RASIS velocity across object types and masses. As with K_e , there are no significant differences between the object masses (B1:B2, $p = 0.618$, B2:B3, $p = 0.786$, B1:B3, $p > 0.999$; S1:S2, $p = 0.707$, S2:S3, $p = 0.178$, S1:S3, $p > 0.999$). Thus, there is no effect of object mass on the kinematics of the legs. The legs are able to accommodate increasing object mass without a decrease in velocity (at least up to the largest object tested).

While object mass does not affect leg kinematics, there is a significant difference between the balls and the spears for RASIS K_e and velocity. Subjects achieved significantly lower K_e and velocity of the RASIS with the spears as compared with the balls ($p < 0.001$). The velocity achieved by the RASIS is a function of stride length (see chapter 7), so this difference could be a

result of subjects taking shorter strides when throwing spears. Figure 6.1c demonstrates stride length across all objects. As expected, subjects took significantly shorter strides with the spears than the balls ($p = 0.004$). Although it is possible that throwing a spear necessitates shorter strides, it is more likely that the size of the lab space where data was collected made subjects feel constrained when throwing a long object.

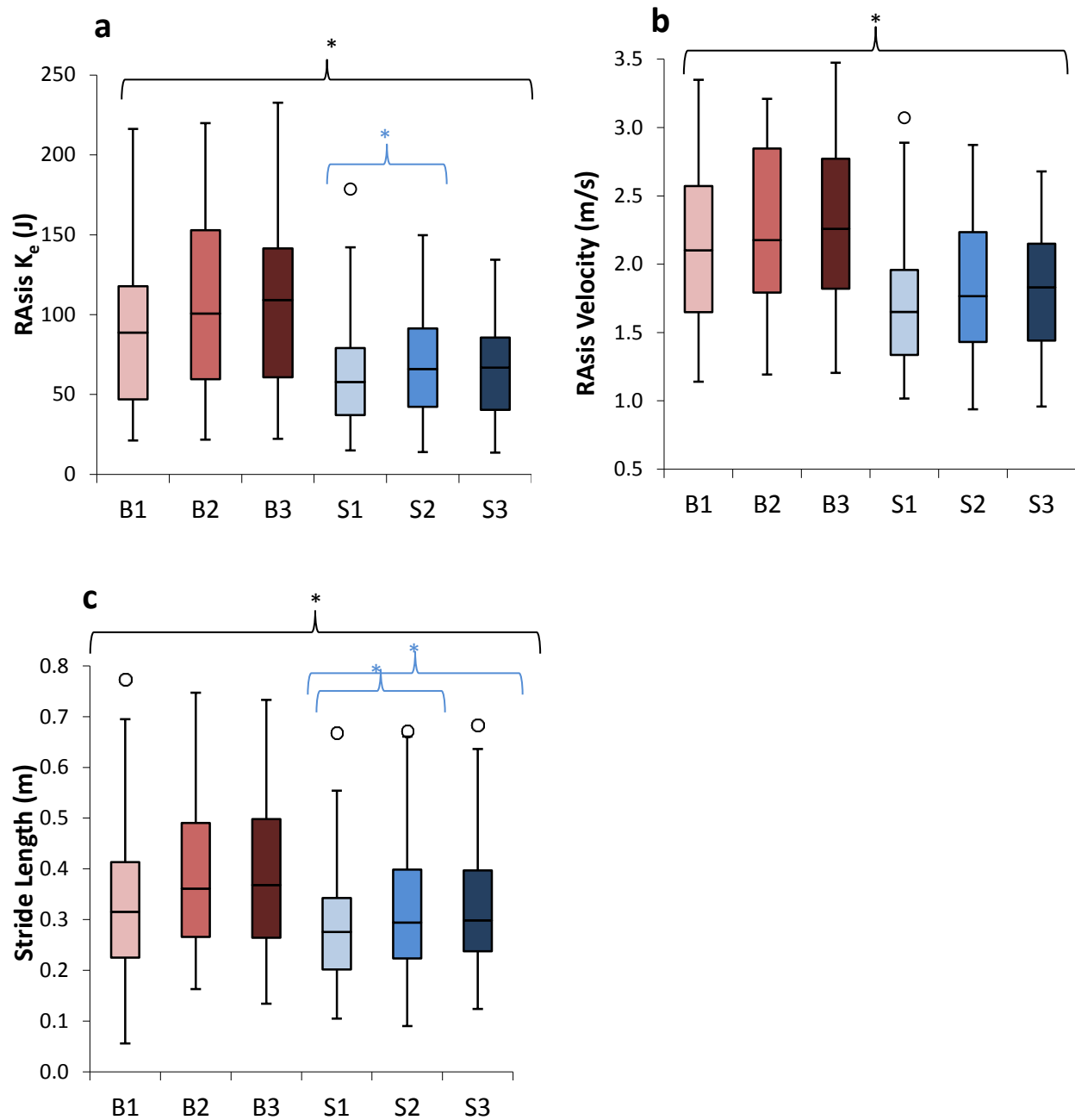


Figure 6.1 Leg kinematics.

Moving up the kinetic chain, comparisons of RShoulder K_e were made within subjects, across object masses and types. The mass of the object is included in the calculation of RShoulder K_e , and thus greater K_e is expected with greater object mass unless concurrent changes in segment velocity occur that counteract the increased mass. Figure 6.2a presents a

boxplot of the results for RShoulder K_e . Within object types, a trend of increasing K_e is observed with increasing object mass, and significant differences were found across most ball and spear masses (B1:B2, $p = 0.695$, B2:B3, $p = 0.018$, B1:B3, $p = 0.005$; S1:S2, $p = 0.010$, S2:S3, $p = 0.004$, S1:S3, $p < 0.001$). Thus, in absolute K_e , there is a clear advantage to throwing a heavier object, as greater K_e is achieved by the body with heavier objects. To determine whether there were concurrent decreases in segment velocity due to the greater object mass, boxplots of RShoulder velocity were compared (figure 6.2b). No significant differences were found across spear masses ($p = 0.113$), but B3 was significantly greater than B1 (B1:B2, $p = 0.629$, B2:B3, $p = 0.283$, B1:B3, $p = 0.045$). Thus, subjects actually increased their dominant shoulder velocity from the smallest to the largest ball mass.

To determine if this variation is a result of differences in kinematics and/or kinetics of the torso (rather than cumulative effects of variation in RAsis K_e), a linear mixed model was employed to assess the independent effects of RAsis velocity and ball mass on RShoulder velocity for the balls. The mixed model found a significant effect of both RAsis velocity ($p < 0.001$) and ball mass ($p = 0.010$), demonstrating that RShoulder velocity during ball throwing increases as a result of cumulative effects from proximal in the kinetic chain and independent effects in the torso. It is unclear why there would be kinetic effects in the torso that would produce greater velocity with a heavier object. Similarly, a mixed effects model was employed to establish whether differences exist between object types independent of any variation in RAsis velocity or object mass. The model found that RAsis velocity significantly explained a portion of the variance in RShoulder velocity ($p < 0.001$), but there was no significant independent difference in RShoulder velocity between object types ($p = 0.059$). Thus, for ball throwing, there is no categorical difference between object types.

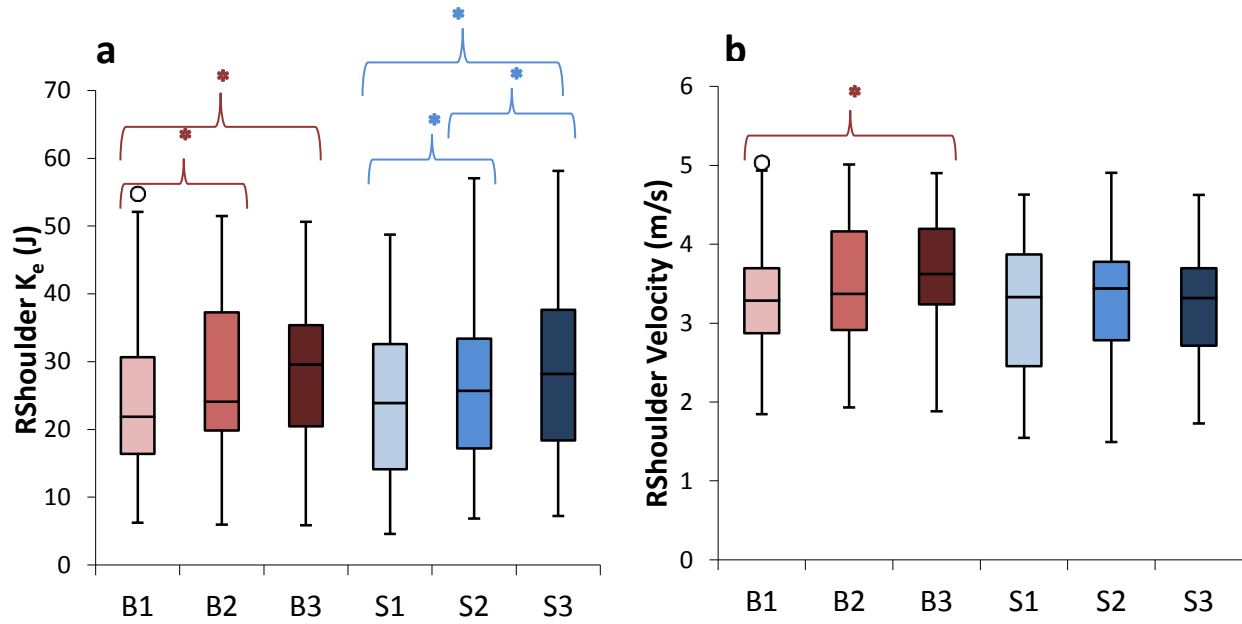


Figure 6.2 Torso kinematics.

II. Kinetics and kinematics of the arm.

1. The shoulder.

The Elbow marker was considered to reflect the cumulative effects of the body, as summarized by the RShoulder, plus the kinetics and kinematics of the shoulder. The absolute K_e of the Elbow across objects signifies the effects of throwing a heavier object on the total energy generated up to that point in the kinetic chain. Figure 6.3a demonstrates that there is a significant trend towards greater Elbow K_e for heavier objects (as expected by the heavier object mass), for both the balls and the spears (B1:B2, $p = 0.291$, B2:B3, $p = 0.014$, B1:B3, $p = 0.004$, S1:S2, $p = 0.001$, S2:S3, $p < 0.001$, S1:S3, $p < 0.001$). When Elbow velocity is considered (figure 6.3b), the only differences are between S3 and the other spears (B1:B2, $p = 0.291$, B2:B3, $p > 0.999$, B1:B3, $p = 0.624$, S1:S2, $p > 0.999$, S2:S3, $p < 0.001$, S1:S3, $p < 0.001$). Thus, there is an absolute advantage to throwing a heavier object for both spears and balls, despite decreased linear Elbow velocity for S3. Furthermore, to demonstrate that shoulder kinematics and/or

kinetics have an effect on Elbow velocity for the spears independent of RShoulder velocity, a mixed model predicting Elbow velocity from spear mass and RShoulder velocity was employed. RShoulder velocity and spear mass were both found to be significant predictors of Elbow velocity at $p < 0.001$. Thus, variation at the shoulder contributes to decreased linear velocity of the elbow for S3.

In addition to the variation observed within objects, there are significant differences between the balls and spears, both in terms of K_e and velocity of the Elbow. A mixed effects model was employed to test for an independent effect of object type on Elbow velocity beyond RShoulder velocity and object mass. The model found a significant effect of both RShoulder velocity and object type ($p = 0.001$ for both), demonstrating that Elbow velocity varies between balls and spears, beyond the effects of ball mass and variation proximal in the kinetic chain. Thus, there is likely variation in shoulder kinematics or kinetics between the balls and spears as well as within spears.

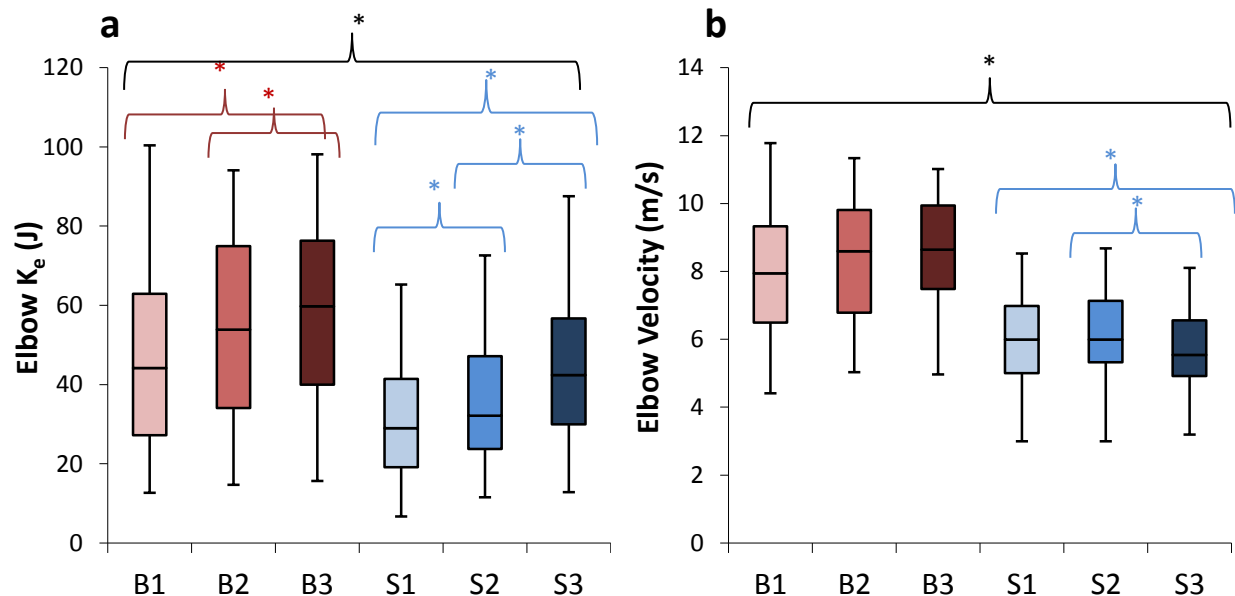


Figure 6.3 Shoulder kinematics.

Previous research on ball throwing has indicated that shoulder internal rotation is of primary importance in generating ball velocity (Feltner and Dapena, 1986). Figure 6.4a demonstrates the patterns of shoulder internal and external rotation ω over the course of a ball throw and a spear throw. The pattern appears on initial inspection to be quite similar within objects, and quite different between objects. Throwers achieve much lower internal and external rotation ω during spear throwing than ball throwing. Repeated measures ANOVA found a significant difference in maximum internal rotation ω between groups ($p < 0.001$), and no significant differences within groups (balls, $p = 0.094$; spears, $p = 0.267$). This difference is due to a much narrower range of motion used during spear versus ball throwing. Figure 6.4b presents the pattern of shoulder internal rotation torque (moment of force, M_f) across the throws. For both types of throwing, relatively small internal rotation torques are generated during the first half of the throw, followed by an external rotation torque. Internal rotation torque magnitudes are not significantly different between objects ($p = 0.116$), despite the extremely large internal rotation ω observed in the ball throws. It may be that subjects are generating optimal torques during both throwing types, but the limited range of motion used during spear throwing does not allow these torques to translate to angular velocity as effectively as during ball throwing. Furthermore, ball throwing is characterized by a very large external rotation torque as compared with the spear throws, probably to resist the large internal rotation ω . Within objects, there were no significant differences in M_f for the balls ($p = 0.125$) or spears ($p = 0.059$).

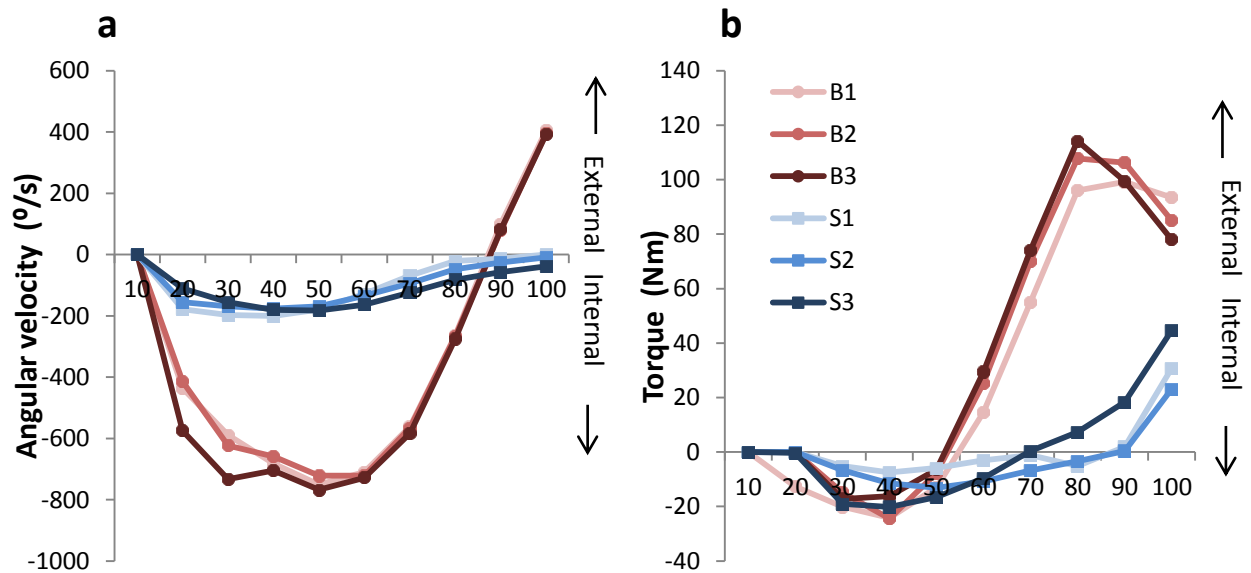


Figure 6.4 Shoulder internal/external rotation.

Figure 6.5 presents the patterns of abduction/adduction ω and Mf generated during throwing. Both ball and spear throwing are characterized by low adduction ω in the first third of the throw, followed by large abduction ω . Abduction ω is similar between objects and object types during the first portion of the throw, but in ball throwing an adduction torque produces adduction during the latter part of the throw. In contrast, during spear throwing the shoulder continues to abduct, ultimately achieving much greater maximum abduction ω ($p = 0.010$). Despite a similar pattern of abduction during the first 60% of the throw, the magnitude of the torque produced between the balls and spear is quite different. Significantly smaller maximum abduction Mf is generated during spear versus ball throwing ($p < 0.001$). Thus, either there are factors involved in producing abduction ω beyond torques, or a difference in the position of the arm results in greater ω for a given Mf during spear throwing. An adduction torque follows the abduction torque for both object types as well, but again the magnitude is significantly smaller, explaining the lack of shoulder adduction during spear throwing. Patterns of abduction ω and Mf

within object types are quite similar, and no significant differences exist for the balls (ω , $p = 0.253$; Mf , $p = 0.193$) or the spears (ω , $p = 0.935$; Mf , $p = 0.332$).

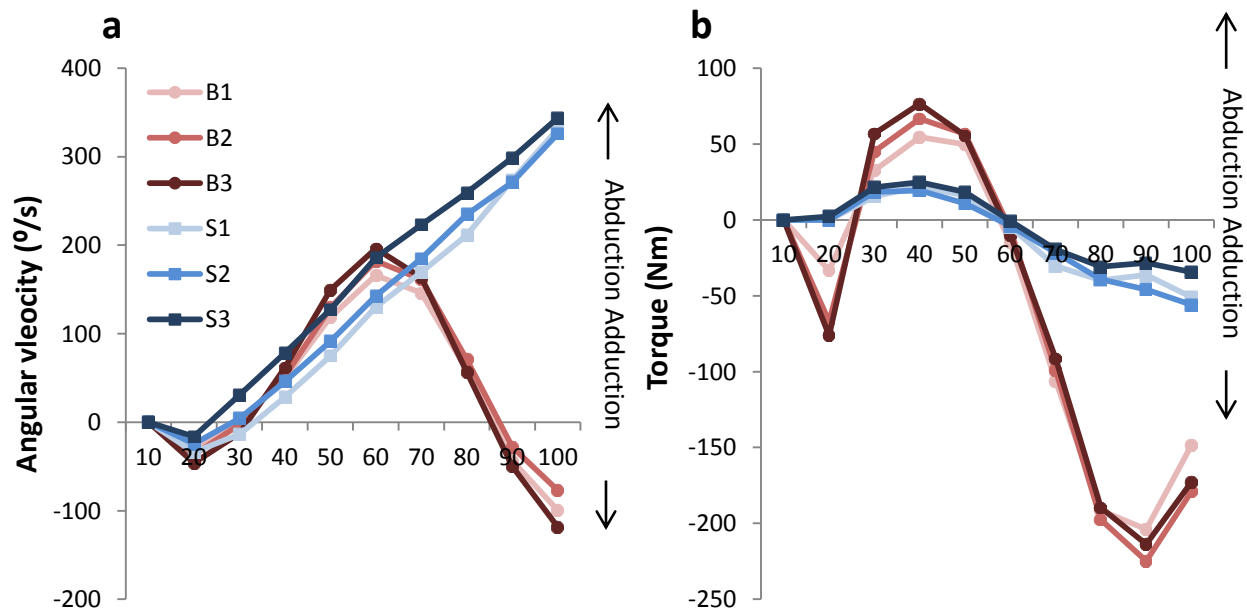


Figure 6.5 Shoulder abduction/adduction.

Patterns of horizontal adduction ω and Mf (forward movement of the humerus in the horizontal plane) are presented in Figure 6.6. Horizontal adduction ω increases until about 70% of the throw, and then begins to decrease. The maximum horizontal adduction ω achieved during spear throws is significantly lower than during the ball throws ($p < 0.001$), and appears to be somewhat delayed in time. This delay corresponds to a small delay in horizontal adduction torque. A significant difference exists in the magnitude of the adduction torque between object types ($p = 0.002$), which could explain the difference in adduction ω , however the magnitude of this difference is quite small compared with the magnitude of the difference in ω . Large horizontal abduction torques are produced during the latter half of the throw for both objects. These are larger for the balls than spears, likely to resist the larger adduction ω . Within objects, no significant differences were found for maximum horizontal adduction ω or Mf for the balls

(ω , $p = 0.717$; M_f , $p = 0.960$). For the spear throws however, horizontal adduction ω was significantly lower for S3 as compared with S1 and S2 (S1:S2, $p = 0.323$, S2:S3, $p < 0.001$, S1:S3, $p < 0.001$). This did not correspond to a difference in maximum horizontal adduction torque, which was not significantly different between spears ($p = 0.766$). One potential explanation is that the muscles responsible for horizontal adduction were taxed when throwing S3, such that they could not maintain the adduction torque as long as with the other spears. Horizontal adduction begins to slow earlier with S3 and does not reach an equivalent peak ω .

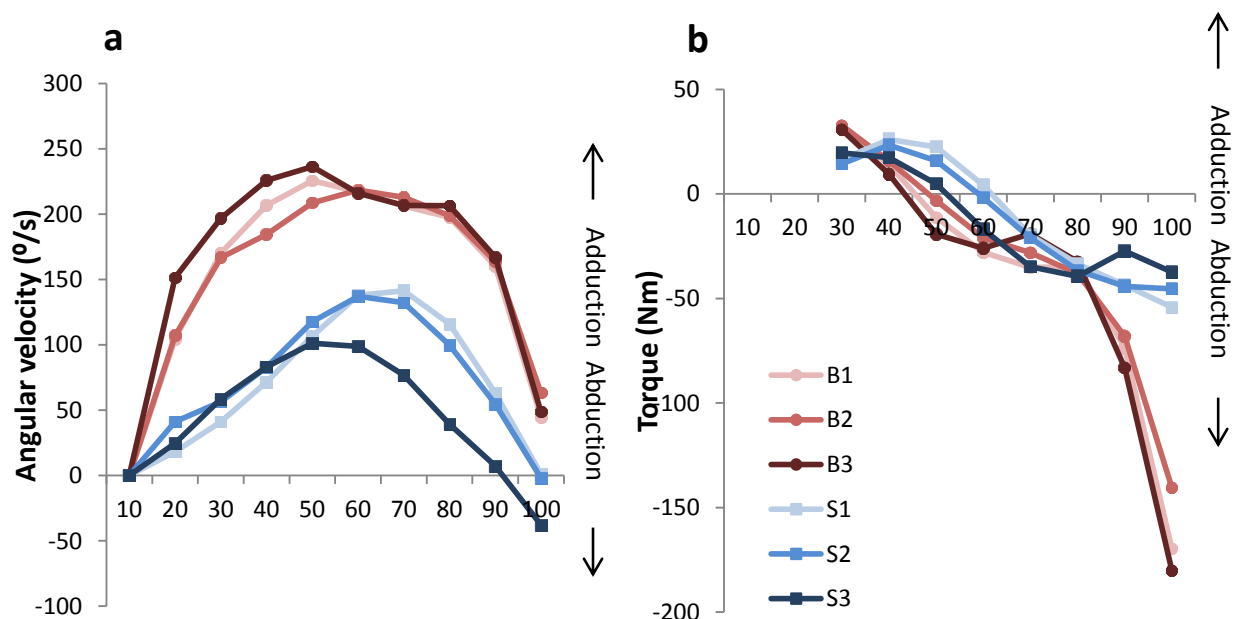


Figure 6.6 Shoulder horizontal abduction/adduction.

The differences in Elbow velocity between object types and between spear masses can now be interpreted in light of this discussion. Spear throws achieve significantly lower internal rotation ω and horizontal adduction ω , which certainly should lead to lesser linear velocities down the chain. The magnitude of the difference in internal rotation ω is quite large, despite very similar torques. Thus, this is not due to differential muscle activation, but instead due to a

narrower range of motion used during the spear throws. Significant differences in Elbow velocity were observed within the spears, primarily due to decreased Elbow velocity in S3. The only kinetic or kinematic factor found to differ significantly between spears is horizontal adduction ω . Thus, the lesser linear velocity observed at the shoulder when throwing a heavier spear is likely due to a reduction in horizontal adduction.

2. *The elbow.*

Moving along the kinetic chain, the kinematics and kinetics of the elbow were compared using the K_e and velocity of the Ulna. To determine if the absolute advantage of throwing a heavier object observed at the previous joints was maintained, Ulna K_e was compared within objects (Figure 6.7a). Significantly greater K_e was found for heavier objects of both object types at $p < 0.001$, except for B1 and B2 ($p > 0.999$). When Ulna velocity was compared (figure 6.7b), differences between object masses were maintained, but in the opposite direction (B1:B2, $p > 0.999$, B2:B3, $p < 0.001$, B1:B3, $p = 0.001$; all spears, $p < 0.001$). Thus, a significant reduction in velocity occurred with heavier objects, but absolute K_e was still significantly greater despite this reduction in velocity. However, significant differences were observed in Elbow velocity between object masses (at least for the spears), which are likely to have been transferred down the kinetic chain. Thus to establish whether differences exist in Ulna velocity independent of variation in Elbow velocity, a mixed effects model predicting Ulna velocity from Elbow velocity and object mass was tested for the balls and spears. The mixed effects model found significant effects of object mass and Elbow velocity on Ulna velocity at $p < 0.001$ for both the balls and the spears.

In addition to the variation within groups, there are significant differences in K_e and velocity of the Ulna between groups ($p < 0.001$ for both). To establish whether these differences are independent of variation in Elbow K_e and object mass, a mixed effects model was used to test

Elbow K_e , object mass, and object type as predictors of Ulna K_e . The mixed model found a significant effect of both object type and Ulna K_e at $p < 0.001$. Thus, there are kinetic and/or kinematic differences between object masses and object types at the elbow that lead to differences in the linear velocity of the distal end of the segment.

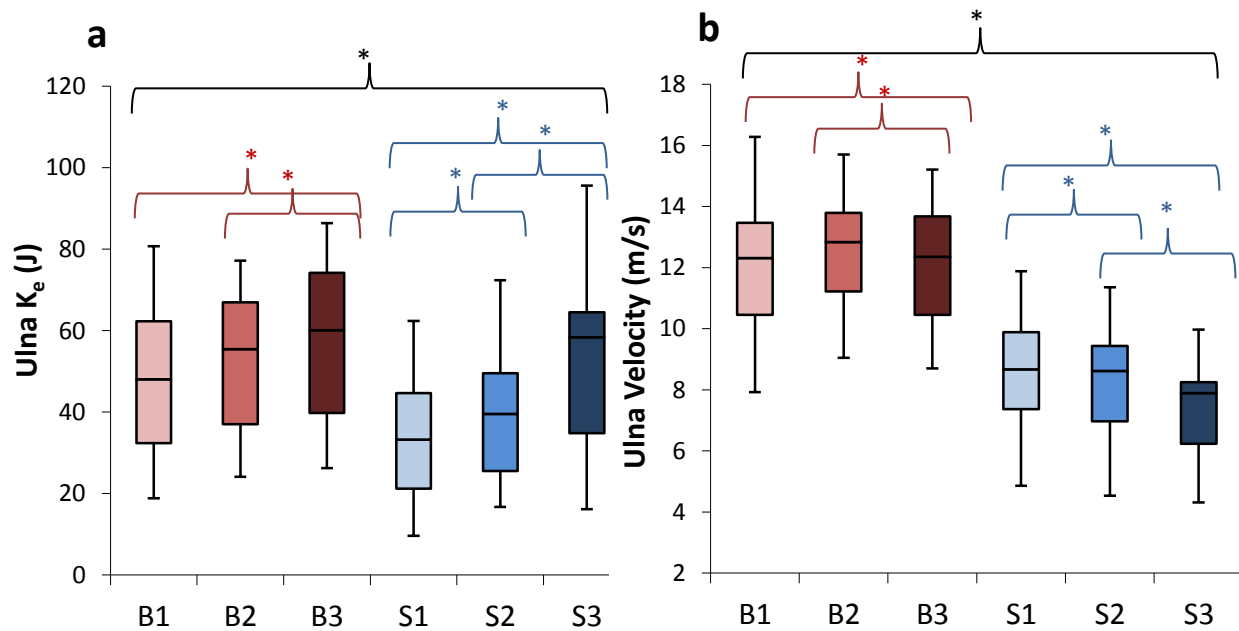


Figure 6.7 Elbow kinematics.

Figure 6.8 presents the patterns of ω , Mf, and muscle activation for the elbow in flexion/extension. The elbow extends during the entire throw, reaching increasingly large extension ω , for both balls and spears (figure 6.8a). Elbow extension ω appears to be slightly greater for the spears, and particularly S3, during the first two thirds of the throw, but ultimately approaches similar maximum extension ω . No significant differences exist between object types for maximum elbow ω ($p = 0.129$). The slightly greater extension ω achieved early in the throw corresponds with a slightly greater extension Mf for the spears (figure 6.8b). Around approximately 70% of the throw however, ball torques exceed spear torques and reach significantly greater maximum Mf ($p = 0.008$). The pattern of muscle activation generally

corresponds with the observed extension M_f and ω across objects. Extensor activity increases over the first half of the throw, and peaks between 60-80% of the throw (figure 6.8c). Flexor activation is quite low during the majority of the throw, but appears to increase slightly around 85% of the throw for the ball trials (figure 6.8d), corresponding with the decreased extension torque observed for the balls. However differences in ω and torque between object types are not explained by the patterns of extensor activation. Subjects begin the throw with greater extensor activity, reaching somewhat larger peak activation during spear versus ball throwing, whereas ball throws achieve greater M_f .

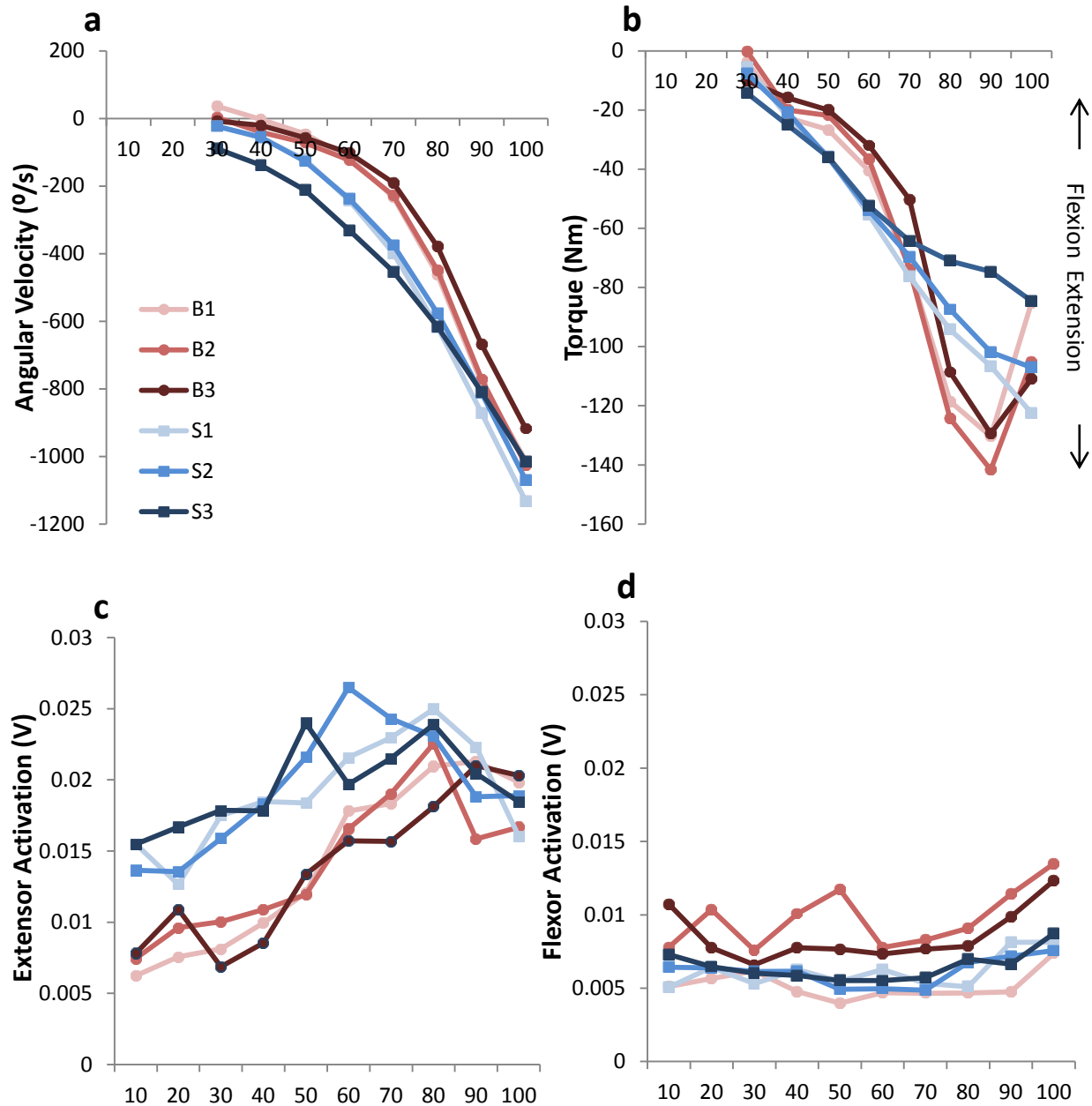


Figure 6.8 Elbow flexion/extension. (c) and (d) are muscle activation measured through EMG.

Within objects, there are significant differences in maximum extension ω for B1 and B3, and all the spears (B1:B2, $p = 0.779$, B2:B3, $p = 0.173$, B1:B3, $p = 0.029$; S1:S2, $p = 0.002$, S2:S3, $p = 0.009$, S1:S3, $p < 0.001$). However, the only corresponding difference in maximum Mf is between S1 and S3 (B1:B2, $p > 0.999$, B2:B3, $p = 0.216$, B1:B3, $p = 0.108$; S1:S2, $p =$

0.186, S2:S3, $p = 0.150$, S1:S3, $p = 0.003$). Although difficult to assess conclusively, there does not appear to be any difference in the magnitude of muscle activation between object masses, with the exception of the flexors for B1. Thus, muscular actions cannot be solely responsible for the angular velocities achieved by the elbow during the throw. Between objects there are differences in M_f that do not translate to differences in ω , and within objects, there are differences in ω that do not correspond to differences in M_f . Furthermore, the patterns of muscle activation observed do not correspond to the observed differences in M_f .

For the balls, significantly lower Ulna velocity was observed for B3, and this corresponds to a significantly lower extension ω . Similarly, the significant differences observed in Ulna velocity for the spears correspond with significant differences in extension ω . Between objects however, there is no significant difference in maximum ω to explain the observed difference in Ulna velocity. It is unclear why this would be the case, but there appears to be some difference in the manner in which rotational energy is translated to linear energy between throwing techniques. Possibly a difference in the position of the arm in space allows a more efficient transfer of energy across the elbow in ball throwing.

3. *The wrist.*

The final joint in the kinematic chain, the wrist, was compared using the K_e and velocity of the fifth metacarpal (Fifthmc). Figure 6.9a presents the pattern of Fifthmc K_e observed across objects. As with the Elbow and Ulna, there are significant differences in Fifthmc K_e between object masses within object types. With the exception of B1 and B2, heavier objects produce significantly more K_e at $p < 0.001$ (B1:B2, $p = 0.112$). Also similarly to the Ulna, when comparing Fifthmc velocity, significant differences exist between all objects (within types) except B1 and B2 in the opposite direction as K_e (B1:B2, $p = 0.814$, B2:B3, $p = 0.001$, B1:B3, p

< 0.001 ; all spears, $p < 0.001$). Thus, at the end of the kinetic chain, the outcome of throwing a heavier object is greater overall energy transferred to the object, despite lower linear velocity of the segments.

Finally, to examine whether differences in Fifthmc velocity are due to kinematics and/or kinetics at the wrist in addition to the effects of variation in Ulna velocity, a mixed effects model tested Ulna velocity and object mass (within objects) as predictors of Fifthmc velocity. The model found a significant effect of object mass as well as Ulna velocity for both object types at $p < 0.001$ (all effects). Between objects, as with Elbow and Ulna, significant differences exist in Fifthmc K_e and velocity ($p < 0.001$ for both). A mixed model was used to test for an effect of object type on Fifthmc velocity independent of Ulna velocity and object mass. The model found significant effects of object type, object mass and Ulna velocity on Fifthmc (type, $p < 0.001$; mass, $p = 0.018$, Ulna, $p < 0.001$). Thus, there appears to be variation at the wrist affecting Fifthmc velocity.

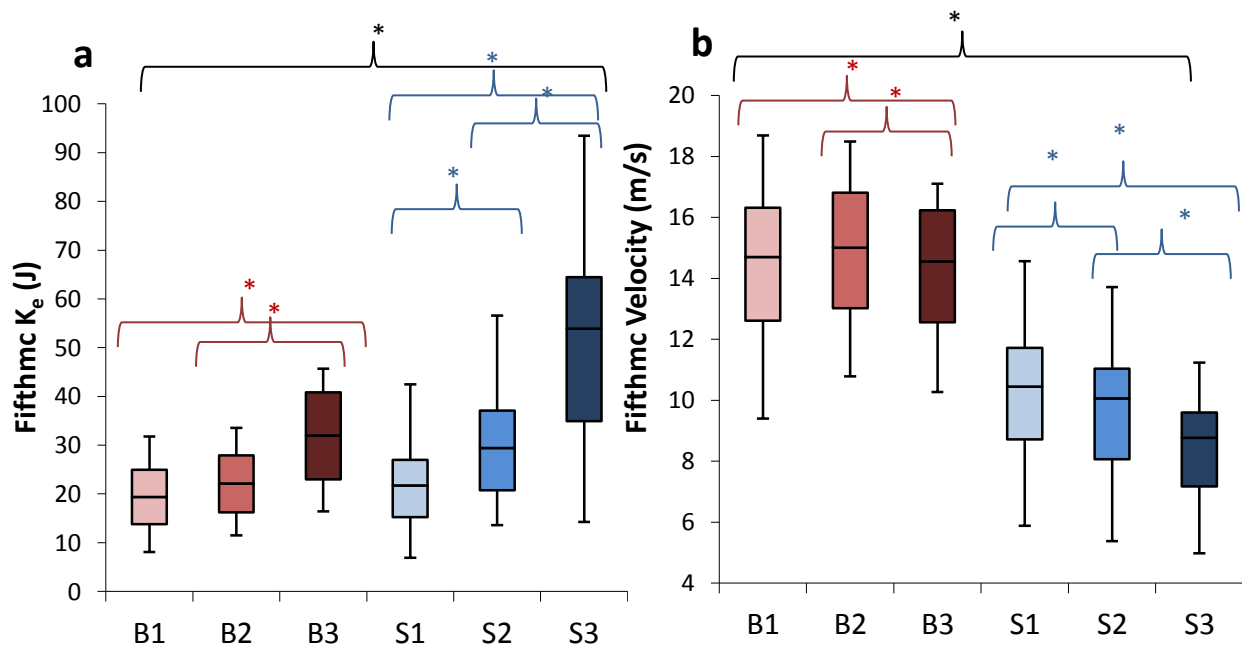


Figure 6.9 Wrist kinematics.

Figure 6.10 presents the patterns of wrist flexion/extension ω , Mf, and muscle activation across the throws. The pattern of ω appears to be relatively consistent for the spears, with low velocities of extension during the first half of the throw, followed by increasingly high velocities of flexion. The ball throws also demonstrate increasing flexion velocities during the second portion of the throw, but there is a great deal of variation in the first half of the throw. Throwers are generally extending during this time (to position the hand for flexion), but the magnitude and pattern is variable between balls. It is unclear why this would be the case, and may simply be due to measurement error. Ultimately, the maximum flexion ω achieved is not significantly different between ball masses ($p = 0.300$), spear masses ($p = 0.142$), or between object types ($p = 0.172$). The Mf measured is also highly variable across all objects. The maximum flexion Mf produced near the end of the throw is not significantly different between ball masses ($p = 0.521$). Within the spears, there is a significantly greater Mf for S3 than S2 or S1 (S1:S2, $p > 0.999$, S2:S3, $p = 0.001$, S1:S3, $p = 0.001$), and Mf is greater for the spears than balls ($p < 0.001$).

The pattern of muscle activation at the wrist (figure 6.10c-d) generally corresponds to the pattern of wrist flexion ω across the objects, but individual differences between object types and masses are not explained by differential muscle activation. Wrist flexors generally increase activation over the throw, peaking between 70-80% of the throw. For the ball throws, the extensors begin highly active, then decrease. This generally corresponds to the extension followed by flexion ω observed, but the measured Mf does not reflect this pattern. For the spear throws, both flexion and extension increase gradually over the throw and in approximately equal magnitude, suggesting the observed ω and Mf are not due primarily to muscle activation. Instead, the muscles are likely stabilizing the wrist to keep the spear at an ideal angle for release.

Furthermore, the flexors and extensors both reach higher peak activation during the ball than the spear throws, but the measured M_f does not reflect this pattern. Flexion M_f is far greater for the spear than ball throws, and ω is not significantly different. Thus, the measured wrist torques are likely not valuable in explaining ball velocity. Small flexion torques were observed for the wrist for ball throwing despite high flexor activation, and the pattern of flexor and extensor activation does not explain the observed ω or M_f for spear throwing.

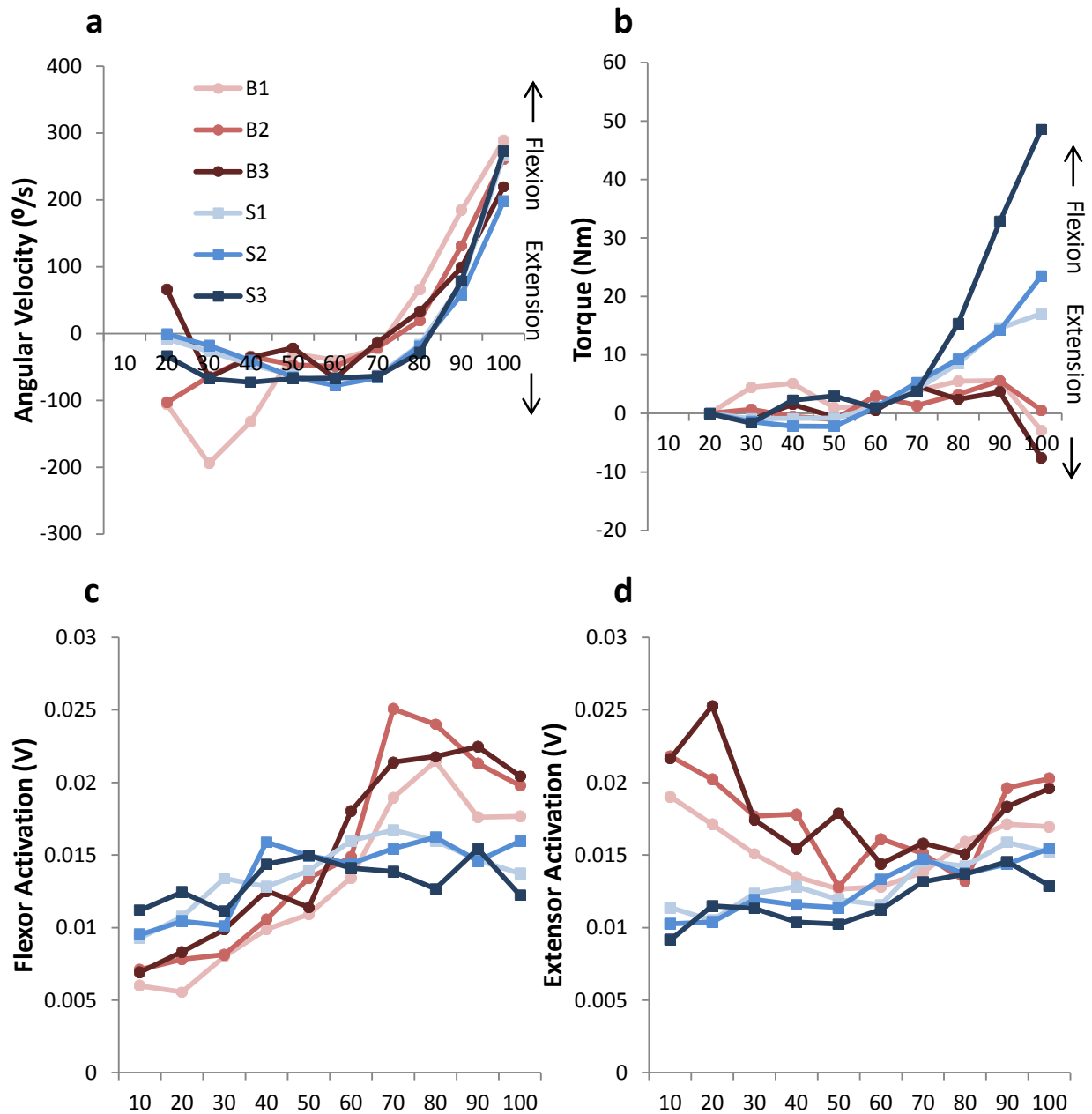


Figure 6.10 Wrist flexion/extension. (c) and (d) are muscle activation measured through EMG.

To summarize, similarly to the elbow, there are significant differences in the velocity of the Fifthmc between object types and masses, and independent of variation proximal in the chain, that are not explained by variation in wrist ω . There are differences in the torques and muscle activation patterns between objects and certain object masses, but these are not translated

into observable differences in ω . No differences exist in maximum flexion ω to explain the observed pattern of lesser Fifthmc velocity with greater object mass and with spears versus balls.

Discussion.

The results presented here demonstrate the patterns of kinetics and kinematics during spear throwing, and highlight several important differences between spear throwing and ball throwing.

1. The legs and torso.

Beginning at the proximal end of the chain, significant differences exist in the velocity of the RAsis, representing the total contribution of the legs to the throw. However this difference may be primarily due to space constraints. Corresponding differences were found in stride length between object types, and this may be due to the relatively confined lab space. Subjects may have felt constrained and reduced their strides when throwing the longer object. Since there is no other obvious reason why spear throwing would induce shorter strides, it is hypothesized that under different circumstances this effect could be eliminated. Despite the difference in K_e and velocity observed at the RAsis, no differences exist between object types in K_e or velocity at the RShoulder. Thus, in terms of the total contribution of the body, spear throwing and ball throwing are quite similar.

2. The shoulder.

At the shoulder, significantly greater abduction ω and significantly lower internal rotation and horizontal adduction ω were observed with spear versus ball throwing. In total, these resulted in significantly lower linear velocity of the Elbow in the spears as compared with the balls. Internal rotation is generally considered to be highly important to producing ball velocity in throwing (Feltner and Dapena, 1986), and as such, it is not surprising that a significant

decrease in Elbow velocity is observed. The shape and positioning of the spear are likely responsible for the difference in internal rotation ω , as these will put considerable limitations on arm position. For effective aerodynamics and target penetration, the spear must be thrown with a relatively straight trajectory at release. To accomplish this, subjects must maintain the shoulder within a much narrower range of motion than is necessary for ball throwing. This is particularly true with respect to internal/external rotation, as greater internal or external rotation would require compensation by the wrist. The narrow range of motion of wrist radial and ulnar deviation will significantly limit the amount of internal or external rotation that the shoulder can employ. In fact, throwers covered on average of 45° of internal rotation during ball throwing, but only 10° during spear throwing. This represents an important difference between the throwing techniques, as it likely reduces the relative importance of internal rotation to the throw as compared with other mechanisms. Adaptations that affect shoulder internal rotation will be less important to throwing performance than would be implied by the literature on ball throwing.

To a lesser extent, shoulder horizontal abduction is also limited during spear versus ball throwing. Subjects covered on average 24° of horizontal adduction during ball throwing, but only 8° during spear throwing. Furthermore, subjects began the throw in $\approx 35^\circ$ less horizontal abduction. To accommodate horizontal abduction/adduction while keeping the spear straight, the forearm must compensate with pronation and supination. In fact, the arm will be most limited when attempting to supinate while horizontally abducting, explaining the relatively horizontally adducted position of the shoulder at the outset of the throw. In contrast, shoulder abduction range of motion is not likely to be affected by the spear position. The arm can abduct as far as necessary without requiring compensation elsewhere in the arm. This may explain why subjects continued to abduct the arm through the throw during spear throwing, rather than returning to the

relatively adducted position used in ball throwing. This may be an attempt to compensate for the lack of mobility of the shoulder in internal rotation and horizontal adduction with increased abduction, although it is unclear how effective this technique might be.

The relative lack of mobility of the shoulder during spear throwing may have implications for the importance of torque production at the shoulder. If subjects are severely limited in their range of motion, increasing torque will only have a very limited effect on ω . Variation in F_m will likely produce only minimal effects on spear velocity, and consequently, it is unlikely that variation in shoulder internal rotator or horizontal adductor aCSA will be correlated with spear velocity. The implications of this finding for interpretations of fossil hominin morphology will be discussed in depth in chapter 10.

3. *The elbow and wrist.*

At both the elbow and wrist, differences in the velocity of the distal segment were found, independent of variation in the proximal segment. However, no corresponding differences in elbow or wrist ω were found to explain the difference. Thus, it does not appear that differences in the kinematics of the elbow or wrist are responsible for the reduced linear velocity. Instead, there may be some positional or temporal difference between the throwing techniques that results in a less efficient transfer of rotational motion to linear motion. Furthermore, patterns of muscle activation at the elbow and wrist do not correspond to patterns of M_f and ω . Thus, it appears the ω of the elbow and wrist are not directly tied to patterns of muscle activation. This suggests that M_f and muscle aCSAs at the elbow and wrist will not be correlated with ball velocity, as predicted in the hypotheses.

4. *Effects of object mass on throwing performance.*

Within object types, these results have highlighted the effects of object mass on throwing velocity. In terms of the contribution of the legs and torso to the throw, there were no differences in linear velocity or K_e between object masses. This is not surprising, since the weight of the objects should not be sufficient to tax the muscles of the legs or torso. However, in the arm, the joints were not able to maintain equivalent angular velocities with greater object mass. Throwers achieved lesser linear velocities of the Elbow with S3 as compared with the other spears, likely due to decreased horizontal adduction ω . Thus, the shoulder horizontal adductors were limited with greater object mass, but only with the heaviest object. For objects up to 0.6 kg, no reduction in horizontal adduction ω occurred. Reduced Ulna velocity was observed between all but the lightest two objects. These differences correspond to differences in elbow extension ω , demonstrating that within objects, elbow extension is inhibited with greater object mass. Similarly, Fifthmc velocity was significantly lower with greater object mass (independent of variation proximal in the chain) for all but the lightest two objects. However, no differences were present in wrist ω to explain the variation in Fifthmc velocity. Thus, it is unclear what mechanism is responsible.

Despite these effects, up to the heaviest object tested, there is a significant benefit to throwing a heavier object. At the end of the kinetic chain, there is an $\approx 38\%$ increase in K_e from the smallest (0.18 kg) to largest (0.31 kg) ball, and an $\approx 57\%$ increase in K_e from the smallest (0.40 kg) to largest (1.40 kg) spear (the magnitude of difference is due to the magnitude of difference in object masses). The largest object tested was 1.40 kg, which is ≈ 1 kg larger than the largest ethnographically described throwing spears (Oakley, 1977; Hughes, 1998). Thus, far beyond the range of known throwing spears, there is a benefit to throwing heavier objects. The

implications of these results for potential projectiles from the archaeological record will be discussed in chapter 10.

The fact that K_e increases with greater spear mass despite decreased velocity provides insight into the potential benefits of choosing objects of different masses as weapons. Up to a 1.40 kg spear, the energy imparted to the spear, and thus the energy imparted by the spear to the prey, increases with spear mass. Consequently, in terms of penetration and killing power, a heavier spear is preferable. However, the decreased velocity with greater spear mass implies that there would be a concurrent decrease in the distance the object travels, as distance is a function of the trajectory of the object and its velocity at release. Although velocity did decrease with greater spear mass, the magnitude of the effect is much smaller than the increase in K_e , where there was only an $\approx 20\%$ decrease in velocity from the smallest to largest spear. In other words, by increasing spear mass from 0.40 kg to 1.40 kg, a hunter gains approximately 57% more energy for penetrating and killing a prey target, but loses about 20% of the maximum throwing distance. However this lost distance will only be relevant if the hunter is attempting to hit prey at the absolute maximum limit of his abilities. Given the loss in energy of the object over the course of the aerial phase and reduced accuracy at very long distances, it is unlikely that hunters regularly throw to the maximum limit of their capability. For throws below the absolute maximum capability of the thrower the loss in throwing distance is likely irrelevant, and the benefits of greater K_e would be crucial.

Chapter 7

Throwing Performance and Anatomy

In this chapter, experimental data is used to test the first hypothesis, H1, that throwing performance is correlated with body form and joint anatomy. It was hypothesized that measures of body proportions, including height, segment lengths, body breadth, body size, arm muscle strength, and mechanical advantage of the elbow and wrist would predict throwing performance. To quantify throwing performance, the maximum kinetic energy (K_e) of the thrown object is used as a measure of the energy transferred by the body to the object. For within-object comparisons the mass of the object is constant, so K_e is a function of the velocity achieved by the object. This makes these results directly comparable to the baseball throwing literature, for which velocity is the primarily reported result. The relationship between anatomy and throwing performance will be examined first for baseball throwing, then for spear throwing, and finally the important differences between the two will be considered. Furthermore, in chapter 6, several interesting kinematic differences were observed between object masses. It will be explored whether these differences affect the relationship between anthropometrics and throwing performance.

Ball results

I. Relationship between anthropometric variables and ball K_e .

To investigate the effects of anthropometric variation on throwing performance, the contributions of the body versus the arm to the throw were examined. Linear, volume, and area measurements across the human body are highly inter-correlated, scaling according to the

principles of allometry. Table 7.1 presents the Pearson product-moment correlation coefficients for the anthropometric variables measured for this study, including body mass, arm aCSA (summed across all upper arm and forearm muscles), and body segment lengths (raw values are found in appendices I-III). With the exception of biasis breadth, most correlations are significant, demonstrating significant inter-correlation of anthropometric variables among these subjects. Thus, if a correlation is found between ball K_e and, for example, upper arm length, it could be due to the correlation of upper arm length with height ($R^2 = 0.623$) rather than causal. If upper arm length is causally producing greater ball K_e , it will be significantly correlated with ball K_e independent of the contribution of the trunk and legs. The contribution of the trunk and legs to the throw can be summarized by the K_e of the dominant shoulder (referred to as RShoulder for simplicity, since the dominant limb was the right in all but three individuals), since the velocity of this marker will be a function of the combined actions of the lower limb and trunk. Figure 7.1 presents the results of least squares linear regression of RShoulder K_e against ball K_e . For all ball masses, the body contributes approximately 52.5% of the energy of the ball at release ($p < 0.001$ for all balls).

Table 7.1 Correlation matrix of subject anthropometrics.

	Body Mass	Total aCSA	Thigh	Shank	Biasis	Torso	Bi- acromion	Upper Arm	Fore- arm	Hand
Height	0.735	0.692	0.533	0.762	0.300	0.676	0.734	0.628	0.678	0.506
Body Mass		0.566	0.293	0.676	0.429	0.684	0.645	0.513	0.496	0.257
Total aCSA			0.333	0.487	-0.166	0.678	0.764	0.317	0.408	0.521
Thigh				0.313	0.255	0.275	0.479	0.444	0.463	0.684
Shank					0.199	0.554	0.506	0.684	0.747	0.316
Biasis						0.209	0.067	0.276	0.316	-0.090
Torso							0.686	0.481	0.555	0.324
Biacromion								0.401	0.436	0.477
Upper Arm									0.817	0.395
Forearm										0.457

Total aCSA is muscle anatomical cross-sectional area summed across all muscles of the upper arm and forearm, remaining variables are segment lengths. Values presented are Pearson product-moment correlation coefficients. Bold indicates significance at $p < 0.05$.

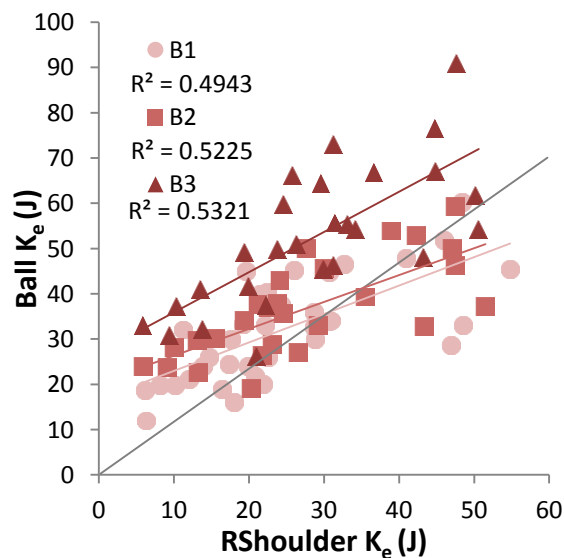


Figure 7.1 Linear regression of RShoulder K_e against Ball K_e . Note: RShoulder K_e was log10 transformed for multiple regression analyses. Grey line represents identity.

The anthropometric measures that could contribute to RShoulder K_e include body mass, height, torso length, shank length, thigh length, bi-axis breadth and biacromion breadth. The contributions of these variables to RShoulder K_e were examined using forward stepwise multiple regression, where each variable was entered sequentially if it met inclusion criteria. Variables were entered if the p-value for the associated F-to-enter value (calculated based on the incremental change in R^2) was < 0.05 , with the lowest p-value entered first. This method allows comparison of the contribution of each individual predictor variable, while also taking into account any possible interaction effects between variables that might be missed with a simple forward or backward procedure (Sokal and Rolf, 1995).

Table 7.2a presents the results of the multiple regression for B1-B3. The pattern varies slightly between balls. For B1, the only significant predictor of RShoulder K_e is height ($p < 0.001$), as all remaining predictor variables do not meet inclusion criteria. All p-values presented are significance for F-to-enter values. Height independently explains approximately 42% of the variation in RShoulder K_e for B1. For balls 2 and 3, biacromion breadth was the only significant predictor of RShoulder K_e (B2: $p = 0.001$, B3: $p < 0.001$), and explained approximately 41.75% of the variation.

Table 7.2 Stepwise multiple regression equations for the relationship between anthropometric variables and ball kinetic energy (K_e).

Variable	Ball 1				Ball 2				Ball 3			
a. RShoulder K_e¹	β	R^2	r	p	β	R^2	r	p	β	R^2	r	p
Height	0.650	0.423	0.650	<0.001			0.219	0.315			0.314	0.144
Biacromion			0.309	0.091	0.626	0.392	0.626	0.001	0.682	0.465	0.682	<0.001
Body Mass			0.025	0.895			0.001	0.997			0.088	0.688
Thigh			-0.084	0.652			0.146	0.507			0.169	0.441
Shank			-0.124	0.506			-0.086	0.698			-0.003	0.988
Torso			0.134	0.474			0.273	0.208			0.325	0.130
Biasis			-0.199	0.284			-0.002	0.994			0.047	0.832
b. Ball K_e	β	R^2	r	p	β	R^2	r	p	β	R^2	r	p
RShoulder K_e¹	0.722	0.522	0.722	<0.001	0.723	0.522	0.723	<0.001	0.729	0.532	0.729	<0.001
Upper Arm			-0.029	0.889			-0.096	0.656			0.010	0.962
Forearm			0.018	0.931			-0.245	0.249			-0.053	0.805
Hand			0.008	0.971			-0.232	0.275			-0.103	0.632
Triceps aCSA ^{1,2,3}			0.330	0.100			0.275	0.193			0.345	0.099
Wrist Flexor aCSA			0.384	0.053			0.262	0.215			0.395	0.056

All anthropometric variables listed are lengths unless otherwise noted. Predicted variable is in top right corner, all variables meeting inclusion criteria are in bold. β is standardized coefficient. R^2 is cumulative for all variables meeting inclusion criteria. r is partial correlation. P-values reported are for F-to-enter statistic (variables included if $p < 0.05$). Variables for which data transformations were required to meet assumptions of normality are noted with a ^{1, 2, or 3} to indicate which set of data was transformed (Ball 1, 2 or 3).

Abbreviations: K_e , kinetic energy; aCSA, anatomical cross sectional area.

Stepwise multiple regression was used as above to examine the relationship between anthropometric variables in the arm and the arm's contribution to the throw. The contributions of RShoulder K_e , upper arm length, forearm length, hand length, elbow extensor cross sectional area (aCSA), and wrist flexor aCSA to ball K_e were examined. RShoulder K_e was entered into the model first as representative of the combined effects of the body, and the residual variation is assumed to represent the potential contribution of the arm to the throw. Table 7.2b presents the results of the multiple regression for B1-B3. As above, the partial correlations varied slightly, but the overall pattern was the same between balls. The only significant predictor of ball K_e is RShoulder K_e and none of the remaining variables met inclusion criteria. Thus, simple linear anthropometric measures of the arm do not explain any of the residual variation in ball K_e .

Thus, the only anthropometric variables that significantly explain either the body's or the arm's contribution to the throw are height for B1 and biacromion breadth for B2 and B3. Height or biacromion breadth explains as much as 48% of the variation in ball K_e . Thus, the best prediction of ball K_e from simple anthropometric variables that can be obtained is based on a single predictor, and explains up to half of the variation in ball K_e . Contrary to predictions, most linear and area measurements of the body and arm do not explain a significant portion of the variation in ball K_e . One explanation is that there is not sufficient variation in body proportions between subjects to detect an effect of segment lengths on throwing performance. If segment lengths and arm muscle sizes are too highly inter-correlated between subjects, each will not independently explain variation in ball K_e . The correlation matrix of all the measured anthropometrics, including body mass, height, aCSA and segment lengths, is presented in table 7.1. With the exception of biasis breadth, most of the anthropometric measures are significantly correlated, with r varying from 0.067 to 0.817, and a mean of 0.480. The corresponding mean

coefficient of non-determination is 0.520, indicating that over half of the variation in body proportions is unexplained. Even assuming a reasonable amount of measurement error, the subjects appear to represent a range of body sizes and proportions, suggesting that a lack of variation is not the explanation for the non-significant correlation between anthropometrics and ball K_e .

Alternatively, it is possible that since each of these variables (as well as ball K_e) were measured with error, the error is compounded to such a degree that measurement of ball K_e cannot detect small but significant effects of anthropometrics. Finally, it is possible that although segment lengths and muscle aCSAs affect kinematics and kinetics as predicted at a given joint, there are inefficiencies in energy transfer across the joints, resulting in ball velocities that are not representative of each joints' contribution. That is, ball K_e may not simply be a result of the additive contributions of each joint, either due to poor technique in these throwers, or the inherent nature of throwing. To explore these possibilities, the following section will examine the effects of anthropometrics on movement and energy at each joint.

I. Relationship between anthropometric variables and K_e at each joint.

1. K_e of the legs and torso.

The difference in maximum linear K_e between the proximal end of a segment and the distal end of the segment should be a function of the forces generated by the muscles acting across that joint, the leverage of those muscles, and the length of the segment. The muscles can potentially create forces (F_m) to rotate the joint, and the resulting angular velocity will be a result of the F_m and the mechanical advantage (EMA) of the joint. Furthermore, for a given angular velocity, the distal end of a longer segment will cover a greater distance in the same time, and should thus have greater linear velocity. Each joint will be examined individually to determine if

EMA (where measured), muscle aCSA (where measured), and segment lengths contribute to the linear velocity of the distal segment, independent of variation in the proximal segment. Table 7.3 summarizes the measured predictor variables that will be tested for each joint and their abbreviations. The analysis begins at the start of the kinetic chain (the legs), essentially building up the contributions of each link in the chain. Figure 7.2 summarizes the relationship between each of the predictor variables tested at each joint.

Table 7.3 Variables used to predict ball/spear K_e .

Joint	Variable	Abbreviation
Legs	Leg length	Leg
	Biasis breadth	Biasis
	Stride length	Stride
	Anterior-Posterior force plate trace scaled to body mass	F_{A-P}/M_b
Torso	Linear kinetic energy of the marker for the anterior superior iliac spine on the dominant side	RAsis K_e
	Torso length	Torso
	Biacromion breadth	Biacromion
	Total arm anatomical cross-sectional area or Total arm strength*	Total aCSA or Total strength
Shoulder	Linear kinetic energy of the dominant shoulder marker	RShoulder K_e
	Upper arm length	Upper arm
	Total arm anatomical cross-sectional area or Total arm strength*	Total aCSA or Total strength
	Shoulder internal rotation angular velocity	Internal rotation ω
Elbow	Linear kinetic energy of the elbow marker	Elbow K_e
	Forearm length	Forearm
	Triceps anatomical cross-sectional area	Triceps aCSA
	Triceps mechanical advantage	Triceps EMA
	Elbow extension angular velocity	Elbow ω
Wrist	Linear kinetic energy of the Ulna marker	Ulna K_e
	Hand length	Hand
	Wrist flexor anatomical cross-sectional area	Wrist flexor aCSA
	Wrist flexor mechanical advantage	Wrist flexor EMA
	Wrist flexion angular velocity	Wrist flexion ω
Total	Height	Height
	Body mass	Body mass

Variables are organized by the joint or link in the kinetic chain where they should have a casual effect. Linear K_e of the element just proximal in the kinetic chain is assumed to summarize the contribution of the chain up to that point, such that the difference in K_e between the proximal and distal end of the segment will be due to variables acting causally at that joint. *Total arm aCSA or strength used as a proxy for the musculature of the torso and shoulder since these were not measured directly.

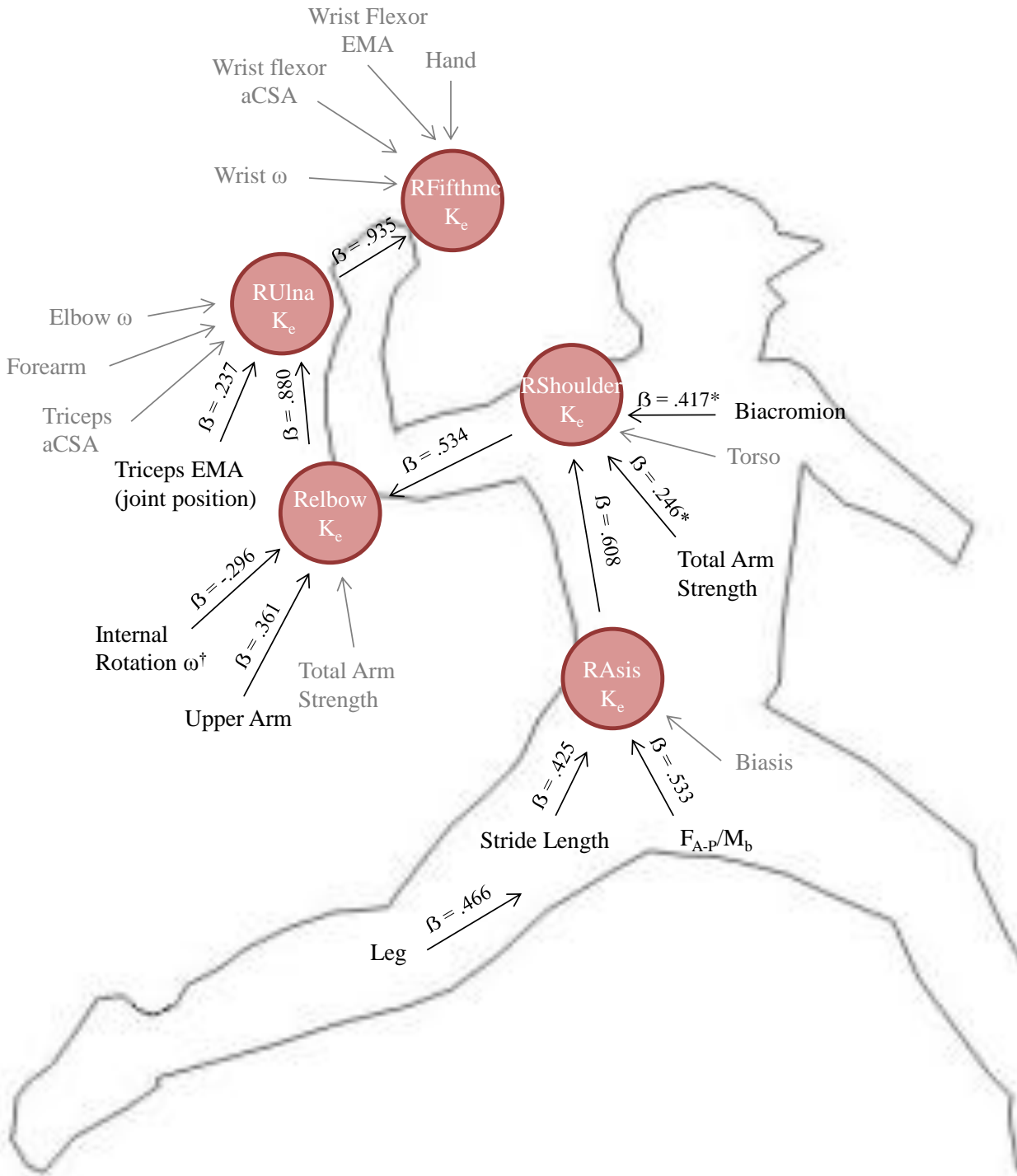


Figure 7.2 Diagram of the relationship between predictor variables and linear kinetic energy (K_e) at each joint for ball throws. See table 7.3 for abbreviations. β values are standardized coefficients for the stepwise multiple regression of all significant predictor variables, averaged across all balls for which the variable was significant (see table 7.4). Variables in black are significant at $p < 0.05$. * β for biacromion is for all balls without total arm strength, β for total arm strength is for B1 with biacromion. Note: shoulder internal rotation is defined as negative.

The K_e of the dominant side of the pelvis (RAsis K_e) will be used to summarize the contribution of the legs to the throw. RAsis K_e should be a function of body mass, the F_m of the leg muscles and the EMA of those muscles, which will produce torques to push off the ground and propel the hips forward. Additionally, the duration of the push-off will determine the length of time over which the legs are able to accelerate and generate velocity. Longer legs should increase stride length and thus the duration of push-off, and the width of the pelvis could affect pelvic rotation velocity, contributing to RAsis K_e . However, muscle sizes and EMA were not measured for the legs, so only leg length and bias breadth are considered here. Stepwise multiple regression of leg length and bias breadth against RAsis K_e was performed (table 7.4a). For B1 and B3, leg length significantly explains approximately 16% of the variation in RAsis K_e ; bias breadth does not meet inclusion criteria for any ball (leg length, B1: $p = 0.030$, B2: $p = 0.077$, B3: $p = 0.043$, bias, B1: $p = 0.987$, B2: $p = 0.895$, B3: $p = 0.659$). Thus, leg length contributes to RAsis K_e , but as it only explains about 16% of its variation, it is of little use in explaining the variation in RAsis K_e .

Table 7.4 Stepwise multiple regression equations for anthropometric variables and K_e at each joint for ball throwing.

Variable	Ball 1				Ball 2				Ball 3			
Legs												
a. RAsis K_e^1	β	R^2	r	p	β	R^2	r	p	β	R^2	r	p
Leg	0.384	0.148	0.384	0.030			0.385	0.077	0.425	0.181	0.425	0.043
Biasis			0.003	0.987			0.030	0.895			0.100	0.659
b. RAsis K_e^1	β	R^2	r	p	β	R^2	r	p	β	R^2	r	p
F_{A-P}/M_b	0.531	0.612	0.641	<0.001	0.579	0.684	0.716	<0.001	0.488	0.567	0.563	0.003
Stride Length	0.430	0.734	0.560	<0.001	0.415	0.795	0.593	0.001	.0430	0.682	0.515	0.007
Torso												
c. RShoulder K_e^1	β	R^2	r	p	β	R^2	r	p	β	R^2	r	p
RAsis K_e^1	0.605	0.624	0.762	<0.001	0.675	0.665	0.801	<0.001	0.513	0.476	0.655	<0.001
Total Strength	0.246	0.751	0.369	0.029			0.233	0.262			0.301	0.144
Biacromion	0.238	0.782	0.355	0.036	0.369	0.781	0.590	0.002	0.500	0.695	0.647	<0.001
Torso			-0.261	0.136			-0.041	0.847			0.160	0.444
Shoulder												
d. Elbow K_e	β	R^2	r	p	β	R^2	r	p	β	R^2	r	p
RShoulder K_e^1	0.792	0.809	0.888	<0.001	0.746	0.772	0.885	<0.001	0.658	0.710	0.832	<0.001
Upper Arm	0.256	0.862	0.589	0.005	0.339	0.869	0.654	<0.001	0.412	0.846	0.684	<0.001
Arm aCSA			0.396	0.050			0.409	0.053			0.402	0.057
Arm strength			0.613	0.627			0.009	0.969			0.024	0.915
e. Elbow K_e	β	R^2	r	p	β	R^2	r	p	β	R^2	r	p
RShoulder K_e^1	0.617	0.819	0.837	<0.001	0.569	0.772	0.823	<0.001	0.415	0.710	0.708	<0.001
Upper Arm	0.277	0.881	0.687	<0.001	0.347	0.869	0.741	<0.001	0.459	0.846	0.816	<0.001
Internal Rotation ω	-0.258	0.920	-0.576	<0.001	-0.279	0.917	-0.602	0.001	-0.350	0.917	-0.682	<0.001

Variable	Ball 1				Ball 2				Ball 3			
Elbow												
f. Ulna K_e	β	R ²	r	p	β	R ²	r	p	β	R ²	r	p
Elbow K_e	0.903	0.857	0.903	<0.001	0.885	0.809	0.929	<0.001	0.851	0.807	0.911	<0.001
Triceps EMA			0.353	0.083	0.244	0.872	0.572	0.003	0.230	0.857	0.512	0.011
Triceps aCSA ^{1,2,3}			0.360	0.077			0.202	0.343			0.252	0.245
Forearm			0.334	0.103			0.091	0.672			0.275	0.205
g. Elbow Extension ω	β	R ²	r	p	β	R ²	r	p	β	R ²	r	p
Triceps EMA			0.036	0.867			0.061	0.772			-0.280	0.185
Triceps aCSA ^{1,2,3}			-0.120	0.576			-0.128	0.541			0.128	0.552
h. Ulna K_e	β	R ²	r	p	β	R ²	r	p	β	R ²	r	p
Elbow K_e	0.929	0.857	0.929	<0.001	0.851	0.809	0.906	<0.001	0.898	0.807	0.898	<0.001
Triceps R			-0.333	0.104	-0.209	0.851	-0.466	0.022			-0.301	0.152
Triceps r			0.157	0.443			0.094	0.669			0.122	0.157
Wrist												
i. Fifthmc K_e	β	R ²	r	p	β	R ²	r	p	β	R ²	r	p
Ulna Ke	0.950	0.902	0.950	<0.001	0.919	0.844	0.919	<0.001	0.935	0.873	0.935	<0.001
Wrist Flexor aCSA			-0.151	0.471			-0.095	0.666			-0.023	0.916
Wrist Flexor EMA			-0.224	0.282			-0.102	0.644			0.270	0.214
Hand			-0.103	0.625			-0.209	0.339			-0.364	0.088
j. Wrist Flexion ω	β	R ²	r	p	β	R ²	r	p	β	R ²	r	p
Wrist Flexor aCSA			-0.235	0.257			-0.259	0.245	-0.464	0.216	-0.464	0.022
Wrist Flexor EMA			-0.303	0.140			0.029	0.899			0.043	0.844

See table 7.3 for abbreviations, see table 7.2 for formatting. Note: elbow extension and shoulder internal rotation ω are defined as negative, so negative r values indicate positive correlation.

The legs contribute energy to the throw primarily by pushing off the ground and propelling the hips forward. Leg length is thus important as it will influence stride length and the duration of push off. As expected, stride length is correlated with RAsis K_e for all three balls at $p < 0.001$ and explains approximately 55.5% of its variation (B1: $R^2 = 0.549$, B2: $R^2 = 0.579$, B3: $R^2 = 0.534$). Furthermore, as predicted, stride length is correlated with leg length. Linear regression demonstrates that leg length explains up to 29 % of the variation in stride length (B1: $R^2 = 0.127$, $p = 0.046$; B2: $R^2 = 0.292$, $p = 0.008$; B3: $R^2 = 0.250$, $p = 0.015$). The remaining variation is likely a function of motivation and technique. Thus, leg length is predictive of the legs' contribution to the throw, but the magnitude of the effect is small because leg length is not a good predictor of stride length, and stride length is not a perfect predictor of RAsis K_e . These additional sources of variation explain why leg length was not found to be predictive of RShoulder K_e (or ball K_e).

Although muscles sizes were not measured for the legs, the force plate data provides valuable information regarding the muscular component of the legs to the throw. Subjects stood with the back foot on the force plate, so the force plate trace represents the ground reaction force for the push-off of the back leg. This occurs during the wind-up and stride phases of the throw, since the back leg lifts off the ground at stride foot contact. Thus, the force plate trace represents primarily the back leg's contribution to the throw, as the torso and arm do not begin to accelerate significantly until the arm cocking and arm acceleration phases. The push-off force in the direction of the throw was examined, as this will generate forward K_e for the throw (MacWilliams et al., 1998). Throwers were oriented to throw approximately in line with the global y axis, so the anterior-posterior (A-P) force was defined as the force trace in the y direction. Since $F=Ma$, the acceleration of the body's center of mass is equal to the A-P force

trace divided by that mass, or $A=F/M$. Thus, maximum A-P force was divided by body mass to compare the acceleration generated by the leg muscles. Body mass scaled A-P force (F_{A-P}/M_b) should be a function of the torques produced by the back leg.

Stepwise multiple regression of stride length and F_{A-P}/M_b against RAsis K_e was performed (table 7.4b). As expected, both stride length and F_{A-P}/M_b were significant predictors of RAsis K_e for all balls (F_{A-P}/M_b , B1: $p < 0.001$, B2: $p < 0.001$, B3: $p = 0.003$; stride length, B1: $p < 0.001$, B2: $p = 0.001$, B3: $p = 0.003$), and together explain up to 80% of the variation in RAsis K_e . Thus, there appears to be a highly significant contribution of the back leg musculature to the throw, in addition to stride length.

Moving up the kinetic chain, the contribution of the torso to the throw was examined based on the relationship between RAsis K_e and RShoulder K_e . The energy of the dominant shoulder should be a function of the energy input from the legs, summarized by RAsis K_e , F_m of the torso muscles, the combined leverages of these muscles, and the length and breadth of the torso. Torso muscle sizes and EMA were not measured here, so only torso length and breadth could be considered. Stepwise multiple regression of RAsis K_e , torso length, and biacromion breadth on RShoulder K_e was performed, and results are found in table 7.4c. RAsis K_e explains up to 67% of the variation in RShoulder K_e ($p < 0.001$ for all balls) and biacromion breadth was also a significant predictor. Together, these two variables explain between 69.5% and 78% of the variation in RShoulder K_e , depending on which ball is considered. Torso length was not a significant predictor (B1: $p = 0.138$, B2: $p = 0.847$, B3: $p = 0.444$).

Although torso muscle sizes were not measured, it may be useful to consider arm muscle sizes, as these are likely correlated with torso muscle sizes. Although the predictive power of arm muscles will be weak compared with actual measures of torso muscle aCSAs, if a

relationship is found between arm musculature and RShoulder K_e , it is unlikely to be for any reason other than a correlation between arm musculature and torso musculature. If the total strength of the arm (sum of all maximum voluntary contractions, MVCs, from strength testing) is entered into the equation from the previous paragraph, both biacromion breadth and arm strength are significant predictors of RShoulder K_e for B1 (table 7.4c, biacromion, B1: $p = 0.036$, B2: $p = 0.002$, B3: $p < 0.001$; arm strength, B1: $p = 0.029$, B2: $p = 0.262$, B3: $p = 0.144$). Total arm aCSA is not a significant predictor in the same equation (when entered in place of total arm strength), probably due to the higher inter-correlation of aCSA with biacromion breadth ($R^2 = 0.583$) as compared with arm strength ($R^2 = 0.417$). RAsis K_e , biacromion breadth and arm strength explain 78% of the variation in RShoulder K_e for B1, and arm strength is in fact a stronger predictor than biacromion breadth for this ball. Given the compounding of error involved in using arm strength as a measure of torso strength, the fact that a significant relationship is found is notable, and it is expected that with a better measure of torso strength, a much greater portion of the variation in RShoulder K_e would be explained. Thus, in addition to the contribution of the legs, biacromion breadth and the musculature of the torso influence RShoulder K_e .

2. *K_e of the arm.*

As discussed above, the K_e of the dominant shoulder (RShoulder) is assumed to summarize energetic contribution of the legs and torso to the throw. Any residual variation in ball K_e not explained by RShoulder K_e may be due to contributions from the shoulder, elbow or wrist. The difference in linear K_e between the shoulder and the elbow should be a function of the action of the muscles acting across the shoulder, the leverage of the shoulder muscles, and the length of the upper arm. Leverage and muscle sizes of the muscles crossing the shoulder were

not measured, so RShoulder K_e and upper arm length were entered as predictors of Elbow K_e (table 7.4d). As expected, upper arm length is a significant predictor of RElbow K_e for all three balls at $p < 0.001$. Upper arm length and the linear K_e of the shoulder explain approximately 86.5% of the variation in Elbow K_e .

The remaining variation in Elbow K_e may be a function of the actions of the muscles crossing the shoulder. As demonstrated in chapter 6, internal rotation is the fastest motion at the shoulder for ball throwing. Although anthropometric measures of muscle size and joint leverage were not measured for the shoulder, if muscle activity is important in generating Elbow K_e , it should do so by generating internal rotation angular velocity (ω). Of course, internal rotation torques (moment of force, M_f) could also reflect muscle activity, but the data presented in chapter 6 demonstrated that despite large internal rotation ω , internal rotation M_f was very small, suggesting that the measured torques would not be useful in predicting throwing performance. Furthermore, total arm aCSA is correlated with shoulder internal rotation ω (note: internal rotation ω is defined as negative, so negative r values indicate positive correlation; B1: $p = 0.001$, B2: $p = 0.002$, B3: $p = 0.003$), and explains approximately 33.7% of the variation in shoulder ω , but it is not correlated with M_f (B1: $p = .208$, B2: $p = .085$, B3: $p = .545$). When internal rotation ω is added to the stepwise multiple regression, all three are significant predictors (table 7.4e; ω , B1: $p = 0.005$, B2: $p < 0.001$, B3: $p < 0.001$), and approximately 92% of the variation in Elbow K_e is explained.

If the arm musculature is entered into the multiple regression equation in addition to RShoulder K_e and upper arm length (instead of internal rotation ω), as a proxy for the total musculature crossing the shoulder, neither total arm aCSA nor total arm strength explains any further variation in Elbow K_e , but aCSA approaches significance for all three balls (table 7.4d,

aCSA, B1: $p = 0.050$, B2: $p = 0.053$, B3: $p = 0.057$, arm strength, B1: $p = 0.627$, B2: $p = 0.969$, B3: $p = 0.915$). Thus, it would appear that the angular excursion of the shoulder is related to muscularity, although not exclusively. With a better measure of torso musculature the relationship between aCSA and Elbow K_e may have been significant, but as much as 87% of the variation in Elbow K_e is explained without active contribution of muscles. Instead, it is likely that the high angular velocities of the shoulder are primarily produced by stretch and release of the tendons of the shoulder, a concept which will be considered further in the discussion at the end of this chapter.

In addition to the contribution from the proximal link in the kinetic chain, the linear K_e of the Ulna should reflect the muscular actions of the elbow extensors, the leverage of the joint, and the length of the forearm. Stepwise multiple regression of Elbow K_e , forearm length, triceps aCSA, and triceps EMA on Ulna K_e was performed, and the results are presented in table 7.4f. Approximately 82% of the variation in Ulna K_e is explained by Elbow K_e alone. In contrast to the shoulder, forearm length was not found to have a significant effect on Ulna K_e (B1: $p = 0.103$, B2: $p = 0.672$, B3: $p = 0.205$). Triceps aCSA also did not meet inclusion criteria, but EMA was found to have a significant effect on Ulna K_e for balls 2 and 3 (aCSA, B1: $p = 0.077$, B2: $p = 0.343$, B3: $p = 0.245$, EMA, B1: $p = 0.083$, B2: $p = 0.003$, B3: $p = 0.011$). Thus, forearm length and triceps aCSA do not appear to be significant in producing Ulna K_e , but EMA is predictive of Ulna K_e .

As with the shoulder, even if muscles are not responsible for the action, the ω of the joint should contribute to the K_e of the distal end of the segment, as greater rotational velocity should result in greater linear velocity (and thus K_e) of the distal segment, independent of the linear velocity of the proximal segment. However, when elbow extension ω and Elbow K_e are entered

as predictors of Ulna K_e , elbow extension ω does not meet inclusion criteria for the stepwise multiple regression (B1: $r = -0.123$, $p = 0.476$, B2: $r = -0.003$, $p = 0.987$, B3: $r = 0.051$, $p = 0.806$). That is, although elbow extension ω is correlated with Ulna K_e (B1: $R^2 = 0.372$, $p < 0.001$, B2: $R^2 = 0.170$, $p = 0.033$, B3: $R^2 = 0.251$, $p = 0.008$), it does not produce linear energy of the distal end of the segment independent of the linear energy contributed by the proximal segment. This implies that the K_e of the distal forearm is produced proximally in the kinetic chain and transferred across the elbow with relatively little direct involvement of the elbow muscles. In fact, Elbow K_e is correlated with elbow ω (B1: $R^2 = 0.349$, $p < 0.001$, B2: $R^2 = 0.208$, $p = 0.017$, B3: $R^2 = 0.334$, $p = 0.002$), which would not be the case unless both are produced proximally.

It was hypothesized that greater ball K_e would be a function of greater elbow extension ω , which would itself be a function of lower EMA and greater aCSA of the triceps. The former is not supported, and if elbow ω is primarily a function of actions proximal in the kinetic chain, it is unlikely that aCSA will be significantly correlated with elbow ω . EMA and triceps aCSA were entered into a multiple regression to predict elbow ω (table 7.4g). EMA and triceps aCSA were not found to be significant predictors of elbow ω for any ball (triceps EMA, B1: $p = 0.867$, B2: $p = 0.772$, B3: $p = 0.185$; triceps aCSA, B1: $p = 0.576$, B2: $p = 0.541$, B3: $p = 0.552$). Thus, the transfer of energy across the elbow appears not to be produced by concentric contraction of the elbow musculature, as the elbow musculature is not significantly correlated with Ulna K_e or elbow ω ; instead elbow ω is produced proximally. Yet, it was demonstrated in chapter 6 (figure 6.8c) and in previous research (Jobe et al., 1984; DiGiovine et al., 1992), that the triceps are active during the acceleration phase of the throw. Thus, rather than generating angular velocity for the throw, the elbow musculature probably contracts isometrically to facilitate, and even

magnify, the transfer of energy across the elbow. This could be produced through spring-like mechanisms of the triceps tendons, or by maintaining the elbow in a position to optimize energy transfer.

Given these results, the correlation between EMA and Ulna K_e deserves further consideration. EMA appears to correlate with Ulna K_e , but it does not do so through an effect on elbow ω . The anatomy of the joint affects EMA, and thus joint anatomy might affect Ulna K_e through the isometric contractions of the triceps. EMA will also be related to the position of the arm, as r and R will be affected by the joint angle and R will be affected by the location and direction of the external force vector which will vary with arm position (see chapter 8 for full discussion). In fact, for B2, correlations are found between R but not r in a multiple regression of Elbow K_e , R , and r on Ulna K_e (table 7.4h, R , B1: $p = 0.104$, B2: $p = 0.022$, B3: $p = 0.152$ r , B1: $p = 0.443$, B2: $p = 0.669$, B3: $p = 0.157$). Furthermore, R is not correlated with ulna length (B1: $R^2 = 0.076$, $p = 0.182$, B2: $R^2 = 0.026$, $p = 0.423$, B3: $R^2 = 0.051$, $p = 0.257$). Thus, the relationship between EMA and Ulna K_e is not due to anatomy (r or ulna length) at all. R predicts Ulna K_e , likely as a function of the position of the arm in space. Subjects who make use of a better arm position have greater elbow EMA and make better use of the isometric contractions of the triceps, thereby generating greater Ulna K_e .

Linear K_e of the distal hand (Fifthmc K_e) should reflect the contribution of the wrist to the throw in addition to the contributions from the proximal links in the kinetic chain. It was examined whether wrist flexor aCSA, wrist flexor EMA or hand length contribute to Fifthmc K_e , independent of Ulna K_e . Neither hand length, wrist EMA, or wrist flexor aCSA were found to have a significant correlation with Fifthmc K_e , and did not meet inclusion criteria for the stepwise regression (table 7.4i). Thus, the energy at the wrist does not appear to be a function of

muscular actions of the forearm flexors or hand length. Instead, as much as 90 % of the variation in Fifthmc K_e is explained by Ulna K_e alone ($p < 0.001$ for all balls), suggesting that there is little active involvement of the wrist in producing movement of the distal hand.

Further support for this argument is found by examining the relationship between wrist flexion ω and wrist kinematics. It was hypothesized in H1 that wrist flexor aCSA and EMA would be correlated with wrist flexion ω , which would in turn be predictive of ball K_e . As with the elbow, there is no correlation between flexion ω and flexor EMA for any ball (table 7.4j, B1: $p = 0.140$, B2: $p = 0.899$, B3: $p = 0.844$), and flexor aCSA is only predictive of ω for B3 (B1: $p = 0.257$, B2: $p = 0.245$, B3: $p = 0.022$). However, for B3, the correlation between aCSA and ω is negative, implying that less musculature is in fact producing greater flexion velocity. This is counterintuitive, and may simply be a false positive result. Furthermore, wrist flexion ω is not correlated with Fifthmc K_e for any ball (B1: $R^2 = 0.002$, $p = 0.784$, B2: $R^2 = 0.002$, $p = 0.838$, B3: $R^2 = 0.122$, $p = 0.075$). Thus, contrary to H1, wrist ω during throwing is not a function of the forearm musculature or mechanical advantage, and wrist ω does not contribute to ball K_e . Given the high correlations between Ulna K_e and Fifthmc K_e , it is likely that the wrist is relatively passive in the throwing process.

In summary, the only anthropometric variable that significantly and directly explains a portion of the arm's contribution to the throw is upper arm length. Total arm aCSA, as a proxy for the musculature crossing the shoulder, approaches significance in predicting Elbow K_e , suggesting that with a direct measure of shoulder muscle aCSA a significant result would be obtained. In contrast, the musculature of the elbow and wrist do not contribute causally to ball K_e , as the rotational velocities of the elbow and wrist are produced proximally through the linear and rotational motion of the legs, trunk, and shoulder. Rather than producing concentric

contractions to extend the elbow, the triceps appear to contract isometrically to facilitate the transfer of energy across the elbow, either through a spring-like mechanism or by maintaining elbow position. To this end, there is some indication that subjects can increase ball K_e by using arm positions that optimize R for the triceps. Contrary to expectations, moment arms of the elbow and wrist, and forearm and hand length do not significantly affect ball K_e .

Discussion.

It was predicted in H1 that ball K_e would be correlated with anthropometric variables such as body mass, height, segment lengths and breadths, and muscle sizes and mechanical advantage (through their effect on joint angular velocity). On first inspection, there appears to be only meager support for H1, in that height and biacromion breadth variously explain a portion of the body's contribution to the throw. None of the anthropometric variables of the arm causally explain the arm's contribution to the throw. Although biacromion breadth and/or height are the only significant predictors of throwing performance, they do explain as much as 48% of the variation in ball K_e . However, this value is likely not a measure of the direct causal relationship between height or biacromion breadth and ball K_e . These can only causally affect ball K_e through their effects on the dominant shoulder, but correlations with RShoulder K_e were slightly lower (table 7.2a). Thus, the correlation with ball K_e likely captures co-variation with other aspects of the anatomy, and as such, it would not be logical to attempt to predict throwing performance solely based on this predictive equation. Instead, the transfer of energy across the kinetic chain was examined to provide insight into which anthropometric variables are important at each joint, even if these do not result in observable relationships with ball K_e in this sample. Figure 7.2 summarizes these results.

1. *The legs and torso.*

Beginning at the start of the kinetic chain, these results demonstrate that forward energy of the pelvis (captured as RAsis K_e) is generated through a forceful push-off by the muscles of the legs. This supports MacWilliams et al. (1998), who found a significant correlation between body mass scaled anterior-posterior push-off force (measured with a force plate) and linear throwing velocity, and Vila et al. (2009) and Ferragut et al. (2011) who found significant correlations between thigh diameter and throwing velocity. Furthermore, these results indicate that A-P push-off force is causally related to ball velocity through its direct effect on pelvis velocity. EMG studies to date have focused on muscle activation in the shoulder and arm rather than the leg, so there is currently no evidence of which leg muscles (if not all) are causally related to A-P force and consequently pelvis K_e . Future research will be necessary to demonstrate patterns of muscle activation with EMG, and examine the relationship between leg muscle sizes and throwing velocity.

In addition to the effects of leg strength, stride length significantly affects RAsis K_e , presumably by increasing stride duration. Stodden et al. (2006) found a similar correlation between stride length and throwing velocity in children at differing levels of throwing skill. These results further suggest a causal link between stride length and ball K_e , demonstrating that stride length is directly correlated with RAsis K_e , and this effect is independent of body size scaled A-P force generated by the leg musculature. Greater stride length allows the thrower to accelerate the mass of the body for a longer duration, thereby increasing velocity.

Stride length is itself correlated with leg length here, although not very strongly, suggesting a significant effect of training or motivation, or large measurement error. Given the small lab space in which the data were collected, some subjects may have felt constrained and

limited their strides, and this would have had a disproportionate effect on taller individuals. There is some indication that training level affects stride length in this sample as well, as there is a significant difference in stride length between the Competitive and Non-Competitive samples ($p = 0.036$; notably, this is not true of the spear throws, for which subjects were all equally experienced). Finally, the measure of stride length used here, the linear distance in the x-y plane of the non-dominant Asis marker between its most posterior (pre-stride) and its most anterior (post-stride) position, is not ideal. This measure should be highly correlated with actual stride length, but certainly introduces additional error. Thus, the relationship between stride length and leg length may in fact be much stronger than these data are able to show. Better data collection circumstances and inclusion of only the best trained subjects would likely find a much higher correlation between leg length and stride length, and consequently a much stronger relationship between leg length and RAsis K_e and ball K_e .

Adding to the energy generated by the legs during stride phase, the torso bends and rotates during arm cocking and arm acceleration. These results indicate that torso bending and rotational motions are very likely generated by forceful muscular activity, as greater muscle strength (assuming a correlation between arm strength and torso aCSAs) and broader shoulders result in greater maximum K_e of the dominant shoulder. This supports Vila et al. (2009), who also found a correlation between biacromion breadth and throwing velocity, although co-variation with other anthropometric measures was not accounted for there. There are currently no EMG data examining the muscle activation patterns in the torso that produce bending and rotational movements. Greater biacromion breadth increases the distance of the shoulder from the rotational axis of the torso, resulting in greater linear velocity of the shoulder for a given rotational angular displacement.

Thus, there does appear to be a relationship between anthropometrics of the legs and torso and ball K_e , although the multiple regression presented in table 7.2a does not fully demonstrate it. The body contributes at least 50% of the energy of the throw, and there is a strong indication that leg length, biacromion breadth, and muscle aCSAs of the legs and torso significantly predict the body's contribution to the throw.

2. *The shoulder.*

The shoulder has traditionally been considered an important contributor to throwing performance by generating very high internal rotation ω (Feltner and Dapena, 1986). The results presented here demonstrate that internal rotation ω as well as upper arm length are significantly and independently correlated with Ulna K_e , supporting a causal relationship between these variables and ball K_e . Furthermore, these results support the hypothesis, proposed elsewhere (Feltner and Dapena, 1986; Jobe et al., 1983, 1994), that internal rotation ω is not produced solely (or even primarily) by the shoulder musculature. Internal rotation torques could be produced or aided by passive stretching of the internal rotators, specifically subscapularis, latissimus dorsi, pectoralis major, and teres major during the maximum external rotation of the humerus. Here, internal rotation ω is weakly correlated with arm muscle aCSAs, and the correlation of arm aCSA and Ulna K_e does not quite reach significance. It seems likely that a better measure of the shoulder internal rotator aCSAs would yield a stronger correlation, but still implies an important contribution of passive forces.

It has been shown that humeral internal rotators are active during the acceleration phase of the throw (Jobe et al., 1984; DiGiovine et al., 1992), and Clements et al. (2001) found a significant correlation between throwing velocity and isometric shoulder internal rotation strength. However, this last study demonstrates a common complication in the research regarding

throwing performance. The assumption of causality is questionable because the correlation with ball velocity is not demonstrated to be independent of co-variation with other variables. The results of this study demonstrate how failure to consider co-variation can lead to erroneous results. Arm muscle strength demonstrates a correlation with throwing kinematics, but not independent of other relevant variables, and not at the joints where it might have a causal effect. Thus, without considering the potential correlation of arm muscle strength and torso muscle strength, one would conclude that arm strength is important to throwing performance (which has been done and will be discussed below).

Thus, the available evidence indicates that K_e produced at the shoulder is likely a result of both muscular activation and passive stretching of tendons to produce internal rotation ω , and this ω is magnified with larger upper arm lengths. Accurate measures of pectoralis major and latissimus dorsi aCSAs would likely yield stronger correlations with internal rotation ω and Ulna K_e , but the relative weakness of the correlation found here suggests room for a significant effect of passive stretching of the internal rotator tendons.

3. *The elbow.*

The available evidence regarding the importance and direct contribution of the elbow to throwing is mixed. EMG studies demonstrate relatively high activity levels of the triceps during the acceleration phase (Jobe et al., 1984; DiGiovine et al., 1992) and correlations between triceps strength and throwing velocity have been reported (Pedegana et al., 1982; Clements et al., 2001). Other researchers did not find a correlation between elbow extension strength and throwing velocity (Bartlett et al., 1989), and some have argued that the high triceps activity observed during the acceleration phase is in fact necessary for positioning the arm, rather than actively producing elbow extension (Feltner and Dapena, 1986; DiGiovine et al., 1992). A study of a

single individual demonstrated that 80% of normal ball velocity could be achieved with the triceps incapacitated with a radial nerve block (Roberts, 1971). Furthermore, in chapter 6, variation was observed in muscle activity and torques for elbow extension, but a corresponding pattern of variation in elbow ω was not observed, supporting that elbow ω is not due to triceps F_m . Instead, it has been suggested that elbow extension angular velocity is a function of centripetal motion produced by abduction and horizontal adduction of the humerus or linear motion of the trunk (Feltner and Dapena, 1986). The results presented here provide clear evidence that the triceps do not directly generate throwing velocity beyond their potential role in positioning the arm. Triceps muscle aCSA does not correlate with elbow ω , and elbow ω does not correlate with Ulna K_e .

This research demonstrates the importance of examining the joints together in series, rather than looking at the correlation between any one variable and throwing velocity. Triceps strength explains approximately 28% of the variation in ball K_e in this study, which is remarkably similar to the 27% reported by Pedegana et al. (1982) (results are not directly comparable to the Clements et al. study). However, this correlation is clearly not causal as triceps aCSA is not correlated with elbow ω or with Ulna K_e when Elbow K_e is entered into the equation (table 7.3i). Rather, this research provides clear evidence that the elbow does not contribute to the throw directly by generating velocity, but transfers the effects of shoulder rotation down the kinetic chain. The positioning of the arm during this process may also be important, as for ball 2 and 3 subjects who make use of better arm positions maximize the EMA of the joint, most likely by minimizing R. Unlike at the shoulder, the length of the forearm does not affect how the energy produced proximally is transferred down the kinetic chain.

4. *The wrist.*

There has been relatively little consideration of the contribution of the wrist to throwing performance, with detailed analysis of the kinematics of the wrist limited to one study (Pappas et al., 2009). EMG analysis has demonstrated that the flexors of the wrist are moderately to highly active during the acceleration phase (DiGiovine et al., 1992), and significant correlations have been noted between wrist flexion and extension strength and throwing velocity (Pedegana et al., 1982). As with the elbow and shoulder, however, a causal link has not been demonstrated for the musculature of the wrist and throwing performance. In fact, the results presented here demonstrate that the musculature of the wrist is not causally related to ball K_e , as wrist flexor aCSA is not correlated with wrist flexion ω , and flexion ω is not correlated with Fifthmc K_e . This suggests that the correlation between flexion and extension strength and ball velocity reported by Pedegana et al. (1982) may be a result of co-variation between wrist strength and torso strength. The wrist is not of great importance in explaining the K_e of the throw, as up to 90% of the variation in Fifthmc K_e is explained without active involvement of the wrist.

The above discussion illustrates the pattern of transfer of energy through the kinetic chain during a baseball throw. Although initial observation suggested that anthropometric variables were not of great importance to ball K_e , examination of the patterns of energy transfer at each joint has highlighted several anthropometric variables that are important in producing K_e at each joint. It was found that approximately 50% of the energy of the throw is provided by the body, a value which corresponds extremely well with values reported in the literature (Broer, 1969; Toyoshima et al., 1974). For this portion of the variation, there is a strong effect of stride length, leg muscularity, torso muscularity and biacromion breadth. Stride length and leg and torso muscularity were only measured indirectly here, but with direct measures and improved data

collection procedures, leg length (through its effect on stride length and stride duration) and muscle volumes would likely be correlated with ball K_e in addition to biacromion breadth. With respect to the arm's contribution to the throw, it has been shown that the majority of the energy contributed by the arm is produced at the shoulder through passive and active internal rotation, and magnified as it is transferred across the elbow by isometric or eccentric contraction of the triceps. The anthropometric variables of the arm that likely influence ball K_e are upper arm length and strength of the latissimus dorsi and pectoralis major. Additionally, the position of the arm in space affects R for the external force acting on the elbow, and there is some evidence that subjects can take advantage of better arm positions to maximize the mechanical advantage of the joint; however, R is not related to body size or shape at all. Thus, with respect to throwing a baseball, there is evidence to support H1a, but not H1b-d.

Spear Results

I. Relationship between anthropometric variables and spear K_e .

This section will follow the same format as that for the ball results above, first exploring the direct relationship between anthropometric variables and spear K_e , then examining the transfer of energy up the kinetic chain. Differences in the relationship between anthropometrics and throwing performance between the ball results and spear results will be noted and discussed in the subsequent discussion section. Variables used to predict spear K_e and their abbreviations are summarized in table 7.3.

As the with ball analysis, the contributions of the body versus the arm to spear K_e were examined separately. The body's contribution to the throw was assumed to be summarized by RShoulder K_e , and RShoulder K_e explains approximately 57% of the variation in spear K_e (figure

7.3). This is comparable to the $\approx 52.5\%$ contribution of the body to the throw for ball throwing. Stepwise multiple regression of body mass, height, leg length, torso length, biasis breadth and biacromion breadth against RShoulder K_e was performed to determine which anthropometric variables are responsible for the body's contribution to the throw (table 7.5a). The only significant predictor of RShoulder K_e for B1 and B2 was height, which was significant for both at $p < 0.001$. For B3, biacromion breadth is the only significant predictor of RShoulder K_e at $p < 0.001$. Biacromion breadth or height explains 39.4% of the variation in RShoulder K_e , similar to that for ball K_e (42%). Thus, most simple linear measurements of body size and proportions are not significant predictors of spear throwing performance.

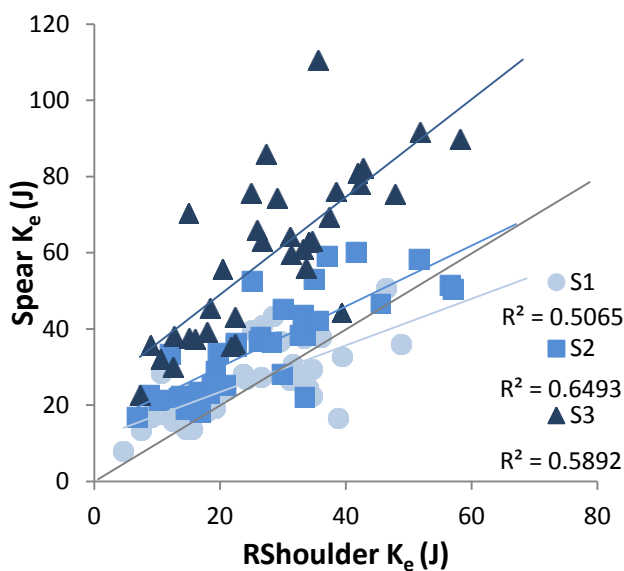


Figure 7.3 Linear regression of RShoulder K_e against Spear K_e . Grey line represents identity.

Table 7.5 Stepwise multiple regression equations for relationship between anthropometric variables and spear K_e .

Variable	Spear 1				Spear 2				Spear 3			
a. RShoulder K_e	β	R^2	r	p	β	R^2	r	p	β	R^2	r	p
Height	0.640	0.409	0.640	<0.001	0.607	0.368	0.607	<0.001			0.320	0.085
Biacromion			0.235	0.212			0.253	0.186	0.636	0.405	0.636	<0.001
Body Mass			0.137	0.469			0.107	0.582			0.174	0.357
Thigh			-0.005	0.978			0.112	0.564			0.110	0.562
Shank			0.057	0.764			-0.025	0.896			0.079	0.677
Torso			0.159	0.401			0.079	0.684			0.116	0.542
Biasis			-0.154	0.415			-0.116	0.548			0.072	0.706
b. Spear K_e	β	R^2	r	p	β	R^2	r	p	β	R^2	r	p
RShoulder K_e	0.712	0.506	0.712	<0.001	0.787	0.619	0.787	<0.001	0.551	0.574	0.651	<0.001
Wrist Flexor aCSA			0.266	0.199			0.374	0.072	0.405	0.694	0.533	0.002
Upper Arm			0.179	0.391			0.251	0.237			0.364	0.080
Forearm			0.133	0.527			0.151	0.483			0.370	0.075
Hand			0.191	0.361			0.178	0.406			0.214	0.316
Triceps aCSA ^{1,2,3}			0.183	0.382			0.234	0.271			-0.243	0.253

All variables are lengths unless otherwise noted. See table 7.3 for abbreviations, see table 7.2 for formatting. Note: elbow extension and shoulder internal rotation ω are defined as negative, so negative r values indicate positive correlation.

To examine the potential contribution of the arm variables to the throw independent of variation in RShoulder K_e , stepwise multiple regression of RShoulder K_e , upper arm length, forearm length, hand length, triceps aCSA, and wrist flexor aCSA against spear K_e was performed. Results were similar to the ball results, with the exception of S3. For S1-S2, the only significant predictor of spear K_e was RShoulder K_e ($p < 0.001$), and all other variables did not meet inclusion criteria (table 7.5b). For S3 however, in addition to RShoulder K_e , wrist flexor aCSA is also a significant predictor of spear K_e ($p = 0.002$). As compared with the 57% of spear K_e explained by RShoulder K_e alone, 69.4% of the variation in spear K_e is explained by the addition of wrist flexor aCSA. It is unclear why S3 would demonstrate a different pattern than S1-S2, but it may be that the additional mass of this object (more than double the mass of the next lightest object) changed the dynamics of the movement. An examination of the pattern of energy transfer between joints may help to shed light on this possibility.

II. Relationship between anthropometric variables and K_e at each joint.

1. K_e of the legs and torso.

As with the ball results, contributions of anthropometric variables to the K_e generated by each joint will be examined, even if these do not lead to a direct relationship with spear K_e in this sample. Figure 7.4 presents the relationship between each of the predictor variables and K_e at each joint. Beginning with the start of the kinetic chain, the contribution of the legs to the throw was examined with a multiple regression of leg length and biasis breadth against RAsis K_e . Leg length was a significant predictor of RAsis K_e for S1 and S2 (table 7.6a, leg, S1: $p = 0.049$, S2: $p = 0.012$, S3: $p = 0.166$; biasis, S1: $p = 0.337$, S2: $p = 0.375$, S3: $p = 0.284$). For S1-S2, leg length explains $\approx 13\%$ to $\approx 21\%$ of the variation in RAsis K_e . Thus, leg length alone does not contribute greatly to RAsis K_e .

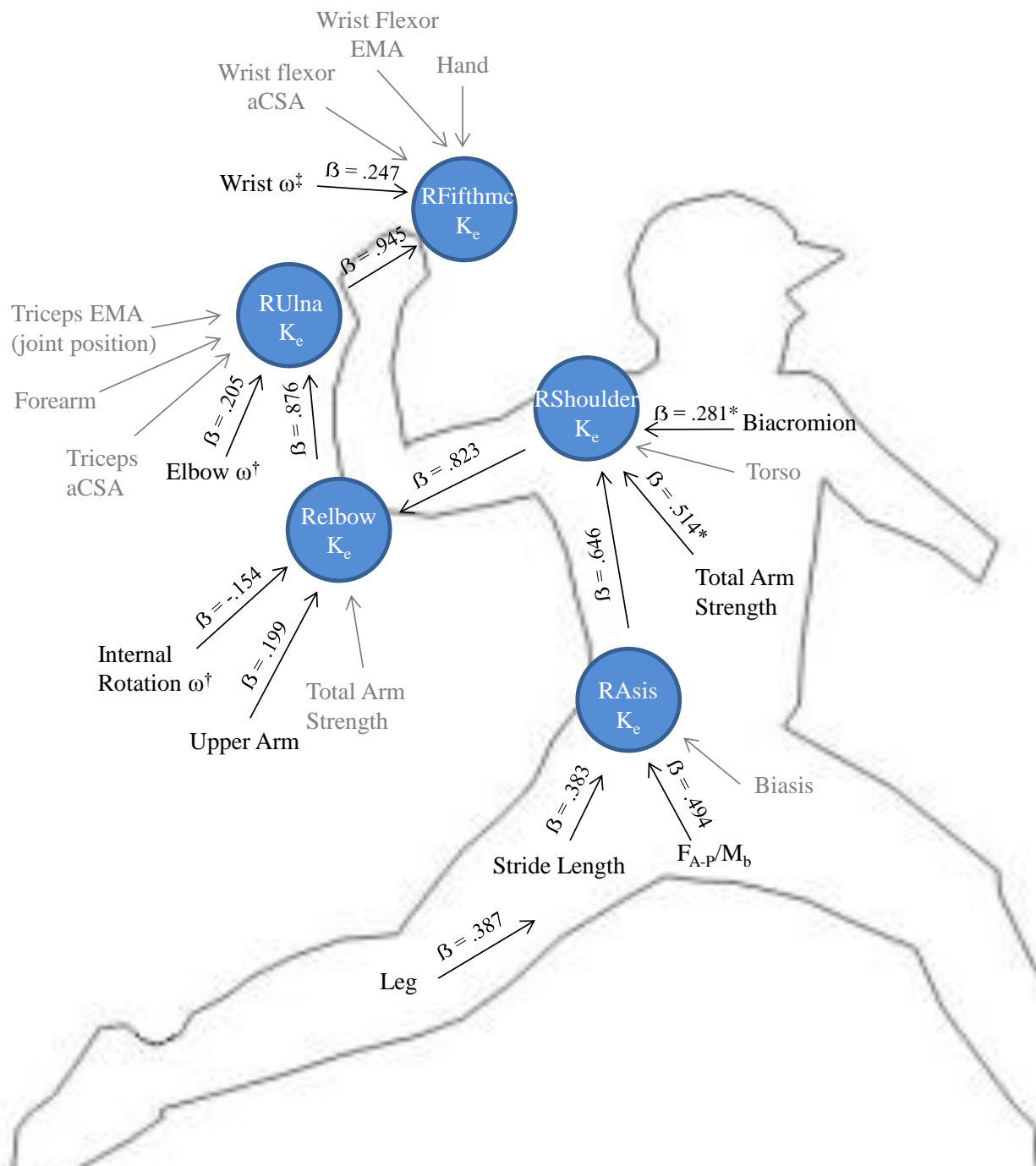


Figure 7.4 Diagram of the relationship between predictor variables and linear K_e at each joint for spear throws. See table 2 for abbreviations. β values are standardized coefficients for the stepwise multiple regression of all significant predictor variables, averaged across all spears for which the variable was significant (see table 7.6). Variables in black are significant at $p < 0.05$. * β for biacromion is for S3 (with total arm strength), β for total arm strength is for S1-S2 (without biacromion). † S2-S3 only. ‡ S1 only. Note: shoulder internal rotation and elbow extension are defined as negative, so positive β for elbow ω with ulna K_e indicates inverse correlation.

Table 7.6 Stepwise multiple regression equations for anthropometric variables and K_e at each joint for spear throwing.

Variable	Spear 1				Spear 2				Spear 3			
Legs												
a. RAsis K_e^1	β	R^2	r	p	β	R^2	r	p	β	R^2	r	p
Leg	0.356	0.127	0.356	0.049	0.462	0.213	0.462	0.012			0.259	0.166
Biasis			0.181	0.337			0.174	0.375			0.202	0.284
b. RAsis K_e^1	β	R^2	r	p	β	R^2	r	p	β	R^2	r	p
F_{A-P}/M_b	0.514	0.570	0.544	0.001	0.489	0.563	0.553	0.001	0.480	0.467	0.516	0.002
Stride ^{1,3}	0.365	0.645	0.419	0.012	0.419	0.670	0.495	0.003	0.365	0.533	0.416	0.013
Torso												
c. RShoulder K_e	β	R^2	r	p	β	R^2	r	p	β	R^2	r	p
RAsis K_e^1	0.647	0.499	0.784	<0.001	0.632	0.442	0.767	<0.001	0.660	0.621	0.871	<0.001
Total strength	0.497	0.742	0.697	<0.001	0.530	0.722	0.708	<0.001	0.287	0.826	0.520	0.002
Biacromion			0.335	0.053			0.347	0.052	0.281	0.871	0.507	0.002
Torso			0.223	0.204			0.270	0.270			0.529	0.180
Shoulder												
d. Elbow K_e	β	R^2	r	p	β	R^2	r	p	β	R^2	r	p
RShoulder K_e	0.811	0.798	0.873	<0.001	0.839	0.819	0.903	<0.001	0.820	0.782	0.873	<0.001
Upper Arm	0.198	0.831	0.400	0.017	0.207	0.857	0.460	0.007	0.192	0.815	0.386	0.022
Arm strength			0.032	0.858			0.056	0.762			-0.025	0.890
e. Elbow K_e	β	R^2	r	p	β	R^2	r	p	β	R^2	r	p
RShoulder K_e	0.811	0.798	0.873	<0.001	0.842	0.819	0.915	<0.001	0.783	0.782	0.875	<0.001
Upper Arm	0.198	0.831	0.400	0.019	0.198	0.857	0.471	0.006	0.194	0.815	0.417	0.014
Internal Rotation ω^3			-0.211	0.237	-0.140	0.877	-0.370	0.037	-0.167	0.842	-0.380	0.027

Table 7.6 cont.

Variable	Spear 1				Spear 2				Spear 3			
Elbow												
f. Ulna K_e	β	R ²	r	p	β	R ²	r	p	β	R ²	r	p
Elbow K_e	0.933	0.870	0.933	<0.001	0.916	0.839	0.916	<0.001	0.778	0.802	0.893	<0.001
Triceps aCSA^{1,2,3}			0.281	0.173			0.143	0.516	0.288	0.871	0.592	0.002
Triceps EMA ^{1,3}			0.365	0.072			0.359	0.093			-0.126	0.557
Forearm			0.376	0.064			0.272	0.209			0.253	0.232
g. Ulna K_e	β	R ²	r	p	β	R ²	r	p	β	R ²	r	p
Elbow K_e	0.933	0.870	0.933	<0.001	1.00	0.839	0.928	<0.001	1.029	0.802	0.892	<0.001
Elbow Extension ω²			0.257	0.137	0.192	0.869	0.431	0.012	0.217	0.831	0.385	0.023
h. Elbow Extension ω²	β	R ²	r	p	β	R ²	r	p	β	R ²	r	p
Triceps aCSA^{1,2,3}	-0.460	0.212	-0.460	0.018			-0.261	0.229			-0.372	0.134
Triceps EMA ^{1,3}			-0.123	0.558			0.072	0.743			0.308	0.067
Wrist												
i. Fifthmc K_e	β	R ²	r	p	β	R ²	r	p	β	R ²	r	p
Ulna Ke	0.933	0.870	0.933	<0.001	0.933	0.871	0.933	<0.001	0.969	0.939	0.969	<0.001
Wrist Flexor aCSA			-0.003	0.990			-0.010	0.963			0.173	0.409
Wrist Flexor EMA ²			-0.132	0.538			0.240	0.270			0.262	0.205
Hand			-0.111	0.606			0.023	0.916			0.250	0.228
j. Wrist Flexion ω^{1,3}	β	R ²	r	p	β	R ²	r	p	β	R ²	r	p
Wrist Flexor aCSA			0.039	0.857	-0.618	0.381	-0.618	0.002			0.180	0.388
Wrist Flexor EMA ²			0.059	0.785			0.200	0.372			-0.343	0.093
k. Fifthmc K_e	β	R ²	r	p	β	R ²	r	p	β	R ²	r	p
Ulna K_e	0.874	0.870	0.953	<0.001	0.933	0.871	0.933	<0.001	0.969	0.939	0.969	<0.001
Wrist Flexion ω ^{1,3}	0.247	0.927	0.665	<0.001			0.316	0.078			0.025	0.885

All variables are lengths unless otherwise noted. See table 1 for abbreviations, see table 2 for formatting. Note: elbow extension and shoulder internal rotation ω are defined as negative, so negative r values indicate positive correlation.

As with the ball results, stride length is an important predictor of RAsis K_e , likely as a result of longer stride duration. Stride length explains approximately 47% of the variation in RAsis K_e , at $p < 0.001$ for all three spears. Furthermore, leg length is significantly correlated with stride length for all spears (S1: $R^2 = 0.138$, $p = 0.040$, S2: $R^2 = 0.170$, $p = 0.021$, S3: $R^2 = 0.143$, $p = 0.036$). Yet, the correlations are quite small, with leg length explaining only about 15% of the variation in stride length. Finally, as with the ball results, there is no additional variation in RAsis K_e explained by leg length beyond stride length. In a stepwise multiple regression of stride length and leg length against RAsis K_e , leg length does not meet inclusion criteria (S1: $p = 0.448$, S2: $p = 0.183$, S3: $p = 0.611$). Thus, as expected, stride length is important in generating linear energy of the pelvis, as it increases stride duration, allowing the legs to generate push-off forces for a longer time. Stride length is influenced by leg length, but there is residual variation in stride length, likely explained by motivation, technique, and measurement error.

In addition to stride length, RAsis K_e should be a function of the actions of the muscles of the push-off leg, as measured by the force plate trace. Body size scaled force in the direction of the throw (F_{A-P}/M_b), in conjunction with stride length, was regressed against RAsis K_e (table 7.6b). Similar to the ball results, both stride length and F_{A-P}/M_b were significant predictors of RAsis K_e for all three spears (F_{A-P}/M_b , S1: $p = 0.001$, S2: $p = 0.001$, S3: $p = 0.002$, stride length, S1: $p = 0.012$, S2: $p = 0.003$, S3: $p = 0.013$). Longer legs allow subjects to take longer strides with longer stride durations, thereby generating forces over a greater period of time and ultimately reaching greater velocities. Together, stride length and body size scaled A-P force explain up to 67% of the variation in RAsis K_e , demonstrating that torques produced by the back leg actively contribute to the throw.

Moving up the kinetic chain, the contribution of the upper body to the throw independent of RAsis K_e was examined. Stepwise multiple regression of RAsis K_e , torso length, biacromion breadth, and arm strength (sum of strength tests for all arm muscle groups) against RShoulder K_e was performed (table 7.6c). Arm strength is used because it is assumed to correlate with torso strength, which was not measured. Arm strength results are presented in place of total arm aCSA because correlations are stronger, but the pattern of results is the same for both. Results were comparable to the ball results, where biacromion breadth, arm strength, or both were significant predictors of RShoulder K_e in addition to RAsis K_e . For S1 and S2, only RAsis K_e and arm strength were significant predictors of RShoulder K_e , all at $p < 0.001$. For S3, RAsis K_e , arm strength and biacromion breadth were all significant predictors of RShoulder K_e (RAsis K_e , $p < 0.001$, arm strength, $p = 0.002$, biacromion breadth, $p = 0.002$). Furthermore, the combination of these three variables explains approximately 87% of the variation in RShoulder K_e , as compared with 78% of the variation explained by biacromion breadth and arm strength for the ball trials. Thus, it seems likely that the breadth and musculature of the torso are important in generating energy for the throw.

In summary, leg length (through an effect on stride length and stride duration), biacromion breadth, and the musculature of the legs and torso appear to contribute significantly to the K_e of the dominant shoulder. These results are very similar to the ball results, suggesting a similar transfer of energy through the legs and torso between ball and spear throwing.

2. *K_e of the arm.*

Using the K_e of the RShoulder to summarize the body's contribution to the throw, the contributions of each of the joints of the arm were examined. The contribution of the shoulder was examined with a stepwise multiple regression of RShoulder K_e , upper arm length, and total

arm strength against Elbow K_e (table 7.6d). As with the ball results, only upper arm length was a significant predictor of Elbow K_e in addition to RShoulder K_e (upper arm, S1: $p = 0.017$, S2: $p = 0.007$, S3: $p = 0.022$; arm strength, S1: $p = 0.858$, S2: $p = 0.762$, S3: $p = 0.890$). However, for the ball trials the arm strength values were quite close to reaching significance ($p = 0.050 - 0.057$), and here there is clearly no correlation. This might indicate a difference in the contribution of the shoulder musculature to the throw between ball throwing and spear throwing. RShoulder K_e and upper arm length explain approximately 83.4% of the variation in Elbow K_e , as compared with 86% for the balls.

With the ball trials, it was found that shoulder internal rotation ω explained a significant portion of Elbow K_e in addition to upper arm length, likely due to actions of the latissimus dorsi and pectoralis major, as well as passive stretching of the tendons crossing the shoulder. For the spear trials, stepwise multiple regression of RShoulder K_e , upper arm length, and internal rotation ω against Elbow K_e found a significant effect of internal rotation ω for S2 and S3 (table 7.6e, S1: $p = 0.237$, S2: $p = 0.037$, S3: $p = 0.027$). The contribution seems relatively small compared with the ball results however, as the partial r values are much smaller. Additionally, shoulder rotation ω is not correlated with arm muscle aCSA (or strength) for any ball (S1: $R^2 = 0.036$, $p = 0.365$, S2: $R^2 = 0.092$, $p = 0.141$, S3, $R^2 = 0.091$, $p = 0.135$). Thus, the angular velocity of the shoulder and the length of the upper arm contribute to the K_e of the elbow, but they have a more minimal effect than for the ball throws, and they probably do not do so through actions of the muscles crossing the shoulder. This is not surprising in light of the results of chapter 6. During spear throwing, shoulder internal rotation is constrained to a much narrower range of motion, reducing the internal rotation ω , and thereby reducing the potential contribution of internal rotation to the throw.

To examine the contribution of the elbow to the throw, the K_e of the Ulna was predicted using stepwise multiple regression of Elbow K_e , forearm length, triceps aCSA, and triceps EMA (table 7.6f). As with B1, the only significant predictor of Ulna K_e for S1 and S2 was Elbow K_e ($p < 0.001$ for all balls), which independently explains approximately 85.5% of its variation, comparable to the 82% for the ball trials. For S3 however, triceps aCSA also explains a significant portion of the variation in Ulna K_e (aCSA, $p = 0.002$). These two variables together explain 87% of the variation in Ulna K_e .

If triceps musculature is contributing to Ulna K_e for S3, this should be captured by the elbow extension ω measured during the trials, which could be a function of the applied F_m acting over a given EMA. In contrast to the ball results, elbow extension ω was a significant predictor of Ulna K_e in addition to Elbow K_e for S2 and S3 (table 7.6g, S1: $p = 0.137$, S2: $p = 0.012$, S3: $p = 0.023$). However, the relationship is negative (note: slope is positive because extension is defined as negative), indicating that greater extension ω is actually detrimental to the throw. Furthermore, when triceps aCSA and EMA are regressed against elbow extension ω , only triceps aCSA is a significant predictor, and only for S1 (table 7.6h, aCSA, S1: $p = 0.018$, S2: $p = 0.229$, S3: $p = 0.134$; EMA, S1: $p = 0.558$, S2: $p = 0.743$, S3: $p = 0.067$). Results are similar if r and R are used in place of EMA, demonstrating that elbow extension ω is not a function of elbow moment or load arms. Thus, for S1, triceps activity appears to be related to elbow extension ω , but elbow ω is not relevant to Ulna K_e . For S2 and S3, elbow extension ω is relevant to Ulna K_e , but it is in the opposite direction expected, and it does not appear to be a function of muscular activity. Thus, in no case is there a simple situation where, as predicted in H1, triceps aCSA and EMA predict elbow ω , and elbow ω predicts Ulna K_e .

Given this discussion, the fact that triceps aCSA predicts Ulna K_e independent of variation in Elbow K_e deserves further exploration. This relationship was visualized by graphing triceps aCSA against the residuals of the regression of Elbow K_e and Ulna K_e . Figure 7.5 demonstrates that the correlation between triceps aCSA and Ulna K_e is likely a statistical artifact, not a true causal relationship. The triceps aCSA values plot in two clouds as a result of the differences in muscularity between the female and male subjects. The male cloud is significantly greater than the female cloud, which pulls the regression line towards significance, but within each cloud there is no significant slope and R^2 values are insignificant. To confirm this, sex was included in the multiple regression of Elbow K_e and triceps aCSA against Ulna K_e . Sex is in fact a strong predictor of Ulna K_e independent of Elbow K_e , while triceps aCSA is no longer significant (sex: $p < 0.001$; triceps aCSA: $p = 0.660$). Thus, triceps musculature does not appear to cause variation in Ulna K_e in a functionally significant way. It is unclear why non-muscular sex differences exist in the elbow's contribution to the throw. This could be an effect of motivation or technique.

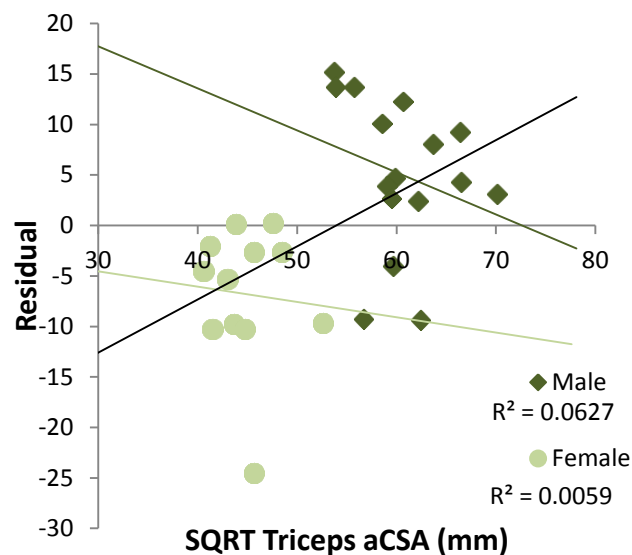


Figure 7.5 Linear regression of triceps aCSA against residuals from regression of Elbow K_e against Ulna K_e . Note: triceps aCSA is square-root transformed.

To examine the contribution of the wrist to the throw, multiple regression of Ulna K_e , wrist flexor aCSA, EMA, and hand length against Fifthmc K_e was performed (table 7.5i). Of these variables, only Ulna K_e was found to be a significant predictor of Fifthmc K_e for all three spears ($p < 0.001$). Ulna K_e explains approximately 87% of the variation in Fifthmc K_e for S1 and S2, and 94% for S3. Thus, the linear energy of the wrist is transferred effectively to the hand with relatively little active contribution of the wrist, particularly for S3.

Furthermore, despite the correlation found between wrist flexor aCSA and spear K_e for S3 discussed above, wrist flexor aCSA is not contributing to spear K_e through an effect at the wrist. To explore this relationship further, flexor aCSA was regressed against the residuals of the regression of RShoulder K_e against spear K_e (figure 7.6). As with the triceps, this relationship may be a statistical artifact. Although the female slope is positive and similar to the total slope, the male data points do not demonstrate a significant positive slope; rather the larger magnitude of the male aCSA values tend to create a slope between the clouds. In confirmation of this, when sex is included in the stepwise multiple regression of RShoulder K_e and wrist flexor aCSA against Spear K_e , sex replaces wrist flexor aCSA as the only significant predictor of Spear K_e independent of RShoulder K_e (sex: $p = 0.001$; aCSA: $p = 0.603$). Given the lack of correlation between flexor aCSA and Fifthmc K_e , it is very unlikely that this correlation is representative of a causal relationship between flexor strength and spear K_e .

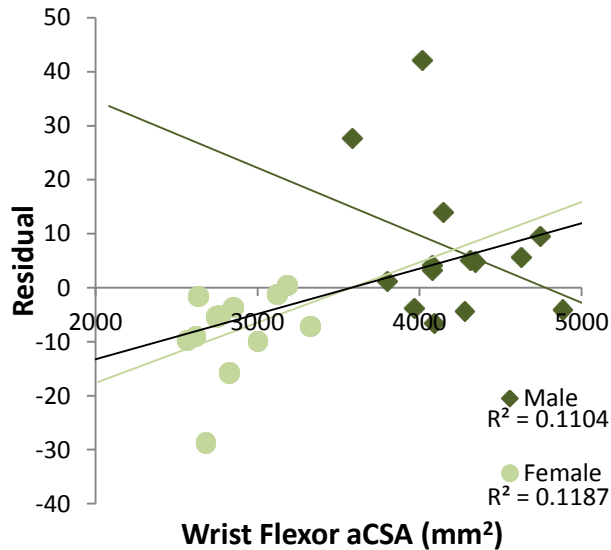


Figure 7.6 Linear regression of wrist flexor aCSA against residuals from regression of RShoulder K_e against Spear K_e .

The ball results demonstrated that, contrary to H1, the wrist flexors do not contribute to flexion ω and flexion ω does not contribute to Fifthmc (or ball) K_e . Similarly, stepwise multiple regression of wrist flexor aCSA and EMA against wrist flexion ω found flexor aCSA to be significantly correlated with flexion ω only for S2, and EMA was not correlated with flexion ω for any spear (table 7.6j, aCSA, S1: $p = 0.857$, S2: $p = 0.002$, S3: $p = 0.388$; EMA, S1: $p = 0.785$, S2: $p = 0.372$, S3: $p = 0.093$). Furthermore, stepwise multiple regression of wrist flexion ω and Ulna K_e against Fifthmc K_e demonstrates that wrist flexion ω is only significantly correlated with Fifthmc K_e for S1 (table 7.6k, S1: $p < 0.001$, S2: $p = 0.316$, S3: $p = 0.885$). Thus, there is no object for which, as predicted in H1, Fifthmc K_e is predicted by flexion ω , and flexion ω is predicted by flexor aCSA and EMA. Instead, it appears that the wrist transfers the energy generated up the chain to the thrown object without concentric muscular activation for both ball and spear throwing.

In summary, the arm does not directly generate energy during a spear throw, and the only anthropometric variable that has a causally significant effect on joint K_e is upper arm length.

Instead, the arm serves to transfer the energy generated by the legs, torso, and to a lesser degree, the shoulder, to the spear without concentric muscular involvement. Where arm muscles are activated during the throw, it is primarily for the purpose of maintaining the spear in the proper position rather than generating velocity.

Discussion.

The above analysis of the kinetics and kinematics of spear throwing has illustrated several important relationships between anthropometrics and spear throwing performance. As with the ball results, initial examination suggested that most anthropometric variables do not significantly affect throwing performance. Only height and biacromion breadth are significant predictors of spear K_e , providing only minimal support for H1. However, by examining the transfer of energy across the joints individually, several important anthropometric variables have come to light, and several interesting differences between the spear throwing results and the ball throwing results were observed. These results are summarized in figure 7.4.

1. The legs and torso.

In the lower portion of the body, the legs contribute to a spear throw very similarly to a ball throw. Kinetic energy is generated by the legs through a muscular push-off with the back leg, and a long stride length increases the duration over which muscular forces are generated by increasing push-off duration. Leg length is significantly correlated with stride length, indicating the anthropometrics of the leg are relevant to RAsis K_e . Although the pattern is very similar between the ball and spear trials, the magnitude of the correlations are somewhat weaker for the spear than ball trials. It is very likely that these weaker correlations are a result of unfamiliarity of the subjects with spear throwing, and with the larger size of spears as compared with the balls. The length of the spears in the small room may have inhibited the throwers, resulting in smaller

strides or less forceful push-off. With more experienced spear throwers (should such a sample exist), a larger data collection space, and the improved data collection techniques discussed for the ball trials, much stronger correlations would have been achieved.

In addition to the legs, RShoulder K_e is generated by the musculature of the torso (as indicated by arm strength) and the breadth of the shoulders. This pattern is very similar to the results of the ball throws, with a potentially greater emphasis on torso strength in the spear throws. Arm strength reaches significance for all three spears, and the partial correlation values are higher for the spear trials. Furthermore, as this measure of torso strength is an admittedly weak one, these correlations would be even higher with an improved measure of torso strength. Thus, there are several important anthropometric variables relevant to the body's contribution to a spear throw. Leg segment lengths, biacromion breadth, and leg and torso muscle sizes are likely all important predictors of throwing performance.

2. *The shoulder.*

The contribution of the legs and torso to the throw appears to be very similar between the ball and spear throws. However, the shape of the spear and the trajectory of the throwing motion are different from baseball throwing, and these might affect how energy is generated by the arm and transferred to the object. At the shoulder, for both the spear and ball throws the internal rotation velocity and length of the upper arm are significantly correlated with Elbow K_e . However, internal rotation ω is less strongly correlated with Elbow K_e for the spear throws than for the ball throws. Furthermore, internal rotation ω is a function of muscular strength for the ball throws but not for the spear throws. This could be due to limitations on the movement of the arm due to the shape and position of the spear in space. As discussed elsewhere, the spear must be held approximately parallel to the ground during the later phases of the throw in order to assure

that it is released with a straight trajectory. When the shoulder internally rotates, this would naturally tend to increase the angle of the spear relative to the ground (make it less parallel to the ground), unless the rest of the limb compensates. The window within which the shoulder can internally rotate and maintain the spear at an appropriate angle will limit its angular displacement. Thus, the internal rotation angular velocities achieved during spear throwing are far less than during ball throwing and will not contribute as much to object K_e . Furthermore, Elbow K_e is less affected by variation in shoulder internal rotator strength for spear throwing than for ball throwing.

3. *The elbow.*

At the elbow, the spear results are comparable to the ball results in that no anthropometric variables are predictive of Ulna K_e independent of Elbow K_e . Furthermore, triceps aCSA and EMA do not significantly correlate with extension ω for most spears. In contrast to the ball results however, elbow extension ω was significantly negatively correlated with Ulna K_e , independent of Elbow K_e for S2 and S3. Thus, *reduced* elbow ω is indicative of greater throwing velocity for this sample. This is a surprising result, and suggests that spear velocity is maximized when the energy generated proximally in the kinetic chain is transferred to the spear with minimal elbow rotation. This might imply that the best spear throwing technique involves a relatively immobile elbow. In ball throwing, the elbow magnifies the energy generated by the legs, torso and shoulder, whereas in spear throwing the elbow serves to keep the spear stable and maintain the proper trajectory through the throw. This partially explains the lesser maximum velocities achieved in spear throwing as compared with ball throwing, demonstrated in chapter 6.

4. *The wrist.*

At the wrist, no anthropometric measures were found to be significant predictors of Fifthmc K_e independent of Ulna K_e . Although wrist ω was significantly correlated with Ulna K_e for S1, it was likely not causal and there were no anthropometric variables which significantly contributed to flexion ω .

Ultimately it can be stated with confidence that with respect to spear throwing, there is support for H1a in that leg segment lengths, biacromion breadth, leg and torso muscle sizes, and upper arm length are all implicated in generating segmental K_e . Although not all of these are significantly correlated with spear K_e in this sample, with reduced measurement error and more experienced throwers, correlations would very likely be significant. On the other hand, there is no support for the hypotheses that EMA and muscle volumes at the wrist or elbow are predictive of angular velocity, or that angular velocity correlates positively with spear K_e . Thus, H1b-d must be rejected.

Chapter 8

Effective Mechanical Advantage

It was hypothesized in H2 that the effective mechanical advantage (EMA) of the elbow and wrist would be correlated with joint angular velocity and joint torque. In chapter 7, limited support for this hypothesis was found, with a correlation between triceps EMA and the kinetic energy of the elbow during ball throwing. However it did not do so through an effect on elbow angular velocity, as predicted. Here, the strength testing results will be used to test whether EMA, along with muscle volume, predicts maximum torque production. However, for these results to be applicable to the fossil record there must be a demonstrable relationship between EMA measured from a static skeletal specimen and functional EMA in the living individual. First, it will be examined whether EMA measured based on skeletal landmarks (as it was measured for skeletal specimens) produces comparable results to EMA measured based on muscular and tendinous landmarks. Secondly, it will be tested whether EMA measured statically in MR imaging is predictive of EMA during throwing. All of these must be supported in order to convincingly draw conclusions about function based on EMA in the fossil record.

I. EMA and maximum external force production.

As discussed in chapter 4, the muscular force (F_m) produced at a joint will act over a given moment arm (r) and load arm (R) to produce an external force (F_e), and the ratio of r to R is called the effective mechanical advantage (EMA) of the joint. Furthermore, it is assumed that across subjects, maximum F_m will primarily be due to variation in muscle cross-sectional area, or aCSA. In the strength tests, subjects contracted maximally against resistance to produce an isometric F_m , and the resulting F_e was measured with a load cell. Each subject's aCSA and r were

measured with MR imaging (raw values can be found in Appendices II and III). External measurements from the approximate center of rotation of the joint to the point of application of the external force (the strap) were used as R .

Based on the principles of lever mechanics, F_e should be strongly correlated with $aCSA \cdot r/R$. Figure 8.1 presents the linear regression of $aCSA \cdot r/R$ against F_e for the elbow and wrist. At the elbow, $\approx 60\%$ of the variation is explained for flexion and 45% of the variation is explained for extension. At the wrist, $\approx 29\%$ of the variation is explained for flexion, and only $\approx 4\%$ of the variation is explained for extension. Thus, as much as 55% of the variation is unexplained at the elbow, and at the wrist there is no correlation between $aCSA \cdot EMA$ and F_e in extension.

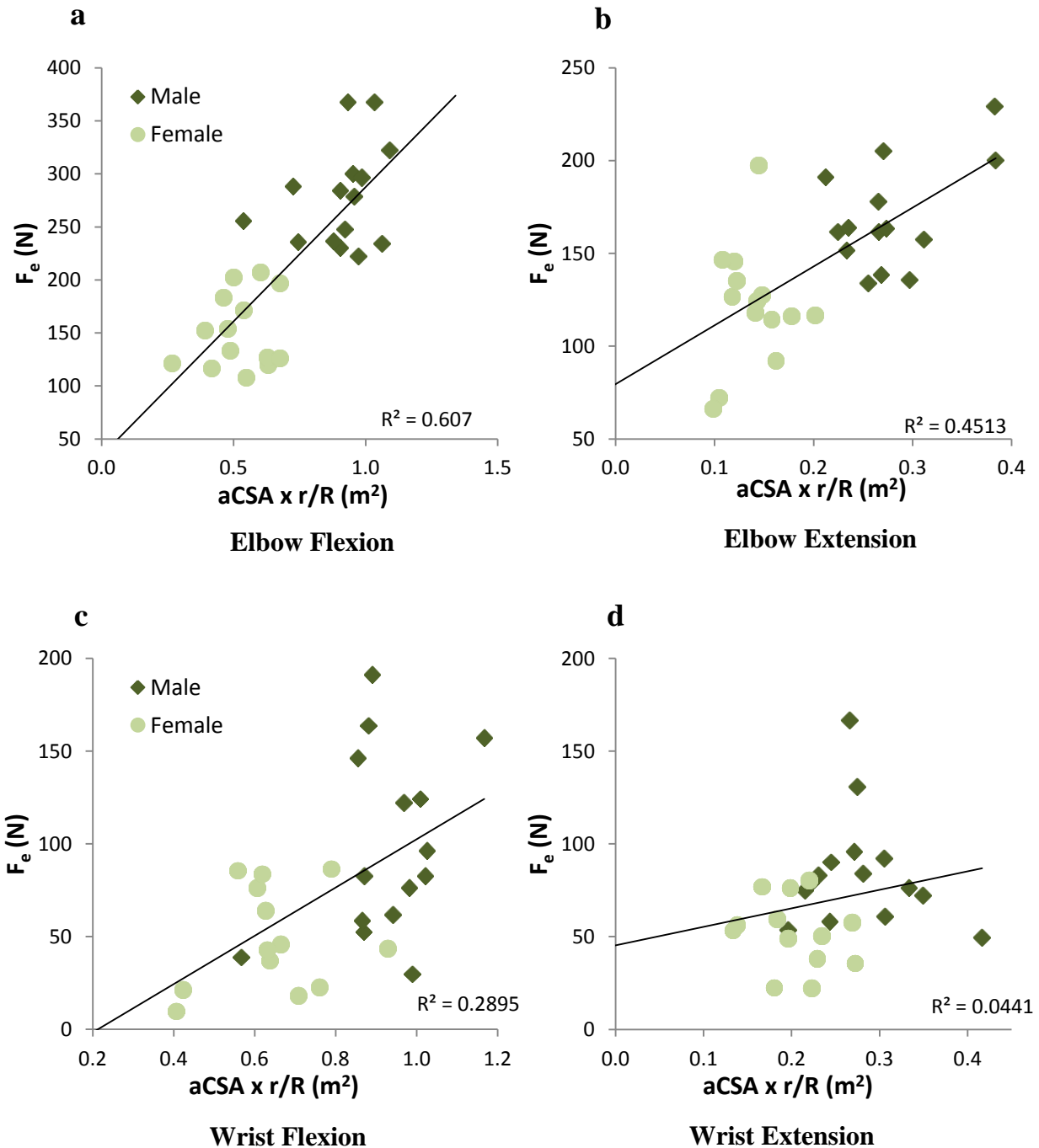


Figure 8.1 Linear regression of external force (F_e) measured with load cell, against muscle cross sectional area (aCSA) multiplied by effective mechanical advantage (EMA). (a) elbow extension, (b) elbow flexion, (c) wrist flexion (d) wrist extension. EMA is moment arm (r) divided by load arm (R).

In order to determine if EMA is contributing to the observed variation in strength, stepwise multiple regression of EMA and aCSA against F_e was performed. Table 8.1 presents the

results of these regressions for elbow flexion and extension and wrist flexion and extension.

Muscle aCSA was significant at $p < 0.001$ for elbow flexion, elbow extension, and wrist flexion, and significant at $p = 0.002$ for wrist extension. However, EMA was not significant for any joint or motion (elbow: flexion, $p = 0.596$; extension, $p = 0.320$; wrist: flexion, $p = 0.785$; extension, $p = 0.252$). Figure 8.2 presents the regression of aCSA against F_e . For both the elbow and wrist, the R^2 values for the regression of aCSA and F_e are greater without the inclusion of EMA. Thus, the EMA values are in fact confounding the relationship between strength and muscle cross-sectional area rather than contributing to it.

Table 8.1 Stepwise multiple regression equations for EMA and muscle aCSA against F_e for the elbow and wrist in flexion and extension.

	Flexion				Extension			
a. Elbow F_e (N)	β	R^2	r	p	β	R^2	r	p
aCSA	0.808	0.653	0.808	<0.001	0.681	0.464	0.681	<0.001
EMA			0.103	0.596			0.191	0.320
b. Wrist F_e (N)	β	R^2	r	p	β	R^2	r	p
aCSA	0.618	0.382	0.618	<0.001	0.549	0.301	0.549	0.002
EMA			0.055	0.785			-0.228	0.252
c. Elbow F_e (N)	β	R^2	r	p	β	R^2	r	p
aCSA	0.808	0.653	0.808	<0.001	0.681	0.464	0.681	<0.001
r			0.152	0.430			0.153	0.427
R			-0.012	0.951			-0.203	0.292
d. Wrist F_e (N)	β	R^2	r	p	β	R^2	r	p
aCSA	0.618	0.382	0.618	<0.001	0.549	0.301	0.549	0.002
r			0.139	0.489			-0.149	0.457
R			0.153	0.445			0.108	0.591

Predicted variable is in top right corner, all variables meeting inclusion criteria are in bold. β is standardized slope. R^2 is cumulative for all variables meeting inclusion criteria. r is partial correlation. P-values reported are for F-to-enter statistic (variables included if $p < 0.05$). Abbreviations: EMA, effective mechanical advantage; F_e , external force measured with load cell; r, moment arm; R, load arm; K_e , Kinetic energy; aCSA, anatomical cross sectional area.

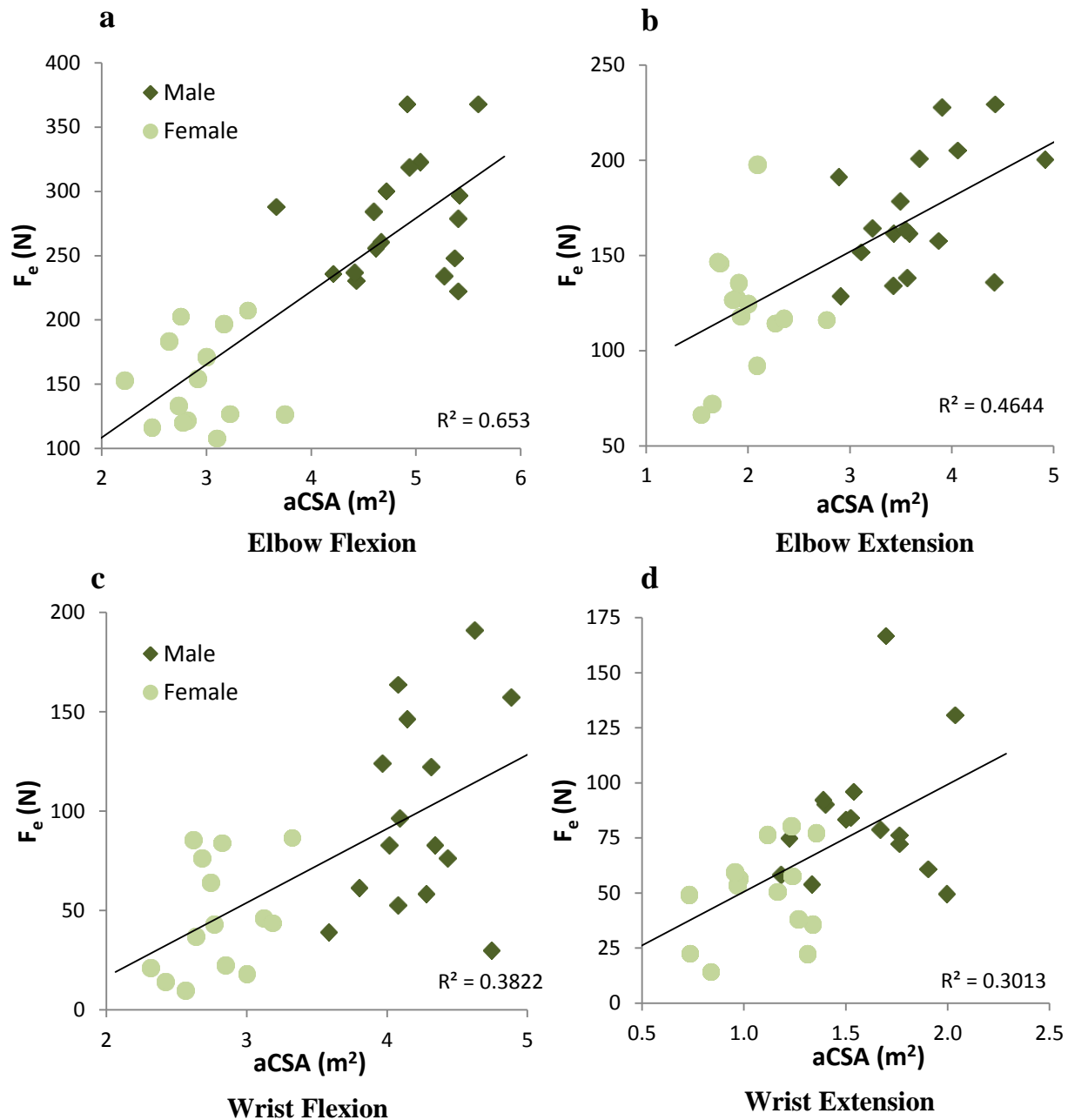


Figure 8.2 Linear regression of aCSA against F_e measured with load cell. (a) elbow flexion, (b) elbow extension, (c) wrist flexion (d) wrist extension. See table 8.1 for abbreviations.

Although EMA may not explain any variation in F_e as a ratio, it is possible that individually r or R is explanatory. To determine if r or R is significantly correlated with F_e

independent of aCSA, stepwise multiple regression of aCSA, r and R against F_e was employed (table 8.1c-d). No significant effect of r or R was found for the elbow (flexion: r , $p = 0.430$; R , $p = 0.951$; extension: r , $p = 0.427$; R , $p = 0.292$), or the wrist (flexion: r , $p = 0.489$; R , $p = 0.445$; extension: r , $p = 0.457$; R , $p = 0.591$). Thus, muscle aCSA explains between 30% and 65% of the variation in F_e , with no significant contribution of moment or load arm.

With the exception of elbow flexion, the correlations of muscle aCSA with F_e are lower than might be expected, with more than half the variation unexplained. This could be due to muscle architectural parameters that were not measured (for example pennation angles or fascicle lengths), failure to isolate the muscle groups during strength testing, or subject motivation. To help tease apart these sources of error, table 8.2 presents the correlation coefficients and partial correlations for aCSA and F_e across all joints and motions. Of note, many of the correlations are stronger between muscle and strength values that should not be causally related than those that should be causally related. In particular, all aCSA values are more strongly correlated with elbow flexion F_e than the relevant F_e value. Furthermore, with only a few exceptions, none of the partial correlations reach significance. If the low correlations were due to error from unmeasured muscle architectural parameters or differential motivation it should serve to lower the correlations overall, but the relevant partial correlations (e.g. triceps aCSA with elbow extension F_e) should still be stronger than the partial correlations with other muscle and strength variables.

Table 8.2 Correlation coefficients and partial correlations for elbow and wrist aCSA and F_e .

		Elbow aCSA				Wrist aCSA			
		Flexor		Extensor		Flexor		Extensor	
		R^2	r	R^2	r	R^2	r	R^2	r
Elbow F_e	Flexion	0.653	0.077	0.711	0.307	0.646	0.094	0.543	0.165
	Extension	0.320	-0.165	0.464	0.432	0.319	-0.115	0.381	0.213
Wrist F_e	Flexion	0.428	0.115	0.456	0.200	0.382	-0.049	0.336	0.094
	Extension	0.397	0.015	0.549	0.616	0.287	-0.416	0.301	0.004

Significant correlations ($p < 0.05$) are in bold. See table 8.1 for abbreviations.

In combination, these observations imply that the strength tests did not successfully manage to isolate the relevant muscles or muscle groups. Instead, many or all of the muscles of the arm were activating during each test. Thus, it is possible that the lack of correlation between EMA and F_e is due to the fact that the F_e values are not exclusively or primarily representing the expected muscles. If, for example, the elbow flexors co-contracted during elbow extension, the F_e value should be a function of each of the activated muscles multiplied by its EMA value. The correlation coefficients and partial correlations between F_e and each of the muscle groups may be used to determine which muscles or muscle groups were likely contributing to the observed F_e , and determine if a greater portion of the variation in F_e is explained by including more muscles and associated EMA values in the predictive equation.

Elbow flexion F_e shows partial correlations of 0.077, 0.307, 0.094, and 0.165 with elbow flexor aCSA, triceps aCSA, wrist flexor aCSA, and wrist extensor aCSA consecutively, none of which are significant. Thus, in the elbow flexion strength test, none of the muscle groups appears to be primary in producing elbow flexion F_e . However, this analysis is complicated by the fact that all the muscle aCSA values are highly inter-correlated (table 8.3). The partial correlations are not significant, likely because the muscle aCSA values explain the same portion of the

variation in F_e , making it difficult to parse out which relationships are causal and which are due to covariation. It's difficult to see how the elbow flexors could have failed to engage in this test, thus the low partial correlation with the elbow flexors should probably not be interpreted functionally. Interestingly, although not significant, the partial correlation between triceps aCSA and flexion F_e is positive ($r = 0.307$, $p = 0.063$). Given that the triceps are antagonists to the elbow flexors, triceps aCSA (and thus extension F_m) should inhibit flexion strength. The fact that the partial correlation is positive may indicate that co-activation of the antagonists was necessary for stability during the flexion test.

Table 8.3 Correlation matrix for muscle aCSA values.

	Brachialis	Triceps	Wrist flexors	Wrist extensors
Biceps	0.755	0.898	0.862	0.703
Brachialis		0.809	0.872	0.721
Triceps			0.904	0.798
Wrist flexors				0.780

Values presented are Pearson product-moment correlation coefficients.
All correlation coefficients are significant at $p < 0.001$.

Thus, it appears that the elbow flexion strength test represents contributions from multiple muscles, but these are not significantly correlated with F_e independent of one another due to covariation. To determine if EMA for the elbow flexors and extensors contributes to the F_e value independent of aCSA, stepwise multiple regression was performed. Unfortunately, the wrist flexors cannot be included in this analysis because the wrist flexor r value represents flexion around a center of rotation in the wrist. The wrist flexors also cross the elbow, and thus can contribute to elbow flexion, but an r value for this joint was not calculated. Furthermore, the muscle aCSAs were entered into the multiple regression as a sum rather than individually. The partial correlations in table 8.2 demonstrate that these are not significantly correlated with F_e independent of one another, but functionally all may be relevant. The results of the multiple

regression are presented in table 8.4a. Summed aCSA is significantly correlated with elbow flexion F_e ($p < 0.001$) and explains $\approx 71\%$ of the variation in flexion F_e . In contrast, elbow flexor aCSA alone explained $\approx 65\%$ of the variation in F_e , so the inclusion of the additional muscles improves the predictive equation (but not significantly, for the reasons described). Triceps r, elbow flexor r and R do not reach significance (triceps r, $p = 0.139$; elbow flexor r, $p = 0.676$; R, $p = 0.440$). Thus, for the elbow, there is no effect of EMA on flexion strength.

Table 8.4 Stepwise multiple regression of muscle aCSA and EMA against F_e for the elbow and wrist in flexion and extension.

Elbow				
a. Flexion F_e (N)	β	R^2	r	p
Total arm aCSA	0.841	0.707	0.841	<0.001
Triceps r			0.293	0.139
Elbow flexor r			0.084	0.676
R			-0.155	0.440
b. Extension F_e (N)	β	R^2	r	p
aCSA*	0.621	0.385	0.621	<0.001
Triceps r			0.181	0.367
Elbow flexor r			-0.035	0.862
R			-0.265	0.182
Wrist				
c. Flexion F_e (N)	β	R^2	r	P
Total arm aCSA	0.665	0.442	0.665	<0.001
Triceps r			0.160	0.436
Elbow flexor r			-0.032	0.878
Wrist flexor r			0.125	0.542
Wrist extensor r			-0.224	0.271
Elbow R			-0.332	0.097
Wrist R			0.067	0.743
d. Extension F_e (N)	β	R^2	r	p
aCSA†	0.661	0.437	0.661	<0.001
Triceps r			0.236	0.245
Wrist flexor r			0.058	0.777
Elbow R			-0.345	0.085
Wrist R			0.034	0.869

See table 1 for abbreviations *summed aCSA for triceps, elbow flexors, and wrist extensors. †summed aCSA for triceps and wrist flexors.

For elbow extension, the observed F_e value demonstrates a more expected pattern, where the R^2 value with triceps aCSA is higher than the R^2 values for the other muscles, and the partial correlation is significant. Thus, the elbow extension test appears to have been more successful at isolating the triceps muscle. Although they do not reach significance, the negative partial correlations with the flexor muscle groups suggest that the low overall correlation between triceps aCSA and extension F_e may be due to co-activation of the antagonists. Greater flexor aCSA resulted in greater flexion F_m , counteracting the F_m produced by the triceps. This trend likely did not reach significance for the same reason described above; the elbow muscles are highly intercorrelated, so they explain the same portion of the variation in extensor F_e . Functionally, both sets of elbow muscles were likely relevant to the observed F_e value. Furthermore, the partial correlation with the wrist extensors is comparable to the elbow flexors, and these muscles may also have contributed to the F_e value.

If the elbow flexors and wrist extensors were relevant to elbow extension F_e , EMA values for these muscles may have been relevant as well. To determine if EMA contributes to elbow extension F_e independent of muscle size, stepwise multiple regression of summed aCSA (elbow flexors and extensors, wrist extensors), elbow flexor r , elbow extensor r , and elbow R was performed. Wrist extensor EMA was not included for the reason described above. The results are presented in table 8.4b. The summed aCSA value is significantly correlated with F_e , and explains 38.5 % of the variation ($p < 0.001$). In contrast, triceps aCSA alone explained 46% of the variation in F_e , so inclusion of the elbow flexors and wrist extensors is not necessary to best explain extension F_e . Triceps r , elbow flexor r , and R did not reach significance (triceps r , $p = 0.367$; elbow flexor r , $p = 0.862$; R , $p = 0.182$). Thus, EMA does not significantly contribute to elbow extension F_e .

At the wrist, R^2 values for flexion F_e are similar across all muscles, suggesting that all muscles were activated. As at the elbow, the wrist extensor groups did not show negative correlations with wrist flexion F_e , indicating that the extensors were not counteracting the flexors, but instead stabilizing the joint. Partial correlations with wrist flexion F_e were actually stronger for the elbow extensors than the flexors, and the partial correlation with the wrist flexors is negative. This is counterintuitive, and very unlikely to be causal. Most likely all the muscles were activating in concert to produce the F_e value observed.

To determine if EMA contributes to wrist flexion F_e independent of aCSA, stepwise multiple regression was performed to predict wrist flexion F_e from total aCSA (summed across all arm muscles), r for all muscle groups, and R for the elbow and wrist (table 8.4c). Elbow EMA can be included here because the elbow muscles do not cross the wrist, so if the elbow muscles are contributing to F_e , it is through an effect at the elbow. Total arm aCSA was significantly correlated with wrist flexion F_e ($p < 0.001$), and explained 44% of the variation. Comparatively, wrist flexor aCSA alone only explained 38% of the variation, so inclusion of the other arm muscles improves the correlation. However, no measure of r or R for any muscle was significantly correlated with F_e . Thus, EMA does not significantly contribute to wrist flexion F_e .

Wrist extension F_e has a greater R^2 value with triceps aCSA than the other muscle groups, and the partial correlation is significant. Thus, the wrist extension strength test appears to have isolated the wrong muscle. Furthermore, the partial correlation with wrist flexor aCSA is also significant, suggesting it may have been functionally important. This correlation is negative, such that the wrist flexors may have been counteracting the F_m produced by the triceps. The partial correlations for the other two muscle groups are quite low, and thus they were not contributing to wrist extension F_e . To establish whether EMA of the wrist flexors and triceps

contributed to the wrist flexion F_e value, multiple regression of summed aCSA (triceps, wrist flexors), triceps r , wrist flexor r , elbow R and wrist R was performed (table 8.4d). Summed aCSA was significantly correlated with extension F_e ($p < 0.001$), and explained $\approx 44\%$ of the variation. The wrist extensors explained only 30% of the variation, so the triceps and wrist flexors better explain extension F_e . Triceps and wrist flexor r and R did not reach significance (triceps r , $p = 0.245$ wrist flexor r , $p = 0.777$; elbow R , $p = 0.085$; wrist R , $p = 0.869$). Thus, EMA does not significantly contribute to the wrist extension F_e value.

Discussion.

The results presented here demonstrate that there is no detectable effect of EMA on isometric strength at the wrist or elbow. The elbow extension strength test successfully isolated triceps activity, and there was no significant effect of triceps r or R on the observed elbow extension F_e value. For the other strength tests, it was determined that the tests did not successfully isolate the correct muscles. However, using the muscles that were actually responsible for the observed F_e values, no significant effect of r or R for any muscle was detected. Thus, under relatively controlled conditions, EMA does not contribute to elbow or wrist strength.

The lack of correlation between EMA and F_e is surprising, as one would expect the joints of the arm to follow the principles of lever mechanics. Despite the complication of failing to isolate the specific muscles intended, the strength tests still represent a highly controlled situation compared with natural behaviors, since the arm position and the point of application of the external load were held constant. Although no prior tests of the relationship between EMA and F_e between subjects have been reported for humans, Lieber and Boakes (1988) found a similar result for the frog. The moment arm for the frog semitendinosus was found to explain

approximately 11% of the variation in its torque production; however when maximum tetanic tension (a direct, in vitro, isometric measure of maximum F_m) was included in the equation, the moment arm explained only 0.4 % of the variation.

The fact that moment and load arms do not explain F_e independent of F_m (whether estimated by aCSA or measured directly) is, at least partly, due to the fact that r and R (approximately ulna length) are both correlated with aCSA. For r , this is partially due to body size scaling, but also because larger muscle cross-sectional areas deflect the tendon farther from the joint, changing the line of action of the muscle. This can be demonstrated with a multiple regression of r and body size against aCSA. For example, a regression of triceps r and height (height is the strongest predictor of triceps aCSA of the body size variables measured) against triceps aCSA finds a significant effect of r in addition to height in predicting triceps aCSA (height, $p = 0.026$; r , $p = 0.046$). This means that r and aCSA at a given joint will always be related, even for subjects with different body proportions. Thus, r will not be functionally important to torque independent of muscle size.

Under the specific conditions tested here, where R is very close to the length of the distal limb segment, R will be correlated with aCSA as an effect of body size scaling. Taller individuals tend to have greater body mass, longer limbs, and bigger muscles. Thus, if subjects have extreme differences in body proportions or muscularity (very short arms for their muscle size), there could potentially be a detectable effect of R under the specific conditions tested here. The subjects included in this study have a relatively low correlation between ulna length and triceps aCSA ($R^2 = 0.309$), implying variation in body proportions and muscularity, and yet no effect of R was detected. Thus, any effect of variation in R is so small as to be functionally

irrelevant. Furthermore, under more natural conditions, R will rarely be related to ulna length, the consequences of which will be discussed in section III.

A second and likely very important reason for the lack of correlation between EMA and strength is the importance of variation in the underlying neural control of muscle activation. The total tension that a muscle develops is a function of how many of its motor units are activated, or recruited, and the rate of discharge of the motor units (Duchateau et al., 2006). Activation is rarely maximal even with full voluntary effort (Aagaard et al., 2000; Duchateau et al., 2006). Many factors affect motor recruitment, including motivation, training (Moritani and Devries, 1979; Patten et al., 2001; Ferri et al., 2003), and task skillfulness (Bernardi et al., 1996), and they do so by influencing the rate of co-activation of antagonists and synergists (Kamen, 2005; Duchateau et al., 2006), altering levels of inhibition of the motor units (Aagaard et al., 2000), and increasing discharge rates of the motor units (Patten et al., 2001). The effect of these factors is measurable variation in strength that is completely independent of the mechanics of the system. In fact, as discussed, activation of antagonists and synergists was observed here, and appears to have contributed to the strength values.

Here a large portion of the variation in isometric strength is unexplained by subject anthropometrics, despite similar training background and skillset of the subjects. Thus, even under relatively controlled and constrained conditions, there appears to be a strong effect of variation in muscle recruitment and activation on strength. It is likely that with specific training for this particular strength testing set-up (improving task skillfulness), some of the variation due to muscle recruitment and discharge rate could be reduced (Bernardi et al., 1996). However, this is not merely a methodological concern, as these patterns of variation in muscle recruitment would certainly affect strength during natural activities as well, likely even more strongly. Given

this, measures such as EMA, which clearly have a relatively small effect (so small as to be undetectable here) do not provide sufficient information to be useful measures of performance in humans. This will have important implications for the ability to make inferences about performance in fossil hominins, and will be discussed at greater length in chapter 10.

II. Skeletal versus tendinous estimation of EMA.

MR images of subjects' dominant arms were used to determine if static measurements of EMA, as can be obtained from a skeleton, are comparable to EMA measured in vivo. Skeletal estimates of r were measured from the MRIs based on bony landmarks observable in a fossilized skeleton. Tendinous estimates of r were measured based on the actual line of action of the tendon as it inserts. Since there is no equivalent static versus tendinous comparison of R , only r is compared here. There should be a strong correlation between skeletal r and tendinous r if EMA measured from fossils is relevant to the living functional anatomy.

At the elbow, r was measured for biceps brachii, brachialis, and triceps brachii. Linear regression of skeletal r against tendinous r was performed, and figure 8.3 presents the results of these regressions. All regressions are significant at $p < 0.001$, and correlation coefficients are quite high. For biceps brachii, skeletal r explains 82% of the variation in tendinous r , for brachialis, skeletal r explains 95% of the variation in tendinous r , and for triceps brachii, skeletal r explains 85% of the variation in tendinous r . Thus, at the elbow, skeletal measures of r are highly accurate in predicting r in vivo, particularly for brachialis. Some of the residual variation may be related to differences in muscle aCSA, as discussed above.

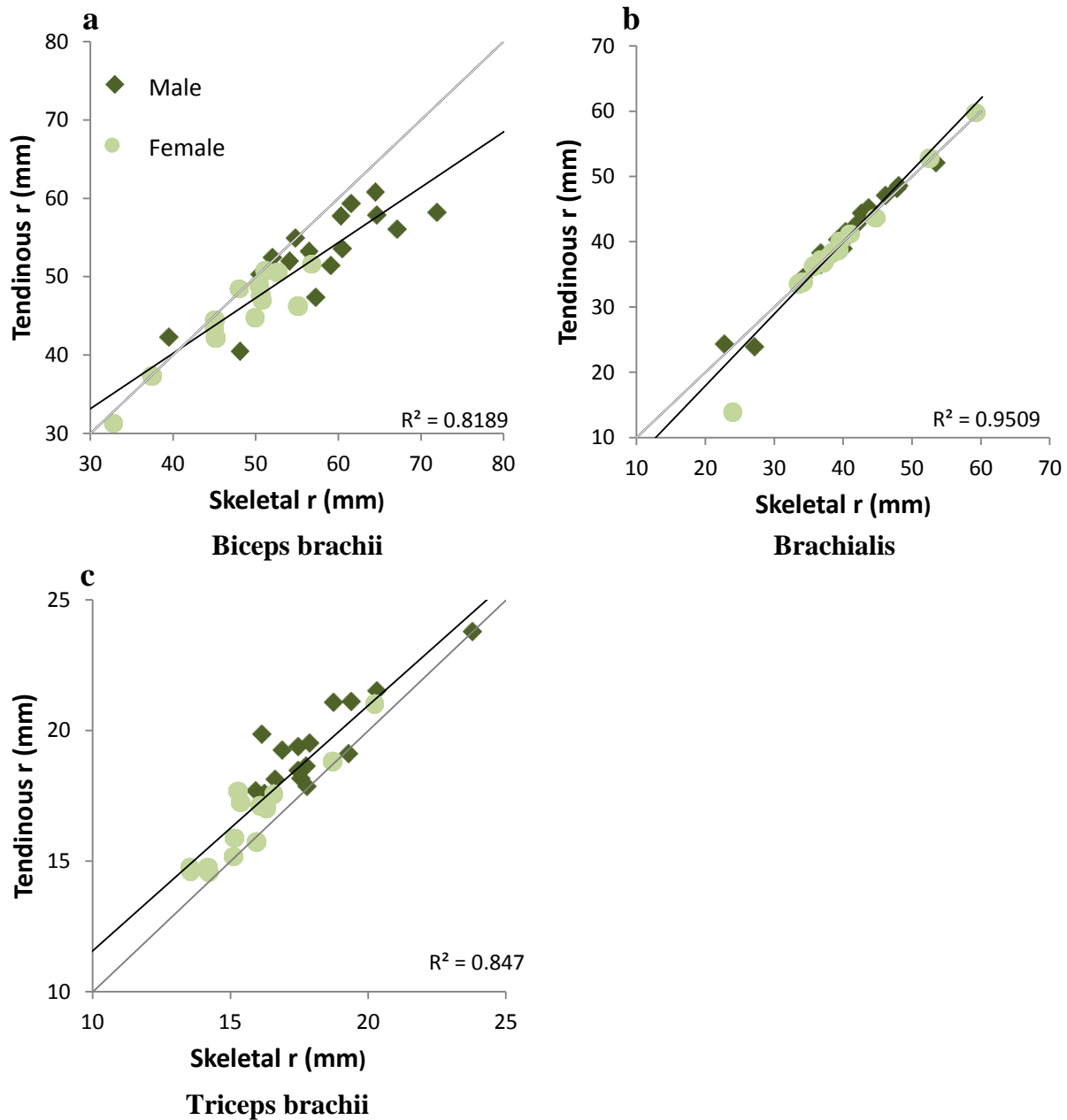


Figure 8.3 Linear regression of skeletal moment arm (r) against tendinous r. (a) biceps brachii, (b) brachialis, (c) and triceps brachii. Grey trendline represents identity.

At the wrist, skeletal and tendinous r were estimated for FCR, FCU, and ECU. A skeletal measure of ECR was not taken because the resolution of the images would not allow a distinct measurement, separate from the tendinous measurement. Linear regression of skeletal r against tendinous r was performed, and figure 8.4 presents the results of these regressions. All

regressions were significant at $p < 0.001$. For FCR, skeletal r explains 53% of the variation in tendinous r, for FCU, skeletal r explains 73% of the variation in tendinous r, and for ECU, skeletal r explains 39% of the variation in tendinous r. Thus, skeletal r is not as strong a predictor of tendinous r for ECU and FCR, but still provides useful information.

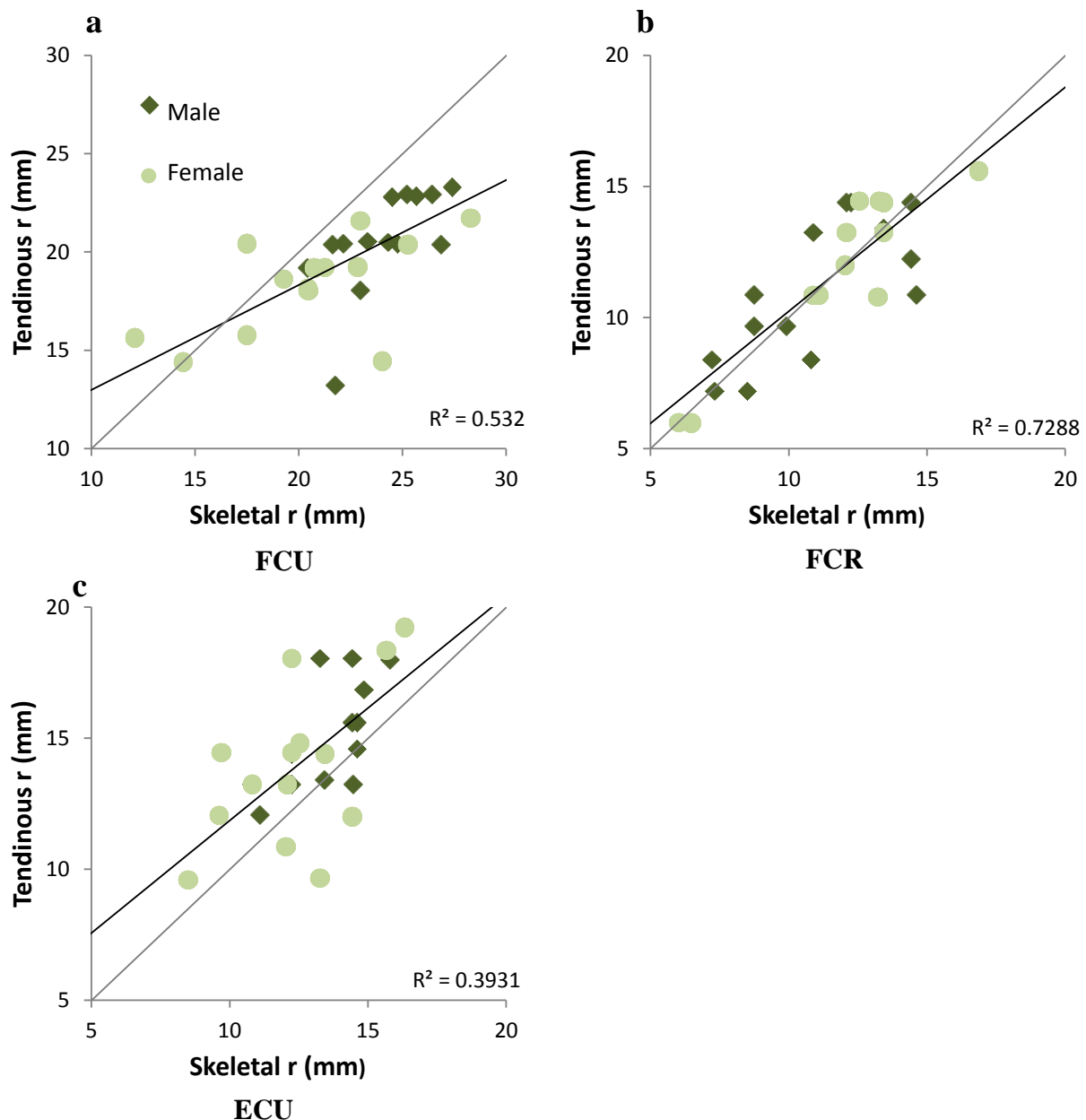


Figure 8.4 Linear regression of skeletal r against tendinous r. (a) flexor carpi radialis (FCR), (b) flexor carpi ulnaris (FCU), (c) extensor carpi ulnaris (ECU). Grey trendline represents identity.

Discussion.

The analyses presented here demonstrate that to the extent that EMA is useful for functional morphology (which is not supported by the results presented thus far), estimates of r from skeletal specimens are generally suitable for predicting r in living individuals. Measures of r from MR images were significantly correlated when measured based on skeletal landmarks and based on tendinous lines of action. Correlation coefficients range between 0.39 and 0.95, indicating that some skeletal estimates are better than others. In particular, skeletal estimates of r for brachialis, biceps brachii, triceps brachii and FCU are highly accurate in predicting tendinous r . Those for FCR and ECU are less reliable, but still significantly correlated. Since, as discussed in the previous section, r is correlated with muscle size independent of body size variation, some of the residual variation is likely due to variation in muscle aCSA. It should be noted, however, that these results are only directly applicable to static conditions such as isometric muscle contractions. The applicability of these results to more dynamic situations will be discussed in the next section.

III. Static versus dynamic EMA.

The results of the previous two sections relate to specific conditions where arm position is controlled and the joint contracts isometrically. However, living people rarely operate under strictly static conditions. Thus, to establish whether estimates of EMA made from fossils are valuable in understanding living functional anatomy, it is necessary to consider how well static EMA predicts EMA during dynamic behaviors. Throwing provides an ideal test as it is a highly dynamic activity, and (specifically for the ball throws) a highly trained activity. Tendinous estimates of EMA from MRIs will be compared with EMA measured during ball and spear throwing.

Under static conditions, the angle of a joint is constrained such that r is constant throughout the motion. In dynamic motion however, r will change as a function of the joint angle. Theoretically, r is predictable across the range of motion of the joint based on the properties of right triangles. However, in living subjects, this relationship may be complicated by variables such as the pennation angle and cross-sectional area of the muscle, and joint anatomy, variation in which might differentially affect r over the range of motion of the joint. In other words, if r were measured using MRI for the same subjects at two different joint angles, it would likely not be perfectly correlated, even ignoring measurement error. Even more importantly, subjects may not consistently use the same joint angle or pattern of joint motion to perform the same activity. If this is the case, r will vary over the course of the motion for reasons that have nothing to do with joint anatomy. Thus, it would be valuable to establish whether a single static measure of r is useful in predicting r during activity. However, it is not currently possible to measure r in vivo during dynamic behaviors. Thus, the following analyses will be limited to R .

During the static conditions considered for strength testing, where the arm contracts against resistance applied perpendicular to the ground at the distal end of the segment, R is approximately equal to the length of the distal segment. The limb is held parallel to the ground and the external force is applied at the wrist or metacarpo-phalangeal joint. Under dynamic conditions, joint angle and position can vary. For the throwing trials, R was measured as the perpendicular distance from the center of rotation of the joint to the vector for the distal resultant force, calculated from the inverse dynamics equations. For the wrist, this is the resultant force acting on the center of mass of the hand, so R will depend on wrist angle and its position in space. At the elbow, R is calculated based on a vector for the resultant force acting on the center of mass of the combined forearm and hand. Thus, R will depend on wrist angle, elbow angle and

the position of the arm in space. If all of these are relatively consistent within and between individuals during the course of the motion, R may be a predictable function of ulna length (based on the properties of right triangles). However, as with r , if subjects do not perform the motion in exactly the same manner, the joint angle and external load may be highly variable, and consequently so will R .

Thus, to determine if static EMA is valuable in predicting EMA in dynamic behaviors, a static measure of R is compared with R measured during throwing. At the elbow, static R was calculated by subtracting r for the triceps from ulna length. In effect, this estimates the length of the ulna without the olecranon process, which is posterior to the center of rotation of the joint, and thus does not contribute to R . At the wrist, static R is first metacarpal length. Since dynamic R varies over the throw, two time points during the throw were chosen for comparison. The first is the point when torque is maximized, since this represents a functionally optimum joint position. However, this does not happen at a consistent time in the throw for different subjects, so a comparison was also made at 90% of the throw. Theoretically, if static R is functionally relevant to throwing, it should be correlated with R throughout the throw.

For the elbow, linear regression of static R against R at maximum torque was performed. No significant correlations were found for static R with dynamic R for any ball or spear (Table 8.5a). Figure 8.5a-b presents the results of these regressions for Ball 1 and Spear 1, as representative of all balls and spears. No pattern is visible in the data to indicate a trend that does not reach significance. Similarly, linear regression of static R against R at 90 % of the throw yielded no significant correlations for any ball or spear (Table 8.5a). Figure 8.5c-d presents the results of these regressions for B1 and S1. It is evident that no trend is present in the data. Thus, there is no correlation between static R and R during throwing at the elbow.

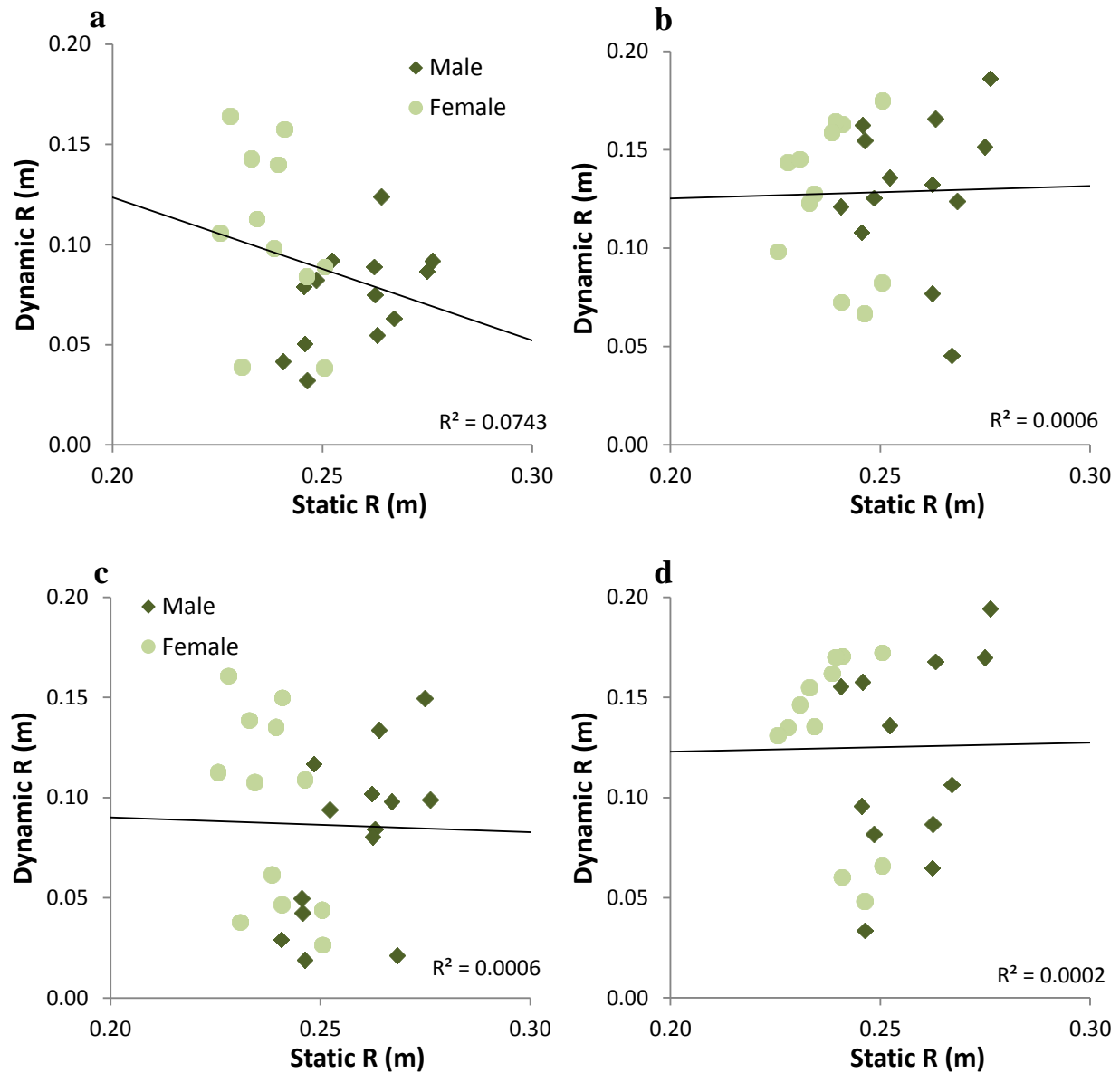


Figure 8.5 Linear regression of static R against dynamic R at the elbow during throwing. Dynamic R measured at maximum elbow torque: (a) B1, (b) S1. Dynamic R measured at 90% of throw: (c) B1, (d) S1. Static R is approximately equal to ulna length.

Table 8.5 Correlation coefficients and significance values for linear regression of static R against dynamic R.

B1			B2		B3		S1		S2		S3	
Elbow												
a. Static R	R ²	p	R ²	p	R ²	p	R ²	p	R ²	p	R ²	p
R (max)	0.074	0.198	0.085	0.167	0.150	0.062	0.001	0.908	0.048	0.294	0.025	0.454
R (90%)	0.001	0.908	0.027	0.443	0.072	0.206	<0.001	0.950	0.041	0.344	0.038	0.348
Wrist												
b. Static R	R ²	p	R ²	p	R ²	p	R ²	p	R ²	p	R ²	p
R (max)	0.084	0.272	0.005	0.744	0.003	0.793	0.014	0.570	0.027	0.430	0.003	0.787

R (max) refers to R measured at the point in the throw when torque was maximal. R (90%) refers R measured at 90% of the throw.

At the wrist, linear regression of 2nd metacarpal length against R at maximum torque was performed. As at the elbow, all correlations were non-significant (Table 8.5b). Figure 8.6a-b presents the results of the linear regression of 2nd metacarpal length against R for Ball 1 and Spear 1. These are representative of all balls and spears. As at the elbow, there is no visible trend, and thus there is no relationship between 2nd metacarpal length and R during throwing at the wrist. Results of the regression of R at 90% of the throw were comparable and thus are not presented.

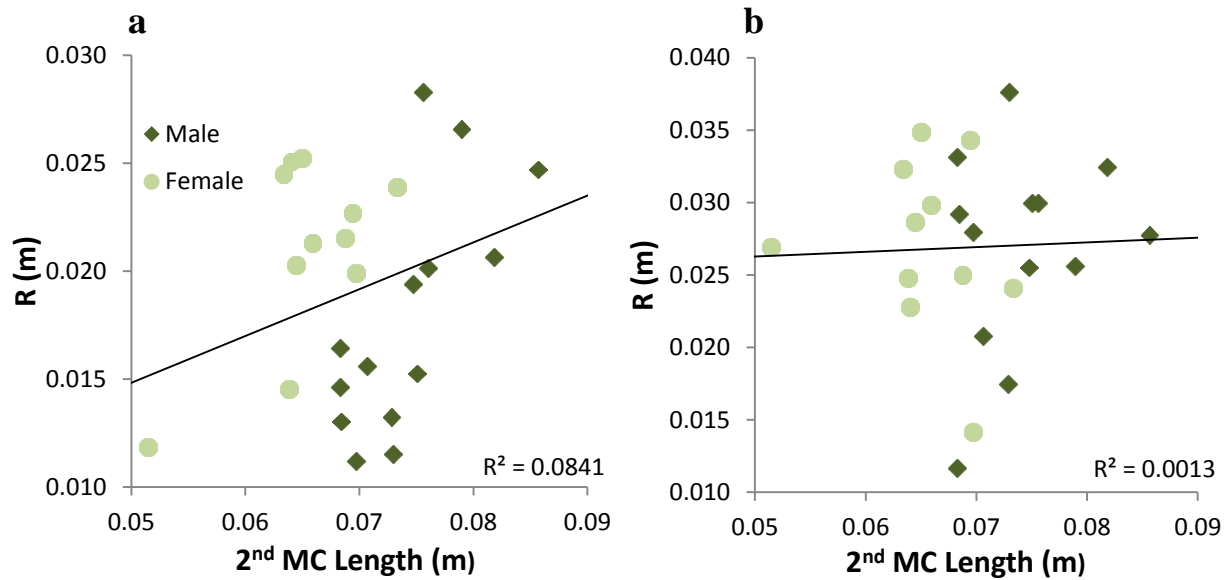


Figure 8.6 Linear regression of 2nd metacarpal length against R at maximum torque for the wrist. (a) B1, (b) S1.

Discussion.

The results of this section demonstrate that under dynamic conditions, there is no correlation between R and distal segment length (ulna or 2nd metacarpal). This result is not surprising in light of the fact that small differences in joint angle and the position of the vector for the external force will produce large differences in R within and between subjects, even performing the same highly trained activity. In fact, despite their extensive training, the subjects in this study exhibited a wide range of variation in joint angles and external force positions. Figure 8.7 presents the average value and standard deviation of elbow angle over the course of the throw for the ball throws. Between subjects, the elbow angles utilized ranged by as much as 90° at the beginning of the throw, and 52° at the end of the throw.

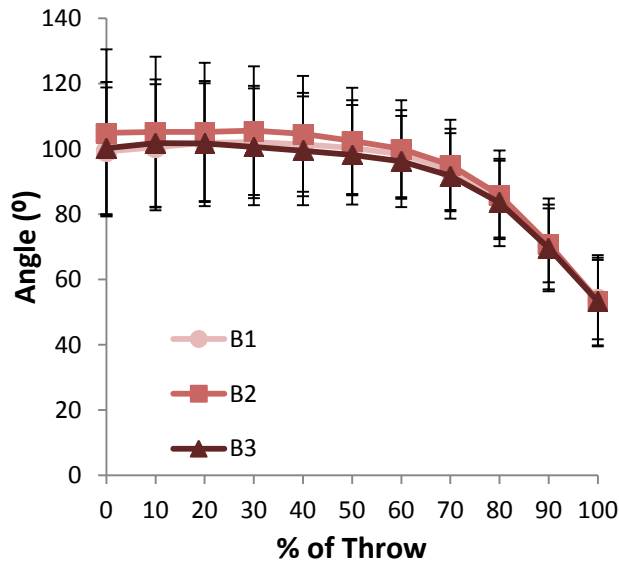


Figure 8.7 Elbow angle during ball throwing. Bars represent one standard deviation from the mean

In addition to elbow angle, the vector for the external force at the elbow is affected by the wrist angle, the position of the arm in space, and the pattern of motion and force production, which are also highly variable. To illustrate this point, figure 8.8 is a representation of the vector for the external force at the elbow and the R value calculated from it for 3 ball throws, each performed by 3 subjects, who are representative of the variation present in the sample. It is visually clear that R is variable both within and between subjects. Each of the subjects presented appears to be using relatively consistent technique between trials, but even small deviations result in significant variation in the external force vector and R. Moreover, between subjects there is an even greater degree of variation, and it is clear that R is unrelated to segment length.

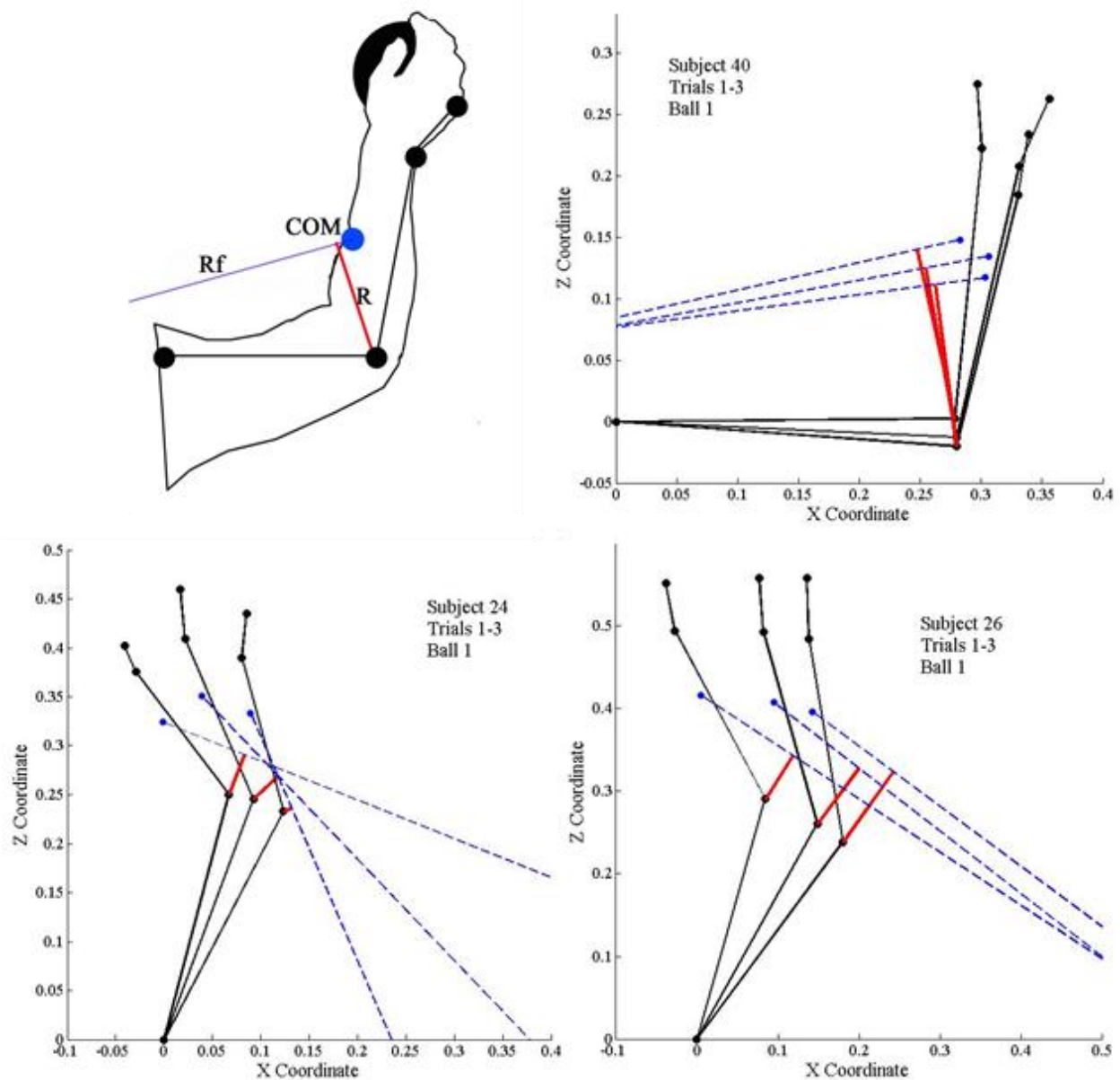


Figure 8.8 Variation in dynamic R at the elbow during throwing. Dotted blue line is the vector for the resultant force (Rf) applied to the forearm and hand at the center of mass (COM) of the forearm and hand. Red line represents R for the elbow, the perpendicular distance from the center of rotation at the elbow to the Rf.

Throwing is an example of an open chain activity, where the distal segment is free to move in space. In light of the discussion above, it is easy to see how under such circumstances the external force vector, and thus R would be highly variable, making these results less

applicable to closed chain activities, where the external force vector is relatively more constrained. However, Warrener (2011) also failed to find a correlation between static skeletal estimates of R at the hip and R measured during a closed chain activity, namely locomotion. In fact, the position of the external force vector during locomotion (the ground reaction force) appears to be variable between individuals, outweighing any potential effect of anatomical variation (Warrener, 2011). Thus, estimates of EMA from skeletal material will not be applicable under natural conditions because variation in the position of the external force vector results in variation in R within and between subjects even performing highly trained or constrained activities. In combination with the results of section I, which established that variation in EMA is not correlated with maximum joint strength, the results of this chapter do not provide support for the use of EMA to draw functional conclusions from fossil skeletons.

Chapter 9

Effective Mechanical Advantage in Paleolithic Fossil Hominins

Skeletal data were collected to estimate effective mechanical advantage (EMA) of the elbow and wrist in samples of Paleolithic hominins and recent modern humans. Previously, EMA has been estimated in skeletal specimens by comparing skeletal features that would affect the moment arm (r), sometimes in conjunction with limb segment length as a proxy for the load arm (R). Here, r and R were measured to more closely represent the living functional anatomy, and it was demonstrated in chapter 8 that skeletal measures of r are highly correlated with r measured from tendinous insertions in living individuals, at least at the elbow and for flexor carpi ulnaris at the wrist. At the elbow, R was calculated by subtracting r for the triceps from ulna length. In effect, this estimates the length of the ulna without the olecranon process, which is posterior to the center of rotation of the joint, and thus does not contribute to R . At the wrist, second metacarpal length was used for R . Despite the problems with static measures of R raised in chapter 8, there is no other skeletal method available, and this will allow the results to be placed into the context of previous research.

These data will be used to test H3: that, as compared with early and recent modern humans, Neandertals had greater EMA of the elbow and wrist. Neandertals are assumed to have had greater EMA as a result of adaptations for strength (Churchill and Rhodes, 2006), or due to a plastic response to loading, since increased loading can hypertrophy the insertion for the muscle and deflect its line of action further from the center of rotation of the joint (Trinkaus, 1983a,b; Villemeur, 1994; Maki and Trinkaus, 2011) or initiate long bone bowing (Galtés et al., 2008b). Due to limitations discussed in chapter 5, the fossil sample sizes are quite small, particularly for

the wrist. Furthermore, many specimens are not complete, requiring approximation of the missing elements, and likely adding an additional level of measurement error (see chapter 5 for how these were handled). Thus, differences between groups presented here should be considered indicative rather than definitive. In the discussion section, these results will be considered in the context of the results presented in the previous chapters.

I. EMA at the Elbow.

At the elbow, r was measured for triceps brachii (TB), brachialis (B), and biceps brachii (BB), and EMA was calculated as r/R . Raw values for all skeletal measures are found in appendix V. Samples were initially separated by sex to reveal relevant sex-specific patterns, but this drastically reduces the already small fossil sample sizes. Furthermore, the Upper Paleolithic early modern human (UPEMH) sample is only male. Two-tailed, unpaired student's t -tests and Mann-Whitney U tests were used to determine if significant differences exist between sexes for the comparative samples and the fossil samples (where sample sizes permit) consecutively. Where sample sizes were not sufficient, between-sex comparisons were made visually. Where sex-specific patterns are absent, sexes were pooled for between group comparisons to maximize sample sizes. These comparisons were made using Kruskal-Wallis tests with Bonferroni adjustments for multiple comparisons.

Functionally, EMA can be considered size independent, as its mechanical consequences are not relative to body size. However, it may also be useful to consider the sources of variation in EMA, rather than just the ratio. A high EMA value at the elbow could be due to a smaller ulna (since R is approximately equivalent to ulna length) or a larger moment arm, and these would have different implications for how the patterns in the fossil record are interpreted. Furthermore, both r and ulna length will be correlated with body size, but where there is variation in body

proportions, the relationship between ulna length and body size will differ, resulting in variation in EMA that is not body size independent. In other words, EMA may vary between samples due to size alone. Although not necessarily functionally relevant, this would have different implications for how patterns in the fossil record are interpreted. Thus, patterns of variation in R and r will be considered in addition to EMA.

Figure 9.1 compares R separated by sex across the fossil and comparative samples. As would be expected, significant differences exist in ulna length, and thus R, between males and females for both the Hamann-Todd (HTH) and Indian Knoll (IK) samples ($p < 0.001$). Although differences between males and females do not reach significance for the fossil samples, the trend is evident, and would certainly reach significance with larger samples. Thus, between-group comparisons were made within each sex. In this situation, pooling sexes might lead to erroneous results because the fossil samples are sex-biased. Kruskal-Wallis tests revealed significant differences between groups for the males ($p < 0.001$), but not for the females ($p = 0.395$). The results of the post hoc comparisons for the males are presented in table 9.1a. Elbow R is significantly greater in the Upper Paleolithic early modern human (UPEMH) sample than all other samples, with the exception of the Middle Paleolithic early modern human (MPEMH) sample. The early *Homo* (EH) specimen is intermediate between the Nean and EMH specimens. No other significant differences in R exist for these samples.

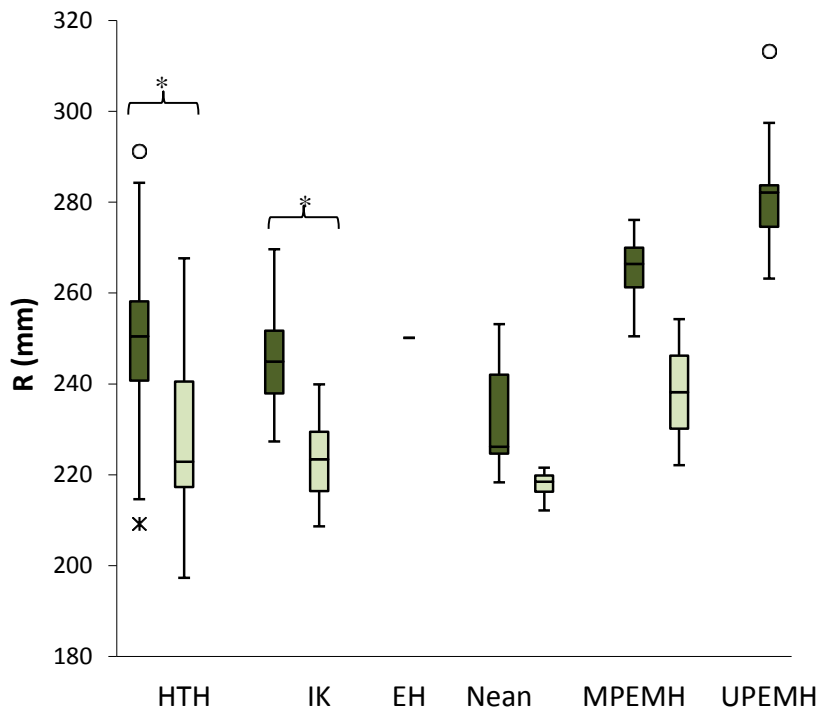


Figure 9.1 Load arm (R) at the elbow. Load arm calculated as ulna length minus r for the triceps. Dark green indicates males, light green indicates females. Abbreviations: HTH, Hamann-Todd modern humans; IK, Indian Knoll modern humans; EH, early *Homo*; Nean, Neandertal; MPEMH, Middle Paleolithic early modern human; UPEMH, Upper Paleolithic early modern human. *indicates significant difference between males and females at $\alpha < 0.05$. P-values for post hoc between group comparisons are found in table 1.

Table 9.1 Results of post hoc significance tests for inter-group differences in moment arms and EMA at the elbow.

a. Elbow R (males)	IK	Nean	MPEMH	UPEMH
HTH	>0.999	0.660	>0.999	0.007
IK		>0.999	0.311	0.002
Nean			>0.999	0.043
MPEMH				>0.999
b. r TB	IK	Nean	MPEMH	UPEMH
HTH	>0.999	<0.001	>0.999	<0.001
IK		<0.001	0.130	<0.001
Nean			0.420	>0.999
MPEMH				0.170
c. EMA TB	IK	Nean	MPEMH	UPEMH
HTH	>0.999	<0.001	>0.999	0.193
IK		<0.001	>0.999	0.025
Nean			0.278	0.196
MPEMH				>0.999
d. r B	IK	Nean	MPEMH	UPEMH
HTH	0.005	0.615	0.327	0.382
IK		0.003	0.053	0.024
Nean			>0.999	>0.999
MPEMH				>0.999

Table 9.1 cont.

e. EMA B		IK	Nea	MPEMH	UPEMH
HTH		0.026	0.015	>0.999	>0.999
IK			0.001	0.168	>0.999
Nea				>0.999	0.278
MPEMH					>0.999
f. r BB (Male)		IK	Nea	MPEMH	UPEMH
HTH		0.045	>0.999	>0.999	0.193
IK			0.109	0.617	0.381
Nea				>0.999	>0.999
MPEMH					>0.999
g. r BB (Female)		IK	Nea	MPEMH	UPEMH
HTH		0.085	>0.999	>0.999	
IK			0.744	>0.999	
Nea				>0.999	
MPEMH					
h. EMA BB (Male)		IK	Nea	MPEMH	UPEMH
HTH		0.195	0.480	>0.999	>0.999
IK			0.023	>0.999	>0.999
Nea				0.641	0.833
MPEMH					>0.999
i. EMA BB (Female)		IK	Nea	MPEMH	UPEMH
HTH		0.096	0.808	>0.999	
IK			0.543	>0.999	
Nea				>0.999	
MPEMH					

P-values include Bonferroni adjustments. Bold indicates significance at $\alpha < 0.05$. Abbreviations: TB, triceps brachii; B, brachialis; BB, biceps brachii; HTH, Hamann-Todd modern humans; IK, Indian Knoll modern humans; Nea, Neandertals; MPEMH, Middle Paleolithic early modern humans; UPEMH, Upper Paleolithic early modern humans.

Figure 9.2 compares r by sex for triceps brachii (TB) across the samples. Moment arms are significantly different between males and females for both the HTH and IK samples ($p < 0.001$). No significant differences were found between males and females for the Neandertal (Nea, $p = 0.311$) or MPEMH ($p = 0.363$) samples. Thus, to compare r between groups, sexes were pooled. A Kruskal-Wallis test revealed a significant inter-group difference for r for TB, and post hoc tests were performed to determine which groups differed (table 9.1b). Bonferroni

adjusted significant differences were found between the Nean sample and both comparative samples, but neither of the EMH samples. Similarly, the UPEMH sample was significantly different from both comparative samples. The MPEMH sample appeared to fall below the Nean and UPEMH samples, but the difference was not significant. Furthermore, the EH specimen falls well within the range of the other Paleolithic samples. Thus, for TB, the primary distinction is between the Paleolithic and modern samples.

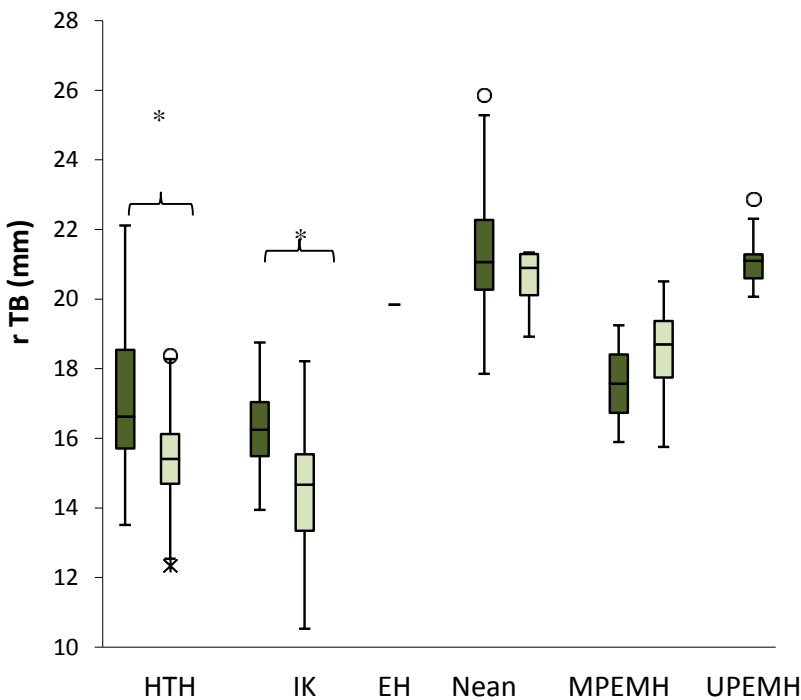


Figure 9.2 Moment arm (r) for triceps brachii (TB). See figure 1 for abbreviations.

The IK sample represents a highly active population with a high degree of sexual division of labor. In contrast, the HTH sample represents a relatively low activity level population, with little relevant division of labor between the sexes. Thus, the differences in r between males and females in these two populations probably do not represent plasticity related to subsistence behaviors or activity level. In chapter 8, it was established that r correlates with muscle aCSA, as

well as other body size measures, such as height. Thus, the sex differences observed here, and potentially some of the group differences, are likely size effects. Given this, the lack of difference between males and females in the fossil samples may be due to random variation in the small samples.

Figure 9.3 presents EMA for TB by sex across the samples. No significant differences were found between males and females for either comparative sample (HTH, $p = 0.517$; IK, $p = 0.751$), or either Paleolithic sample (Nea, $p = 0.796$; MPEMH, $p = 0.564$). Thus, males and females within each sample are similar in EMA. As noted above, EMA is not entirely size independent, specifically where variation exists in body proportions. However, it is unlikely that dramatic differences in body proportions exist between males and females within a population. Thus, the lack of difference between males and females in EMA is strongly suggestive that the differences in r were due to body size differences alone.

A Kruskal-Wallis test revealed a significant between-group effect with sexes pooled ($p < 0.001$), and table 9.1c presents the results of the post hoc comparisons. In contrast to the r values, there is a visual separation of the Neandertals as compared with all other groups, but the differences do not reach significance for the fossil samples. Although the trend does not reach significance, the EMH specimens are at the low end of the Nea range, and might reach significance with larger sample sizes. Additionally, the UPEMH sample is significantly different from the IK sample. The EH specimen falls at the low end of the Nea range, and well within the range of the EMH specimens. Thus, the main distinction in TB EMA is between the Neandertals and all other samples, although significance testing was not able to establish this conclusively.

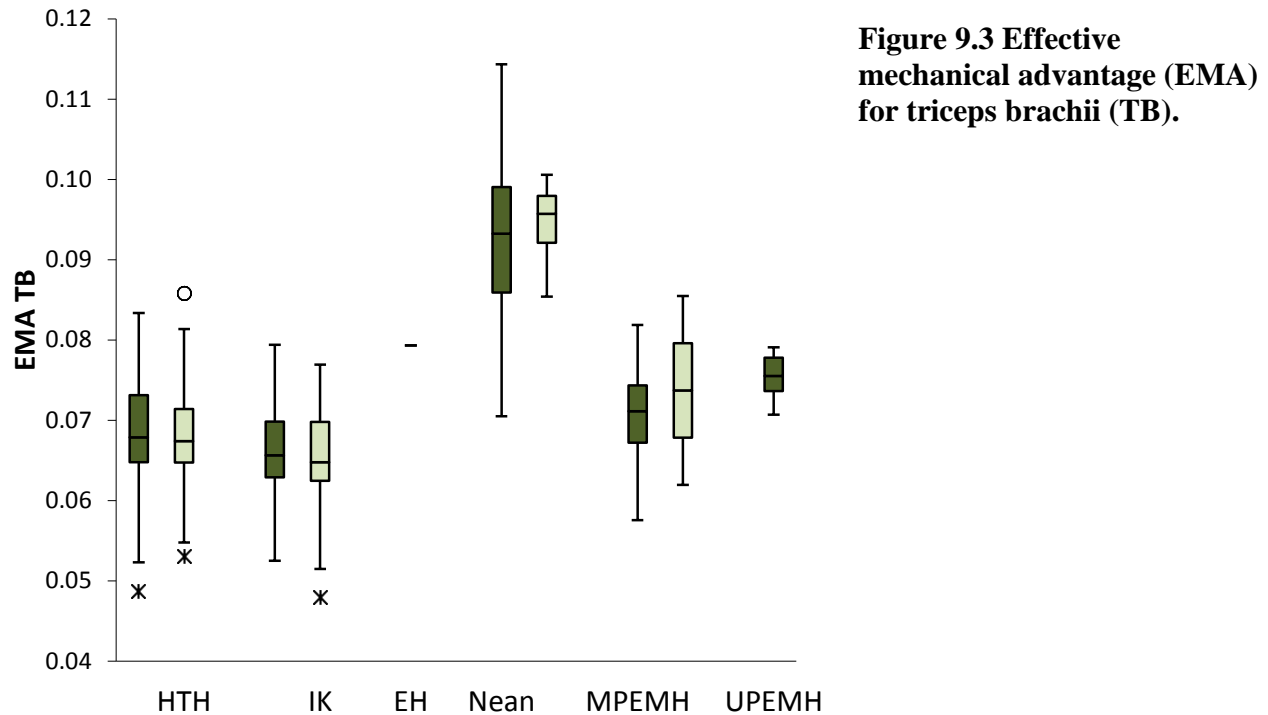
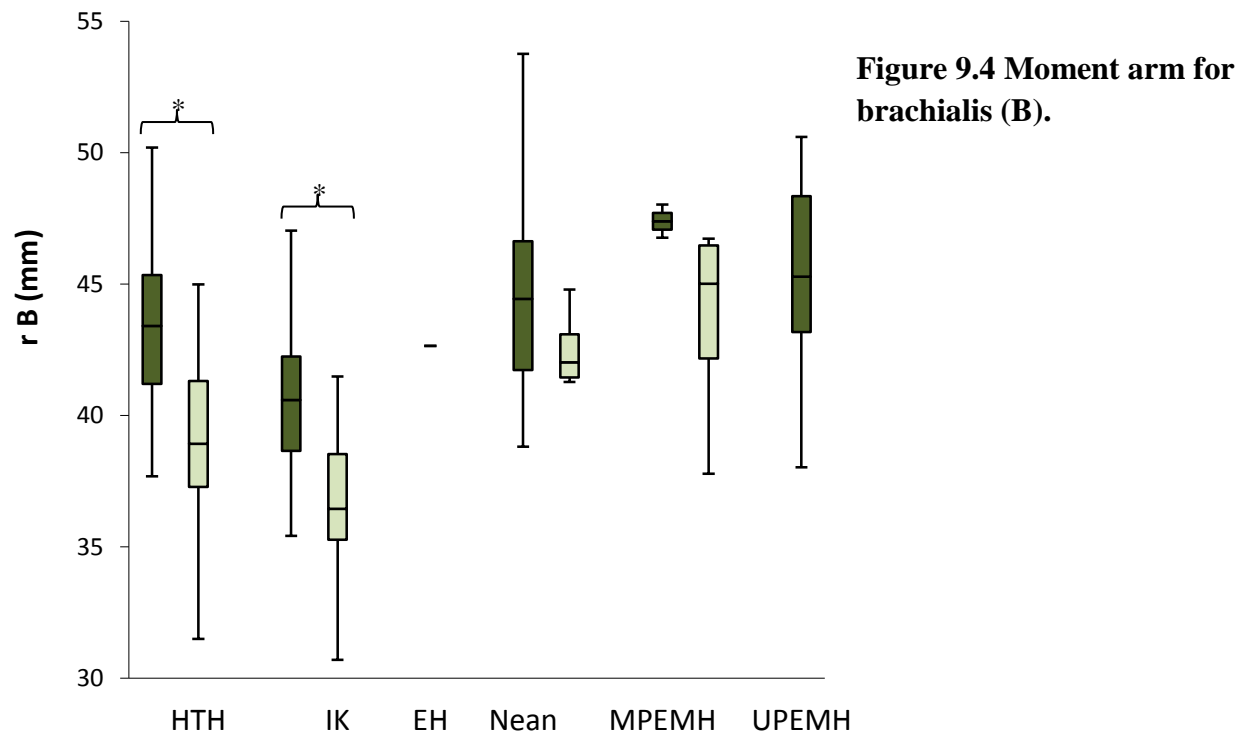


Figure 9.4 presents the results for r for brachialis (B) across all samples. Males were found to have significantly greater r for B than females for both the HTH and IK samples ($p < 0.001$). No significant differences were found between males and females for either the Nean or MPEMH samples (Nean, $p = 0.231$; MPEMH, $p = 0.198$). A significant between group effect was found for r ($p < 0.001$), and table 9.1d presents p -values for the post hoc comparisons. No significant differences exist between any fossil samples. In fact, the only significant differences are between the IK sample and all other samples (the comparison with the MPEMH sample is quite close but does not reach significance). It is unclear what might explain this pattern, but it may be partially due to smaller body size in this sample. In fact, body mass, as estimated from femoral head diameter (Ruff et al. 2005), is significantly lower in the IK sample as compared with the HTH sample ($p < 0.001$). Given that differences did not exist between the HTH and IK samples for R (approximately ulna length), this implies that ulna lengths are longer for body

mass in IK versus HTH individuals. In contrast, the fossil samples appear to be quite consistent, all falling within a similar range of variation.



The results for B EMA are presented in figure 9.5. No significant differences between the sexes are present for any sample measured (HTH, $p = 0.626$; IK, $p = 0.495$; Nean, $p = 0.302$; MPEMH, $p = 0.564$). Thus, once any potential size effects are accounted for, there is no difference in B between sexes. A Kruskal-Wallis test indicated a significant difference between groups ($p < 0.001$), and table 9.1e presents the p-values for the post hoc comparisons. The IK sample has significantly lower EMA for B than the HTH sample ($p = 0.026$). This pattern is probably not due to greater loading during life, as any plastic effects of loading should result in greater EMA for IK. Instead, this probably reflects the different body proportions between the samples. Ulna lengths are smaller for body mass in the HTH sample, thus EMA is not size independent for these samples. In fact, when scaled to body mass, B EMA is, in fact,

significantly larger in the IK sample compared with the HTH sample ($p < 0.001$). Thus, the observed differences in EMA in the comparative samples reflect, at least in part, body size differences. The Neandertal sample has significantly greater EMA than the HTH and IK samples, and trends towards greater EMA than the UPEMH sample, although this comparison is not significant. The EH and MPEMH samples fall within, but at the low end of the Nean range of variation. Thus, although not all comparisons are significant, the Nean sample trends towards greater EMA.

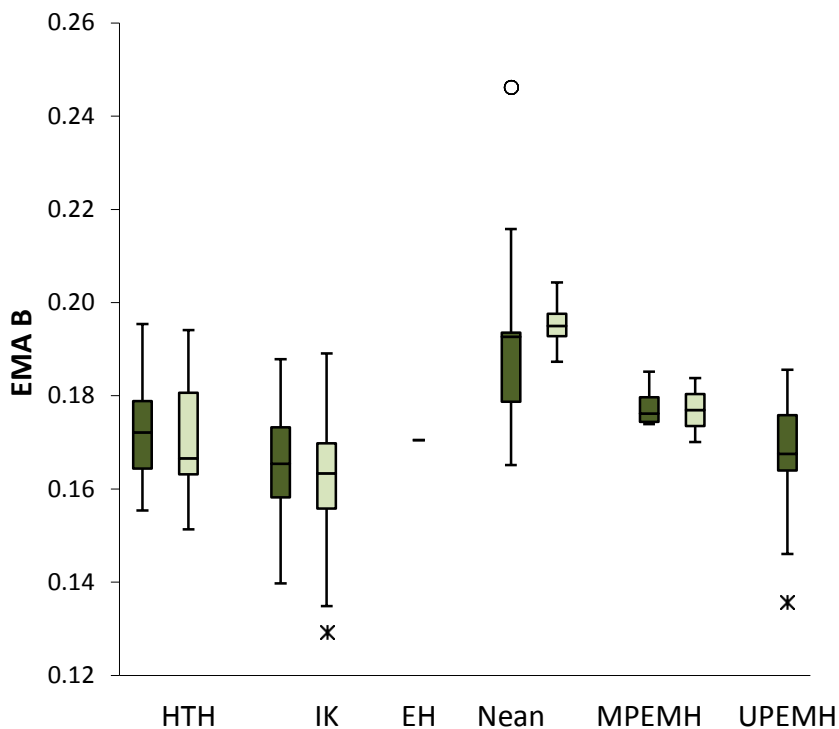


Figure 9.5 EMA for brachialis (B).

Moment arms for biceps brachii (BB) for all samples are presented in figure 9.6. As with the other moment arms at the elbow, significant size variation exists for BB between males and females of the modern human comparative samples ($p < 0.0001$ for both). In addition, significant differences exist between males and females of the MPEMH sample ($p = 0.042$), and the

Neandertal sample approaches significance ($p = 0.074$). Thus, between-group comparisons were made within each sex. For the male samples, a Kruskal-Wallis test revealed a significant difference between groups ($p = 0.004$), and the results of post hoc comparisons are found in table 9.1f. The only significant difference between any of the samples is between the HTH and IK males. As with r values for the other muscles, the IK males are smaller than HTH males, which is likely an effect of their smaller body size. None of the male fossil samples demonstrate any significant variability between groups. For the female samples, significant between group differences were indicated by a Kruskal-Wallis test ($p = 0.023$), and p -values for post hoc comparisons are found in table 9.1g. No significant differences were found between any female groups. Although the original Kruskal-Wallis test found a significant between group effect, the post hoc tests with Bonferroni adjustments are more conservative. The only groups approaching significance are the HTH and IK samples, none of the female fossil samples demonstrate any trend towards significance.

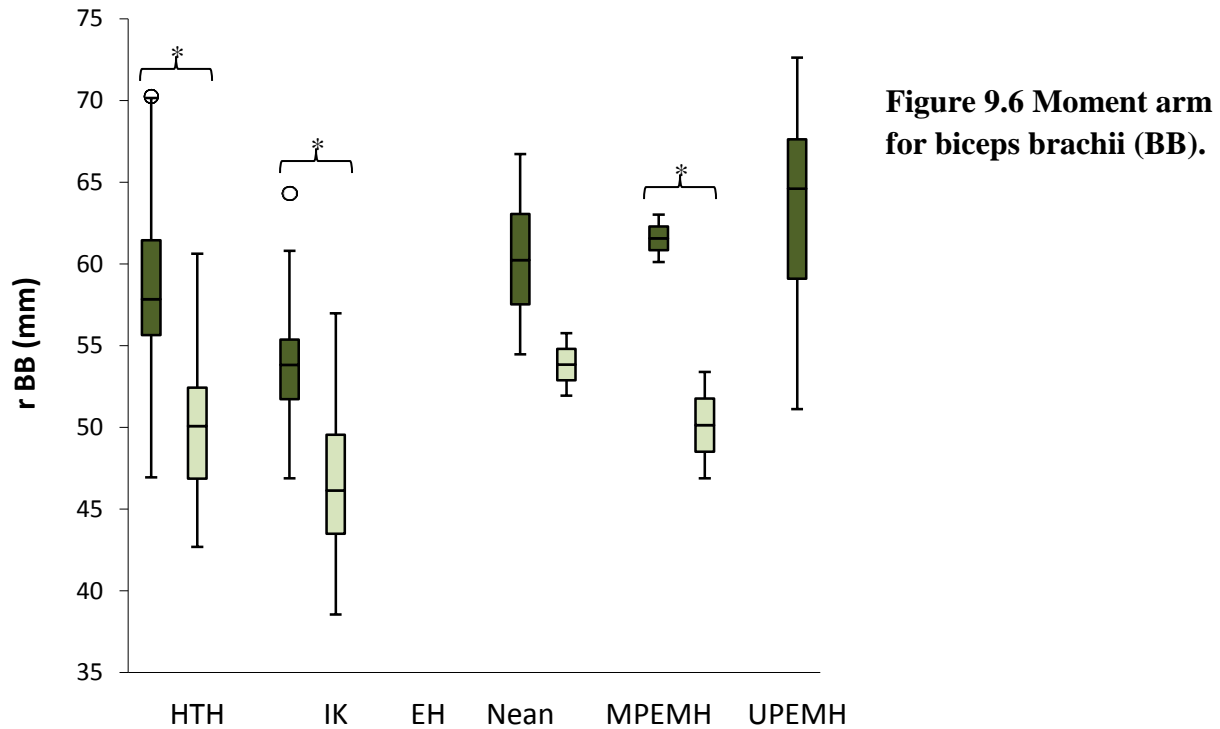
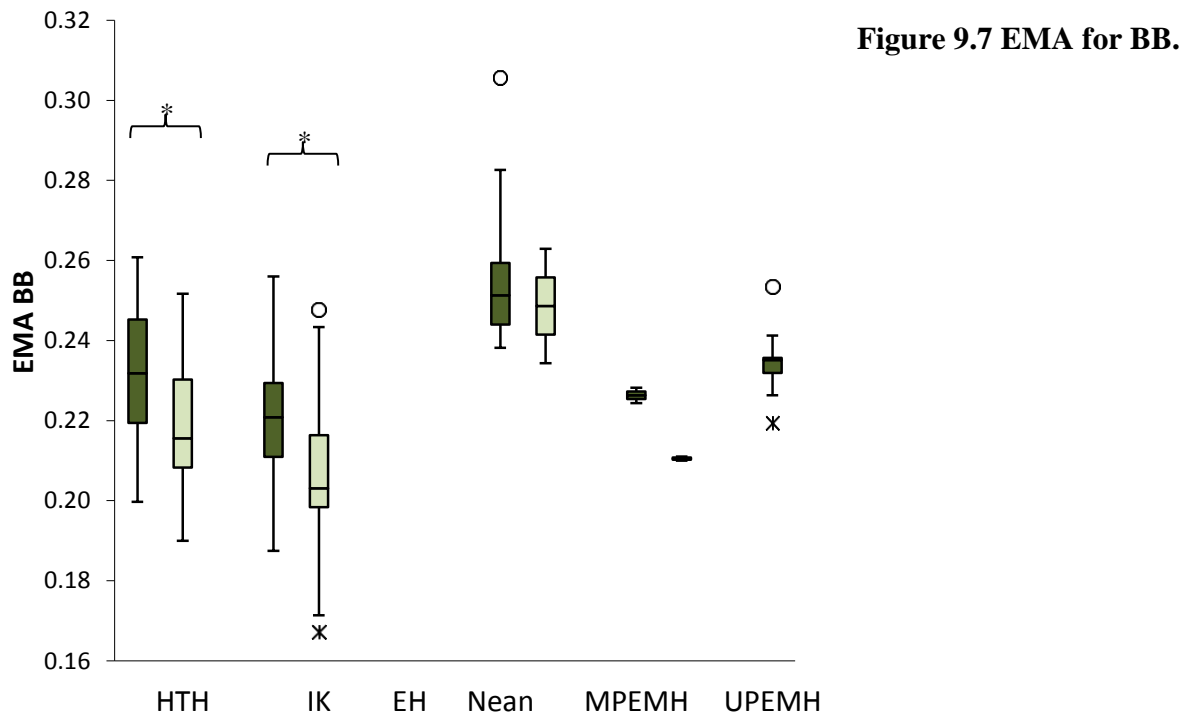


Figure 9.7 presents the EMA values for BB across groups. The sex differences in r present in the HTH and IK samples are present for EMA as well, and the MPEMH sample approaches significance (HTH, $p = 0.012$; IK, $p = 0.011$; MPEMH, $p = 0.059$), demonstrating that the effect is not merely due to variation in body size. This variation may be due to differential muscularity of BB between males and females, an interpretation which will be considered further in the discussion section. Thus, inter group comparisons were made within each sex. Kruskal-Wallis tests revealed significant differences between groups for both the males ($p = 0.015$) and females ($p = 0.016$). Post hoc comparisons between groups were performed, and associated p -values are found in table 9.1h-i. For the males, the only significant difference is between the IK and Nean samples, and for the females, no significant differences were found. This is due to the fact that the Bonferroni adjustment on the post hoc comparisons is more conservative than the original Kruskal-Wallis test. Thus, for BB EMA, the only significant

differences are between males and females of HTH and IK, and between Nean males and IK males. Although not significantly different, the Neandertal males appear to trend above all other samples, and larger sample sizes might reveal significantly greater EMA.



II. EMA at the wrist.

At the wrist, r was estimated for flexor carpi radialis (FCR), flexor carpi ulnaris (FCU), extensor carpi radialis longus and brevis (ECR) and extensor carpi ulnaris (ECU), and EMA was calculated as $r/2^{\text{nd}}$ metacarpal length. Due to the fragmentary nature of the carpal specimens and the extremely small sample sizes for the wrist, between group comparisons could not be performed within sexes, even where relevant sex specific patterns exist. Instead, results are presented visually with sexes separated, but statistical tests were performed with sexes pooled. Tests of between sex differences were performed for the comparative samples using two-tailed,

unpaired student's t-tests for independent samples, to determine the potential consequences of pooling sexes. Where sample sizes allowed (only for Nean, and only for several measures), Mann-Whitney U tests were used to test for between sex differences in the fossil samples. Between group comparisons were made using Kruskal-Wallis tests, and post hoc pairwise comparisons using Bonferroni adjustments were made where sample sizes allowed. Unfortunately, no wrist specimens were available for the EH or UPEMH samples, so between group comparisons were between the HTH, IK, Nean, and MPEMH samples.

Second metacarpal (2MC) length is presented in figure 9.8. Student's t-tests revealed significant differences between males and females for HTH ($p = 0.002$) and IK ($p < 0.001$). A similar trend of size variation was observed in the Nean and MPEMH samples, although this pattern was not significant (Nean, $p = 0.800$). Thus, pooling sexes may have resulted in a slight bias in the Nean sample (slightly increasing the mean), as this sample is male-dominated. Significant between-group differences were indicated by a Kruskal-Wallis test, and post hoc comparisons with Bonferonni adjustments were performed (table 9.2a). The IK sample was found to have significantly shorter 2MCs than the HTH and Nean samples, consistent with the smaller body sizes of this group. No significant differences were detected between the fossil samples, however the MPEMH sample appears to fall below the Neandertal sample.

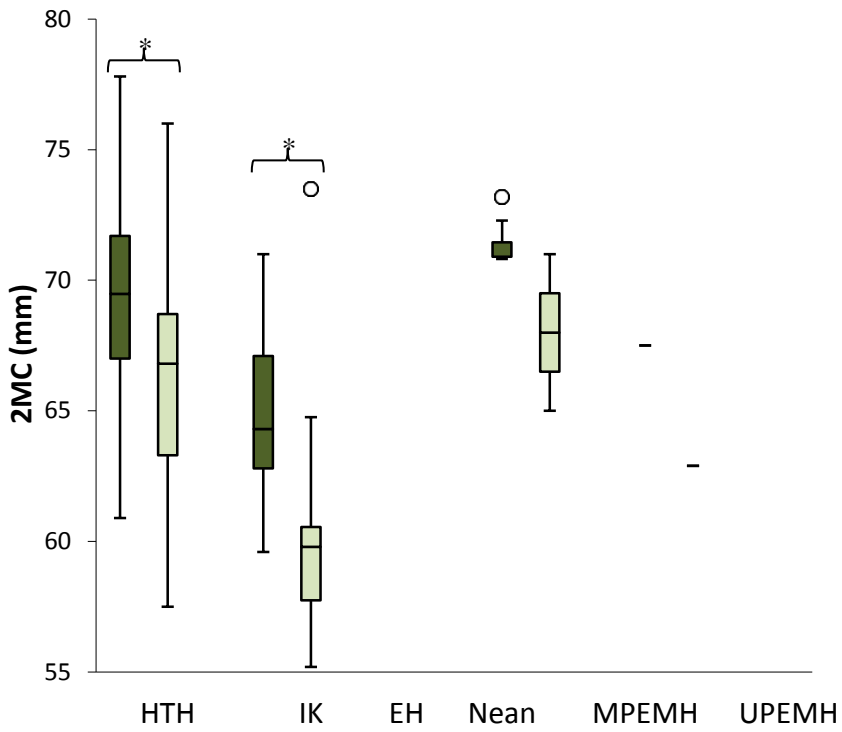


Figure 9.8 Second Metacarpal (2MC) length.

Table 9.2 Results of post hoc significance tests for the wrist.

a. 2MC Length	IK	Nea	MPEMH
HTH	< 0.001	0.687	>0.999
IK		0.003	>0.999
Nea			0.546
b. rHam FCU	IK	Nea	MPEMH
HTH	0.005	0.816	>0.999
IK		0.090	0.702
Nea			>0.999
c. r FCR	IK	Nea	MPEMH
HTH	< 0.001	>0.999	>0.999
IK		>0.999	>0.999
Nea			>0.999
d. EMA FCR	IK	Nea	MPEMH
HTH	0.102	0.600	>0.999
IK		>0.999	>0.999
Nea			>0.999
e. r ECU	IK	Nea	MPEMH
HTH	0.024	>0.999	>0.999
IK		>0.999	>0.999
Nea			>0.999
f. r ECR	IK	Nea	MPEMH
HTH	0.024	0.546	0.600
IK		0.018	0.624
Nea			0.942

P-values include Bonferroni adjustments. Bold indicates significance at $\alpha < 0.05$. Abbreviations: FCU, flexor carpi ulnaris; FCR, flexor carpi radialis; ECU, extensor carpi ulnaris; ECR, extensor carpi radialis brevis and longus. See table 1 for additional abbreviations.

The most accurate measurement of r for FCU would define the line of action (LOA) based on the maximum palmar projection of the pisiform (rPis). However, most fossil specimens do not retain a pisiform. Thus, r was measured based on the projection of the hamate (rHam) for the fossil specimens. Figure 9.9 presents the results of the least squares regression of rHam against rPis in the modern human samples. rHam explains approximately 60 % of the variation in rPis for the HTH sample (the IK sample is smaller as it retained fewer pisiforms). Thus,

estimates of r for FCU based on the hamate alone are probably sufficient to draw inferences regarding EMA for this muscle.

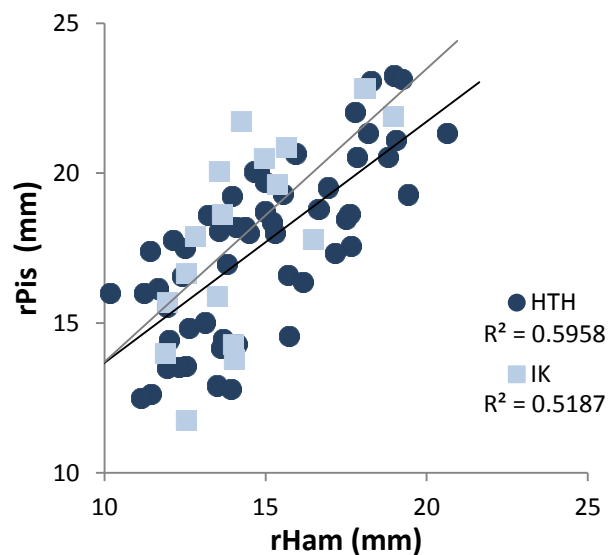


Figure 9.9 Linear regression of r for flexor carpi ulnaris (FCU) measured from the hamate (rHam) against r measured from the pisiform (rPis).

Figure 9.10 presents rHam for each group, separated by sex. Significant differences were found between males and females in the HTH ($p < 0.001$) and IK ($p = 0.033$) samples. The fossil sample sizes do not allow between-sex comparisons, but the single male specimen falls between the two female specimens. A Kruskal-Wallis test indicated a significant between-group effect ($p = 0.001$), and the results of post hoc comparisons are presented in table 9.2b. The only significant difference detected is between the HTH and IK samples, with significantly smaller rHam in the IK sample. Given the pattern of variation in the 2MC lengths, the between-sex and between-group differences in the modern samples are likely due to size variation. It would be difficult to detect significant differences in the fossil samples with the given sample sizes, but the available data do not visually suggest any differences between the fossil samples. Both fossil samples fall at the upper end of the modern human range of variation, suggesting these might be significantly larger with larger samples.

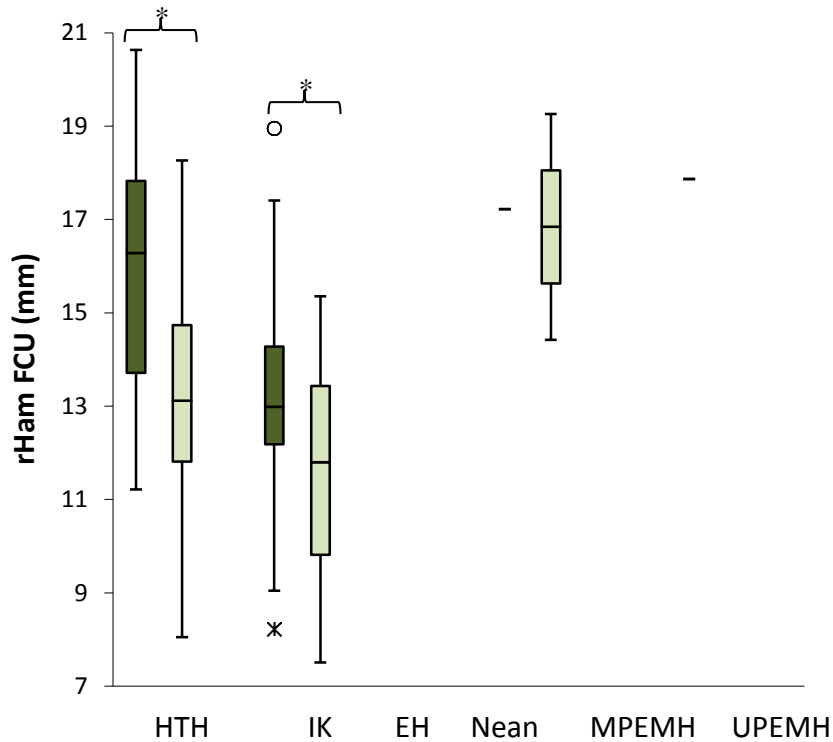


Figure 9.10 Moment arm for FCU (rHam).

EMA values for FCU are presented in figure 9.11. Student's t-tests revealed significant differences between males and females for the HTH sample ($p = 0.003$), but not the IK sample ($p = 0.375$). No significant between-sex differences are visible in the Nean sample. Visually, the HTH female sample appears to fall almost exactly in line with the male and female IK samples, with the male HTH sample above all three. In fact, the HTH males are significantly greater than the IK males ($p = 0.012$) while the females do not differ significantly ($p = 0.631$). Thus, it appears that the hamate is larger than would be expected from 2MC length in the HTH males (or vice versa). In fact, this may be due to known differences in relative index finger length between males and females (Phelps, 1952). In the HTH sample, body size scaled 2MC length is significantly smaller in females than males ($p < 0.001$), but the same is not true in the IK sample ($p = 0.460$). It is interesting that 2MC length reflects sex in the HTH but not IK sample, and it is unclear why this would be the case. Yet, when scaled to body size, no significant differences

exist between the HTH males and HTH females ($p = 0.651$), or IK males ($p = 0.445$). Thus, the observed pattern in EMA for FCU in the comparative samples is reflective of body size variation. With sexes pooled, no significant differences are present between any group ($p = 0.064$), although the fossil samples remain on the upper end of the modern human range of variation.

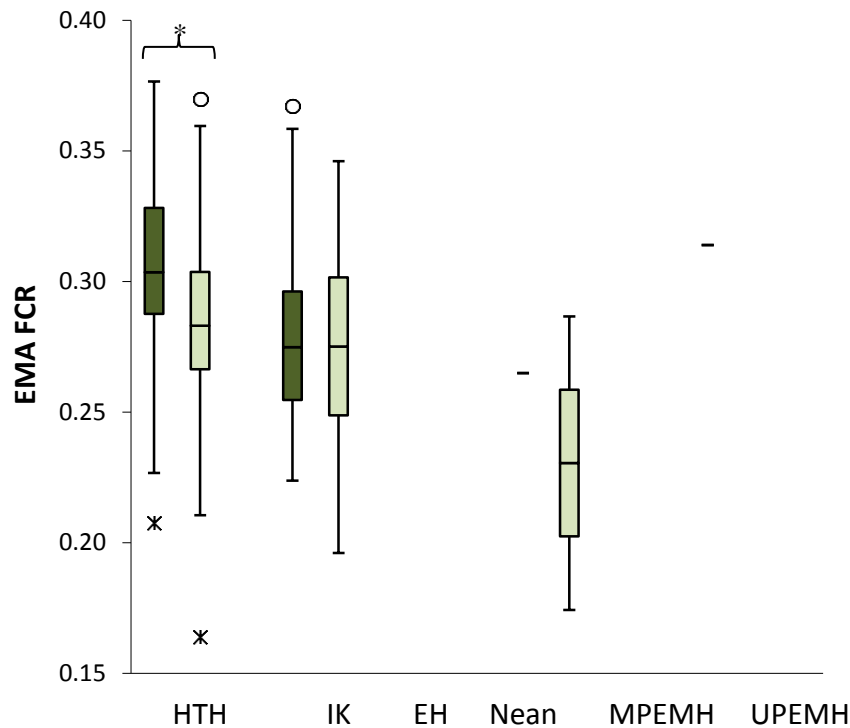


Figure 9.11 EMA for FCU (from rHam).

Figure 9.12 presents the moment arm results for FCR. Sex differences are present in the HTH ($p < 0.001$) and IK ($p = 0.010$) samples. No differences between males and females are suggested by the Neandertal data. A Kruskal-Wallis test revealed significant between-group differences ($p < 0.001$), and the results of the post hoc comparisons are presented in table 9.1c. The sole difference between groups is between the HTH and IK sample. As with r for FCU, the between-sex and between group differences for HTH and IK are likely due to size variation. In

contrast to *r* for FCU, however, the fossil samples appear more similar to the IK sample than the HTH sample. It is unclear if this pattern would remain with larger samples.

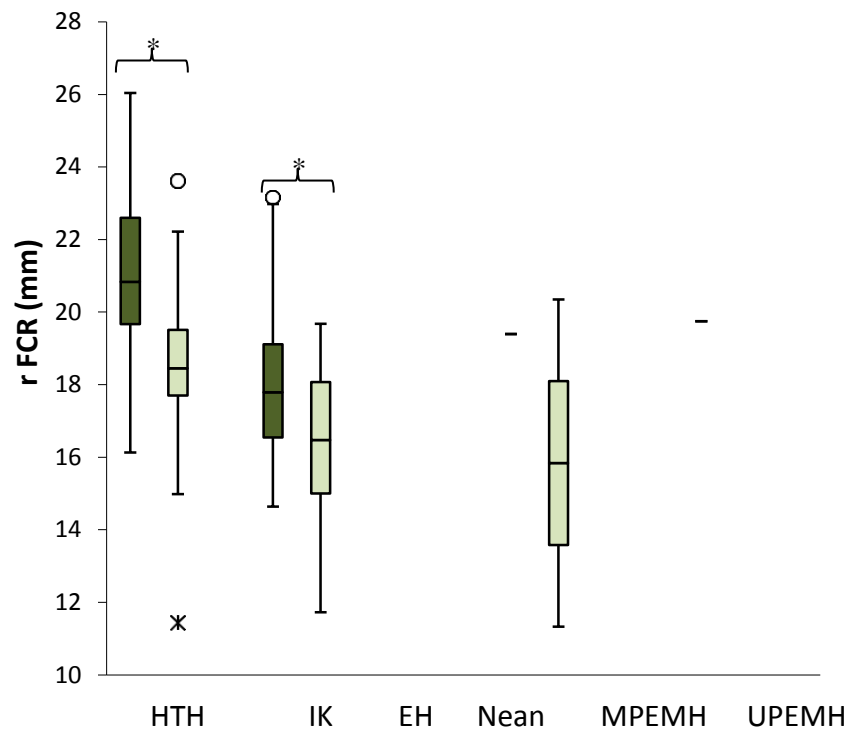


Figure 9.12 Moment arm for flexor carpi radialis (FCR).

EMA for FCR is presented in figure 9.13. As with EMA for FCR, males from the HTH sample appear to have slightly larger EMA than females of this group, but males are not significantly greater for either the HTH ($p = 0.070$) or IK ($p = 0.670$) sample. There is no indication of significant sex differences in the Neandertal sample either. Although a Kruskal-Wallis test indicated a between group effect ($p = 0.035$), more conservative post hoc tests with Bonferroni adjustments did not detect significant differences between groups. The only groups approaching significance were the HTH and IK samples. Although not significant, the Nean sample, particularly the females, appears to fall at the low end of the range of variation as compared with all other samples. Thus, the Neandertals might, in fact, have lower EMA of the FCR musculature than other human groups.

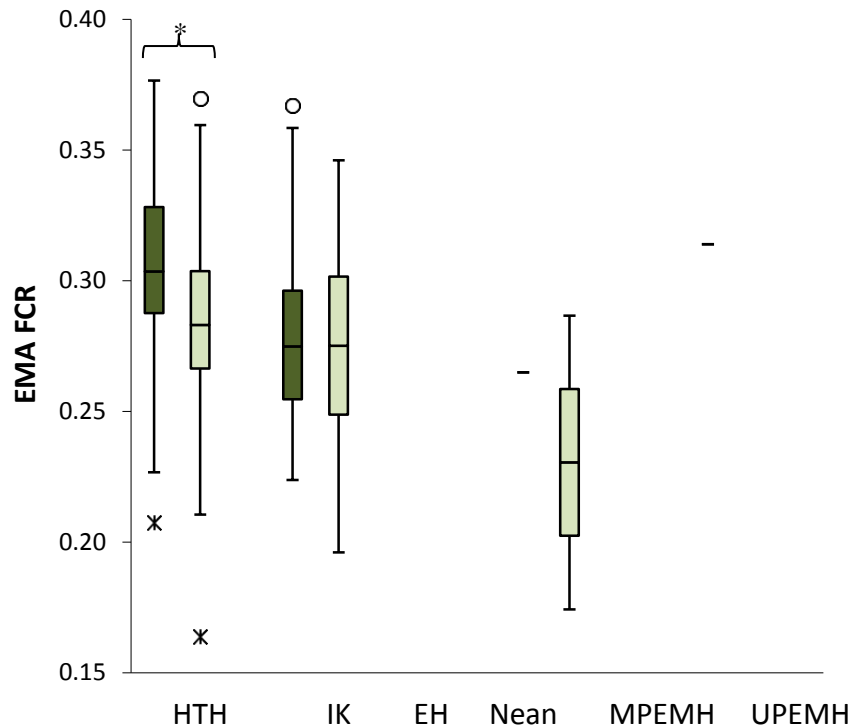


Figure 9.13 EMA for FCR.

The moment arm for ECU is presented in figure 9.14. T-tests revealed significant differences between males and females for HTH ($p < 0.001$) and IK ($p = 0.001$), but a Mann-Whitney U test did not indicate a significant difference between males and females for Nean ($p = 0.667$). Although too small for significance testing, the MPEMH male and female are quite different from one another, at the extremes of the modern human range of variation. Thus, there is likely variation in r for ECU between the sexes, at least in part due to size variation. With sexes pooled, there are significant differences among groups ($p = 0.041$), and post hoc tests indicated a significant difference between the HTH and IK samples (table 9.1e). Visually, the Neandertal and MPEMH sample appear to fall within the modern human range, although the two MPEMH individuals are at opposite ends of the range.

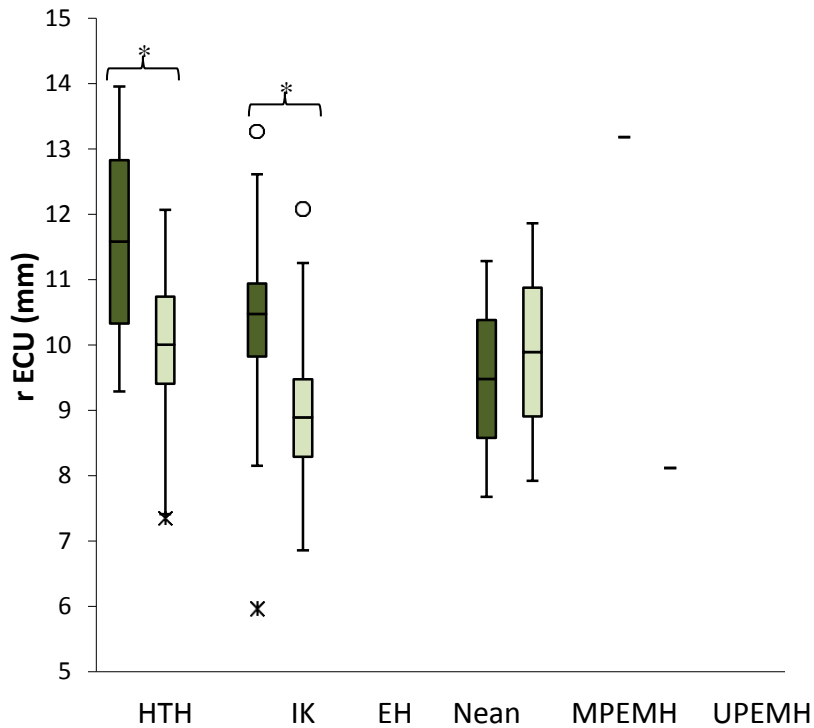


Figure 9.14 Moment arm for extensor carpi ulnaris (ECU).

EMA for ECU was compared between groups, and the results are presented in figure 9.15. The males of the HTH sample are significantly larger than the females of this group ($p = 0.007$), while the IK males and females are not significantly different ($p = 0.316$). As with EMA for the flexors, this is due to differential 2MC length between males and females in the HTH sample. A Mann-Whitney U test did not indicate significant differences between the Nean males and females, and these appear very similar for ECU EMA. As with r , the MPEMH male and female remain quite far apart, at the extremes of the modern human range. No between group effect was detected with a Kruskal-Wallis test ($p = 0.647$), however the Nean males appear lower than the males of all other samples. As there are only two specimens, this may simply be random variation, or the Nean males may, in fact, have lower EMA for ECU.

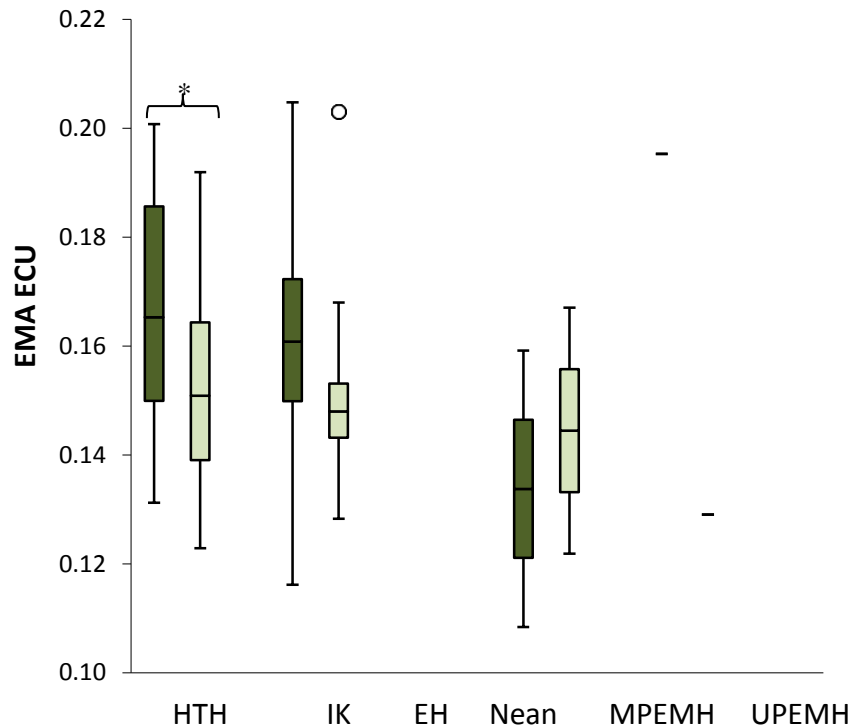


Figure 9.15 EMA for ECU.

Figure 9.16 presents the results for r for ECR. Males of HTH and IK have significantly greater r for ECR than the females of each group (HTH, $p < 0.001$; IK, $p = 0.002$). The Nean males and females are not significantly different ($p = 0.439$), although the males appear slightly elevated as compared with the females. With sexes pooled, a significant difference was detected among the groups ($p = 0.001$), and post hoc comparisons were performed (table 9.2f). The IK sample was found to have significantly lower r for ECR than both the HTH and Nean samples. No other significant differences exist. Although significance tests are not likely to reveal differences given the sample sizes, the Nean female sample falls at the upper end of the HTH female sample, while the males are comparable. This is suggestive that the Nean females may be more similar to males than in the modern human sample. The single MPEMH female specimen falls at the low end of the HTH and IK range, suggesting that MPEMH females may have relatively small r for ECR.

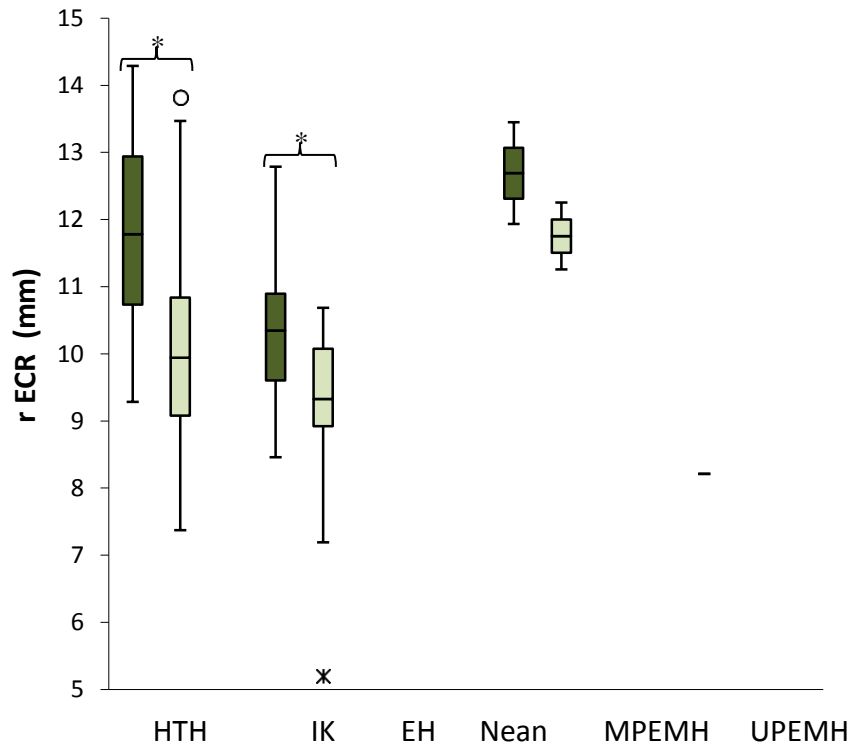


Figure 9.16 Moment arm for extensor carpi radialis longus and brevis (ECR).

EMA results for ECR are presented in figure 9.17. As with EMA for the other muscles, the males from HTH are significantly greater than the females of this group ($p = 0.009$), but the males and females from IK are comparable ($p = 0.447$). Visually, the Nean males and females appear very similar. With sexes pooled, no significant between-group effect was observed with a Kruskal-Wallis test ($p = 0.156$). The Nean males and females appear to fall well within the range of variation for the HTH males, again suggesting that the Nean females may be more comparable to the male than the female modern humans with respect to ECR. The single MPEMH specimen remains at the low end of the female modern human range of variation. It is unclear if this represents a pattern of low EMA for ECR in the MPEMH sample (or just MPEMH females), or if this single specimen is unusual.

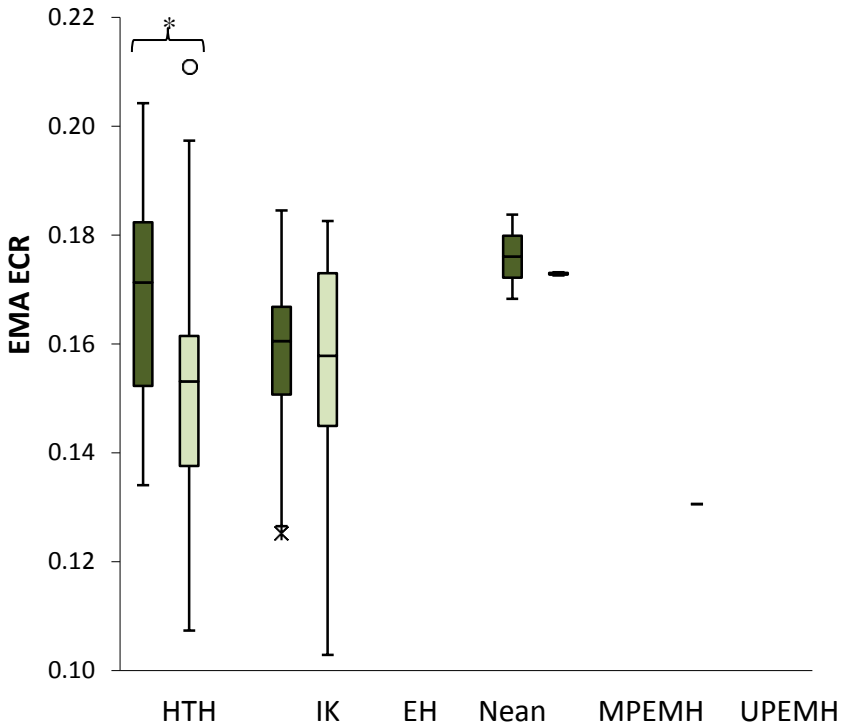


Figure 9.17 EMA for ECR.

Discussion.

1. *The elbow.*

In summary, at the elbow, there are no significant differences among any of the fossil samples for r for any muscle. With the exception of the MPEMH sample, which appears to have lower r for TB than the other fossil samples (but not significantly so), the fossil samples are remarkably consistent. In contrast, Neandertals demonstrate a trend towards greater EMA for all muscle groups, but the trend is not significant. It would likely be significant with larger sample sizes. This is consistent with Churchill and Rhodes (2006), who found greater triceps, biceps and brachialis EMA in Neandertals as compared with all early and recent modern humans sampled (with the exception of MPEMH for brachialis). Additionally, although the difference was only significant for the UPEMH sample, Neandertals had lower R values (shorter ulnae) than the other fossil samples. Combined with the similar r values across samples, this indicates that

differences in EMA between the Nean sample and the other fossil samples are due to variation in ulna length, not moment arms. Churchill and Rhodes (2006) do not provide moment arms for comparison across groups to confirm if this pattern is consistent with moment arms measured there.

The similarity in TB and B EMA at the elbow between males and females for the HTH and IK samples, and the pattern of variation in EMA between these samples further supports that the raw EMA values for these muscles are not indicative of habitual loading. As discussed in chapter 4 (II.2), moment arms can increase with habitual loading (particularly during development) by deflecting the muscle's insertion farther from the center of rotation (Trinkaus 1983a,b; Villemeur, 1994; Maki and Trinkaus, 2011) or by initiating long bone bowing (Galtés et al., 2008b). Furthermore, it was demonstrated in chapter 8 that moment arms are correlated with muscle size independent of body size, demonstrating plasticity in the moment arm as a result of muscle size. The IK sample (particularly males) is expected to have experienced far greater habitual load levels than the HTH sample, but no differences exist in EMA for TB, and EMA is in fact lower for B and BB (only males). Rather, the raw EMA values are not size independent, such that the smaller body size of the IK sample results in lower EMA for this group. Likewise, raw EMA values should not be used to infer habitual loading in the fossil samples either.

The variation in EMA between Neandertals and the other Paleolithic samples is due to variation in ulna length, and ulna length in these groups at the population level is primarily a function of body size and proportions, as influenced by adaptation to climatic conditions. Both upper and lower limb segments are shorter in Neandertals compared with MP and UP early modern humans (Ruff, 1994; Holliday, 1997a, b), but the difference is more extreme with distal

limb segments (Holliday, 1997a, b, 1999). This pattern results in low brachial indices (ulna length relative to humerus length). Thus, whatever the functional implications, the greater EMA in the Neandertal sample is due to variation in body proportions, rather than a plastic response to loading.

The fact that greater EMA in Neandertal elbows is a consequence of variation in body proportions has important implications regarding Neandertal adaptation. Patterns of increased EMA have been used to argue that Neandertals were adapted for greater force producing potential compared with early and recent modern humans (Churchill and Rhodes, 2006). However, these results indicate that at least for flexion and extension of the elbow, greater EMA does not reflect selection for strength. Rather, shorter ulnae, as a result of cold adaptation, have the unrelated effect of raising the ratio of r/R in the Neandertal sample. Ultimately, this group may be capable of greater strength as a result of their shorter ulnae (but see below), however it should not be interpreted as an adaptation.

For BB EMA, significant differences exist between sexes for the HTH, IK, and MPEMH samples. Given that the relationships between body size and ulna length and body size and r should be consistent between males and females of a given sample (i.e., body proportions should scale similarly), this pattern of variation is likely due to a plastic response to loading. Increased muscularity of BB in males could result in hypertrophy of the bony insertion for BB on the radius, potentially increasing its maximum distance from the COR. Thus, the pattern of variation in BB EMA between males and females may represent greater relative muscularity in MPEMH, HTH, and IK males. Interestingly, males and females are more similar in the Nean sample, although the sample sizes are too small to determine if this is a true pattern or just random variation.

2. *The wrist.*

At the wrist, no significant differences exist between the available fossil samples (Neanderthal and MPEMH) for r or EMA for any muscle, although the sample sizes are too small to expect significant results in most cases. Visually, the Neanderthal and MPEMH specimens appear comparable, with the exception of ECR. Both r and EMA are very small in the single MPEMH specimen, with respect to all other samples. As it is only a single specimen, however, it is impossible to assess whether this is representative. With respect to the comparative samples, the Neanderthal and MPEMH moment arm values fall within the recent modern human range of variation for all muscles. Thus, as at the elbow, it does not appear from these data that differences in moment arms exist between fossil and recent humans at the wrist. Although not significant, the Neanderthal EMA values for FCR (particularly females) and ECU (particularly males) were slightly beyond the recent modern human range of variation. This is suggestive that variation might exist in EMA for these muscles with larger sample sizes. However, in both cases the Neanderthal values are low relative to the other samples rather than higher, as expected.

The fact that Neanderthal moment arms at the wrist are not significantly greater than early and recent modern human samples is surprising in the context of previous research. Neanderthals are known to have had large palmar tuberosities of the carpals, which provide insertion for the wrist flexors (Trinkaus 1983a, b; Villemeur, 1994). These have been assumed to have the effect of increasing the moment arms for FCU or FCR by moving the line of action for the muscle farther from the center of rotation. Yet, Neanderthal r values for FCR are at the low end of the modern human range of variation, indicating that the greater palmar tuberosity of the trapezium observed elsewhere does not translate to a larger r value.

This demonstrates the complex anatomy of the carpals, where small changes in one aspect of the anatomy may be offset by changes elsewhere. Specifically, since FCR was measured with the capitate, trapezium, scaphoid and trapezoid articulated, small changes in how these bones relate to one another will result in variation in r . Furthermore, the COR was defined as the head of the capitate, such that differences in capitate morphology will strongly affect r . Although this method may not have perfectly captured r , it demonstrates the numerous sources of variation in r , which likely outweigh any pattern of variation in the length of the palmar tuberosity of the trapezium. Alternately, it is possible that the previous measures of r have overestimated differences between samples due to the difficulties of adequately scaling such measurements. In either case, these results indicate that caution should be used when drawing conclusions about EMA from a single skeletal dimension.

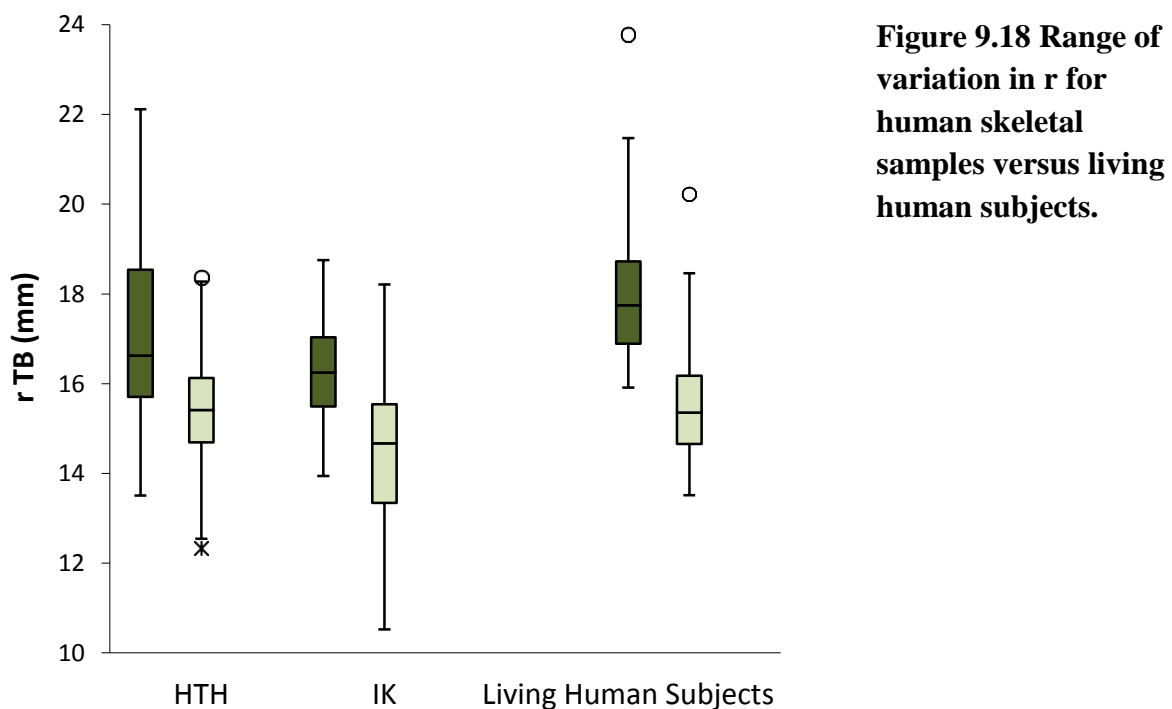
The data presented above provide cautious support for the hypothesis that Neandertals have greater EMA of the elbow, and hint at greater EMA for FCU and ECR at the wrist. Given these results, it is necessary to consider the functional and behavioral implications of this pattern in the context of the results of the previous chapters. It was hypothesized that greater EMA in Neandertals would have had functional implications for strength and throwing performance. However, in chapter 7, it was demonstrated that EMA of the elbow and wrist do not contribute to throwing velocity. Variation in EMA between subjects has no bearing on the ultimate velocity of the thrown object. In fact, the elbow and wrist do not contribute directly to throwing performance at all, leaving little room for EMA to have an important effect.

Furthermore, the results of chapter 8 demonstrate that the use of the distal limb segment length as R is invalid in most situations. The true load arm was measured during throwing, and there was no correlation between R during throwing and distal segment length for either the

elbow or wrist. Rather, the true load arm varies greatly between trials within and between subjects, overwhelming any effect of anatomical variation. This will be true for most natural behaviors. Given that there is no effective method for estimating R in skeletal specimens besides using distal limb segment length, the estimates of EMA for the fossil samples provided here would not be relevant to living conditions, except under very specific circumstances. Moreover, it was demonstrated in chapter 8 that even under the strict conditions where R is approximately equal to the length of the distal segment, EMA does not correlate with isometric force production. EMA was not correlated with the strength of the flexors or extensors for the elbow or wrist. This is partially due to the fact that r is correlated with muscle aCSA, independent of height (as a general measure of body size), making r an uninformative measure. Likewise, there is a great degree of variation in the neural control of muscle activation, overwhelming any (apparently minor) effects of anatomy on strength. Thus, EMA does not provide sufficient information about strength to be a useful measure in the fossil record.

An important consideration here is whether the results of chapters 7 and 8 can be applied to fossil hominins, given the potentially limited range of variation present in modern humans compared with other populations or species. With respect to EMA, it is possible that there is insufficient variation present in r in modern humans as a group, or in this sample of modern humans, to observe a pattern that would exist between fossil populations or species. Certainly, the principles of lever mechanics must affect joint function at some scale. Exactly what magnitude of difference in EMA is necessary to obtain an observable effect on torque is as yet unknown, and will require further research. However, for these purposes it is sufficient to say that moment arms would not have had any functional effect on the groups examined. Moment arms for all fossil samples fall essentially within the range of modern human variation, and the

modern skeletal samples display a comparable range of variation as the living human subjects. To demonstrate this point, figure 9.18 presents the moment arm values for r for TB (as representative of all muscles) for the human skeletal samples as compared with the living human subjects. The magnitude and range of variation in the living subjects falls in line with the fossil samples. Thus, the principles demonstrated in chapters 7 and 8 are applicable to the Paleolithic hominins studied here. Moreover, with respect to fossil samples that might fall outside the range of modern human variation, it is still not possible to accurately assess or interpret EMA, as there is no meaningful way to measure R .



In total, the results of chapters 7 and 8 render the results of this chapter of very little use. Even though Neandertals appear to have had greater r relative to ulna length, this is not relevant to any known behaviors. Even if EMA could accurately be measured in fossil specimens it does not matter to throwing performance, as there is no correlation between EMA and throwing

velocity, and it is not relevant to strength as the variation in other factors such as muscle recruitment are far greater, overwhelming any effect of variation in EMA. Thus, variation in r or EMA should not be used to infer strength or throwing performance in fossil hominins.

Furthermore, the assertion made elsewhere that Neandertals would have been deficient throwers as a result of greater EMA (Churchill and Rhodes, 2006) must be rejected. Similarly, there is no evidence that Neandertals would have been capable of greater force production as a result of variation in moment arms or EMA. If they were stronger, it can only be due to greater muscularity or recruitment.

Chapter 10

Conclusions

The purpose of this dissertation has been to 1) demonstrate the biomechanics of spear throwing, independently and in comparison with ball throwing, 2) examine the morphological and anatomical correlates of spear and ball throwing to demonstrate which hominin traits may reflect or influence throwing performance, 3) empirically test the biomechanical assumptions regarding the relationship between effective mechanical advantage (EMA) and joint performance, and demonstrate its relevance and measurability in the fossil record, and 4) examine whether patterns of variation in EMA exist in the fossil record that would be relevant to throwing performance. Each of these sections has independent implications, and taken as a whole they have the potential to provide valuable insight regarding the functional morphology and adaptation of Paleolithic fossil hominins. In this chapter, the results and important conclusions of each of the previous chapters will be discussed separately, and then integrated so as to consider the implications of the results as a whole.

I. The biomechanics of spear and ball throwing.

In chapter 6, the kinetics and kinematics of ball and spear throwing were demonstrated and compared. A primary goal of this chapter was to determine how spear throwing differs from ball throwing, in order to clarify whether and how the existing literature on ball throwing can be applied to spear throwing, and to establish the basic biomechanical principles relevant for spear throwing. Additionally, the kinetic and kinematic effects of throwing objects of increasing mass were investigated. Given the large degree of variation in projectile mass observed across the

Paleolithic, this is valuable in establishing the relative pros and cons of choosing various objects to throw.

The results presented demonstrate that the contribution of the legs and torso to a spear throw are comparable in magnitude to that of a ball throw. Although significant differences were observed in the velocity of the hip on the dominant side (RAxis, representing the contribution of the legs) between ball and spear throws, these were likely due to the constrained laboratory space, not some aspect of throwing technique. Furthermore, the velocity of the dominant shoulder (RShoulder) did not differ significantly between ball and spear throws, demonstrating that in total the contribution of the legs and torso was quite similar. In contrast, the contribution of the arm to the throw differs significantly between ball and spear throwing. At the shoulder, internal rotation angular velocity (ω) is significantly and considerably smaller for spear throws. This is very likely due to the shape and positioning of the spear in space. When throwing a spear, the subject is constrained to a very narrow range of motion for internal rotation, in order to maintain the spear at an appropriate angle relative to the ground. This does not allow the shoulder to reach the very high internal rotation ω observed with ball throwing, and significantly limits the maximum linear velocity achieved by the spear.

This conclusion is highly important for researchers interested in throwing during the Paleolithic, as it implies that the literature on the shoulder during ball throwing is probably of limited value to spear throwing. Ball throwing is characterized by extremely high internal rotation ω and torque (Meister, 2000), and these have been implicated in high incidences of shoulder injuries in throwing athletes (Atwater, 1979; Jobe, 1979; Cofield and Simonet, 1984). The same is not likely to be true for spear throwing, and it is interesting to note that if the human shoulder reflects adaptations for throwing, it would be for spear throwing, not ball throwing.

Such high incidences of shoulder injuries might well reflect the fact that the shoulder is not adapted for such large internal rotation ω and torques.

A number of researchers have considered the shape of the glenoid fossa in the context of throwing (Churchill and Trinkaus, 1990; Trinkaus, 2008; Churchill and Rhodes, 2009), based on the assumption that the shoulder experiences large joint reaction forces during throwing. It has been suggested that the relative breadth of the glenoid fossa may reflect adaptation for throwing, for example to protect against osteoarthritis (Churchill and Trinkaus, 1990; Trinkaus, 2008; Churchill and Rhodes, 2009). Similarly, humeral retroversion angles have been argued to reflect habitual throwing (or lack thereof) in the fossil record, as modern throwing athletes develop reduced retroversion angles (Crockett, 2002; Osbahr, 2002), and retroversion has functional implications for external rotation range of motion (Roach et al., 2012).

Specifically, it is noted that Neandertals and EUP early modern humans have dorso-ventrally narrow glenoid fossae, and this has been taken to represent a lesser frequency of throwing activities prior to the MUP (Trinkaus, 2008; Churchill and Rhodes, 2009). Furthermore, Neandertals do not demonstrate a predictable pattern of variation between dominant and non-dominant limbs and between males and females for humeral retroversion angle, and this has been used to argue that throwing was not habitual in this group (Rhodes and Churchill, 2009). The results presented here, that internal rotation range of motion, angular velocity, and torque are extremely constrained during spear throwing, strongly suggest a reassessment of the relevance of glenoid fossa shape and humeral retroversion angle for spear throwing. It is unlikely that the glenoid fossa experienced selection or remodeling in response to spear throwing, as it does not produce large internal rotation torques or make use of large

internal rotation ranges of motion. Thus, the variation in these traits between groups should not be used to argue for a lack of habitual throwing in Neandertals (or any other group).

As a result of the reduced ω achieved at the shoulder, as well as similar differences in the elbow and wrist due to the limitations imposed by the positioning of the spear, the ultimate velocities achieved during spear throwing were less than that during ball throwing. However, the kinetic energies (K_e) of the spear throws were in fact comparable to or larger than the ball throws, as a result of the larger mass of the objects. This pattern holds with respect to variation in object mass within an object type as well. With heavier objects, the velocity of the throw is reduced, but this is more than compensated for in terms of K_e by the additional mass. Given that the distance and penetration of the throw is a function of the K_e of the object at release, this demonstrates a clear benefit to throwing heavier objects, at least within the range of masses tested.

These results have important implications for the interpretation of projectile sizes in the fossil record. The spears tested ranged from ≈ 0.4 to 1.4 kg, and ethnographically known throwing spears range from ≈ 0.11 to 0.45 kg (Oakley, 1977; Hughes, 1998). Although exact masses are not available, some of the earliest known spears appear to be significantly larger than any ethnographically known throwing spears (Movius, 1950; Oakley et al., 1977; Thieme, 1997, 2007), and this has been used as evidence that these early objects were not thrown but thrust (Schmitt et al., 2003, Shea, 2006). Yet, the results presented here demonstrate that rather than being a detriment, heavy spears would have been beneficial for throwing performance. Subjects in this study were able to successfully throw objects much heavier than ethnographic spears, and in fact imparted 57% more energy to the heaviest spear relative to a spear within the range of ethnographic spears. Thus, there is no reason to conclude based on their size that these early

spears were not thrown. Instead, it may be that the small size of modern spears reflects some other factor, such as efficient use of resources, a desire to minimize the weight of carried tools, or smaller prey size.

II. Throwing performance and anatomy.

Chapter 7 explored the anatomical and morphological correlates of ball and spear throwing performance. It was investigated whether body mass, height, segment lengths and breadths, muscle sizes and mechanical advantage (EMA) are correlated with ball and spear K_e at release. The anatomical and morphological variables that determine the leg's and torso's contributions to the throw are consistent for ball and spear throwing. Either height or bi-acromion breadth (alternately for different objects) best predict the body's contribution to the throw, although these two factors are highly correlated with each other, leaving it unclear which is primary. Other aspects of leg and torso morphology did not reach significance in explaining ball or spear K_e , but were important in predicting each joint's individual contribution to the throw. Leg length (through its effect on stride length) and musculature significantly predict the legs contribution to the throw, and torso strength and bi-acromion breadth significantly predict the torso's contribution to the throw. Thus, for ball and spear throwing, the magnitude of the contribution of the body (legs and torso) to the throw is comparable (section I above) and the anatomy has comparable effects on performance.

With respect to the arm's contribution to the throw, no aspect of arm anatomy or morphology was significantly and independently correlated with the K_e of the thrown object. However, when the joints were considered independently, upper arm length was a significant predictor of the shoulder's contribution to the throw for both ball and spear throwing. Contrary to expectations, forearm length, hand length, elbow and wrist musculature, and mechanical

advantage of the elbow and wrist were not (causally) significantly correlated with any measure of performance for ball or spear throwing. The musculature of the shoulder is likely predictive of the shoulder's contribution to the throw for ball throwing, but it was not measured directly here. Thus, in terms of the arm's contribution to a spear throw, the only significant anatomical measure is upper arm length. This result is surprising, and implies that variation in throwing performance is primarily affected by the anatomy of the body, not the throwing arm. This represents a significant departure from the emphasis of the throwing literature to date, and suggests that future research should focus on the legs and torso rather than the throwing arm.

With this information, it is now possible to consider the significance of known differences in relevant aspects of anatomy between fossil populations. As discussed in chapter 4, differences in body size and proportions are known between Paleolithic hominin groups (Trinkaus, 1983a; Feldesman et al., 1990; Ruff, 1994; Ruff et al., 2005), and differences in musculature have been proposed (e.g. Trinkaus, 1983, 2006; Hambucken, 1993, Villemeur, 1994; Churchill and Rhodes, 2006, 2009). Neandertals are of shorter stature, with shorter limbs, compared with all early modern humans and *H. erectus* (Trinkaus, 1981; Feldesman et al., 1990; Ruff and Walker, 1993; Ruff, 1994; Holliday, 1997a, b; Ruff et al., 2005). However, bi-acromion breadth appears to be greater in Neandertals as compared with early modern humans, at least relative to humeral length (Trinkaus, 1983a, 2007; Vandermeersch and Trinkaus, 1995; Voisin, 2004, 2006). Furthermore, Neandertals are often described as having greater muscular hypertrophy than other Paleolithic hominins (Churchill and Rhodes, 2006). Unfortunately, it is not yet clear which muscles of the legs and torso are relevant to throwing performance to compare these between samples.

Thus, based on height and limb length, Neandertals would be expected to produce lower K_e throws than *H. erectus* and early modern humans, but based on bi-acromion breadth and musculature this would be reversed. Unfortunately, within this sample, bi-acromion breadth, height and body segment lengths are too highly correlated to tease apart which is primary, and strength of the leg and torso muscles was not measured directly. Thus, these data do not provide the resolution necessary to determine whether a shorter, broader body form would be superior, inferior, or comparable to a taller, narrower body form. Instead, further research will be necessary to determine conclusively if differences in Neandertal and early modern human body size and shape produce differences in throwing ability.

What can be said with confidence, however, is that no known differences between Neandertals and other hominin populations are due to differential selection for throwing performance. The relevant factors (height, leg length, arm length, and bi-acromion breadth) have been firmly established as reflecting climatic adaptation (Ruff, 1994; Holliday, 1997a,b; Weaver, 2003). Given that these factors also affect throwing performance, where populations were engaging in throwing, selection for climatic adaptations clearly outweighed any potentially conflicting selection pressures for throwing performance (i.e., selection for broader torsos in a hot climate, or selection for taller stature and longer limbs in a cold climate). Muscular hypertrophy is more difficult to address because it is so highly plastic, and variation in musculature between populations could certainly reflect habitual throwing. Populations engaging in habitual throwing would likely have developed greater musculature, but it remains to be seen which muscles would be affected and if these vary significantly between populations.

On the other hand, other anatomical measures that have been used to infer a lack of habitual throwing in Neandertals can now be conclusively rejected. Specifically, the purportedly

larger size of the deltoid muscle (involved in shoulder abduction during throwing), and the lower EMA of the elbow and wrist in early modern humans as compared with Neandertals has been inferred as resulting from selection for throwing performance (Churchill and Rhodes, 2006). In fact, neither of these measures is relevant to spear or ball throwing, and thus cannot be used to infer selection (or lack thereof) for throwing.

In addition to the implications for variation between Neandertals and early modern humans, this research may also provide insight into the australopithecine to *Homo* transition. Along with changes in shoulder, humeral, and torso anatomy that occur across the transition from the genus *Australopithecus* to the genus *Homo* (particularly *H. erectus* onward) that enable the throwing motion (see chapter 3:II), there are concurrent increases in height and absolute leg lengths (McHenry and Coffing, 2000; Pontzer, 2012) which would have improved throwing ability in the latter. These changes also roughly coincide with ecological and dietary changes, including greater frequency of meat in the diet (Ungar et al., 2006), either from hunting or scavenging (Domínguez-Rodrigo, 2002). Although preceeding the archaeological evidence, it is possible these shifts in ecology and anatomy represent the first use of projectile weaponry (for hunting or scavenging), creating selection pressure for throwing performance, and directly causing increases in height and leg length in *H. erectus*. However, there are other explanations for increased height and leg length as well, including climatic adaptation (Ruff, 1994) and locomotor efficiency (Pontzer, 2012). Thus, it may be that increases in height and leg length in the genus *Homo* are exaptations for throwing, such that once these traits evolved, it allowed or even promoted the adoption of projectile weaponry. At a minimum, this research demonstrates a significant increase in throwing ability from *H. erectus* onward.

III. Energy transfer across the kinetic chain in throwing.

This research has highlighted several important aspects of the transfer of energy across the kinetic chain that were previously poorly understood. To summarize, for both ball and spear throwing, the legs and torso propel the body forward, producing large forward linear velocities. With ball throwing, the shoulder internally rotates over a large range of motion, producing large angular velocities both passively and actively, and rather than directly generating velocity, the elbow magnifies the linear and angular velocities achieved proximally in the chain, transferring this energy to the ball. With spear throwing, the shoulder produces lesser internal rotation angular velocities, and the energy generated by the legs, torso, and shoulder are transferred to the spear through a much less mobile elbow.

Previous research had proposed that the angular velocities of the shoulder and elbow achieved during ball throwing involve passive mechanisms (Feltner and Dapena, 1986; Jobe et al., 1983, 1984), and this research strongly supports this conclusion. The musculature of the arm (as a proxy for the shoulder musculature) is correlated with the angular velocity of the shoulder during ball throwing, but explains only about 38% of its variation. Furthermore, as much as 87% of the variation in elbow velocity is explained without the active contribution of the musculature. For spear throwing, arm strength is not correlated with shoulder angular velocity at all. Thus, the angular velocity of the shoulder during both forms of throwing is partly or largely produced by passive mechanisms, likely the stretching of the internal rotator tendons. This conclusion is important for coaches and trainers interested in maximizing athlete performance. Training for strength of the internal rotators is likely to be less effective than, or could be strongly supplemented by, improving the potential for passive stretching of these muscles. One way that

this can potentially be achieved is by improving the external rotation range of motion to more strongly pre-load the tendons (Roach et al., 2012).

Similarly, the angular velocity of the elbow produced during ball throwing is not due to concentric contractions of the elbow musculature. Elbow angular velocity is not correlated with the size of the elbow musculature, but instead with the linear and angular velocities of the proximal segments of the chain. The elbow musculature may contribute to the throw by ensuring appropriate positioning of the arm in space, but it does not generate elbow velocity. Thus, as with the shoulder musculature, there will be little benefit to training the musculature of the arm. Instead, coaches and trainers can focus on improving strength in the proximal segments of the chain, and maximizing the transfer of energy across the elbow with optimal technique. This also highlights the importance of taking into account the covariation of morphological and anatomical variables. Previous researchers have found correlations between various measures of arm strength and throwing performance (Pedegana et al., 1982; Clements et al., 2001), but these are very likely due to correlations between body strength and arm strength rather than causal. Furthermore, during spear throwing, energy is maximally transferred to the spear with a relatively less mobile elbow, providing little room for the musculature of the elbow to play a role in generating throwing velocity; instead the elbow musculature likely aids in stabilization and positioning of the spear in space.

IV. The relevance and measurability of effective mechanical advantage.

Measures of EMA taken from fossil skeletons have been widely used to infer functional adaptation (e.g., Smith and Savage, 1956; Hall-Craggs, 1965a, b; McArdle, 1981; Anemone, 1990), but the biomechanical principles upon which they are based had not been tested empirically. Furthermore, even if EMA is a valuable measure of performance in living subjects,

it had not been demonstrated that it could be reliably and accurately measured from skeletal specimens. In chapter 8, the relationship between EMA and maximum torque production, independent of muscle size, was investigated. Contrary to expectations, it was found that neither the moment arm (r), the load arm (R), nor the ratio of the two (EMA) significantly explains maximum external force production at the elbow or wrist. This is at least in part due to the fact that r is correlated with muscle cross-sectional area (aCSA), as a result of body size scaling and because greater muscle aCSA moves the line of action of the moment arm further from the joint center.

Additionally, there is very likely variation in the underlying neural control of muscle recruitment and activation present that vastly outweighs any effects of anatomy on strength. This will be a large source of variation in strength during natural behaviors, and creates an added level of complexity for making inferences about strength from skeletal material. In fact, Walker (2009) suggests that the extreme differences in strength often noted between chimpanzees and humans could be due to different patterns or control of muscle recruitment and activation. Chimpanzees appear to be relatively stronger compared with humans than would be expected from muscle dimensions, and it is hypothesized that this is due to the presence of fewer motor neurons controlling chimpanzee muscle fibers, thereby activating a larger ‘unit’ of muscle with a given neural stimulus (Walker, 2009). In contrast, humans are capable of more fine-tuning of muscle recruitment patterns, and do not regularly activate the entire muscle maximally. If this hypothesis is correct, such differences could be present in fossil populations as well. Besides speculating about potential selective benefits, it would be impossible to predict what pattern existed in a given fossil population, and thus very large differences in strength might exist between populations that are entirely invisible in the fossil record.

Beyond the issue of the value of EMA in living subjects is the question of whether it can be measured reliably in the fossil record. It was found that measures of moment arms taken from soft tissue are in fact correlated with measures taken from skeletal landmarks, demonstrating that where r is determined to be meaningful, it can be measured reasonably well from skeletal specimens. However, r is not useful without some measure of the external load arm, and it was determined that R measured during activity is not correlated with the length of distal limb segment (traditionally used as a proxy for R). This is due to the fact that slight differences in joint angles and the position of the arm in space produce very large differences in R , which completely overwhelms any potential correlation with segment length. The natural variation in R both between and within subjects for the same activity (even a highly trained activity like throwing) is very large, making relevant and reliable estimations of EMA from a skeleton impossible. The results presented here are specifically relevant to open chain activities, where the limb moves freely through space, but Warrener (2011) also failed to find a correlation between R and anatomy for a closed chain activity, namely locomotion. Taken together, these results provide strong opposition for the practice of inferring adaptation or performance from estimates of EMA in the fossil record. At a minimum, the biomechanical inferences of a particular activity should be tested empirically prior to drawing functional conclusions from measures of mechanical advantage.

V. Effective mechanical advantage in Paleolithic fossil hominins.

Despite the significant problems raised in the previous sections regarding the usefulness and measurability of EMA, since it is a measure that has been so widely compared between fossil hominins and important implications drawn from it, an attempt was made in chapter 9 to elucidate the presence and magnitude of any differences between Neandertal, early modern

human, and where possible, *H. erectus* samples. Moment and load arms were measured in a more comprehensive way than in previous research, taking into account all possible sources of skeletal variation. The results of this analysis can then be placed into the larger context of the previous chapters.

No significant differences were found between fossil samples for r for any muscle or muscle group at the elbow or wrist. Thus, contrary to expectations, when moment arms are measured in the most comprehensive way possible, there appears to be no significant differences between samples. Admittedly the sample sizes were quite small, but the data do not visually suggest any trends that fail to reach significance, and there is no reason to assume a larger sample would find different results. On the other hand, when r is considered relative to R (approximately ulna length), Neandertals demonstrate a trend of increased EMA at the elbow as compared with all other samples. Although the trend only reaches significance for some comparisons, there appears to be a pattern of greater EMA in this group.

Given the similarity in r values, the difference in EMA at the elbow between Neandertals and the other samples is due to variation in R , specifically ulna length. Shorter ulnae in Neandertals have been documented previously and are a result of climatic adaptation (Holliday, 1997a, b). Thus, variation in EMA is not in fact an adaptation for strength in this population, but simply a secondary effect of selection for shorter distal limb segments in a cold climate. Furthermore, based on the results of chapter 8, there is no support for the principle that variation in EMA, particularly when measured from a skeletal specimen, has any functional implications. EMA is not correlated with joint strength or speed independent of muscle cross-sectional area, and the length of the ulna is not predictive of the actual load arm for the joint during activity.

Thus, variation in EMA between Neandertals and other hominin populations does not indicate greater strength or adaptation for greater strength in this group.

VI. Spear throwing performance in Paleolithic fossil hominins.

Taken as a whole, this dissertation provides valuable insight into the selective pressures and differential abilities for spear throwing of our hunter-gatherer ancestors. Spear throwing, either used for hunting or protection from predators, must have played a significant role in survival in the Upper Paleolithic and earlier. The results presented here demonstrate that despite the potential for selective pressure for greater limb (particularly leg and upper arm) lengths, broader shoulders, and greater musculature, there is no clear trend towards adaptation for throwing performance in any Paleolithic hominin population. Each hominin sample has traits that would have been advantageous for throwing performance (height and limb length in early modern humans and *H. erectus*, broad shoulders in Neandertals), however these primarily reflect climatic adaptation. In fact, climatic adaptation appears to outweigh selection for throwing performance, as each group has traits that are less well adapted to throwing performance as well. Future research will be necessary to fully resolve whether these different body forms produce significant differences in throwing performance.

Although it has been suggested that Neandertals had greater muscular hypertrophy than early and recent modern humans, and this certainly would have been beneficial for throwing performance, it is unclear whether this is true for any relevant muscles. It has been shown that the musculature of the arm is not relevant for throwing performance, and it is not yet known which leg and torso muscles are important in order to make comparisons between groups. Future research will be necessary to investigate the contribution of the leg and torso musculature to throwing performance and to then make comparisons between hominin samples (but note that

comparisons of muscle marking size and rugosity are considered somewhat questionable). The great degree of plasticity in muscular hypertrophy makes interpretation of this trait slightly more complicated, however. If it is found that Neandertals have greater hypertrophy of relevant muscles, but the Neandertal body form is found to be detrimental to throwing performance, greater musculature may be a plastic response to compensate and maximize throwing ability with the given body form.

On the other hand, most of the traits that have been described previously as adaptations for or reflective of habitual throwing, including upper limb EMA and muscle sizes, glenoid fossa morphology, and humeral retroversion angle, can now be conclusively rejected. All of these are traits related to the shoulder or arm, and it is now seen that the arm does not actively produce the energy of the throw. Thus, variation in the arm will not produce variation in throwing performance. Furthermore, EMA is not a useful or measurable trait in skeletal samples. In addition, the angular velocity and torque experienced by the shoulder during spear throwing is much smaller than previously thought. The torques and joint reaction forces experienced are very unlikely to provide sufficient pressure to induce anatomical changes through selection or plasticity. Thus, previous research using the morphology of the shoulder or arm to infer that Neandertals did not habitually throw must be rejected. No aspect of anatomy or morphology that is known to differ between Neandertals and early modern humans is indicative of selection for or more frequent throwing in early modern humans.

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APPENDICES

Appendix I. Subject anthropometrics (measured externally).

Subject	Age	Sex	R vs L Handed	Height	Body Mass (Kg)	Bi-Acromion Breadth	Upper Arm	Forearm
2	27	M	R	1.78	80.83	0.35	0.35	0.27
3	29	F	R	1.70	68.76	0.35	0.32	0.26
4	24	M	R	1.80	68.04	0.40	0.30	0.28
5	39	M	R	1.75	63.50	0.39	0.30	0.23
6	25	M	R	1.70	64.23		0.29	0.29
7	27	F	R	1.68	79.20		0.33	0.24
8	26	F	R	1.68	76.84	0.38	0.30	0.25
9	21	M	R	1.88	68.95	0.36	0.31	0.28
10	24	F	R	1.47	57.61	0.27	0.27	0.23
11	24	F	R	1.49	68.86	0.32	0.32	0.25
12	26	F	R	1.52	63.96	0.34	0.30	0.28
13	19	F	L	1.68	65.68	0.36	0.29	0.26
14	20	F	R	1.73	70.94	0.32	0.31	0.26
15	21	F	R	1.71	70.94	0.33	0.29	0.26
16	20	F	R	1.73	75.39	0.32	0.29	0.25
17	19	F	R	1.64	62.41	0.31	0.31	0.23
18	20	F	L	1.63	59.24	0.31	0.27	0.26
19	18	F	R	1.65	70.31	0.33	0.33	0.26
20	19	F	R	1.80	77.20	0.32	0.29	0.24
21	19	F	R	1.57	55.88	0.33	0.25	0.24
22	19	F	R	1.68	86.91	0.35	0.29	0.24
23	21	M	R	1.91	79.11	0.38	0.30	0.28
24	20	M	R	1.73	71.03	0.36	0.29	0.26
25	21	M	R	1.91	92.99	0.37	0.34	0.31
26	21	M	R	1.96	105.41	0.40	0.35	0.26
27	21	M	R	1.85	88.09	0.37	0.32	0.29
28	20	M	R	1.75	72.30	0.35	0.29	0.24
29	19	M	R	1.75	71.12	0.36	0.27	0.24
30	21	M	R	1.93	87.09	0.38	0.34	0.31
31	20	M	R	1.93	96.89	0.39	0.32	0.28
32	21	M	R	1.75	72.85	0.38	0.33	0.26
33	21	M	R	1.78	83.91	0.37	0.30	0.27
34	22	M	R	1.82	84.46	0.36	0.33	0.26
35	20	M	R	1.80	72.30	0.36	0.30	0.30
36	20	M	R	1.78	84.37	0.40	0.30	0.29
37	20	M	R	1.83	82.83	0.36	0.32	0.26
38	21	F	R	1.78	94.53	0.34	0.32	0.27
39	20	F	L	1.63	67.13	0.32	0.29	0.24
40	21	F	R	1.70	78.20	0.32	0.28	0.25
41	21	F	R	1.60	62.78	0.32	0.31	0.26
42	20	F	R	1.65	59.87	0.30	0.27	0.22

Appendix I. cont.

Subject	1st MC (cm)	2nd MC (cm)	Arm	Bi-Asis Breadth	Thigh	Shank	Leg
2	6.10	8.60	0.68	0.29	0.38	0.43	0.81
3	6.35	8.10	0.64	0.29	0.35	0.43	0.77
4		6.67	0.58	0.28	0.39	0.38	0.77
5	6.99	9.21	0.60	0.30	0.41	0.38	0.79
6	6.67	8.89	0.65	0.26	0.44	0.38	0.83
7	5.72	6.99	0.63	0.30	0.40	0.39	0.79
8	5.50	6.99	0.61	0.29	0.38	0.42	0.80
9	6.67	5.72	0.65	0.25	0.45	0.46	0.91
10	4.45	6.35	0.54	0.27	0.31	0.35	0.65
11	5.40	7.30	0.62	0.29	0.36	0.39	0.76
12	6.30	7.50	0.64	0.25	0.41	0.42	0.83
13	6.80	8.50	0.61	0.28	0.39	0.41	0.80
14	5.40	7.00	0.62	0.27	0.41	0.42	0.83
15	6.50	8.20	0.62	0.27	0.40	0.40	0.80
16	4.60	7.70	0.58	0.29	0.36	0.41	0.77
17	6.50	7.50	0.60	0.25	0.39	0.40	0.79
18	5.90	8.20	0.58	0.26	0.38	0.38	0.76
19	5.00	8.30	0.64	0.24	0.41	0.41	0.82
20	5.80	8.80	0.59	0.29	0.31	0.40	0.71
21	5.60	7.80	0.54	0.23	0.36	0.35	0.71
22	5.50	8.40	0.59	0.32	0.38	0.38	0.76
23	5.70	8.00	0.64	0.28	0.43	0.47	0.90
24	7.00	7.90	0.62	0.26	0.34	0.39	0.73
25	5.50	8.10	0.70	0.29	0.42	0.47	0.89
26	6.00	9.00	0.67	0.28	0.39	0.41	0.80
27	4.80	8.50	0.65	0.29	0.41	0.43	0.84
28	5.80	6.80	0.59	0.27	0.40	0.37	0.78
29	6.50	8.20	0.58	0.27	0.41	0.39	0.80
30	7.20	9.60	0.73	0.29	0.47	0.48	0.95
31	5.40	9.90	0.65	0.33	0.42	0.45	0.87
32	5.00	7.90	0.65	0.22	0.40	0.41	0.81
33	6.50	8.20	0.63	0.26	0.42	0.42	0.84
34	6.00	8.00	0.65	0.28	0.44	0.42	0.86
35	6.20	7.50	0.66	0.27	0.39	0.43	0.82
36	5.00	8.50	0.64	0.26	0.38	0.43	0.81
37	5.80	7.90	0.63	0.25	0.42	0.42	0.84
38	6.00	7.50	0.65	0.30	0.43	0.42	0.85
39	5.90	7.50	0.59	0.26	0.34	0.41	0.75
40	5.20	7.90	0.58	0.27	0.38	0.38	0.76
41	6.40	6.90	0.63	0.23	0.36	0.38	0.74
42	5.80	7.50	0.55	0.26	0.37	0.42	0.79

All measurements are lengths in meters unless otherwise noted. MC: metacarpal.

Appendix II. Subject muscle cross-sectional areas (aCSA) measured from MRIs.

Subject	TB	BB	B	Wrist Flexors	Wrist Extensors
2	3901.21	3095.90	1943.40		
5	2888.27	2633.46	1034.37	3584.28	1221.65
13	1882.90	1931.88	887.43	2314.38	1116.94
14	1722.99	1176.99	1462.23	2634.90	979.63
15	1849.76	1780.61	1380.12	3124.00	1336.90
16	1699.94	1457.91	1459.35	2619.06	1355.63
17	1648.08	1469.44	1303.00	2565.75	734.72
18	1537.15	1184.19	1296.56	2420.25	838.44
19	2090.51	1442.07	1310.97	3002.26	1234.62
20	1929.00	1395.97	1332.58	2851.95	969.54
21	2266.10	1675.45	1426.22	3182.34	730.40
22	1905.95	1266.31	952.25	2681.00	1312.45
23	3561.23	3045.48	2356.86	4078.41	1400.29
24	3581.39	3045.48	2356.86	4278.66	1390.20
25	3427.25	2227.21	2391.44	4743.98	1996.71
26	3865.20	3026.75	2243.05	4342.04	1903.07
27	3421.48	2143.65	2065.86	4432.8	1761.88
28	3489.19	2516.77	2077.39	3803.25	1499.69
29	3541.06	2521.08	1907.39	3967.48	1524.18
30	2904.30	2447.62	2217.12	4015.02	1334.02
31	4056.80	2685.33	2031.00	4314.67	1538.59
32	3680.80	2789.05	2146.53		
33	4913.97	3124.72	2469.23	4625.85	2037.04
34	4414.08	2820.74	2548.47	4883.72	1671.13
35	3107.43	2322.29	2090.35	4143.24	1181.31
36	3215.48	2734.31	2682.44	4076.97	1763.33
37	4421.28	2590.24	2325.17	4091.38	1697.06
38	2349.66	1655.28	1344.10	2823.63	1165.47
39	2087.47	1485.28	1738.83	2745.83	1267.75
41	2001.03	1619.26	1773.41	3323.52	956.58
42	2196.95	1597.65	1547.23	2768.88	1238.94

All measurements are in mm². Abbreviations: TB: triceps brachii, BB: biceps brachii, B: brachialis.

Appendix III. Subject moment arms (r) measured from MRIs.

Subject	TB (skel)	TB (tend)	BB (skel)	BB (tend)	B (skel)	B (tend)
2	19.27	19.14	67.11	56.10	53.39	52.10
5	15.91	17.72	51.98	52.47	41.96	42.85
13	18.69	18.81	32.76	31.33	23.97	13.96
14	15.26	17.69	51.14	50.79	38.41	38.40
15	15.14	15.91	50.71	47.00	59.21	59.83
16	15.11	15.19	45.02	44.53	33.50	33.60
17	14.20	14.58	56.76	51.64	52.46	52.83
18	15.94	15.73	45.01	43.46	39.33	38.73
19	15.35	17.25	52.63	50.62	39.58	40.18
20	16.56	17.56	45.15	42.20	44.66	43.73
21	13.55	14.61	37.43	37.40	37.09	36.89
22	14.18	14.77	49.90	44.85	35.73	36.33
23	18.72	21.09	64.47	60.80	36.79	38.32
24	17.55	18.18	60.44	53.57	34.16	34.57
25	17.75	18.65	39.44	42.30	27.16	24.00
26	20.30	21.52	61.50	59.37	47.83	48.24
27	17.46	19.39	50.52	50.27	40.29	41.57
28	17.78	17.88	54.10	52.04	39.14	40.34
29	16.60	18.14	59.04	51.51	42.64	44.40
31	16.23	17.60	64.60	57.96	48.08	48.60
32	23.79	23.81	48.09	40.55	22.72	24.40
33	17.86	19.53	56.44	53.29	39.92	39.01
34	17.46	18.49	60.29	57.77	36.76	36.60
35	16.14	19.89	71.89	58.25	46.11	47.15
36	16.89	19.25	54.78	54.96	40.42	40.63
37	19.38	21.12	57.21	47.42	43.67	45.22
38	20.23	21.03	55.09	46.30	40.91	41.29
39	16.29	17.04	47.94	48.49	36.72	37.28
41	16.07	17.13	50.57	47.58	37.42	37.44
42	13.52	14.75	50.37	48.94	34.13	33.86

Appendix III. cont.

Subject	FCU (skel)	FCU (tend)	FCR (skel)	FCR (tend)	ECU (skel)	ECU (tend)	ECR (tend)
5	7.20	8.40	21.74	13.21	14.46	13.26	10.80
13	6.45	5.99	21.23	19.23	12.51	14.82	9.66
14	13.42	14.40	19.24	18.63	13.25	9.67	9.60
15	12.07	13.26	14.41	14.41	10.80	13.26	13.21
16	12.01	12.01	22.81	19.25	14.41	12.01	6.00
17	6.00	6.00	24.01	14.46	15.65	18.36	13.26
18	13.26	14.46	20.44	18.05	9.60	12.07	6.12
19	12.53	14.46	17.48	15.79	12.24	14.46	8.40
20	16.85	15.61	22.94	21.61	8.49	9.60	9.60
21		9.60	17.47	20.44	16.32	19.24	8.40
22	13.42	13.26	12.07	15.65	9.68	14.46	7.20
23	8.74	10.87	24.49	22.81	14.60	15.61	12.01
24	8.49	7.20	22.14	20.44	15.79	18.01	12.01
25	10.87	13.26	22.94	18.05	13.26	18.05	13.26
26	14.41	12.24	25.21	22.94	12.07	13.26	10.80
27	14.60	10.87	25.65	22.83	12.24	14.40	14.40
28	12.24	14.41	23.31	20.55	11.07	12.07	9.68
29	14.41	14.41	21.61	20.41	10.80	13.26	12.01
30	10.80	8.40	32.44	27.08	14.41	15.61	8.49
31	13.42	13.42	24.28	20.51	13.42	13.42	13.26
33	8.74	9.68	27.38	23.31	14.60	14.60	8.49
34	16.85	15.61	20.41	19.21	12.01	10.87	8.49
35	9.90	9.68	24.75	20.44	14.85	16.85	13.26
36	7.30	7.20	26.41	22.94	14.41	18.05	9.60
37	12.07	14.41	26.84	20.41	12.24	13.26	8.49
38	11.07	10.87	20.72	19.21	13.42	14.41	13.21
39	13.21	10.80	20.41	18.17	12.01	10.87	12.01
41	10.87	10.87	25.24	20.41	12.07	13.26	12.07
42		6.00	28.26	21.74	12.24	18.05	8.40

All measurements are in mm. Abbreviations: TB: triceps brachii, BB: biceps brachii, B: brachialis, FCU: flexor carpi ulnaris, FCR: flexor carpi radialis, ECU: extensor carpi ulnaris, ECR: extensor carpi radialis brevis and longus, skel: r measured based on skeletal landmarks, tend: r measured based on tendon insertions. ECR (skel) could not be measured.

Appendix IV. Subject strength measured with load cell.

Subject	Elbow Flexion (N)	Elbow Extension (N)	Wrist Flexion (N)	Wrist Extension (N)
2	322.63	227.88	119.21	83.63
3	129.29	68.06	21.80	32.77
4	247.47	145.90	113.13	77.99
5	288.10	191.13	39.00	74.88
6	218.56	151.24	50.86	57.23
7	171.70	134.93	83.03	65.98
8	176.45	124.25	49.08	40.63
9	230.12	145.46	56.20	59.31
10	164.14	140.25	50.13	66.41
11	122.64	85.85	12.46	38.83
12	153.91	125.13	40.92	69.08
13	121.88	127.66	21.35	76.36
14	183.41	145.90	37.07	56.49
15	196.91	126.63	45.96	35.73
16	154.06	146.79	85.55	77.10
17	120.10	72.21	9.79	22.54
18	116.54	66.43	14.23	14.23
19	202.54	197.65	18.24	80.51
20	133.30	117.88	22.69	53.53
21	107.80	114.32	43.74	49.08
22	152.72	135.52	76.21	22.39
23	278.61	138.34	52.64	90.30
24	222.26	161.62	58.57	92.08
25	255.77	161.62	29.80	49.67
26	233.98	157.60	82.87	60.81
27	235.89	134.02	76.20	76.20
28	284.11	178.24	61.70	83.32
29	230.55	163.38	124.24	84.07
30	260.22	128.55	82.87	53.82
31	300.12	205.20	122.33	96.08
32	318.80	200.93	180.91	91.19
33	367.73	200.17	191.27	130.78
34	247.77	135.80	157.33	78.87
35	236.65	151.68	146.35	58.14
36	296.56	164.14	163.69	72.37
37	367.73	229.39	96.53	166.67
38	171.26	116.99	83.94	50.58
39	126.77	92.21	64.05	38.12
40	176.91	134.78	144.12	32.92
41	207.29	124.55	86.61	59.47
42	126.64	116.23	43.01	57.69

Appendix V. Skeletal measurements for fossil specimens.

Specimen	Sample	Ulna Length	TB	BB	B	2 nd MC	FCU	FCR	ECU	ECR
KNMWT 15000	Early <i>Homo</i>	270.00 ⁺	19.84		42.64					
Amud 1	Nean					70.82 [*]	17.22		7.68	
La Chapelle 1	Nean	246.50	23.14	54.47	38.81	70.90			11.28	
La Ferrassie 1	Nean	271.00	19.90	59.80	48.39	70.90				11.93
Kebara 2	Nean	271.00	17.85	65.76	41.80	71.00	14.42	20.35	11.86	12.25
Neandertal 1	Nean	239.00	20.64	66.73	53.76					
La Quina 5	Nean	240.50	21.28		44.79					
Reourdou 1	Nean	225.00		60.24	46.05					
Shanidar 4	Nean	252.00	25.86	55.25	43.97	73.20		19.40		13.45
Shanidar 5	Nean	247.00	21.07		41.52					
Shanidar 6	Nean	233.49 [†]	21.34	55.77	41.28					
Tabun 1	Nean	240.50	18.92	51.93	41.51	65.00	19.26	11.33	7.92	11.26
Qafzeh 7	MPEMH	271.00	20.51		46.38					
Qafzeh 9	MPEMH	270.00	15.75	53.39	46.73	62.90	17.87	19.75	8.12	8.21
Skhul 4	MPEMH	292.00	15.89	63.02	48.02					
Skhul 5	MPEMH	287.18	19.25	60.13	46.76	67.51 [*]			13.18	
Skhul 7	MPEMH	241.11	18.99	46.88	37.78					
Dolní Věstonice 13	UPEMH	336.00	22.88	72.63	42.48					
Dolní Věstonice 14	UPEMH	290.00	21.10	68.15	43.87					
Dolní Věstonice 16	UPEMH	284.00	20.82	57.76	48.85					
Pavlov 1	UPEMH	304.00	20.07		50.61					
Prědmostí III	UPEMH	299.00		66.06						
Sungir 1	UPEMH	305.00 [‡]	21.45		47.85					

All measurements are in mm. Abbreviations: TB: triceps brachii, BB: biceps brachii, B: brachialis, FCU: flexor carpi ulnaris, FCR: flexor carpi radialis, ECU: extensor carpi ulnaris, ECR: extensor carpi radialis brevis and longus, MC: metacarpal. ⁺ Ruff and Walker, 1993. ^{*} Estimated from MC1 length using predictive equation from modern human comparative sample.

[†] Estimated from radius length using predictive equation from modern human comparative sample. [‡] Mednikova, 2005.