ON THE EVOLUTION OF THE SEX DIFFERENCES IN THROWING: THROWING IS A MALE ADAPTATION IN HUMANS

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abstract
The development of the ability to throw projectiles for distance, speed, and accuracy was a watershed event in human evolution. We hypothesize that throwing first arose in threat displays and during fighting and later was incorporated into hunting by members of the Homo *lineage because nonhuman primates often throw projectiles during agonistic interactions and only rarely in attempts to subdue prey. Males, who threw more often than females in both combat and hunting, would have been under stronger selection than females to become proficient at the ability to throw, intercept, and dodge projectiles as throwing skills became critical to success in combat and hunting. Therefore, we predict that males, more than females, should display innate anatomical and behavioral traits associated with throwing. We use data from a variety of disciplines to discuss: the sex differences in throwing speed, distance, and accuracy; sex differences in the development of the throwing motion; inability of training or cultural influences to erase the sex differences in throwing; sex differences in the use of throwing in sports, combat, and hunting; and sex differences in anatomical traits associated with throwing that are partly responsible for male throwing superiority. These data contradict the view held by many commentators that socialization rather than innate sex differences in ability are primarily responsible for male throwing superiority. We suggest that throwing is a male adaptation.*

Introduction

"throwing like a girl"

GIRLS and women typically do not throw as fast, far, or accurately as boys and men (Thomas and French 1985). The reasons for these differences have been the subject of debate for decades. Many scholars and commentators in the popular media have claimed that the sex differences in throwing are not as

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large as the public believes and that they are the result of sex differences in socialization and not differences in innate abilities (Table 1). Indeed, the commentary on this topic often includes statements such as: the pejorative trope to "throw like a girl" has at its "source in the particular *situation* of women as conditioned by their sexist oppression in contemporary society. . . . Women in sexist society are physically handicapped" (Young 1980:152); "'throwing like a girl' is quite likely to be a recent, idiosyncratic, culturally imposed sexual dimorphism" (Bingham and Souza 2010); and "Young women learning to throw in North America thus face a quadruple whammy of obstacles. We *are* girls, therefore we throw like ourselves. We are learners, therefore our bodies naturally perform the early throwing mechanics that have been culturally labeled in a negative way. Even post-*Title IX*, many of us come to this experience later and have fewer opportunities to practice overhand throwing. So our early-learning phase lasts longer and looks more acute by contrast with age-cohort boys, who have moved through those early learner phases more quickly. All this is a powerful disincentive to keep picking up the ball. Because throwing is such a complex, learned activity, . . . this vicious cycle can have a disproportionately large effect" (Rowe 2012).

Few commentators have discussed at length the possibility that the origin of the sex differences are innate differences between males and females that have been shaped by selection. The view of many feminists, journalists, political theorists, and scientists, including evolutionarily oriented ones, is that girls "throw like girls" *only* because of sex differences in socialization (Table 1). However, from an evolutionary perspective this view is fatally flawed because it explicitly rejects our modern understanding about how an individual's traits are expressed. This is because throwing is a phenotype and like all other phenotypes arises from the complex interactions between an individual's genotype and its environment (Plomin et al. 2008). Therefore, it is surprising that few scholars and commentators have hypothesized that the sex differences in throwing have partly innate causes (Table 1).

Why There are Sex Differences in Throwing is an Interesting Question

It is not surprising that males throw faster and farther than females for two related reasons. First, adult males are larger than females (Ellis et al. 2008). The length of the body and limbs synergistically contribute to throwing velocity (Stodden et al. 2006a,b; Maki 2013; Roach and Lieberman 2014). Second, males have more muscle mass in both absolute terms and relative to fat-free body mass (Janssen et al. 2000; Lassek and Gaulin 2009) and consequently are stronger than females. Muscle mass contributes to the amount of force that can be used during the throwing motion. Numerous studies comparing athletically trained and untrained males and females have shown that female strength, even when controlling for differences in fat-free body mass and limb or body size, ranges from 40–75% of male strength (Bishop et al. 1987; Lassek and Gaulin 2009). Especially relevant to the sex difference in throwing velocity, the difference is greater for upper-body than lower-body strength (Bishop et al. 1987; Janssen et al. 2000; Lassek and Gaulin 2009). Moreover, male muscle fibers are shorter and have greater angles of pennation (i.e., the angle of the muscle fibers to the force-generating axis of the muscle) contributing to the sex differences in muscular strength (Chow et al. 2000). Finally, males tend to have a greater proportion of "fast twitch" (Type IIA) muscle fibers than females (Miller et al. 1993) making male muscles better at producing the anaerobic power (Mayhew and Salm 1990) used during the rapid, intense actions that occur during throwing. Thus, the larger size and greater strength of males are responsible for some of the sex differences in throwing. However, what makes the sex differences in throwing especially interesting is that they are greater than the sex differences in running and jumping.

A comparison between male and female performances in track and field events demonstrates the large gap in male and female overhand throwing performance relative to the other basic physical actions of running and jumping. The sex differences in world records, top 10 all-time performances, the per-

TABLE 1
A sample of some published discussions about the evolution of throwing

No discussion of sex differences in throwing	Sex differences in throwing attributed solely to environmental effects	Sex differences in throwing attributed to biology x environment interaction
Darlington (1975)	Young (1980, 1998)	Thomas and French (1985)
Calvin (1983)	Fallows (1996)	Isaac (1987)
Knüsel (1992)	Williams (1996)	Thomas and Marzke (1992)
Young (2003)	Dunsworth et al. (2003)	Ehl et al. (2005)
Bingham and Souza (2009)	Evaldsson (2003)	Young (2009)
Roach et al. (2012, 2013)	Fredrickson and Harrison (2005)	Downey (2010)
Roach and Lieberman (2014)	Anthamatten (2014)	
Roach and Richmond (2015)		
Larson (2015)		

formances of 2016 Olympic finalists, and U.S. youth record holders show that males, on average, run about 10% faster and jump about 15–20% higher than females (Table 2). There are four throwing events: shot put, discus, hammer, and javelin. Males throw heavier implements than females in each event (Table 2). The sex difference in javelin throwing is the most relevant because the javelin is the only implement thrown overhand. In general, there is little difference between males and females in the distances that the shot put, discus, and hammer are thrown, but boys and men throw the javelin more than 30% farther (Table 2). Given that the difference between the weights of the javelins thrown by the sexes is relatively small compared to the differences in weights between the shot put, hammer, and discus thrown by the sexes (Table 2), we would expect there to be relatively little difference in the distance that the sexes throw the javelin if male and female throwing abilities were roughly equivalent. The large sex difference in javelin throwing is *not* because male champion javelin throwers are from the U.S. where overhand throwing is highly valued because of the cultural importance of baseball and softball to Americans. The senior male world record holder is a European as are eight of the top 10 all-time performers (the top eight are Europeans, a Kenyan is ranked ninth, an American is ranked 10th), and none of the top eight finishers in the 2016 Olympics were Americans (six of eight were Europeans, the two others were a Kenyan and a competitor representing Trinidad and Tobago; https://www.iaaf.org; https://www.olympic.org/rio-2016/athletics/javelin-throw-men).

Interestingly, the sex difference for throwing baseballs for speed is similar to that for javelin throwing for distance; men throw baseballs 39% faster (169 km/hr versus 105 km/hr) than women (Glenday 2007). Because they are throwing the same weight implement (range 141.75–148.83g), the difference in baseball throwing speed clearly illustrates the sex difference in throwing performance.

In summary, the sex difference in javelin throwing performance is larger than those in running and jumping and the magnitude of the difference is paralleled by the sex difference in throwing baseballs for speed. Collectively, these patterns suggest that there may be a fundamental difference between the sexes in throwing ability that goes beyond the differences in size and strength.

An Evolutionary Theory of Throwing

Our overarching purpose is to develop an evolutionary theory of throwing in humans. Elsewhere, we hypothesized that throwing likely evolved first within the ecological context of agonistic interactions and then transitioned into use during hunting because throwing in nonhuman primates occurs almost exclusively during threat displays and agonistic interactions (Lombardo and Deaner

TABLE 2
Sex differences in performance in track and field events

Event	Percent sex difference in senior world record performances	Percent sex difference in senior all-time top 10 performances	Percent sex difference in 2016 Olympic final performances	Percent sex difference in U.S. youth performances
		Running events		
100m	8.7	8.8	9.4	6.5
200m	10.1	9.8	9.5	6.2
400m	9.6	10.2	12.6	8.0
800m	10.9	11.1	11.5	7.7
1500m	10.5	10.6	8.3	7.6
3000m	9.3	10.3	—[3]	6.6
5000m	11.0	11.1	11.1	14.6
10,000m	10.2	11.0	9.3	12.7
Marathon	10.2	11.0	9.9	—[4]
		Jumping events		
High jump	17.2	17.0	20.1	12.5
Pole vault	21.3	23.4	21.4	23.7
Long jump	19.0	18.6	18.6	13.8
Triple jump	18.0	17.8	16.6	18.3
		Throwing events[1]		
Shot put	2.2	3.4	9.5	23.3
Discus	3.5[2]	2.4[2]	1.5	25.0
Hammer throw	4.5	8.4	2.6	18.6
Javelin	**36.2**	**33.2**	**31.9**	**33.7**

All data from International Association of Athletics Federations (https://www.iaaf.org) or USA Track & Field (http://usatf.org). Data represented are the percent differences between male and female performances; instances where female performance is superior to male performance are indicated in the table. Sex differences in top 10 all-time performances based on mean performance in each event, 2016 Olympic final based on mean performance by the eight finalists in each event, and U.S. youth athletic performances are based on the mean sex differences in each event averaged across all age groups; male performances were superior to female performances in all events across all youth age groups. U.S. youth age groups are <= 8, 9–10, 11–12, 13–14, 15–16, and 17–18 years. The percent sex difference in the javelin throw is in bold font to emphasize the magnitude of the difference compared to the differences in male and female performances in other events.

[1]Implements used by males are heavier than those used by females. Senior throwing implements: male shot = 7.26kg; female shot = 4kg; male discus = 2kg; female discus = 1kg; male hammer = 7.26kg; female hammer = 4kg; male javelin = 800g and 2.6–2.7m in length; female javelin = 600g and 2.2–2.3m in length. As youth age, the implements thrown by girls become lighter than those thrown by boys. Shot: ages 8 and under = 2kg; ages 9–12 = 2.72kg; ages 13–14, boys = 3.63kg, girls = 2.72kg; ages 15–18, boys = 5.44kg, girls = 4kg. Discus: ages up to 10 depends on local rules; ages 11–14 = 1kg; ages 15–18, boys = 1.6kg, girls = 1kg. Javelin: ages 8–12 = 300g; ages 13–14 = 600g; ages 15–18, boys = 800g, girls = 600g (http://www.usatf.org/groups/officials/files/resources/weights-and-measures/Throws-Implement-Specs-Feb2014.pdf).

[2]Female performance is superior to male performance.

[3]3000m event is not contested in Olympics.

[4]Not an official U.S. youth event.

2018). Here we focus on the evolutionary consequences of over two million years of selection on the biology of throwing in the human lineage (Roach et al. 2013). In this article, we demonstrate the weakness of the claims that socialization alone is responsible for the sex differences in throwing by showing that the differences are large and primarily due to the evolution of male-specific anatomical and behavioral adaptations that evolved during a long history of stronger selection on the throwing biology of males than on females. First, we review our hypothesis that the ecological causes of selection that shaped the evolution of throwing were stronger on males than on females. This hypothesis yields the predictions that males should be superior throwers than females and that males, more than females, should possess innate behavioral and anatomical traits associated with throwing. Second, we briefly review the evidence showing that males are superior throwers and the developmental and cross-cultural literature reporting sex differences in throwing behavior. Finally, we review the anatomical literature that demonstrates that there are sex differences in the anatomical traits associated with throwing and shows that some of these differences cannot be attributed solely to sex differences in usage.

Others have documented some of the data that we discuss here, including those that show that there is a substantial sex difference in throwing performance, the sex difference is relatively impervious to environmental input, and anatomical traits advantageous for throwing are more pronounced in males than females. However, they did not use these data to develop a complete evolutionary theory of throwing. In contrast, we use several lines of converging evidence (i.e., a consilience of inductions; Wilson 1998) from a variety of disciplines to make a strong argument that the traits underlying the sex difference in throwing are evolved consequences of a long history of selection on male throwing ability.

The Ecological Causes of Selection that Shaped the Evolution of Throwing Ability Were Stronger on Males than on Females

Several lines of evidence suggest that the ecological causes of selection shaping the evolution of throwing were stronger on males than on females. First, throwing during agonistic interactions is widespread in nonhuman primates (Shumaker et al. 2011). More importantly, male chimpanzees throw more often than females during agonistic interactions (Sugiyama and Koman 1979; Goodall 1986). For example, male chimpanzees at Gombe, Tanzania, were responsible for 94% of throwing incidents recorded in 1968 and 1977–1982 (Goodall 1986). These observations are especially relevant to our theory because it suggests that male hominins were more likely than female hominins to use throwing to manipulate the behavior of other individuals. Thus, selection would have more strongly favored the evolution of superior throwing skills in male, rather than female, hominins if those skills led to increased success during fighting or dominance displays that increased their access to food or mates.

Second, throwing and projectile use during primitive (i.e., without firearms) and modern warfare are common (van Creveld 1989; Isaac and Isaac 2011). Indeed, one of the most common sex differences is that males more often than females throw projectiles during warfare (Murdock and Provost 1973; Wood and Eagly 2002). Throughout human history, lethal violence has been common (Gómez et al. 2016) and males have been far more likely than females to fight and participate in warfare (Turney-High 1971; Wilson and Daly 1985; Keeley 1996; Puts 2010). These circumstances suggest that there would have been stronger selection for throwing abilities in males than in females. Moreover, the effects of selection on throwing ability generated by frequent warfare were likely very strong because of the effects warfare can have on male survival. Archeological and ethnographic data suggest that 15–30% of male mortality in some groups may be caused by warfare and its consequences (Keeley 1996; Otterbein 2004). These levels of male mortality during primitive warfare suggest intense selection on the physical attributes, including throwing ability, that would promote success during combat and fighting (Lombardo and Deaner 2016). The advantages of being skilled at throwing, the use of projectile weaponry, and avoiding projectiles during combat are obvious and would lead to survival and reproductive advantages. Successful fighters and warriors are often rewarded with material goods and achieve high status, and are thereby able to gain greater access to fertile women, and thus obtain greater reproductive success, than nonwarriors (Chagnon 1988; Zerjal et al. 2003) resulting in selection for throwing ability and projectile use.

Finally, throwing projectiles is common in primitive hunting, especially for large game (Oswalt 1976; Shea 2009). Because hunting large game with thrown projectile weapons has been and remains primarily a male activity (Murdock and Provost 1973; Marlowe 2007), selection on throwing abilities would have been stronger on males than on females. Men who are good hunters, and therefore likely to be highly skilled at using projectiles, typically obtain high status and tend to have high reproductive success (Smith 2004; Gurven and Hill 2009) further augmenting selection for throwing ability.

Collectively, the adaptive advantages of being successful during fighting and as a hunter would have accelerated the evolution of superior male skills at throwing and projectile use because of the synergistic interaction between natural selection driven by the outcomes of male-male competition during combat and hunting and sexual selection driven by female mate choice for superior warriors and hunters. Moreover, the evolution of superior throwing abilities would have been rapid if there were large differences of fitness between individuals that had heritable differences in throwing ability (Fisher 1958).

Evidence of Sex Differences in Throwing Ability

The sex differences in throwing include differences in throwing velocity, distance, and targeting ability (Kimura 1999) and are among the largest documented behavioral sex differences (Thomas and French 1985; Hyde 2005). The sex differences in adult throwing ability are not strongly influenced by sex differences in the amounts of sports activity, especially throwing games, undertaken (Watson and Kimura 1991) and extensive practice does not eliminate them (Duffy et al. 2004).

males throw faster than females

At all ages, males throw faster, on average, than females. The sex differences in throwing velocity emerge during the preschool years before sex differences in sports involvement appear. By ages 4–7, 90% of boys throw faster than the average of same-age girls (Thomas and French 1985) and boys 6 years of age throw faster, on average, than do girls who are 9 years old (Rippee et al. 1990). Practice improves female throwing velocity but, when compared to males with similar throwing experience, the sex difference remains (Thomas and Marzke 1992; Petranek and Barton 2011). By age 12, the fastest throwing girls are comparable to the slowest throwing boys (Thomas and French 1985). Sex differences in throwing velocity persist through adolescence into middle age and although the differences decrease in the oldest age groups, they remain large (Lorson et al. 2013).

males throw farther than females

Throwing distance is positively and highly correlated with throwing speed and is influenced by the point in the throw when the projectile is released (Axe et al. 1996, 2014; Zhu et al. 2009). The magnitude of the sex differences in the development of distance throwing exceeds that of any other motor skill (Espenschade 1960) and manifests itself early; boys 6 years of age throw farther than girls who are 9 years old (Rippee et al. 1990), and only the very best girls throw as far as the least skilled boys at age 17 (Thomas and French 1985). Practice improves throwing distance for both sexes (Zhu et al. 2009), but females do not "catch up" to males (Thomas et al. 1994). The inability of girls to catch up to boys suggests that there may be a biological component that limits the ability of females to improve their throwing with training (Haubenstricker and Seefeldt 1986).

The sex differences in throwing the javelin demonstrate that highly trained women, even when they throw lighter projectiles, do not throw as far as men (Table 2). It is interesting to note that the javelin is most weapon-like of all of the projectiles thrown during track and field competitions.

The difference between the sexes in throwing for distance has consequences during warfare and hunting. Because males can throw farther than females, male warriors and hunters need not approach rival combatants or dangerous prey, respectively, as closely as females would thereby reducing their risks of detection and injury. The potential consequences of sex differences in throwing ability remain relevant in modern warfare (Browne 2007). For example, men in the U.S. Army are required to throw fragmentation grenades 35m whereas women are required to throw them 25m; the blast radius of the grenades is 15m (Department of the Army 2005). Therefore, a toss of only 60% of the required distance could have lethal consequences for female but not male grenade throwers.

males have better aimed throwing than females

The ability to throw a projectile and hit a target would have been an important cause of selection on ancient warriors and hunters. The sex difference in targeting ability while throwing manifests itself early and persists throughout life (Jardine and Martin 1983; Watson and Kimura 1991). Overall, 75% of men outperform the average woman at hitting a target with a thrown object (Watson and Kimura 1991). Differential sports experience with unimanual games, especially throwing games, contributes only a small proportion to the sex difference in throwing accuracy (Watson and Kimura 1988, 1991). This difference in throwing accuracy can have sex-biased fitness consequences in warfare and hunting because it makes males more effective than females as warriors and hunters.

males are better at intercepting projectiles than females

The advantages of being able to intercept or dodge projectiles during combat are obvious. Males are better, on average, than females at judging the velocity of moving objects (Schiff and Oldak 1990; Law et al. 1993; Sanders and Sinclair 2011), which is advantageous in judging the expected location of a projectile targeting them. Males outperform females at hitting a moving target with a thrown ball, although physical strength affecting accuracy at hitting distant targets and experience may be responsible for some of the sex difference (Peters 1997). The intercepting abilities of both males and females improve with practice and feedback, but the sex difference remains (Law et al. 1993).

Sex Differences in the Development of Throwing Ability

Throwing begins early in life when infants begin to manipulate objects. The first attempts at throwing are usually underhand tosses that eventually transition to overhand throwing (Cratty 1979). Boys tend to achieve mature throwing actions before girls (Butterfield and Loovis 1993; Marques-Bruna and Grimshaw 1997). Throwing proficiency involves flexion and extension of the trunk and arm with weight shifting from the foot on the same side as the throwing arm to weight shifting to the foot opposite the throwing side and with lower trunk and pelvis rotation occurring before upper trunk rotation (Williams and Monsma 2007). For example, boys, on average, show throwing proficiency at 69 months of age while girls do not show throwing proficiency until nearly three years later at 102 months of age (Williams and Monsma 2007). By age 3, boys throw much faster, farther, and more accurately than girls (Thomas and French 1985). There is no other motor skill early in life, middle childhood, or adolescence that boys perform so much better than girls. Before adolescence there is little sex difference in height, weight, and muscle mass (National Center for Health Statistics 2017), so male superiority in throwing cannot be attributed to sex differences in size or strength.

Many scholars of throwing attribute this developmental sex difference in throwing to greater male participation in ball sports and social encouragement of throwing skills by boys (Cratty 1979; Sakurai and Miyashita 1983; Bingham and Souza 2009). However, Butterfield and Loovis (1993) showed that sex differences in the throwing motion and performance remained after age and Tee-ball (simplified baseball), softball, or baseball participation were statistically controlled during analyses. These results are consistent with our hypothesis that the sex difference in throwing may have a biological component.

Our hypothesis predicts sex differences in throwing by children even in cultures where overhand throwing is not encouraged. Cross-culturally, many sex differences in interests and activities emerge before 2 years of age and continue to manifest themselves throughout childhood, adolescence, and adulthood (Cohen-Bendahan et al. 2005; Berenbaum 2011; Ceci and Williams 2011) and are related to adult reproductive strategies (Low 1989, 2000; Geary 1999). Some of these differences, including observations that boys show greater interest than girls in imitating propulsive actions, playing with weapons, and playing hunting and war games (Hoffman 1890; Eibl-Eibesfeldt 1989; Goldstein 1995; Loy and Hesketh 1995; Chagnon 1997; Benenson et al. 2011; Deaner and Smith 2013) likely reinforce the innate sex differences in throwing.

Environmental Influences Have Little Effect on Sex Differences in Throwing

The overhand throwing motion is a human universal; it develops naturally and appears before children learn to walk (Wickstrom 1977). The early onset of throwing, the pattern of development of the throwing motion, the age-related improvement in throwing ability, and the development of sex differences in throwing ability have been recorded wherever they have been studied, including Brazil, England, Germany, Japan, Mexico, New Guinea, Nigeria, Senegal, Tasmania, and the U.S. (Young 2009).

Male infants may have a greater predisposition for throwing than female infants because they imitate more frequently the propulsive movements (e.g., pushing, throwing, and kicking) associated with throwing (Benenson et al. 2011). Benenson et al. (2011) speculated that these forceful propulsive actions are behavioral expressions of masculinity and that masculine children (i.e., mostly boys) may derive greater pleasure from them than do nonmasculine children (i.e., mostly girls). Research in nonhuman primates and prenatally androgenized girls, (e.g., girls with Congenital Adrenal Hyperplasia) support the hypothesis that prenatal androgen exposure predisposes males to performing propulsive actions such as throwing. These observations led Benenson et al. (2011) to argue that this innate predisposition, and the pleasure that males derive from it, may provide the foundation for the male preference for games involving projectiles.

Training Does Not Eliminate the Sex Differences in Throwing Mechanics

There is individual variation in the effects of training on the development of throwing skills (Langendorfer and Roberton 2002). Individuals who reach the most advanced developmental levels for the major components of expert and efficient throwing are almost always boys (Stodden et al. 2006a, b). Boys tend to more quickly develop the mature throwing motion because they play more ball games than girls (McKenzie et al. 2002; Vandaele et al. 2011). However, girls and women, even with training, do not often display the most advanced components of the mature throwing motion (Stodden et al. 2006a, b), although training can produce improved throwing motions in preschool girls (Lorson et al. 2013; Veldman et al. 2017). These observations suggest the possibility that innate factors may limit the ability of girls to produce the mature throwing motion.

Culture Has Little Effect on Sex Differences in Throwing

Cultural norms regarding sports, hunting, and warfare have little effect on sex differences in throwing. Thomas et al. (2010) studied throwing in Australian Aboriginal boys and girls aged 6, 8, and 10 years. Both male and female Australian Aborigines throw during hunting and defense (Clarke 2003) leading Thomas et al. (2010) to predict that there would be few sex differences in throwing in this population. However, contrary to their prediction, boys still outperformed girls and the mean effect sizes were large ($d = 1.6$; Cohen 1992) but smaller than in same-aged populations in the U.S. (mean effect size, $d = 2.3$; Thomas et al. 2010). Australian Aboriginal girls outperformed girls from Germany and the U.S. indicating that throwing experience was responsible for their superior performance (Thomas et al. 2010). Indeed, Australian Aboriginal girls threw balls at 78% of the velocity of those thrown by Australian Aboriginal boys, the smallest sex difference in ball velocity recorded in non-Aboriginal Australian, German, Japanese, Thai, and U.S. populations (Young 2009; Thomas et al. 2010). The throwing abilities of the Aboriginal boys were comparable to boys from elsewhere.

Sex differences in throwing also occur in cultures where throwing games are not popular. Ehl et al. (2005) compared the throwing velocity of 13-year-old boys and girls in the U.S. and Germany. Throwing sports and games are more popular with boys and girls in the U.S. than they are in Germany where the most popular sport that involves frequent overhand throwing is team handball, which is not very popular compared to soccer. Ehl et al. (2005) predicted that sex differences in throwing would be smaller in Germany than in the U.S. where there are more sex differences in throwing experience. They found sex differences in both populations and the relative differences between the sexes were about the same. In terms of effect sizes, and contrary to the authors' expectations, the differences between boys and girls were larger in Germany (d = 5.36) than in the U.S. (d = 1.82). The observation that German boys threw much better than girls in the U.S. even though they do not throw much, have U.S.-like cultural support or encouragement for throwing, and throw as well as U.S. boys (Ehl et al. 2005) is consistent with our hypothesis and challenges the hypothesis that sex-biased training significantly contributes to the sex differences in throwing.

In summary, the evidence from a variety of disciplines is inconsistent with the hypothesis that environmental influences account for a large proportion of the sex differences in throwing. Nevertheless, the idea that sex differences in throwing result solely from environmental influences, including the idea that females are "conditioned by their sexist oppression in contemporary society" to be poor throwers (Young 2009:152) appears to be the dominant view among scholars and journalists (e.g., Haspel 2012; Anthamatten 2014).

SEX DIFFERENCES IN THROWING BEHAVIOR IN SPORTS

Most hypotheses about the functions of sport agree that it likely had its origins as a way for males to develop and practice the skills necessary for primitive warfare and/or hunting (Sipes 1973; Chick et al. 1997; Carroll 2000; Lombardo 2012). Numerous studies demonstrate that boys consistently attain higher scores than girls on tests of motor proficiency skills that require the same kinds of bursts of power (e.g., jumping, sprinting, and throwing; Venetsanou and Kambas 2016) that are advantageous during fighting and hunting. The connection between primitive warfare and hunting techniques and sports that involve throwing, intercepting, and dodging projectiles is obvious. These observations are consistent with our hypothesis that throwing evolved as a male adaptation in the context of greater male than female participation in fighting and hunting. Because weapons are thrown much less frequently during modern combat or hunting than they were in the past, we predict that vestiges of the importance to males of developing throwing ability are present today in the prominence of throwing, intercepting, and dodging projectiles in sports.

Although sports are a human universal (Brown 1991) and despite the recent rapid increase in participation by females, especially in the U.S. (Shulman and Bowen 2001), they remain primarily a male endeavor (Guttmann 1991, 2004a,b). Deaner et al. (2012) confirmed the generalization that males not only play sports more often but are also more motivated to play sports than are females even when accounting for a country's gender inequality (Deaner et al. 2012, 2016; Deaner and Smith 2013; Balish et al. 2016). The generalizations that sports played by boys and men often either involve throwing projectiles for distance, velocity, or accuracy or avoiding getting hit by, catching, or hitting projectiles in clear parallel to the use of projectiles in primitive hunting and warfare (Deaner et al. 2012).

Boys in traditional societies throw projectile weapons during play more often than girls because boys play war and hunting games more often (Hoffman 1890; Eibl-Eibesfeldt 1989; Loy and Hesketh 1995; Chagnon 1997). For example, Himba boys in Namibia practice throwing stones for distance and accuracy more often than girls (Eibl-Eibesfeldt 1989) and Yanomamö boys start practicing with bows at a very early age (Chagnon 1997).

Sex Differences in Throwing During Combat

If throwing first evolved in the context of agonistic interactions, then we predict that throwing and projectile use would be male-biased and play a central role in primitive warfare. Primitive warriors used human muscle power to throw bolas (i.e., a number of balls connected by a cord that when thrown entangles the legs of prey), boomerangs, darts, knives, spears thrown with and without the aid of atlatls, sticks, and stones (Turney-High 1971; Oswalt 1976; van Creveld 1989). More advanced weapons (arrows, catapults, bullets, and missiles) rely on mechanical or chemical sources of energy to "throw" projectiles (van Creveld 1989; Crosby 2002). Although sticks and stones were undoubtedly the first thrown projectiles, they are used much less often by modern warriors. However, they remain effective weapons and are commonly used during conflicts with rivals, including against those with much more lethal weapons such as firearms. For example, modern rioters commonly throw stones, bricks, and bottles at police or soldiers armed with firearms. The threat of being injured or killed by thrown projectiles is treated as serious by targets who have been known to fire their guns at stone-throwing protestors (President's Committee on Campus Unrest 1988).

In Australia, the bow was not yet invented so men and women used throwing sticks for defense before the introduction of firearms but, as elsewhere, men were much more likely than women to be warriors (Davidson 1936; Clarke 2003). Even though throwing is an important skill for Australian Aboriginal girls, they remain inferior throwers compared to Australian Aboriginal boys. Aboriginal girls are even inferior throwers compared to boys in modern Germany where hunting and fighting by throwing is virtually nonexistent and sports that involve throwing are not popular (Thomas et al. 2010).

Collectively, these observations are consistent with our hypothesis that the causes of selection on throwing ability were stronger on males than on females and have resulted in the evolution of sex differences in throwing that are resistant to change by training. Nevertheless, environmental influences such as the different treatment of boys and girls by parents, teachers, and coaches during development and differential throwing and sports experience and opportunities due to cultural norms and expectations likely account for some of the sex differences in throwing (Cratty 1979; Young 1980; Sakurai and Miyashita 1983; Nelson et al. 1986; Thomas and Thomas 1988).

Sex Differences in Throwing Behavior During Hunting

Throwing and the use of projectiles are common in primitive hunting, especially against large game (Oswalt 1976; van Creveld 1989; Churchill 1993; Hitchcock and Bleed 1997; Shea 2009). Hunting large game with projectile weapons is primarily a male activity (Murdock and Provost 1973; Marlowe 2007). Modern hunter-gatherer women may hunt but with the exception of the Agta of the Philippines (Goodman et al. 1985), they rarely use weapons capable of penetrating the flesh of their prey (Testart 1986 in Villotte and Knüsel 2014).

The Sex Differences in Anatomical Features Associated with Throwing are Evolutionary Consequences of Selection Favoring Male Throwing Biology

If the causes of selection are stronger on one sex, then the evolutionary consequences of that selection are more prominently expressed in that sex (Darwin 1871). The scientific literature is replete with examples of sex differences in anatomy and behavior that have evolved as consequences of different causes of selection on males and females. An especially compelling example is the derived curvature (i.e., lumbar lordosis) and reinforcement of the lumbar vertebrae of human females to compensate for the ways that the expanded abdomen of pregnancy and enlarged breasts during lactation compromise locomotion by relocating the female's center of mass from over her pelvis to a position anterior to her hips (Whitcome et al. 2007; Masharawi et al. 2010; Hay et al. 2015). This female-only skeletal adaptation may have arisen with the advent of bipedalism in the Australopithecines prior to 2 million years ago (Whitcome et al. 2007). Males have not evolved these skeletal adaptations because the biomechanical challenges associated with being bipedal and pregnant or lactating are not causes of selection on male anatomy.

Given the biomechanical demands of the very rapid and coordinated movements of the humerus and forearm, trunk rotation, and striding toward the target during the mature throwing action (Wild 1938) and the historically important sex differences in throwing behavior during combat and hunting, we predict that selection has produced sex differences in anatomy associated with throwing.

If the consequences of throwing ability were stronger causes of selection on males than on females, then we predict sex differences to have evolved in the anatomical traits associated with throwing. However, intrasexual variation in these traits are also expected because bone morphology is affected by the interaction between the genetic information shaping it and the mechanical forces it is subjected to during development (Ruff 2003). Observations of little inter- or intrasexual variation in bone morphology are evidence of strong selection favoring a particular phenotype (Williams 1985; West-Eberhard 2003).

Sex Differences in the Pectoral Girdle

Anatomical sex differences in the pectoral girdle relevant to throwing performance are summarized in Table 3. Below we discuss how sexual dimorphism in each of these features may contribute to the sex differences in throwing performance.

Shoulder Width

Shoulder width is a significant predictor of the torso's contribution to the kinetic energy of thrown projectiles (Maki 2013). That males, on average, have wider shoulders than females is well established (Stoudt et al. 1970; Malina and Zavaleta 1976; Lohman et al. 1988). Moreover, sex differences in shoulder width are large in both an Australian Aboriginal population in which both males and females throw in hunting and defense (Abbie 1957) and in 20th-century populations in the U.S. (Montoye et al. 1965) and England (Hiorns and Harrison 1985) in which throwing was likely much less important to survival. The large effect sizes in all of these studies indicate little overlap between men and women (Table 3). The sexual dimorphism in shoulder width develops during the pubertal growth spurt (Gasser et al. 2000) producing large sex differences in shoulder width in adolescents (Table 3). This sex difference suggests that there was strong selection on males beginning in puberty favoring arm and shoulder power production, both of which would contribute to throwing performance (Lundh et al. 2011) even if the primary cause of selection on arm and shoulder power production was success in hand-to-hand combat (Lombardo and Deaner 2016).

Glenoid Fossae

The articulations between the glenoid fossae of the scapulae and humeral heads form the shoulder joints. The orientation and size of the glenoid fossa affect throwing by affecting the range of motion (ROM) of the arms.

Glenoid Inclination

The upward/downward tilt of the glenoid fossa relative to the scapula is referred to as glenoid inclination (Figure 1). The cranial orientation of the glenoid fossae of other primates is inferred to be an adaptation for the overhead use of the arms during arm-hanging

TABLE 3

Sex differences in the anatomical characteristics of the pectoral girdle associated with throwing by modern humans

Anatomical characteristic	Condition that enhances throwing ability	Population time period	Population age group	Population identity and/or location (side measured)	Sample sizes M, F	Direction of sex difference	P	d	Reference
Shoulder width	Wider	20th century	Adults	Njalia Aboriginies, Australia	22, 20	M > F	***	1.88	Abbie (1957)
		20th century	Adults	U.S.	418, 475	M > F	***	2.12	Montoye et al. (1965)
		20th century	Adolescents	England	61, 38	M > F	***	2.16	Hauspie et al. (1985)
		20th century	Adolescents	India	49, 38	M > F	***	1.89	Hauspie et al. (1985)
		20th century	Adults	England	132, 130	M > F	***	13.66	Hiorns and Harrison (1985)
Glenoid inclination	Lateral orientation	20th century	Adults	African and Euro-Americans (mean of right and left)	100, 72	Male more lateral than female	NS	0.14	Churchill et al. (2001)
Glenoid version	Greater retroversion	20th century	Adults	Japan (mean of right and left)	97, 108	M > F	***	0.33	Matsumura et al. (2014)
Glenoid breadth	Wider	20th century	Adults	African and Euro-Americans (mean of right and left)	100, 72	M > F	***	2.80	Churchill et al. (2001)[1]
		20th century	Adults	Guatemala (left)	65, 38	M > F	***	2.60	Frutos (2002)
		Pre-1800	Adults	New Zealand Polynesian (not indicated)	31, 37	M > F	***	2.53	Murphy (2002)
		10th and 11th centuries	Adults	East Anatolia (left)	47, 45	M > F	***	2.12	Özer et al. (2006)
		20th century	Adults	African and Euro-Americans (mean of right and left)	184, 184	M > F	***	2.04	Merrill et al. (2009)[1]

continued

TABLE 3
Continued

		20th century	Adults	African and Euro-Americans (left)	447, 277	M > F	***	1.98	Dabbs and Moore-Jansen (2010)[1]
		20th century	Adults	Black South Africans	60, 60	M > F	***	2.08	Macaluso (2011)
		19th and 20th centuries	Adults	Crete (left)	81, 66	M > F	***	2.51	Papaioannou et al. (2012)
Glenoid height	Taller	20th century	Adults	African and Euro-Americans (mean of right and left)	100, 72	M > F	***	2.61	Churchill et al. (2001)[1]
		20th century	Adults	Guatemala (left)	65, 37	M > F	***	2.50	Frutos (2002)
		Pre-1800	Adults	New Zealand Polynesian (not indicated)	17, 22	M > F	***	2.55	Murphy (2002)
		10th and 11th centuries	Adults	East Anatolia (left)	45, 45	M > F	***	1.70	Özer et al. (2006)
		20th century	Adults	African and Euro-Americans (mean of right and left)	184, 184	M > F	***	1.25	Merrill et al. (2009)[1]
		20th century	Adults	African and Euro-Americans (left)	447, 277	M > F	***	2.35	Dabbs and Moore-Jansen (2010)[1]
		20th century	Adults	Black South Africans (left)	60, 60	M > F	***	2.27	Macaluso (2011)
		19th and 20th centuries	Adults	Crete (left)	81, 66	M > F	***	2.29	Papaioannou et al. (2012)
Glenoid area	Larger	20th century	Adults	Germany (not indicated)	114, 100	M > F	***	2.48	Prescher and Klümpen (1995)
		20th century	Adults	Black South Africans (left)	60, 60	M > F	***	2.37	Macaluso (2011)
Glenoid index = glenoid breadth/height	Larger	20th century	Adults	Euro-Americans (mean of right and left)	46, 50	M < F	NS	0.20	Churchill and Trinkaus (1990)

continued

TABLE 3
Continued

Anatomical characteristic	Condition that enhances throwing ability	Population time period	Population age group	Population identity and/or location (side measured)	Sample sizes M, F	Direction of sex difference	P	d	Reference
		20th century	Adults	African and Euro-Americans (mean of right and left)	184, 184	M > F	***	1.40	Merrill et al. (2009)[1]
		20th century	Adults	Euro-Americans (right)	40, 39	M > F	NS	0.31	Churchill and Rhodes (2009)
		20th century	Adults	African Americans (right)	25, 25	M > F	NS	0.20	Churchill and Rhodes (2009)
		20th century	Adults	Aleutian Islanders (right)	24, 20	M > F	NS	0.19	Churchill and Rhodes (2009)
Clavicle length	Longer	20th century	Adults	African Americans (right)	50, 50	M < F	*	0.42	Terry (1932)
		20th century	Adults	Amritsar Zone, India (right)	236, 112	M > F	***	1.74	Jit and Singh (1966)
		20th century	Adults	Varanasi Zone, India (right)	97, 97	M > F	***	1.99	Singh and Gangrade (1968)
		20th century	Adults	Chandigarh Zone, India (right)	280, 80	M > F	***	1.82	Jit and Sahni (1983)
		Pre-European Settlement	Adults	New Zealand Polynesian (right)	12, 15	M > F	***	2.28	Murphy (1994)
		20th century	Adults	Chandigarh Zone, India (right)	748, 252	M > F	***	1.63	Kaur et al. (2002)
		21st century	Adults	Iran (left)	60, 60	M > F	***	1.77	Akhlaghi et al. (2012)
		21st century	Adults	Southern India (right)	185, 135	M > F	***	0.92	Nagarchi et al. (2014)
		21st century	Adults	North Karnataka Zone, India (right)	39, 30	M > F	***	0.87	Shobha et al. (2014)
		21st century	Adults	Spain (right)	45, 32	M > F	***	2.41	Alcina et al. (2015)

continued

TABLE 3
Continued

Humeral torsion—"twisting" of the humerus from medial orientation	Less (i.e., more retroversion—humerus head oriented posteriorly)	20th century	Adults	Sardinia (mean of right and left)	100, 99	M > F	NS	0.12	Gualdi-Russo (1998)
		Unknown	Adults	Euro-American (right)	17, 11	M < F	**	1.22	Edelson (1999)
		Unknown	Adults	African American (right)	15, 11	M < F	NS	0.68	Edelson (1999)
		Unknown	Adults	Alaskan Inuit (right)	15, 13	M < F	NS	0.87	Edelson (1999)
		Unknown	Adults	Northern Chinese (right)	16, 12	M < F	NS	0.12	Edelson (1999)
		Unknown	Adults	Bedouin (right)	14, 15	M < F	NS	0.73	Edelson (1999)
		Unknown	Adults	Native American—New Mexico (right)	16, 13	M < F	**	1.21	Edelson (1999)
		Unknown	Fetuses aged 5–9 months	African and Euro-American (right)	29, 21	M > F	NS	0.08	Edelson (1999)
		20th century	Adults	Euro-American (right)	26, 26	M < F	***	1.01	Rhodes and Churchill (2009)
		20th century	Adults	African American (right)	25, 25	M < F	**	0.74	Rhodes and Churchill (2009)
		Pre- and early post-Russian contact	Adults	Aleutian Islander (right)	25, 24	M < F	NS	0.29	Rhodes and Churchill (2009)
		21st century	Adults	Japan (mean of right and left)	97, 108	M < F	***	0.45	Matsumura et al. (2014)

See the text for complete descriptions of how the characteristics are related to throwing. To be included, sources of data needed to report the means, standard deviations, sample sizes, the time period when the individuals sampled lived, the age class of individuals, and the identity of the population to which individuals belonged. A *t*-test was used to statistically compare the sexes.
NS = Not Significant.
*= $P \leq 0.05$, **= $P \leq 0.01$, ***= $P \leq 0.001$. d = effect size (Cohen 1992).
[1]Samples overlap because investigators used samples in the Hamann-Todd Collection at the Cleveland Museum of Natural History, Cleveland, Ohio.

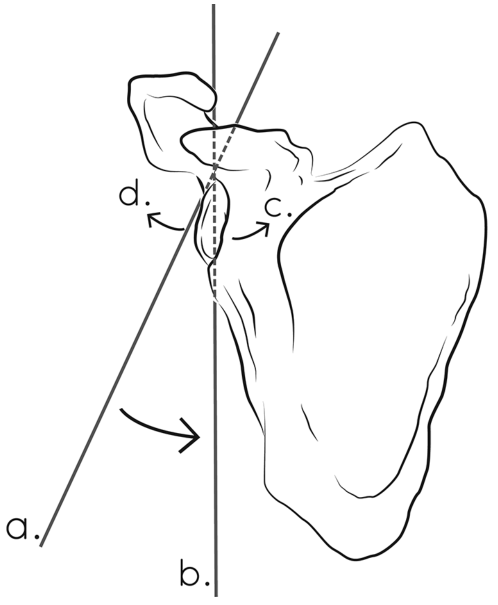

FIGURE 1. DORSAL VIEW OF LEFT SCAPULA INDICATING GLENOID FOSSA INCLINATION AND VERSION

a. Cranial inclination of the glenoid fossa. The cranial orientation of the glenoid fossa in other primates is inferred to be an adaptation for the overhead use of the arms during arm-hanging and climbing (Hunt 1991; Young et al. 2015). b. Lateral orientation of the glenoid fossa found in *Homo* facilitates throwing. c. Glenoid retroversion (i.e., dorsal tilt of the glenoid) facilitates throwing performance. d. Glenoid version (i.e., ventral tilt of the glenoid).

and climbing (Hunt 1991; Young et al. 2015). The Australopithecines had cranially oriented glenoid fossae leading to the inference that, although they were bipedal, they had not yet anatomically abandoned their ability to climb (Stern 2000; Green and Alemseged 2012; Larson 2012; Churchill et al. 2013). In contrast, members of the genus *Homo* have laterally oriented shoulder joints (Walker and Leakey 1993; Larson 2009; Young et al. 2015, but see Lordkipanidze et al. 2007) that facilitate throwing.

If the lateral orientation of the glenoid fossa facilitates high-speed throwing (Roach et al. 2013), they should, on average, be more laterally oriented in males than in females. Contrary to this prediction, there is no evidence of statistically significant sexual dimorphism in this trait (Table 3). However, the trend of the sex difference is in our predicted direction (Table 3). For example, the glenoid fossae of adult African American and European American males, on average, were more laterally oriented than those of females (Churchill et al. 2001). The lack of statistically significant sexual dimorphism in glenoid inclination suggests two nonmutually exclusive explanations. First, there may be developmental constraints on adult glenoid inclination. Second, glenoid inclination, within a relatively wide range, may not affect throwing performance.

GLENOID VERSION

Glenoid version refers to the dorsal/ventral orientation of the glenoid surface and is defined as the angle between a line connecting the anterior and posterior rims of the glenoid and the line perpendicular to the scapular axis (Friedman et al. 1992; Figure 1). Glenoid fossae tilted ventrally relative to a lateral orientation are described as having positive version; those tilted dorsally are described as being retroverted. External rotation of the glenohumeral joint, and therefore throwing performance, improves with increased retroversion (Crockett et al. 2002; Whiteley 2007; Wyland et al. 2012; Roach et al. 2013). Glenoid version is influenced by activity and typically becomes retroverted with frequent throwing. For example, increased glenoid retroversion is commonly observed in the dominant shoulder of throwing athletes and is likely due to the mechanical stresses of throwing during skeletal development. Accordingly, glenoid retroversion is not well developed in the dominant shoulders of nonthrowing athletes (Crockett et al. 2002; Wyland et al. 2012).

Matsumura et al. (2014) reported the glenoid fossae of males being significantly more retroverted, on average, than those of females but the effect size was moderate (Table 3). As expected, individuals with a history of playing throwing sports had greater glenoid retroversion in their dominant shoulders. High glenoid retroversion and low humeral torsion (see below) increase shoulder external rotation (Matsumura et al. 2014) and thus they may be skeletal adaptions for overhand throwing.

GLENOID SHAPE

The glenoid fossa's size and shape affect throwing performance (Crockett et al. 2002; Wyland et al. 2012; Roach et al. 2013) because they influence the upper arm's ROM (Churchill and Trinkaus 1990). The glenoid fossa is pear-shaped (Merrill et al. 2009; Figure 2). Sexual dimorphisms in the breadth and height of the glenoid fossae of anatomically modern humans are large (Table 3), well known by anatomists (Prescher and Klümpen 1995; Merrill et al. 2009), and are used to identify the sex of the dead from skeletal remains (Di Vella et al. 1994; Frutos 2002; Murphy 2002). The wide glenoid fossae of modern humans may have resulted from selection on glenoid shape during a history of frequent overhand throwing (Churchill and Trinkaus 1990). Male shoulders have larger joint surfaces because their glenoid fossae area is larger than that of females (Table 3). The larger joint surfaces relative to body stature in males are likely related to greater male muscularity and skeletal robusticity (Churchill and Trinkaus 1990). The dimensions of the glenoid fossae develop early in fetal life (Hrdlička 1942) and the sex differences are apparent by 4.2 years of age (Humphrey 1998) suggesting that selection shaped these sex differences.

The ratio between the glenoid's greatest breadth and height, glenoid index (Figure 2), is related to the degree of dorsoventral glenohumeral movement (Churchill and Trinkaus 1990). The glenoid index of Neanderthals was less than that of modern humans. This likely limited the ROM of Neanderthal upper arms and consequently their ability to throw projectiles with an overhand motion (Churchill and Trinkaus 1990). Modern males typically have larger glenoid indices than females, but the difference is not always statistically significant and effect sizes range from small to moderate (Table 3). The sexual dimorphism of the glenoid is not due solely to sex differences in body size; when the ratios between humerus length and either glenoid breadth or height are used to control for body size, male glenoid fossae are larger (Churchill and Trinkaus 1990). Consequently, resulting greater ROM in the glenohumeral joints of males likely contributes to the male advantage in throwing speed.

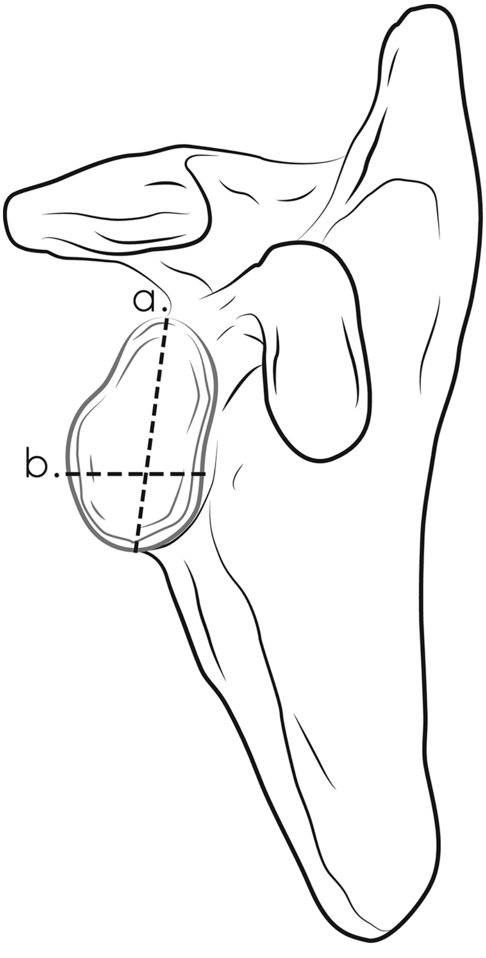

FIGURE 2. GLENOID FOSSA SHAPE
Glenoid index = (b/a); a larger glenoid index and glenoid area facilitate throwing by increasing the range of motion of the glenohumeral joint.

Interestingly, the dimensions of the glenoid, especially the lower glenoid where it articulates with the humeral head, show the least individual variation of all of the anatomical structures of the scapula (Hrdlička 1942). This suggests that the ROM requirements of the overhead arm actions needed for throwing, and possibly overhand clubbing (Young 2009), were important causes of selection on glenoid shape.

CLAVICLE LENGTH

The clavicle anchors the shoulder complex to the torso and its length may influence throwing performance (Larson 2007b, 2015; Roach and Richmond 2015). Short clavicles are thought to result in poor throwing ability mostly because individuals with pathologically short clavicles report an inability to throw well (Larson 2007b). If clavicle length is directly related to throwing ability, we predict that the clavicle lengths of males would be more advantageous for throwing than those found in females. Indeed, males have longer clavicles, on average, than females and the difference between the sexes is large (Table 3) and is used to identify the sex of the dead from skeletal remains (Terry 1932; Singh and Gangrade 1968; Murphy 1994; Frutos 2002; Kaur et al. 2002; Özer et al. 2006; Akhlaghi et al. 2012; Papaioannou et al. 2012; Alcina et al. 2015). However, the sex difference in clavicle length is related to larger male body size. In one study, relative clavicle length was not related to throwing performance in Daasanach men in East Africa who are expert throwers and frequently use throwing sticks during hunting (Roach and Richmond 2015).

HUMERAL TORSION

A central assumption in the clinical and sports medicine literature is that the normal condition of the shoulder joint is a laterally facing glenoid fossa with a medially facing humeral head (Larson 2007a). In reality, the humeral head is slightly twisted and thus does not often face directly medially. This condition is referred to as humeral torsion and is measured as the angle between a line bisecting the proximal head of the humerus and one between the lateral and medial epicondyles of the distal humerus (Figure 3; Krahl and Evans 1945). Both heredity and the muscular forces acting on the upper arm and shoulder joint during development affect the degree of torsion (Evans and Krahl 1945). However, once growth has stopped, increased training does not alter the degree of torsion (Meyer et al. 2011). Low humeral torsion (Figure 4) is typically described as a skeletal adaptation to frequent, excessive external rotation from overhand throwing during growth (Pieper 1998).

Low humeral torsion is advantageous for throwing because it enables throwers to increase the cocking phase of their throw producing increased projectile velocity (Rhodes and Knüsel 2005; Roach et al. 2012). Observations of low humeral torsion in modern athletes playing sports requiring frequent overhand throwing are common (Crockett et al. 2002; Osbahr et al. 2002; Whiteley et al. 2009). From these observations, Roach et al. (2013) hypothesized that *Homo erectus*, because of its low humeral torsion, was capable of high-speed overhand throwing. Early hominins were characterized by low humeral torsion (Walker and Leakey 1993; Larson et al. 2007; Lordkipanidze et al. 2007; Lovejoy et al. 2009; Churchill et al. 2013). However, Larson (2015) cogently argued that it is difficult to reconcile the inference of the growing importance of throwing to the survival of post-*H. erectus* hominins with the subsequent increase rather than expected decrease in humeral torsion. Nevertheless, because low humeral torsion facilitates high-speed throwing, we predict that males exhibit lower humeral torsion than females.

Consistent with our prediction, humeral torsion is (with few exceptions) lower in males, on average, than in females (Table 3). However, the extensive variation in humeral torsion angles between dominant and nondominant arms within individuals (e.g., throwing arms show significantly less torsion than nonthrowing arms in baseball pitchers; Pieper 1998; Whiteley et al. 2009), between sexes, and within and among populations (Table 3) suggests three, nonmutually exclusive explanations. First, within a fairly wide range, the actual angle of humeral torsion may have only a modest direct effect on throwing ability. Therefore, humeral torsion angle may not have been an important target of selection during the evolution of throwing in hominins (Maki 2013). Second, because frequent throwing decreases humeral torsion (Krahl

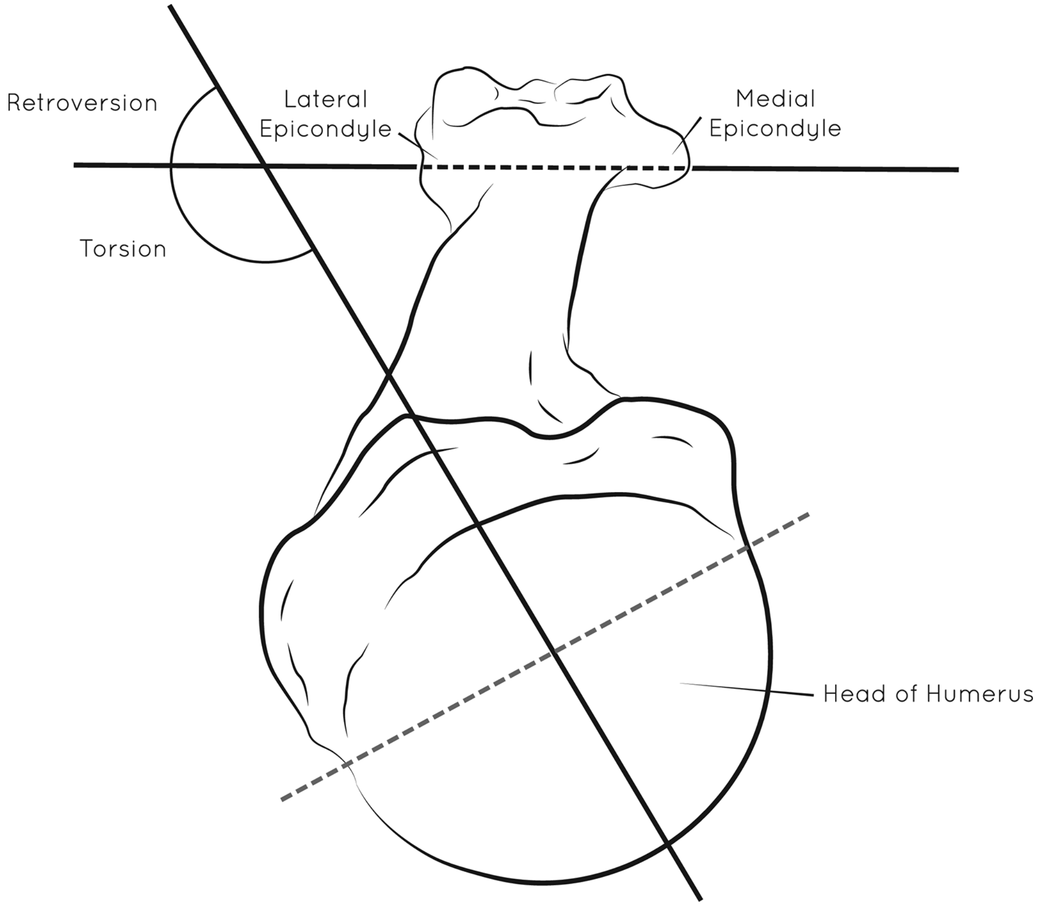

FIGURE 3. TORSION OF LEFT HUMERUS
Humeral torsion is measured as the angle between a line bisecting the proximal head of the humerus and one between the lateral and medial epicondyles of the distal humerus (Krahl and Evans 1945).

and Evans 1945; Edelson 1999; Rhodes 2006; Cowgill 2007), especially in dominant arms, the relatively wide range of humeral torsion angles observed in modern humans suggests there are population, sex, and individual differences in activities requiring external rotation of the arm (Cowgill 2007). Third, we hypothesize that the wide variation in humeral torsion reflects evidence of relaxed selection on this trait during the evolution of anatomically modern humans. The transition from hunter-gatherer to agricultural subsistence economies may have relaxed selection on throwing adaptations in humeral torsion. For example, male Native American hunter-gatherers in southern California from groups that used spears and atlatls displayed greater bilateral asymmetry in humeral torsion than did males in contemporaneous groups that were agriculturalists (Gjerdrum et al. 2003). This pattern suggests important differences between these populations in the frequency of overhand motions such as throwing.

SUMMARY OF THE SEX DIFFERENCES IN THE PECTORAL GIRDLE RELATED TO THE SEX DIFFERENCES IN THROWING

The sex differences in the anatomy of the pectoral girdle are, with few exceptions, in the direction that would result in superior

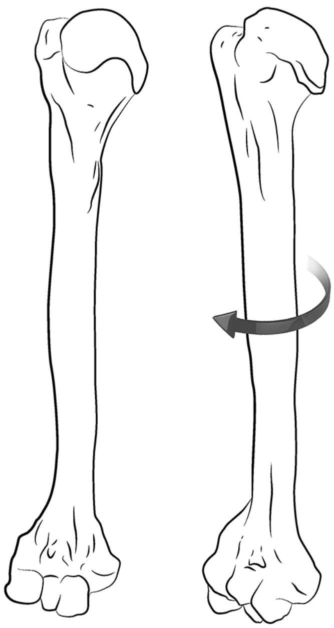

FIGURE 4. VIEW OF RIGHT HUMERUS COMPARING A HUMERUS SHOWING NO TORSION AND ONE WITH INCREASED TORSION

Low humeral torsion is advantageous for throwing because it increases the cocking phase of the throw resulting in increased projectile velocity (Rhodes and Knüsel 2005; Roach et al. 2012).

throwing performance by males. Moreover, they are consistent with the nonmutually exclusive hypotheses that overhand motions during growth are performed more often by males than females and shape the pectoral girdle in ways that result in superior male throwing performance and throwing ability was a more important cause of selection on male than female throwing ability. Whether the skeletal structures of male pectoral girdles are more responsive to frequent overhand throwing than those of females remains an open question.

OTHER SEX DIFFERENCES IN ANATOMY AFFECTING THROWING ABILITY

Several anatomical sex differences that are not specific to throwing contribute to male throwing superiority. Bodies that are taller, have more muscle mass, and longer limbs are capable of generating more muscular torque and power during throwing (Chu et al. 2009). Some of these features may have been targets of selection for reasons (e.g., climatic adaptations; Ruff 1991, 1994) other than throwing but once evolved would have contributed to the sex differences in throwing performance. Thus, some traits may be considered to be exaptations for throwing (Maki 2013). Therefore, regardless of the multiple synergistic causes of selection that favored larger males than females during the course of human evolution, sex differences in various components of body size have produced superior male throwing performance. As these traits evolved and produced superior throwing performance, they also may have reinforced the adoption of throwing weapons by *H. erectus* and its successors.

SEX DIFFERENCES IN BODY SIZE

Males, on average, are larger than females. Van den Tillaar and Ettema (2004) studied the relationship between sex, body size, isometric strength, and throwing velocity in Norwegian team handball players and concluded that fat-free body mass, independent of sex, is the factor that contributes the most to throwing velocity. From that result, they argued that the greater muscle mass of males is the primary cause of the sex difference in throwing velocity. Within sexes, larger athletes typically throw faster (Pyne et al. 2006) and farther (Morrow et al. 1982).

SEX DIFFERENCES IN STRENGTH

Muscular strength is positively correlated with the ability to throw fast and far. The muscular strength differences between males and females are well established (Bishop et al. 1987; Lassek and Gaulin 2009). For example, female strength even when controlling for differences in fat-free body mass, limb, or body size ranges from 40–75% of male strength (Bishop et al. 1987). The upper-body strength of males (Bishop et al. 1987; Lassek and Gaulin 2009) contributes to the sex differences in throwing velocity.

SEX DIFFERENCES IN ARM LENGTH

Longer arms produce greater external arm rotation during throwing resulting in faster throws (Roach et al. 2013). Males have longer upper arms and forearms than females (Gindhart 1973; Dittrick and Suchey 1986; Steyn and İşcan 1997; İşcan et al. 1998; Kranioti and Michalodimitrakis 2009; Wyland et al. 2012; Waidhofer and Kirchengast 2015). Arm bone lengths can be used to identify the sex of the dead from skeletal remains (Krogman 1962; Stewart 1979; Bass 1995). Moreover, males have relatively longer forearms than females (Fullenkamp et al. 2008) and this difference emerges in utero (Tanner 1978). The sex difference in forearm development is consistent with a hypothesis of strong selection on male forearm length for throwing because disproportionately long forearms increase the extent of arm external rotation thereby increasing throwing velocity.

SEX DIFFERENCES IN HAND AND FINGER LENGTH

The longer hands and fingers of males at the ends of their longer arms (Peters et al. 2002) contribute to greater external arm rotation and thus greater throwing speed. Young (2009) argued that this advantage during overhand clubbing in hunting and combat may have favored the evolution of longer arms, hands, and fingers in males than in females.

SEX DIFFERENCES IN WAIST LENGTH

A tall, mobile waist decouples the hips and thorax during throwing permitting more torso rotation to produce the high torque needed to load the shoulder's elastic elements and produce faster throws (Roach et al. 2013). When height is controlled for, anatomically modern males have taller waists than females (Fullenkamp et al. 2008) facilitating faster throwing by males. It is not yet known whether the greater lumbar lordosis of females (Whitcome et al. 2007; Hay et al. 2015) compromises female ability to throw by inhibiting torso rotation.

SEX DIFFERENCES IN LEG LENGTH

Regardless of the primary causes of selection that shaped the sexual dimorphism in leg length, longer legs help males throw faster and farther than females (Maki 2013). Males have longer legs, on average, than females and femur length is used to identify the sex of the dead from skeletal remains (Krogman 1962; Stewart 1979; Bass 1995). Moreover, leg length is important because stride length during overhand throwing contributes nearly 70% of the variation in throwing velocity (Stodden et al. 2006a). The overhand throwing stride length, as measured as percent of height, of elite female baseball pitchers (approximately 70%) was significantly shorter than that of elite male pitchers (approximately 78%; Chu et al. 2009).

Sex Differences in Injuries Associated with Throwing

If throwing was primarily a male activity, then we predict the existence of sex differences in injuries associated with throwing. For example, lesions of tendon attachments (i.e., enthesopathies) of the medial epicondyle were more common in males than females in prehistoric, preindustrial historic, and modern European populations (Villotte and Knüsel 2014). These injuries are evidence indicative of a sexual division of labor in those populations in arm movements that involve external rotation of the arm like those used in throwing, overhand clubbing, or in the use of an adze or axe. Sex differences in extensive training in these activities during growth may have contributed to the greater frequency of male medial epicondyle enthesopathies (Villotte and Knüsel 2014).

Although there are few sex differences in injury rates in college athletes in the U.S., females are more likely than males to injure their shoulders in swimming and water polo (Sallis et al. 2001), sports that require repetitive overhand shoulder motions, including external and internal rotation, against water resistance. Water polo also requires throwing. The greater frequency of shoulder injuries in females suggests a history of stronger selection on males than females for repetitive forceful movements of their shoulders such as those that would be caused by the frequent throwing of weapons. Similarly, during ergonomic studies females had a higher prevalence of upper musculoskeletal disorders associated with repetitive motions (Nordander et al. 2009). Together, these injury data are consistent with our hypothesis because they are indirect evidence that males have evolved greater resistance than females to injuries caused by repetitive forceful movements of their upper extremities such as those associated with throwing.

Concluding Remarks

Sex differences in human behavior are subjects of notoriously contentious debates. However, there can be little doubt that there are innate sex differences in strength and speed. Throwing must be now added to that list.

We do not dispute the observation that *all* modern humans have the basic adaptations for throwing. Our hypothesis is that males are better adapted for throwing than females because during human evolution the consequences of throwing success or failure on fitness have been a stronger cause of selection on males. To be clear, we are not arguing that socialization has no effect on the sex differences in throwing or that females cannot become effective throwers. In fact, we presented evidence that training can improve female throwing performance and that some females are expert throwers. The evidence that socialization plays a role in producing sex differences is not incompatible with the evolutionary approach we take here. The patterns of sex differences in a variety of traits often reflect differences in cultural norms and practices and are related to adult reproductive strategies and the causes of selection that shaped those strategies (Low 2000). Therefore, from an evolutionary perspective it is extremely unlikely that socialization alone can explain all of the sex differences in throwing. We have presented several lines of evidence that support our hypothesis that sex differences in throwing have a partly innate basis. Moreover, the evidence is inconsistent with the view held by many that sex differences in throwing are due solely to environmental causes (Table 1). In our view, the consilience of multiple, independent lines of evidence from anatomy, anthropology, archeology, childhood development, ethology, primatology, and sports sciences that were collected for purposes other than testing our hypothesis strengthens its support (Wilson 1998).

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