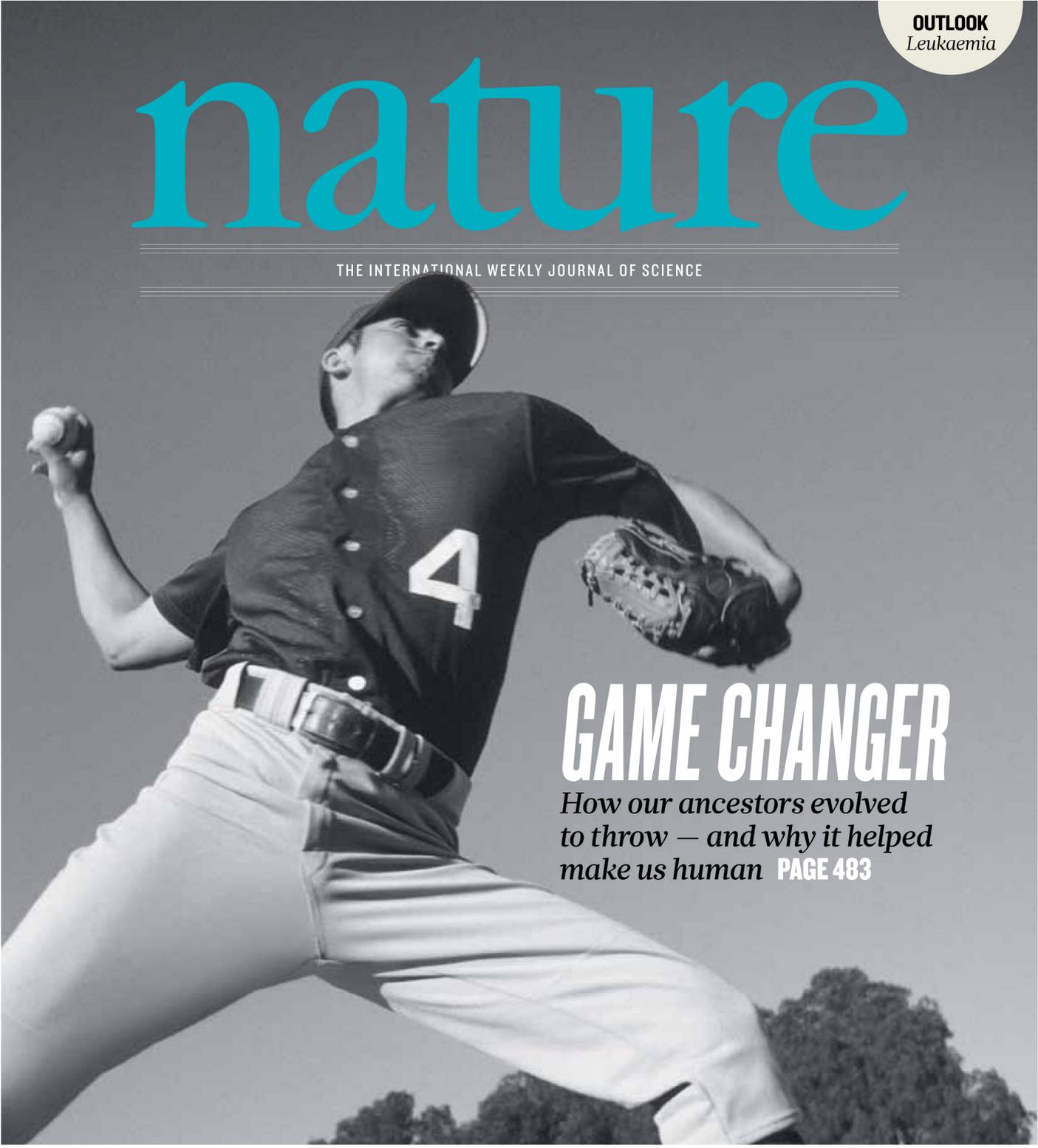


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Elastic energy storage in the shoulder and the evolution of high-speed throwing in *Homo*

Neil T. Roach^{1,2}, Madhusudhan Venkadesan³, Michael J. Rainbow⁴ & Daniel E. Lieberman¹

Some primates, including chimpanzees, throw objects occasionally^{1,2}, but only humans regularly throw projectiles with high speed and accuracy. Darwin noted that the unique throwing abilities of humans, which were made possible when bipedalism emancipated the arms, enabled foragers to hunt effectively using projectiles³. However, there has been little consideration of the evolution of throwing in the years since Darwin made his observations, in part because of a lack of evidence of when, how and why hominins evolved the ability to generate high-speed throws^{4–8}. Here we use experimental studies of humans throwing projectiles to show that our throwing capabilities largely result from several derived anatomical features that enable elastic energy storage and release at the shoulder. These features first appear together approximately 2 million years ago in the species *Homo erectus*. Taking into consideration archaeological evidence suggesting that hunting activity intensified around this time⁹, we conclude that selection for throwing as a means to hunt probably had an important role in the evolution of the genus *Homo*.

Compared with other carnivores, hominins are slow, weak and lack natural weapons such as fangs and claws. However, hominins were eating meat at least 2.6 million years (Myr) ago, and were probably hunting large prey 1.9 Myr ago (Supplementary Note 1). Although contemporary hunter-gatherers rarely rely on throwing to kill prey, earlier hominins probably needed to throw projectiles frequently to acquire and defend carcasses before the relatively recent inventions of the atlatl and bow¹⁰. We can therefore surmise that the ability to throw well would confer a strong selective benefit to early hunters. However, to test when and how hominins evolved the ability to throw projectiles effectively, it is necessary to understand both throwing biomechanics and how changes in hominin anatomy affect throwing performance.

Throws are powered by rapid, sequential activation of many muscles, starting in the legs and progressing through the hips, torso, shoulder, elbow and wrist^{11–14}. Torques generated at each joint accelerate segmental masses, creating rapid angular movements that accumulate kinetic energy in the projectile until its release. It has been shown that internal (medial) rotation around the long axis of the humerus makes the largest contribution to projectile velocity¹⁵. This rotation, which occurs in a few milliseconds and can exceed 9,000° per s (ref. 13), is the fastest motion that the human body produces. Although previous research has focused on the internal rotator muscles of the shoulder^{11,16,17}, these muscles alone cannot explain how humans generate so much internal rotational power. Calculations of the maximum power-production capacity of all of the shoulder's internal rotator muscles indicate that these muscles can contribute, at most, half of the shoulder rotation power generated during the throwing motion (Supplementary Notes 2 and 3). Peak internal rotation torque also occurs well before the humerus starts to rotate internally¹². Furthermore, variation in muscle fibre orientation in these muscles produce actions other than internal humeral rotation that reduce power output for this action.

Elastic energy storage has been shown to be an important source of power amplification for many high-powered movements^{18,19}. We propose

that several evolutionarily novel features in the human shoulder help to store and release elastic energy to generate much of the power needed for rapid humeral rotation during human throwing. According to this model, energy storage occurs during the arm-cocking phase (Fig. 1a), which begins with completion of a large step towards the target. As the foot hits the ground, the arm is already externally rotated, horizontally extended, and abducted nearly 90° at the shoulder, with forearm flexion approaching 90° at the elbow¹³. As the cocking phase begins, large torques are generated by rapid rotation of the torso towards the target and by the activation of the major shoulder horizontal flexor, pectoralis major^{11,16}. The positioning of the shoulder and elbow at this time increases the mass moment of inertia around the long axis of the humerus, causing the forearm and hand to lag behind the accelerating torso. Furthermore, a flexed elbow during the cocking phase enables passive inertial forces to externally counter rotate the arm, stretching the short, parallel tendons, ligaments and elastic components of muscles that cross the shoulder, potentially storing elastic energy in the large aggregate cross-sectional area of these structures (Supplementary Note 4). When the biceps deactivate and elbow extension begins, the arm's moment of inertia is reduced, allowing these stretched elements to recoil, releasing energy and helping to power the extremely rapid internal rotation of the humerus (Supplementary Note 5).

Three derived morphological features of humans that are not present in chimpanzees, our closest extant relatives, have a major role in storing and releasing elastic energy during throwing (Supplementary Note 6). First, the tall, mobile waists of humans decouple the hips and thorax, permitting more torso rotation²⁰, in turn enabling high torque production over a large range of motion (ROM), which is needed to load the shoulder's elastic elements. Second, humeral torsion, the angle between humeral head orientation and the axis of the elbow, is 10–20° lower in human throwers' dominant arms compared to chimpanzee humeri⁵. Decreased torsion extends the rotational ROM at the shoulder externally^{21,22}, potentially enabling more elastic energy storage during the cocking phase. Finally, humans have a more laterally oriented glenohumeral joint, which aligns the pectoralis major flexion moment around the same axis as the torso rotation moment. This orientation allows humans to increase the arm's moment of inertia by abducting the humerus in line with the torso rotation and shoulder flexion torques, maximizing resistance to both (Fig. 1b, c, d). In contrast, chimpanzees have a more cranially oriented glenohumeral joint and limited ability to produce torso rotation torque, and this requires them to maximize inertial loading by abducting their humeri more than humans to bring their arm in line with the pectoralis major flexion moment. However, this increased abduction would force chimpanzees to position their elbow in a more extended posture to maximize the arm's moment of inertia, resulting in a costly reduction in elbow extension during the throw.

We tested the effects of these derived features on throwing performance using high-speed, three-dimensional kinematic and kinetic data from 20 human throwers with considerable prior training to quantify power production at the shoulder during overhand baseball throwing

¹Department of Human Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138, USA. ²Center for the Advanced Study of Hominid Paleobiology, Department of Anthropology, The George Washington University, Washington DC 20052, USA. ³National Centre for Biological Sciences, Tata Institute of Fundamental Research, Bangalore, Karnataka 560065, India. ⁴Spaulding National Running Center, Department of Physical Medicine and Rehabilitation, Harvard Medical School, Cambridge, Massachusetts 02138, USA.

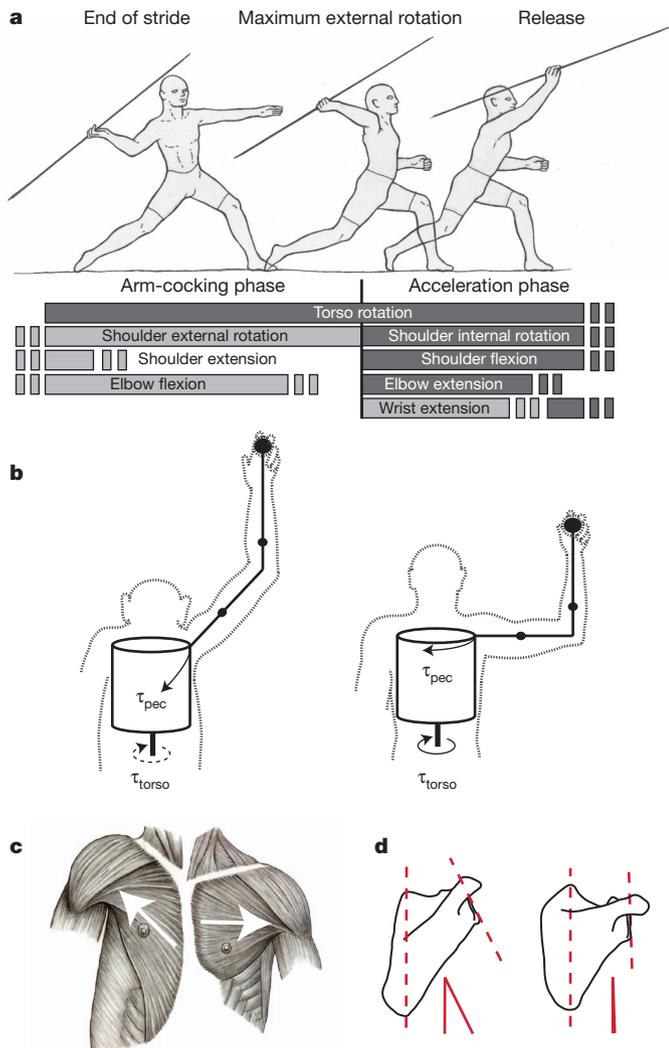


Figure 1 | Model of elastic energy storage. **a**, Arm-cocking and acceleration phases of the overhand throw. Light grey text boxes show the relative timing of the ‘cocking’ motions; dark grey boxes indicate the relative occurrence of the opposing ‘acceleration’ motions. Short boxes illustrate variation in timing of onset and cessation. **b**, **c**, Humans (right) and chimpanzees (left) differ in arm abduction and elbow flexion during throwing (**b**; a free-body diagram shows the torso (cylinder), arm and forearm, with black dots representing segmental centres of mass and τ vectors showing input torques), because of differences in shoulder orientation, that alter the major line of action (white arrows) of the pectoralis major (human, right; chimpanzee, left) (**c**). In humans, aligning the long axis of the humerus with the major axis of the pectoralis major and flexing the elbow maximizes inertia to shoulder flexion torque and loads the elastic elements in the shoulder. However, in chimpanzee morphology there is conflict between maximizing humeral rotation or maximizing elbow extension, hence chimpanzees are unable to achieve the same elastic energy storage. **d**, Signatures of shoulder orientation found in the scapula (human, right; chimpanzee, left) can be used to reconstruct hominin shoulder orientation; for example, the vertebral–glenoid angle is shown in red.

(Supplementary Note 7). During the arm-cocking phase, the throwers’ humeri externally rotate $57 \pm 15^\circ$ (mean \pm s.d.) past the active ROM limit achieved using their own muscular power, indicating passive stretching of the ligaments, tendons and muscles crossing the shoulder. Inverse dynamics analysis shows that during this period, the shoulder produces an opposing internal rotation torque, causing a sustained period of power absorption (Fig. 2). During arm-cocking, the negative work of shoulder rotation averages -201 ± 70 J, with an average power of -631 ± 337 W. In contrast, the total rotational work of the subsequent internal rotation motion is 346 ± 116 J, with power during acceleration averaging $3,847 \pm 1,697$ W. If 90% of the negative work

during arm-cocking is stored and returned elastically²³, this energy can account for $54 \pm 15\%$ of the internal humeral rotation work done during a typical throw.

Elastic energy storage at the shoulder also augments the generation of joint velocity and power at the elbow. During acceleration, the elbow extends at very high angular velocities ($2,434 \pm 552^\circ$ per s) despite large amounts of negative power and work (-246 ± 63 J), indicating that the triceps alone are not powering this rapid extension (Fig. 2). As previous studies have shown, elbow extension is powered primarily by segments proximal to the elbow^{15,24}, particularly the shoulder.

An additional line of evidence to support the idea that elastic energy storage is important comes from experimentally limiting shoulder rotational ROM with therapeutic braces (Supplementary Notes 8–11); restricting external rotation by $24 \pm 9^\circ$. During brace trials, shoulder rotation beyond the active ROM decreased by $50 \pm 36\%$ and shoulder work during arm-cocking decreased by $39 \pm 16\%$ (repeated measures analysis of variance (ANOVA), $P < 0.001$) (Fig. 3). Shoulder rotation work during the subsequent acceleration phase was not significantly different between conditions, but average shoulder rotation power during acceleration decreased significantly ($-16 \pm 35\%$, repeated measures ANOVA, $P = 0.036$). Wearing a shoulder brace also decreased elbow negative work during acceleration by $20 \pm 21\%$ (repeated measures ANOVA, $P < 0.001$). Overall, these work and power reductions from less elastic energy exchange significantly reduced humeral rotation angular acceleration ($-24 \pm 29\%$, repeated measures ANOVA, $P < 0.001$) and elbow extension angular velocity ($-21 \pm 10\%$, repeated measures ANOVA, $P < 0.001$), reducing ball speed by $8 \pm 6\%$ (multivariate ANOVA, $P < 0.001$).

Natural variation in humeral torsion (Supplementary Note 12) produces similar performance effects. It has been known for a long time that athletes such as pitchers have lower degrees of humeral torsion, by

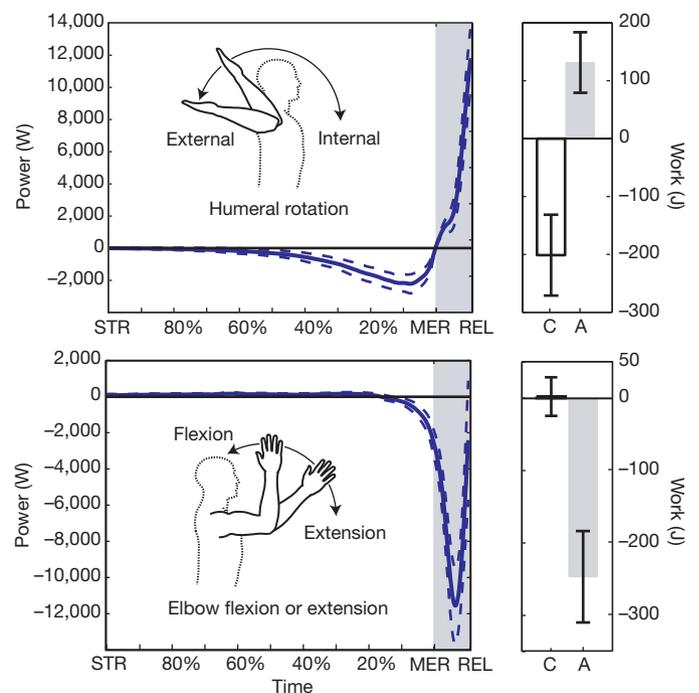


Figure 2 | Shoulder rotation and elbow flexion–extension power. Mean shoulder rotational power (solid blue line) with 95% confidence intervals (dotted blue lines) shows a sustained period (white) of negative power and work during arm-cocking (C), between stride (STR) and maximum external rotation (MER). This negative work is recovered (grey) during acceleration (A), between MER and release (REL). Recovered work powers both internal rotation at the shoulder and extension of the elbow. All power values are normalized by phase duration, with relative time and per cent arm-cocking duration shown on the x axis. Graphs on the right show the mean \pm s.d.

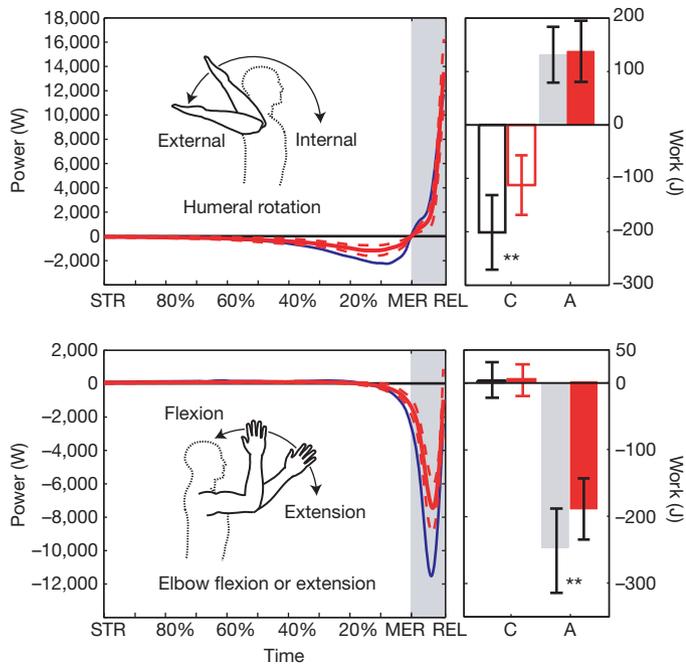


Figure 3 | Shoulder-brace restriction condition. Brace restricted mean power (solid red line) with 95% confidence intervals (dotted red lines) for shoulder rotation and elbow flexion-extension. Values for the unrestricted condition (no brace) are shown by the solid blue line. In the right panels, work values are shown in red bar and red solid bar (restricted using a brace) or white bar and solid grey bar (unrestricted). Significant reductions (** $P < 0.05$) in shoulder-rotation work occur during arm-cocking (C) and during elbow flexion-extension work when accelerating (A). Graphs on the right show the mean \pm s.d.

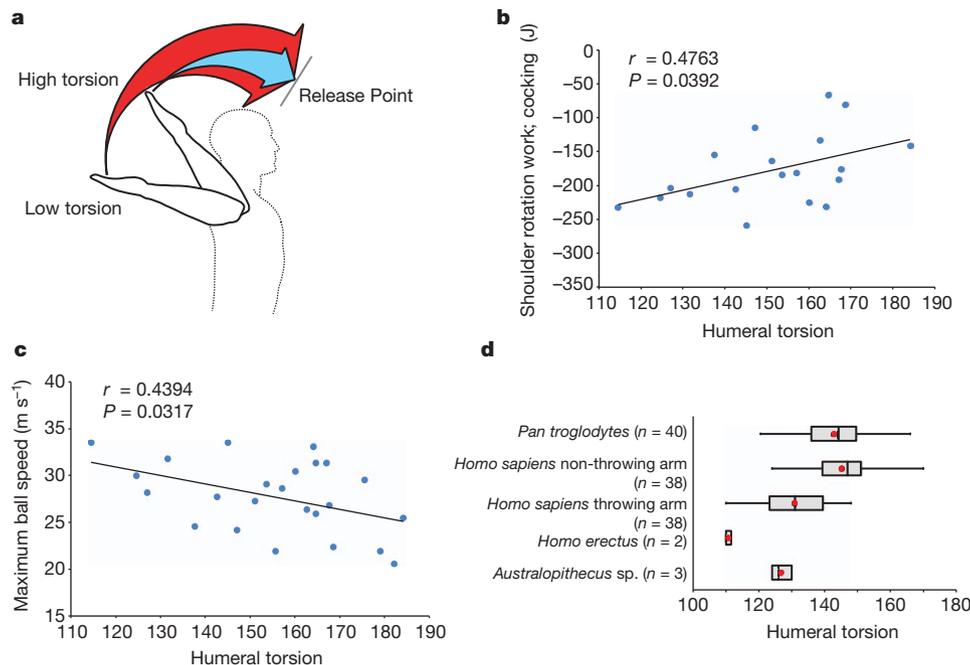


Figure 4 | Humeral torsion and throwing performance. a–c Low humeral torsion shifts the shoulder rotational ROM externally (a), enabling increased negative work during arm-cocking to be stored as elastic energy (b), and resulting in faster projectile speed (c). d, Humans and chimpanzees show comparable degrees of torsion⁵, although throwing athletes show reduced dominant-arm torsion²⁵ consistent with low torsion in *Australopithecus* and

10–15°, in their throwing versus non-throwing arms^{21,22,25}. By maintaining relatively lower, juvenile levels of torsion into adulthood²⁶, throwing athletes increase power generation by shifting the rotational ROM of the humerus externally^{21,22}. This shift enables further external rotation during arm-cocking and increases internal rotation during acceleration (Fig. 4a), permitting more elastic energy storage and release (Fig. 4b, c). It is unknown whether the plasticity of humeral torsion is greater in humans than in other taxa, but we speculate that plasticity in humans may be advantageous, enabling low torsion to persist in the throwing arm, whereas higher torsion (useful for manipulative tasks) develops in the non-throwing arm^{5,25}.

It is difficult to establish when high-speed throwing first evolved because the first projectiles were probably rocks and untipped wooden spears (Supplementary Notes 7 and 13). However, many of the derived morphological features that help human throwers to store elastic energy can be assessed in the fossil record (Supplementary Note 14). These features evolved in a mosaic fashion, some pre-dating the evolution of *Homo*. Tall, decoupled waists first appear in *Australopithecus* as adaptations for locomotion²⁰. Low humeral torsion also appears in *Australopithecus*, probably resulting from the release of the forelimbs from weight-bearing during quadrupedal locomotion, and is present in early *Homo*⁵ (Fig. 4d). Although variation in glenoid orientation exists within *Australopithecus*²⁷, a fully lateral glenoid position is first definitively present in *Homo erectus*²⁸ (Supplementary Notes 15 and 16). Such laterally oriented shoulders probably decreased the mechanical advantage of the scapular rotator muscles during climbing, and probably had little or no effect on stone-tool production. Throwing performance may also have benefited from low, wide shoulders, long legs, and hyperextendable wrists, which are all present in *H. erectus*^{20,29}. Although some of these features were probably selected for functions other than throwing, their combined configuration, first present in *H. erectus*, would have benefited throwing performance by enabling elastic energy storage in the shoulder, providing a selective advantage during hunting (Supplementary Note 1). Furthermore, high-speed

*Homo erectus*⁵. Chimpanzees are a combined sample as they do not show arm dominance, whereas human values are split between dominant and non-dominant arms as they show arm dominance. In d, the black and grey boxes and whiskers show torsion-angle quartiles, and the red dot shows the torsion-angle mean.

throwing was probably a critical component of a suite of hunting behaviours that enabled early members of the genus *Homo* to thrive in new and varied habitats both in and out of Africa.

Today, technological advances such as the bow and arrow, nets and firearms have reduced contemporary hunter-gatherers' reliance on thrown projectiles, but the human ability and proclivity to throw persists in many sports, in which athletes rely on the same mechanics (Supplementary Note 7). In this modern context, the evolution of adaptations for elastic energy storage during human throwing has implications for the high prevalence of injuries in throwing athletes. Paleolithic hunters almost certainly threw less frequently than modern athletes, who often deliver more than 100 high-speed throws over the course of a few hours. Unfortunately, the ligaments and tendons in the human shoulder and elbow are not well adapted to withstanding such repeated stretching from the high torques generated by throwing, and frequently suffer from laxity and tearing^{12,30}. Although humans' unique ability to power high-speed throws using elastic energy may have been critical in enabling early hunting, repeated overuse of this motion can result in serious injuries in modern throwers.

METHODS SUMMARY

Anthropometric and kinematic data were collected from 20 male subjects (Supplementary Note 17) after written consent was given in accordance with the Harvard Committee on the Use of Human Subjects. Kinematic data were collected at 1,000 Hz using an eight-camera Vicon T10s 3D infrared motion capture system (Vicon). Each subject had 21 passive reflective markers taped on the throwing arm and torso (Supplementary Note 18). Subjects were tasked to throw a 144-g baseball at a 1-m-radius target from 10 m away, both normally (8 to 10 pitches) and when restricted using a brace (Donjoy Shoulder Stabilizer, Donjoy) that limited external rotation ROM at the shoulder (8 to 20 pitches) (Supplementary Note 19). Ball speed was measured using a Sports Radar Model 3,600 radar gun. Ball release was timed using a synched FlexiForce A201 force sensor (Tekscan) collected at 1,000 Hz taped to the palmar side of the distal phalanx of the third digit and synchronized with a 30-Hz Canon Vixia HV30 digital video camera (Canon). A Butterworth second-order low-pass filter (cut-off of 25 Hz) was applied and marker gaps up to 100 frames were interpolated using C-Motion Visual3D software (v4) (Supplementary Note 20). For analysis, each motion was then subdivided into five phases of the throw¹⁴ and standardized by phase length (Supplementary Note 21). Joint Euler angles were calculated and inverse dynamics analyses were performed in Visual3D (Supplementary Note 22). Joint angular velocities, moments and power were calculated using each joint's instantaneous axis of rotation (Supplementary Note 23).

Full Methods and any associated references are available in the online version of the paper.

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Supplementary Information is available in the online version of the paper.

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Author Contributions N.T.R. and D.E.L. designed the study and wrote the paper. N.T.R. collected and analysed the data with help from D.E.L., M.V. and M.J.R. All authors helped to edit the paper.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to N.T.R. (ntroach@email.gwu.edu).

METHODS

Subjects. Data were collected from 20 male subjects (aged between 19 and 23 years). Nineteen of the subjects were collegiate athletes (16 baseball players, 3 non-throwing athletes). Prior to enrolment in the study, all participants were required to pass a throwing performance task (Supplementary Note 17) to exclude poor throwers. For all subjects, we collected information on relevant injury, medical history, and basic anthropometric data (height, weight, segment lengths and circumferences, joint ROM). Humeral torsion was estimated using ROM measures³¹. All subjects provided informed written consent in accordance with the Harvard Committee on the Use of Human Subjects.

Kinematics. Kinematic data were collected at 1,000 Hz using an eight-camera Vicon T10s 3D infrared motion capture system (Vicon). Each subject had twenty-one passive reflective markers taped on the throwing arm and torso (Supplementary Note 18). Subjects were given approximately 5 min to stretch and warm up before recording. After the warm-up period, subjects were tasked to throw a 144-g baseball at a 1-m-radius target from 10 m away. The subject then threw 8 to 10 normal pitches and 8 to 20 pitches using a Donjoy Shoulder Stabilizer (Donjoy) brace that restricts external rotational ROM at the shoulder (Supplementary Note 19). As a control, data were collected for an intermediate (sham) condition in which the brace was applied but not tightened (Supplementary Note 8). Ball speed was measured using a Sports Radar Model 3,600 radar gun. Ball release was timed using a synched FlexiForce A201 force sensor (Tekscan) collected at 1,000 Hz taped to the palmar side of the distal phalanx of the third digit and synched with a 30-Hz Canon Vixia HV30 digital video camera (Canon). To filter the kinematic data, a residual analysis³² of the entire throwing trial and the critical period during

the humeral internal rotation motion was calculated in MATLAB (version R2010b) (Supplementary Note 20). A Butterworth second-order low-pass filter (cut-off of 25 Hz) was applied and marker gaps up to 100 frames were interpolated using C-Motion Visual3D software (v4). For analysis, each motion was then subdivided into five standard phases of the throw: windup-stride, arm cocking, arm acceleration, arm deceleration and follow through¹⁴.

Kinetics. Joint Euler angles were calculated and inverse dynamics analyses were carried out using mass distribution data from Dempster³³ in Visual3D. Joint angular velocities, moments and power were calculated using each joint's instantaneous axis of rotation (Supplementary Note 23). The sequence of rotations at each joint is described in Supplementary Note 22. Joint work was calculated in MATLAB using the trapz function.

Statistics. Kinetic data were standardized to phase length, interpolated and resampled using custom MATLAB code to produce comparable data across all trials and subjects (Supplementary Note 21). Individual subject means were compared across experimental conditions using repeated measures ANOVA or multivariate ANOVA as appropriate. All statistical analyses were conducted using JMP software (v5). Differences were considered to be significant at $\alpha < 0.05$.

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Supplementary Note 1. *Throwing in human evolution* - In *The Descent of Man*, Darwin proposed that the evolution of bipedality, which freed the forelimb from its primary locomotor roles, likely had profound effects on the evolution of hominin anatomy and behavior¹. He specifically noted that the ability to hunt using thrown projectiles was made possible by bipedal posture. Despite Darwin's observations, the role of throwing in human evolution has been understudied compared to other derived human abilities such as walking, running, and tool making. In addition, while several researchers have inferred that throwing may have been a component of early hunting and scavenging behaviors²⁻¹⁵, recent research on the evolution of throwing has focused more on throwing's role in the evolution of the brain^{3-6,16} or in the establishment of social bonds and cooperation^{3,12,13,17-19}. Without discounting these hypotheses, we propose that the most fundamental adaptive benefit of throwing must have been for hunting, given evidence for the incorporation of animal foodstuffs, such as meat and marrow, into the hominin diet^{2,20-25}. Calories added from meat and fat would have helped make possible selection for larger bodies, larger brains, and more offspring^{2,22-25}. When hominins first began to eat meat regularly is difficult to pinpoint²⁶⁻²⁹, but evidence of this behavior in the fossil record appears by 2.6 million years ago²⁷ (and possibly earlier²⁹) and seems to intensify around 1.9 Myr ago³⁰⁻³³.

How hominins gained access to meat is the subject of debate^{9,34-41}, but regardless of whether meat was gained by persistence hunting, approach, ambush, or scavenging, the ability to kill or injure other animals at a distance using a thrown projectile would have provided a significant evolutionary benefit. Throwing a projectile such as a rock or spear could kill an animal, wound the animal making it easier to track, or drive another carnivore away from a kill. This ability to kill or wound from a distance also provides crucial space between the hunter and dangerous prey/carnivores. Without this separation, hominins would have been very poorly suited to obtaining or defending meat. First, we lack large canines and claws to fight prey or defend carcasses. We also lack the strength, speed, and stability of other carnivores. Further, our lack of fur removes some protective insulation from horn thrusts, bites, and kicks. Even helpful technologies such as thrusting spears or clubs need to be used at very close range, exposing hominins to risk of serious injuries. Similarly, while increased group size could spread the risk of close interaction with a dangerous animal between more individuals, the fitness costs of a broken bone or punctured lung are extremely high, difficult or impossible to share, and would have been a strong negative selective force. Reducing these injury risks, even slightly, using thrown projectiles would have given any throwing hominin a potential fitness advantage. Even the relatively short distances over which modern hunter-gatherers throw spears (approximately 7m on average)¹¹ could significantly reduce the likelihood of being seriously hurt. Furthermore, an isolated report of hand thrown spears being used to hunt prey from 30-40m away suggests that these short distances over which spears are currently thrown may represent modern usage practices and not a limit on the capacity of such weapons⁴². Thrown projectiles may also have been used in conjunction with other hunting strategies, as has been recorded in San hunters, who after a persistence hunt have been witnessed dispatching exhausted, but still unpredictable and dangerous game, with a thrown spear^{43,44}. Such examples of flexible, situationally adaptable hunting behavior may have been an especially important subsistence strategy as hominins left Africa and encountered new environments and prey species.

Finally, it is possible that throwing instead evolved in the context of providing a selective advantage during aggression. Numerous ethnographic and historical accounts document the importance of throwing during intergroup conflicts⁴⁵⁻⁶², and occasionally between members of the same group^{54,63-66}. Throwing proficiency could have enabled better throwing groups to monopolize desirable resources or provided good throwing males an advantage over weaker throwers in gaining access to reproductive opportunities. Although we do not discount the potential selective advantage throwing may have conferred in male aggression, there are several reasons to believe that the selective benefit of throwing during hunting was more important. First, the evidence for high-speed throwing first appears in *H. erectus*, a species that exhibits a marked reduction in sexual body size dimorphism compared to earlier hominins⁶⁷⁻⁷⁰. Such a reduction in dimorphism may represent reduced male-male aggression (or a shift to projectile aided aggression), but appears to be driven more by increases in female body size^{67,68,71} suggesting a shift in dietary quality or food availability at this time⁷¹⁻⁷³. The increased inclusion of meat into the diet could explain this shift in female body size. Further, animal carcasses represent high-quality, monopolizable resources that can be shared or traded⁷⁴⁻⁷⁶. Such a shift in food economy has been suggested to increase cooperation, likely resulting in reduced aggression^{73,77}. Therefore, while thrown projectiles are used during male-male and intergroup aggression, we propose that such usage is likely exapted and that selection for throwing in order to hunt/scavenge is better supported by multiple lines of evidence.

Regardless of what drove the evolution of our throwing capacity, humans today are still capable of being excellent throwers. While technological improvements in armature have made hunting more effective and safer, modern foragers still occasionally employ thrown projectiles to effectively hunt even large animals^{1,7,11,78-87}.

Supplementary Note 2. Modeled vs. actual power output - One way to test the hypothesis that elastic energy provides most of the rotational power for throwing is to compare estimates of the maximum power production capacity of all the muscles potentially responsible for internally rotating the humerus with the actual calculated power. The maximum power production of all internal rotators of the humerus is calculated using the average actual power during the acceleration phase, thus minimizing the effects of instantaneous changes in angular acceleration. This average actual power value is then adjusted by a mass estimate for all potentially contributing muscles (see Supplementary Note 3). This mass specific power estimate (in $W\ kg^{-1}$) is then compared to published maximum mass specific power values from the literature, which range from $\sim 250\text{-}500\ W\ kg^{-1}$ ⁸⁸⁻⁹⁰. This conservative model shows that the average actual power at the shoulder exceeds the maximum isotonic power production capacity for muscle by at least 3-7 fold (Table S1).

Supplementary Table S1 – Modeled Power Comparison	
Maximum isotonic power - skeletal muscle ($W\ kg^{-1}$)	250-500
Adjustment for force enhancement due to stretching	1.75x
Maximum modeled muscle power - skeletal muscle ($W\ kg^{-1}$)	438-800
<hr/>	
<i>Predicted values</i>	
Shoulder rotation work during acceleration (J)	132 ± 52
Time of acceleration (sec)	0.034 ± 0.013
Average joint power (W)	3,847 ± 1967
Estimated total muscle mass (kg)	2.16
Adjusted average kinetic power - acceleration ($W\ kg^{-1}$)	1,781 ± 911
<i>Average kinetic power > Maximum muscle power</i>	

Table S1 | Modeled power comparison. Average kinetic power (shoulder rotation) adjusted by modeled total internal rotator muscle mass compared to known maximum power values for skeletal muscle.

However, it is well known that when muscle is actively stretched during or just prior to concentric contraction there is a notable increase in force production⁹¹⁻⁹⁴. Plyometric models propose that the pre-stretching of the shoulder internal rotator muscles

during arm-cocking augment force enhancement during the subsequent acceleration phase of the throw⁹⁵. Accordingly, we also compared our average actual power values to force enhancement adjusted ($1.75 \times$ ⁹³) values of maximum muscle force, ranging from ~ 438 - 875 W kg^{-1} . Even with this significant force enhancement, our measured average rotational power in the shoulder exceeds the maximum muscle values by 2-4 times. Thus, in order to achieve this joint power using muscular power alone, the individuals in this analysis would require internal rotator muscles at least 2-4 times larger than those used here. Given that the muscle masses used are the largest published⁹⁶, this is highly unlikely and suggests that elastic energy stored in the shoulder is used to enhance the internal rotation power output.

Supplementary Note 3. Muscle data – Muscle volumes used for muscle modeling are taken from the Visible Human Project data set⁹⁷. These volumes are calculated from a single male subject and are the largest available in the literature (which contains other males in the 95th percentile in height and the 90th percentile in weight)⁹⁸. Muscle volumes for forelimb muscle (Table S2) were calculated from MR images by Garner and Pandy⁹⁶. The values used for the anterior deltoid were calculated by dividing the entire deltoid volume by three. These volumes were then converted to masses by multiplying by an empirically derived measure of mammalian muscle density from the literature⁹⁹. The summed muscle mass of all internal rotators of the humerus was then used to normalise our power data by potentially contributing muscle mass. Our use of these very large muscle volumes in our analysis, as well as the assumption that all fibers are contributing at 100% of their capacity and solely to humeral internal rotation, intentionally overestimate the potential muscular contribution to joint power at the shoulder. This significant overestimation is designed to reduce the effects of error within the inverse dynamics torque estimates.

Supplementary Table S2 – Shoulder Internal Rotator Muscle Volumes (cm ³)	
<i>Muscle (Garner & Pandy 2003)</i>	
pectoralis major	676.40
latissimus dorsi	549.69
anterior deltoid	792.87/3 = (264.29)
teres major	231.40
subscapularis	318.52
Total internal rotator volume (cm³)	2040.30
<i>Muscle Density (Mendez & Keys, 1960)</i>	
	1.06 g/cm ³
Total internal rotator muscle mass (kg)	2.16

Table S2 | Calculated total muscle volume and mass for internal rotators of the shoulder. The largest volumes for each are taken from the literature.

Supplementary Note 4. Location of elastic energy storage – The purpose of our study is to determine whether elastic energy storage is indeed occurring during throwing and to propose a mechanism for the role of elastic energy storage at the level of the joints and segments. However, exactly where elastic energy is being stored at the shoulder is currently unknown. We hypothesize that elastic energy storage predominantly occurs at the glenohumeral joint, as movements at the scapulothoracic joint during the critical acceleration phase are minimal^{100,101}. While resolving the precise location of elastic energy storage requires better data on scapular motion as well as *in vivo* soft tissue imaging of the ligaments, tendons, and muscles crossing both joints, clinical data on repetitive injuries in the shoulder do provide some preliminary insight. Throwing athletes show an increased prevalence of shoulder instability and stretching related tears and laxity in the glenohumeral ligaments and at the origin of the biceps tendon on the superior glenoid labrum¹⁰²⁻¹⁰⁴. Over-stretching injuries to these elastic structures suggest they may be involved in storing elastic energy. For example, by actively positioning the arm during the early cocking phase a number of shoulder ligaments are pulled taut (anterior band of the inferior glenohumeral ligament, the middle glenohumeral ligament, and the coracohumeral ligament)¹⁰⁵. It is quite likely that during the following late cocking phase, when the humerus is further passively rotated, these already taut ligaments stretch considerably. Furthermore, microscopic analyses of the glenohumeral ligaments in those suffering from shoulder instability (found frequently in throwing athletes¹⁰⁶) show higher amounts of elastin present in these ligaments and an increase in the number of large diameter collagen fibrils¹⁰⁷, effectively making these ligaments more tendon-like.

The internal rotator muscle tendons are a likely energy store. Similar to ligaments, muscle tendons are also frequently injured in throwing athletes¹⁰⁸⁻¹¹⁰. For example, the attachment site of the long head of the biceps muscle on the superior glenoid labrum is often the site of SLAP tears or lesions. These tears occur when large stresses are repetitively applied to the labrum via the biceps tendon¹¹¹, such as occur during the isometric and eccentric contraction of the biceps during the throwing motion. During normal, injury free throwing, such muscular contractions will pull the biceps tendon taut and potentially stretch this tendon, allowing for elastic energy storage. Rotator cuff tendon tears are also frequent in throwing athletes^{109,112}, although many of these tears likely do not result from elastic energy storage, but rather from impingement^{106,110,113,114} or tensile failure as these muscles resist high distraction forces¹¹⁵⁻¹¹⁷. However, it is worth noting that the subscapularis muscle is highly eccentrically activated during the arm cocking phase¹¹⁸, despite lower distraction forces during this phase than during the acceleration and deceleration phases¹¹⁶. Given this muscle's action (as an internal rotator of the humerus), eccentric contraction of the subscapularis as the humerus externally rotates during cocking could stretch the subscapularis tendon and store elastic energy. Likewise, forceful eccentric contractions of the other internal rotator muscles (pectoralis major, latissimus dorsi) during the cocking phase¹¹⁸⁻¹²⁰ could also result in their tendons stretching and storing elastic energy.

While the elastic structures in the shoulder are not typical of those used by many animals to store elastic energy, it is important to make a distinction regarding how most animals use such stored energy. Many animals use long tendons (such as the achilles), attached to pennate muscles to store elastic energy for increased locomotor efficiency

^{88,93,121-123}. However, while such long tendons can stretch considerably and store large amounts of elastic energy, the rate at which long tendons recoil and release that energy will be slower than for a shorter elastic element. When returning elastic energy very quickly is important, as is the case for power amplification, shorter tendons and ligaments can be more effective. Such may be the case in the human shoulder, where the average length (weighted by cross-sectional area - CSA) of the internal rotator muscle tendons (58 mm ¹²⁴) is comparable to (patellar tendon – 48 mm ¹²⁵) or shorter than (Achilles – 120 mm ¹²⁶) the large tendons in the lower limb. Furthermore, although there is no single elastic element in the shoulder that could store all of the elastic energy essential to throwing mechanics, the CSA of the internal rotator muscle tendons alone is 3.5-6 fold greater than that of either large tendon in the leg ¹²⁴⁻¹²⁸. Accordingly, we propose that as a complex, the short length and large aggregate CSA of the numerous ligaments and muscle tendons act in parallel across the shoulder allowing these elements to return large amounts of elastic energy very rapidly (a hypothesis that requires further study).

Finally, it is worth noting that the failure stresses of the shoulder ligaments (~5-11.5 MPa ¹²⁹⁻¹³²) and muscle tendons (biceps ~32.5 MPa ¹²⁸; subscapularis ~ 43 MPa ¹³³) are lower than the failure stresses measured in the elastic elements of the lower limb ¹³⁴⁻¹³⁶. We suggest that these differences likely reflect the differential frequency and repetitiveness of locomotor versus throwing behaviors. Given the comparative weakness of the shoulder elements, it is likely crucial to spread all forces involved in storing elastic energy in the shoulder across multiple ligaments and tendons. We further hypothesize that when this force distribution is poorly controlled (such as when a throwing athlete fatigues), the repetitive overreliance on single elastic elements could lead to their failure and result in injury.

Supplementary Note 5. Countermovement power enhancement - Many rapid, powerful movements are preceded by an initial countermovement in the opposite direction. Such countermovements have been shown to increase the performance of the following motion¹³⁷⁻¹⁴¹. For example, countermovement jumps, in which an athlete quickly squats before jumping, show increased jump height when compared to non-countermovement squat jumps¹³⁸⁻¹⁴⁴. Numerous studies have shown that the knee and ankle extensor muscles responsible for powering jumps are highly active during the initial countermovement¹⁴⁵⁻¹⁴⁷. The eccentric lengthening of these muscles during countermovement followed by the rapid concentric shortening as the motion occurs have also been termed the “stretch-shortening cycle” or “SSC”¹⁴⁸⁻¹⁵⁰. However, how this countermovement enhances performance is unknown. Previous studies have suggested that countermovement/the SSC enables more time for muscles to become fully active^{141,151,152}, that muscle pre-stretch allows them to reach optimal sarcomere lengths for maximal force production¹⁵³⁻¹⁵⁵, that stretching induces further reflexive muscle activation^{149,156}, and/or that this stretching enables elastic energy storage^{137,157,158}.

While the mechanics and performance enhancement of countermovement/SSC have been well studied for running and jumping, few studies have examined this phenomenon in the upper body¹⁵⁹⁻¹⁶⁴. Although the throwing windup is frequently described as an important countermovement^{141,149,160,165-167}, very little attention has been paid to the mechanics of this portion of the throw. Mathematical modeling of the windup during throwing suggests that “moment reversal” from countermovement to forward movement results in increased throwing distance and velocity¹⁶⁸⁻¹⁷⁰. An experimental study of seated throwers with their throwing arms resting on a table showed improved wrist velocity with an unimpeded countermovement external rotation of the shoulder¹⁶². Elliott and colleagues¹⁶² further suggest that elastic energy likely played a minimal role in this velocity enhancement. Another study of a two-handed, overhead medicine ball throw from a supine position found a countermovement power enhancement at the shoulder¹⁶⁴. However, although these studies suggest that countermovement may play a significant role in throwing performance, the experimental/modeling conditions have been largely artificial. To date, no study of this phenomenon has been conducted under normal, high-speed throwing conditions. Furthermore, the role of elastic energy storage in the human forelimb is currently unknown for all mechanical tasks, including throwing.

We seek to address the effects of countermovement at the shoulder under normal throwing conditions and specifically test whether elastic energy storage plays an important role in determining throwing performance. The mechanism we propose is used to enhance throwing power relies on an external rotation of the humerus occurring just prior to the rapid internal rotation motion around the same joint axis. While this arm-cocking countermovement is similar in a number of respects to the squat preceding a countermovement jump, we hypothesize that this counter rotation is driven by a different and novel mechanism (the inertial mass of the forelimb). We further propose that this countermovement during throwing enhances performance by loading the elastic elements crossing the shoulder, storing elastic energy and powering the subsequent internal rotation motion.

Supplementary Note 6. Chimpanzee throwing performance – Although data exist on the frequency of chimpanzee throwing behavior¹⁷¹⁻¹⁷⁴, all published descriptions of their throwing performance have been qualitative. We collected preliminary throwing velocity data (Table S3) from 3 chimpanzees with previous overhand throwing training at a sanctuary in Auburn, CA. While not directly comparable to human throwing data due to limited practice and training, these data further illustrate the lack of projectile velocity, corroborating previous published accounts.

Although chimpanzees are facultative rather than skilled throwers, chimpanzee throwing behavior and anatomy can provide insight into the performance effects of morphological differences between these two species. We use a model that compares human and chimpanzee throwing performance because we are interested in assessing how differences in skeletal morphology affect throwing ability. Furthermore, because many aspects of early hominin upper body anatomy more closely resembles that of chimpanzees¹⁷⁵⁻¹⁷⁷, they are a useful comparator for humans and are helpful in assessing throwing performance in the fossil record. Regardless of whether the human-chimpanzee last common ancestor was behaviorally chimpanzee-like¹⁷⁶⁻¹⁷⁸ or not^{179,180}, comparisons of human throwing mechanics and performance to that of chimpanzees can provide valuable insights for interpreting how throwing performance and skeletal anatomy are related.

Supplementary Table S3 – Chimpanzee throwing velocity (mph)			
	<i>Juvenile Male (3 years)</i>	<i>Juvenile Male (9 years)</i>	<i>Adult female (~30 years)</i>
Mean velocity	12.4	12.5	19*
N	17	18	12*
Maximum velocity	14.3	15.5	22.4*
Standard Deviation	1.4	1.7	2.4*

Table S3 | Throwing velocity data from 3 chimpanzees. Note: while the adult female had previously been trained to throw overhand, during data collection she chose to throw underhand (while standing bipedally). Her data has been asterisked accordingly.

Supplementary Note 7. *Effects of projectile type* – For practical reasons, we chose to collect data on individuals throwing standard baseballs. However, given that hominin throwers were likely throwing objects such as rocks and untipped spears, it is worth noting how throwing kinematics differ between projectile types. While the throwing literature largely focuses on baseball throwing, there are a number of studies addressing the throwing kinematics of footballs^{120,181-183}, handballs¹⁸⁴⁻¹⁸⁶, and javelins¹⁸⁷⁻¹⁸⁹. These projectiles differ from baseballs in both mass and shape. Results from these studies show that a standard sequence and timing of motions is conserved across all throw types^{181,190}. Importantly, these standard kinematic patterns include consistent external rotation of the arm into the passive ROM during the arm-cocking phase, when we propose that elastic energy is stored^{181,191,192}. Modeling research by Alexander¹⁹³ suggests that projectile mass may be important in dictating arm position differences during the arm-cocking phase. These positioning differences, where heavier projectiles are positioned closer to the shoulder joint by reducing arm abduction angle and increasing elbow flexion, may help to reduce the arm's moment of inertia during cocking to prevent damage to the ligaments and tendons crossing the shoulder. Data on arm positioning during the cocking phase suggest that this may be the case for a number of heavier projectiles (handball ~ 450g; shot put - 7260g)^{192,194}. Such a constraint may have compromised hominin throwing performance when throwing heavy projectiles or affected the choice of how heavy a projectile was thrown. Scarce ethnographic data on hand-thrown spears suggests that human hunter-gatherers choose lighter spears (averaging 184g)¹⁹⁵, potentially to avoid injury or compromised throwing mechanics. Projectile shape likely also has effects on throwing kinematics, especially in the positioning of the hand.

Elongated projectiles (such as footballs, javelins, or spears) require that the palm of the hand is positioned alongside the elongated axis the projectile, as opposed to spherical projectiles (such as baseballs, handballs, etc...) where the palm is typically positioned behind the projectile^{196,197}. When throwing elongated projectiles, this is accomplished through a more supinated position of the forearm. While this more supinated forearm position is required of both football quarterbacks and javelin throwers, the kinematics of hominin spear throwing were likely more similar to those of football passing than javelin throwing. This is because spear throwing for hunting as well as football passing require both power and accuracy in order to be effective, while javelin throwing requires only power, as the marker of performance is simply the distance the javelin has travelled from the thrower. For this reason, the differences between baseball pitching and javelin throwing (including the run up and unstable release) will not be discussed here. Detailed comparisons of the football passing and baseball throwing motions show that while these motions are largely similar, football quarterbacks tend to achieve slower torso rotational velocities and faster shoulder flexion velocities¹⁸¹. Quarterbacks also externally rotate their arm ~9° less than baseball pitchers during the cocking phase¹⁸¹. It has been suggested that these differences in football passing kinematics may be accommodations to the increased mass of the football (~ 415g), in order to reduce the risk of injury to the shoulder and elbow¹⁸¹. Similar kinematic accommodations may have been employed by spear throwing hominins for the same purpose. It is also worth noting that throwing athletes from all sports show reduced humeral torsion in their dominant arm versus non-dominant arm¹⁹⁸⁻²⁰².

Supplementary Note 8. Intermediate/sham condition – Data were collected for an intermediate condition in which the shoulder brace was applied, but the restriction mechanism was not loaded. This intermediate condition allows for the analysis of the effect of the brace itself somewhat independently of the restriction. In this condition, the shoulder brace acted like a tight-fitting jacket and reduced external rotational range of motion at the shoulder approximately -11° (compared to the restricted condition which limited external rotational ROM -24°). This intermediate level of restriction resulted in a small but significant reduction in maximum projectile velocity from the normal trials. However, the intermediate condition showed significantly higher projectile velocity than the restricted condition. Kinetic data show this intermediate condition is largely indistinguishable from the normal condition (Figure S1), with the exception of the shoulder rotation work done during the arm cocking phase which drops $-9\pm 13\%$ ($p < 0.05$) from the normal condition.

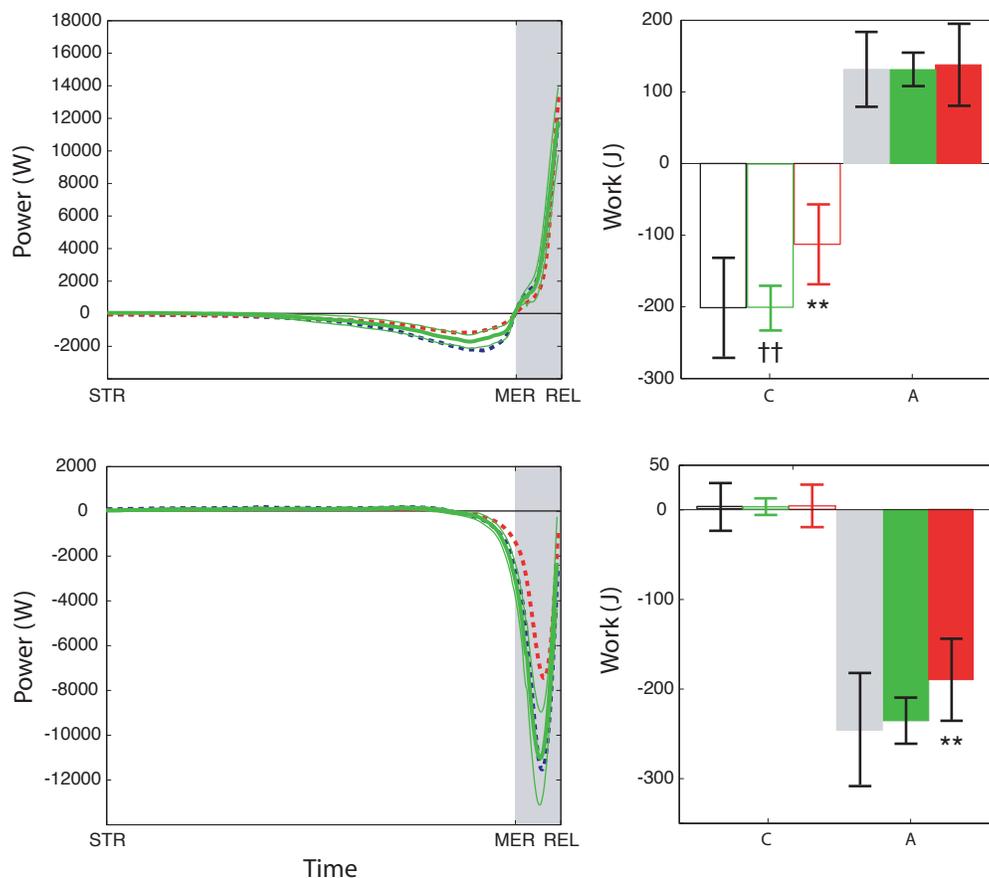


Figure S1 | Intermediate/Sham condition. Mean joint power and work (green) for the sham condition. The mean values for the normal condition (blue dashed, grey) and restricted condition (red dashed, red) are shown for comparison. A 95% confidence interval (± 2 st. error) bounds the mean sham values in the power curve and all work values. Significant reductions ($p < 0.05$) from both the normal and intermediate conditions are indicated by **, while the †† indicates significant differences from both the normal and restricted conditions.

Supplementary Note 9. Ball speed & accuracy – Mean maximum ball speed was compared across experimental conditions (Figure S2). Significant differences were found between condition means (MANOVA – $p < 0.0001$), but not between condition variances (Levene's – $p = 0.94$). Post-hoc pairwise comparisons showed significant differences between all three conditions. As expected, the intermediate condition in which the brace was worn but not tightened showed an intermediate reduction in ball speed, while the full restriction showed a greater reduction. Mean accuracy was also compared across conditions. No significant differences were found between conditions for mean accuracy (repeated measures ANOVA – $p = 0.1485$) or variance (Levene's – $p = 0.4574$). Within all conditions, no condition order effects were found in either speed or accuracy.

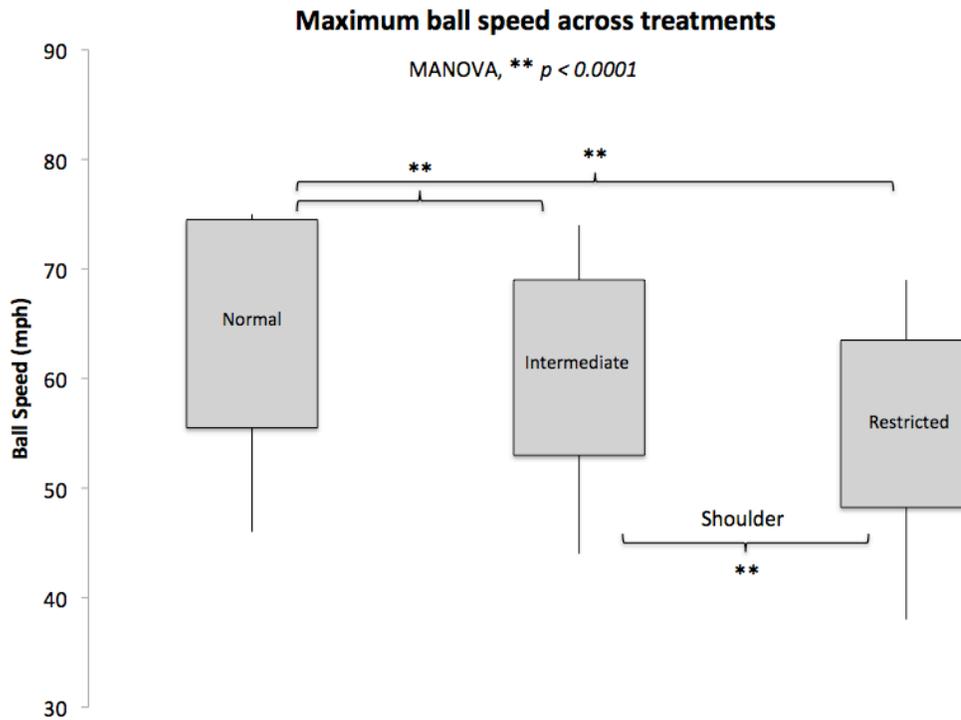


Figure S2 | Maximum ball speed across conditions. Maximum ball speed across treatment conditions showed significant differences between all conditions as expected.

Supplementary Note 10. Timing differences between experimental conditions – Experimental conditions involving the brace showed significantly different timing in both the duration and relative duration of the arm-cocking (repeated measures ANOVA, $p = 0.0255$, Mauchly's sphericity = 0.2404) and acceleration phases (MANOVA, $p = 0.0024$, Mauchly's sphericity < 0.0001) (Figure S3). Post-hoc pairwise testing shows these differences are due to reduction of the arm-cocking phase and elongation of the acceleration phase in the restricted condition. The reason for the change in cocking duration is not clear, but the elongated acceleration seems to represent a slowdown associated with reduced acceleration of the arm due to the lack of elastic energy storage in this condition. Such reduced acceleration could delay the moment of release and elongate the acceleration phase.

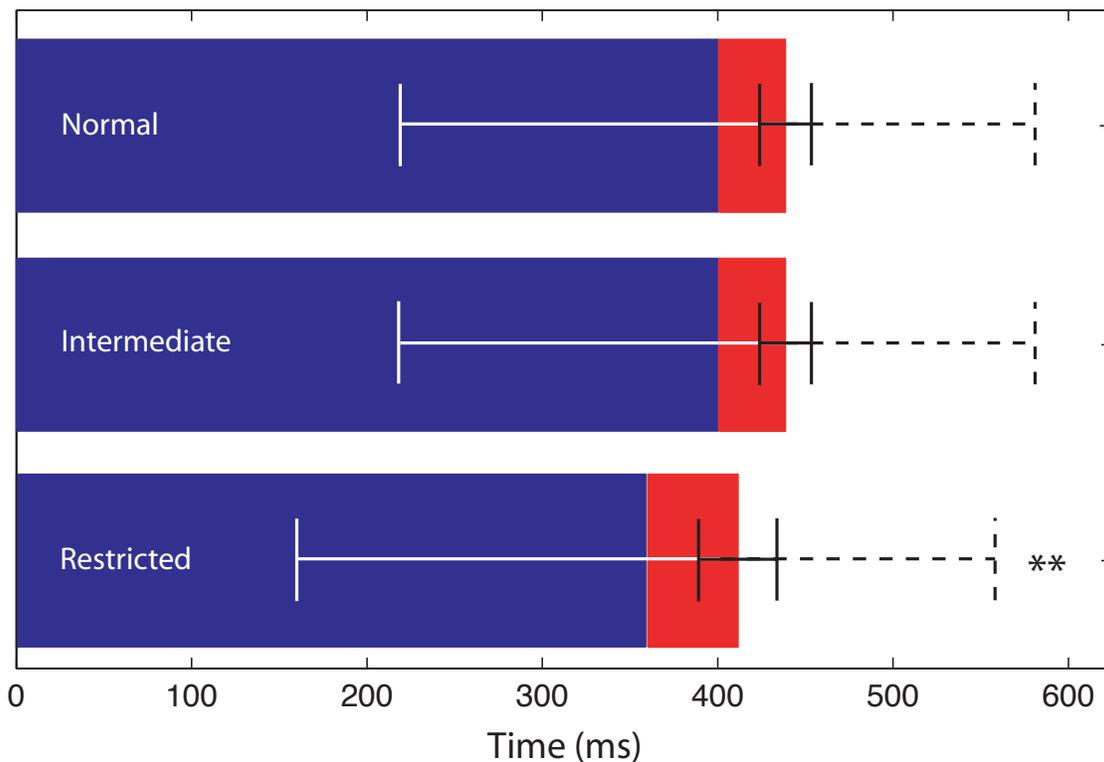


Figure S3 | Phase duration. Duration of the arm cocking phase (blue) and acceleration phase (red) for the normal and shoulder brace conditions. Restricted throw timing differed significantly from both normal and intermediate throws.

Supplementary Note 11. *Effects of the brace on force production* - Any range of motion (ROM) restriction will necessarily alter the degree to which the ligaments, muscles, and tendons that cross a restricted joint are stretched. In the case of the shoulder brace used in our experiments, this restriction was intended for precisely this purpose. We have argued that the performance reductions that accompanied our shoulder restriction are largely due to a reduction in elastic energy storage. However, the effects of this brace restriction may not be solely limited to elastic structures. It is possible that by altering the excursion of the internal rotator muscles, that these muscles may have achieved less optimal sarcomere lengths and thus produced less force. Such an effect could complicate our findings related to elastic energy storage. However, we propose that there are several reasons to believe such muscle effects are minimal and that the brace's effects are largely, although not wholly, confined to more elastic structures.

First, while the brace restriction reduced the external rotation during the restricted trials by an average of 24° , this reduction was entirely within the shoulders' passive ROM. Therefore, the active external rotation of the throwing arm at the beginning of the cocking phase is unimpeded. This "pre-cocking" of the humerus by the external rotator muscles results in stretching of the internal rotator muscles, tendons, and ligaments and presumably an increase in their stiffness^{203,204}. This active external rotation should continue until the point where the passive (or minimally active) resistance of the internal rotators, tendons and ligaments equals the active force generated by the external rotators (the active ROM limit). Thus, even before the passive external rotation of the humerus during the cocking phase, the internal rotator muscles have been stretched.

Second, measures of resting sarcomere length in p. major, anterior deltoid, and biceps show these muscles are close to optimal length ($2.8 \mu\text{m}$ ²⁰⁵) when in anatomical position. Furthermore, comparison of resting muscle length in anatomical position to estimates of optimal muscle length^{124,206} for the other internal rotators (subscapularis, l. dorsi, t. major) suggest that positioning the arm at the beginning of the cocking phase (shoulder abducted, horizontally extended, externally rotated) likely brings these muscles to near optimal lengths as well. Therefore, the force generation potential of these muscles at the active ROM limit should be near peak. This near optimal force production potential of the internal rotators at the active rotational ROM limit is important to our model, providing the counter torque required to oppose the inertial forces acting on the arm during rotation into the passive range. Electromyography studies show that during the late cocking phase (when the arm is being passively externally rotated), the internal rotator muscles are highly active^{118,119,182,207}. Such high activation at near optimal muscle length could provide large counter forces to stabilize the internal rotator muscle lengths, oppose the external rotation motion, and enable the tendons/ligaments to stretch and store elastic energy.

Finally, it is worth noting that despite the brace restriction, a mass-corrected estimate of joint power during the restricted condition ($1162 \pm 994 \text{ W kg}^{-1}$) still exceeds even adjusted estimates of peak muscle force by 1.5-3 fold. As our model predicts, this indicates significant amounts of elastic energy storage is still occurring in the restricted condition.

Supplementary Note 12. Humeral torsion - Humeral torsion (or retroversion) is a commonly used measure to describe the twisted shape of the humeral shaft. This angle is measured perpendicular to the long axis of the humerus at the intersection of two chords: one that evenly bisects the articular surface of the humeral head, the other connecting the distal epicondyles at the elbow (Figure S4). Previous research has shown torsion differs between human populations²⁰⁸⁻²¹¹, between the sexes^{208,209,211,212}, and between the dominant and non-dominant arms^{208,211,213}. It is known that such differences occur during development²¹⁴⁻²¹⁷ potentially due to variation in habitual usage of the arm^{198,209,218,219} or a muscular imbalance between the shoulder rotator muscle groups^{167,217,220,221}. Recent work has shown that throwing athletes have significantly lower torsion in their throwing arm than do non-throwers^{198-200,222,223} and that this lower torsion is linked both to shifts in the rotational range of motion (ROM) at the shoulder^{199,200,222,223} and to a reduction in shoulder injury risk¹⁹⁸. Here, we test the hypothesis that lower torsion in the throwing arm enables increased elastic energy storage and thus increases throwing velocity. We estimate humeral torsion in our subjects using measures of the active rotational ROM limits²²³. The performance data reported in the text come from the normal unrestricted throwing condition.

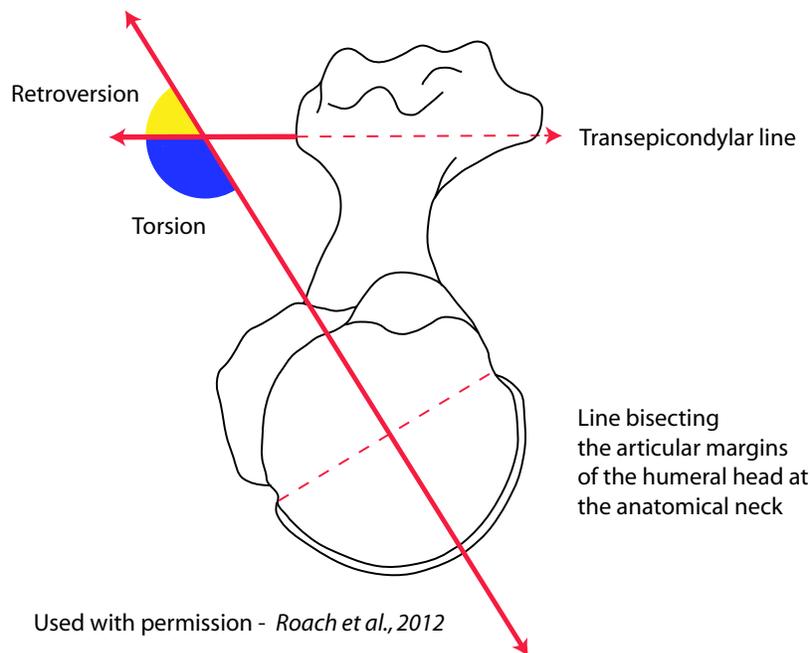


Figure S4 | Measuring humeral torsion. Humeral torsion (in blue) is measured at the intersection of the chords defining the orientation of the humeral head proximally and the transepicondylar line distally. In clinical settings, this angle is measured in the opposite direction and is termed humeral retroversion or retrotorsion.

Supplementary Note 13. *Lethality of hand thrown projectiles* – In modern sports contexts, hand thrown projectiles rarely cause (or are intended to cause) serious harm. However, despite the use of light, round balls and protective gear such as helmets and significant padding, minor injuries such as contusions, concussions, and bone fractures are common and fatalities sometimes occur^{224,225}. Moreover, these modern projectiles differ significantly from the stones, throwing sticks, and untipped wooden spears likely used by early hominins. While the precise effectiveness of these projectiles at causing lethal damage is unknown, there is some indirect evidence that such weapons are able to kill game. For example, there are reports of throwing sticks and boomerangs being used to hunt small animals^{81,226,227}. Darwin reports on the effectiveness of rocks thrown by Fuegian foragers at killing birds¹. Similarly, there are reports of wooden spears being used to kill game as large as wallabies, dugong, and crocodiles^{81,228}. Furthermore the presence of untipped wooden spears in both the ethnographic^{81,228-234} and fossil records²³⁵ further suggests they must have been effective weapons. While much remains unknown about throwing behavior in human evolution, there is good reason to believe such behavior could have been an effective means of early hunting and may have played an important role in our evolutionary past.

Supplementary Note 14. Osteological signatures of throwing – The archaeological record for throwing before the relatively recent appearance of lithic projectile points²³⁶⁻²⁴¹ is sparse and controversial^{235,238,242-248}. Accordingly, a number of studies have sought to use fossil material to address whether earlier hominins produced high-powered throws^{8,10,14,15,249-252}. Contrary to our approach, previous osteological studies have largely focused on asymmetries in anatomical features of the upper body thought to be related to throwing behavior. However, such studies often address only more recent taxa (such as *H. neanderthalensis*) and frequently do not test the validity of proposed functional anatomical hypotheses.

Results from these analyses have been equivocal and problematic. A study of later hominin humeral torsion asymmetry found, with a limited sample, that bilateral asymmetry in torsion angle was lower in Neanderthals than modern humans¹⁵. The authors suggest that this asymmetry pattern suggests that Neanderthals did not throw. However, it is worth noting that the Neanderthals sampled had lower torsion than most of the modern human groups measured. Our data on humeral torsion and throwing performance suggest that it is not the presence of asymmetries in torsion, but rather the maintenance of lower torsion into adulthood that provides a performance advantage during throwing. Differences in ulnar supinator crest size and asymmetry have also been interpreted as evidence that Neanderthals did not throw¹⁴. However, the supinator muscles are not involved in generating high-speed throws and accordingly show low activity during all phases of the throw²⁵³. Furthermore, no asymmetries in supinator index were found in any group studied. The variable presence of a supinator crest in males across a number of diverse hominin taxa suggests this trait is a signature of skeletal robusticity rather than throwing behavior²⁵⁴⁻²⁵⁶. Analyses of humeral cross-sectional geometry and glenoid index have also been used to suggest that Neanderthals lacked the ability to throw effectively^{14,15,257,258}. While the performance or injury reduction benefits of both features are unknown and untested, significant difference between Neanderthals and modern humans were found. However, it is worth noting that in both cases when non-size corrected values are analyzed, Neanderthals have absolutely more robust humeri and glenoid fossae. These data suggests that Neanderthals might actually be better adapted to withstand the forces generated during throwing than modern humans. Churchill and Rhodes²⁵⁹ point out that Neanderthals have significantly longer olecranon processes than do modern humans, which would increase the mechanical advantage of the triceps, but potentially also reduce elbow extension speed during throwing. However, it is worth noting that our data and that from a number of other studies of throwing biomechanics²⁶⁰⁻²⁶² show that the moment at the elbow during rapid elbow extension is antagonistic and in fact acts to slow extension. This suggests that a minor increase in olecranon length would have little effect on throwing performance. Thus far, the most useful osteological marker of throwing behavior is the unilateral presence of enthesopathies on the medial epicondyle of the distal humerus of the throwing arm^{10,263-268}. However, it is worth noting that this bone stress indicator is not present in all throwers and further work is needed to determine whether throwing alone is responsible for creating these bone lesions. Furthermore, these enthesopathies may be of limited utility in addressing whether earlier hominins threw, as excellent preservation of the bone surface on both humeri is required and rarely found.

Supplementary Note 15. Clavicle length in *Homo erectus* - Previous research reconstructing the hominin shoulder has suggested that early *H. erectus* fossils have relatively short clavicles when standardized by humeral length²⁴⁹. Given that the clavicle is the only bony attachment of the shoulder girdle to the torso, clavicle length is inferred to affect scapular positioning and thus range of motion at the shoulder²⁴⁹. Using the claviculohumeral ratio (clavicle length/humeral length*100) from the KNM WT 15000 and LB1 fossils, Larson²⁴⁹ reconstructs early *H. erectus* as having novel, intermediate shoulder morphology with low, very anteriorly positioned scapula and suggests that as a result early *H. erectus* may have had compromising throwing ability.

However, while the KNM WT 15000 claviculohumeral ratio (40.9) is low for modern humans, it does fall within the measured range of normal variation seen in east african populations today²⁴⁹. Additionally, fossil clavicles from the early *H. erectus* site of Dmanisi show reconstructed claviculohumeral length ratios squarely within the modern human range (adult male – 46.5L, 46R; juvenile – 43.7)²⁶⁹. Given that both the Dmanisi and Nariokotome clavicle fossils are incomplete, assessing the accuracy of the length reconstruction methods used is important to resolve this discrepancy. However, these methods are not reported in the Dmanisi analysis. Further research is required to address this interesting discrepancy.

Finally, while standardizing clavicle length using the humerus has been shown to be a useful method to correct for species-specific differences in body mass^{249,270}, it is unclear whether the claviculohumeral ratio is useful for reconstructing shoulder position. Chimpanzees for example have low claviculohumeral ratios and yet have *dorsally* positioned, cranially oriented scapula. This dorsal shoulder position is not a function of the length of the clavicle relative to body mass, but instead derives from the length of the clavicle relative to the breadth of the superior portion of the ribcage, which is evolving independently of body mass²⁵. Recent work investigating clavicular length in apes suggests that when chimpanzee clavicles are normalised to thorax width they fall closer to the rest of the apes in having a relatively elongated clavicle relative to monkeys²⁷¹. Such a thorax width standardization better accounts for the shoulder positioning seen in chimpanzees and humans. In sum, better data are needed to determine how clavicle length/shape, as well as thorax width/shape, relate to shoulder positioning in hominins, and existing data on clavicle length in *H. erectus* do not preclude high-speed throwing.

Supplementary Note 16. Glenoid orientation as a throwing adaptation – The “relaxation” or caudal rotation of the scapula in *H. erectus* likely had significant effects on many behaviors. It is possible that this modification to shoulder position may be an adaptation for throwing, because it would result in large increases in throwing performance while having relatively minor or even negative effects on the performance of other important behaviors. For instance, laterally oriented shoulders likely positioned the glenohumeral joint further inferiorly on the thorax, resulting in a wider shoulder breadth that would reduce the mechanical advantage of the shoulder muscles during climbing. In addition, a more relaxed shoulder would result in a lateral reorientation of the p. major muscle, removing any useful flexion contribution of this muscle during stick digging. The effects of shoulder position on knapping are more difficult to address. The power requirements of stone tool manufacture are probably much lower than during high-speed throwing and the muscle most significantly affected by a change in shoulder positioning, p. major, is likely minimally active during knapping. In this regard, a lower shoulder would have little effect. However, Larson²⁴⁹ notes that a laterally oriented glenoid in combination with very low torsion in *H. erectus* (below most modern human values, including most throwing athletes) could result in reduced range of motion for manipulative tasks such as knapping or tool use. This problem, in combination with potentially short clavicles relative to humerus length, have led Larson to propose that the shoulder in *H. erectus* was more anteriorly positioned. To address this hypothesis, further data on tool manufacture and use are needed to test whether shifts in shoulder morphology alter performance or result in compensatory motions. The only other context in which a low laterally oriented shoulder has been suggested to improve performance is during running²⁵. Bramble and Lieberman suggest that shifts in shoulder position represent a decoupling of the head and shoulders and help to increase gaze stability during running. However, it is unclear to what extent decoupling of the shoulder from the head is related to lower, wider shoulders, and the body has additional mechanisms to insulate the head from jarring motions^{272,273}. In sum, much additional research is needed to quantify the performance effects of a laterally oriented shoulder on many diverse activities, but there is reason to hypothesize that shifts in shoulder position have important performance effects during throwing and may represent an adaptation for this behavior.

Supplementary Note 17. *Pre-enrolment performance task & data exclusion criteria* – Collegiate age male subjects with no current torso or forelimb injuries were recruited for this study. All subjects were required to pass an initial performance task prior to enrolment. Each potential subject was given 5 tries to hit a 1m x 1m target with a baseball from 10 meters away at a minimum speed of 22.35 m/sec (50 mph). Twenty-five subjects successfully completed the task and were enrolled in the study (one subject subsequently removed himself prior to data collection). Of the 24 total subjects, 3 failed to achieve any throw of at least 22.35 m/sec during the full data collection and were excluded from the study. One further subject was removed from normal vs. restricted analysis due to an abnormal response to the shoulder restricted condition, rendering him an outlier in all analyzed data. The final sample size for all conditions is 20 subjects.

Supplementary Note 18. Kinematics – Twenty-one 25mm passive reflective markers were used to define the torso, arm, forearm and hand (Figure S5). The markers were placed on bony landmarks using both double-sided toupee tape and cloth medical tape. The torso was defined with 5 markers (C7, C7 prominens; ThrowAcro, throwing side acromion; ContraAcro, contralateral side acromion; ThrowHip, throwing side greater trochanter of the femur; and ContraHip, contralateral side greater trochanter of the femur). A rigid cluster containing 4 markers was also placed on the back between the scapula on trials were no brace restricted its application (TorsoSup, superior; TorsoInf, inferior; TorsoThrow, throwing side; and TorsoContra, contralateral side). Two markers were placed on the scapular spine (ScapLat, lateral; and ScapMed, medial). The arm was defined using a functionally defined shoulder joint (see Supplementary Note 22) and two distal markers (ElbLat, lateral humeral epicondyle; and ElbMed, medial humeral epicondyle). On some trials a second rigid cluster was applied to the dorsal side of the arm (ArmProx, proximal; ArmDist, distal; ArmMed, medial; and ArmLat, lateral). The forearm was defined using the calculated midpoint between ElbLat and ElbMed proximally and two markers distally (WriLat, radial styloid; and WriMed, ulnar styloid). The hand was defined again using the calculated midpoint of the wrist markers as well as two distal markers (MC2, distal end of the 2nd metacarpal; and MC5, distal end of the 5th metacarpal). All markers were identified using Vicon Nexus v1.7.1 software.

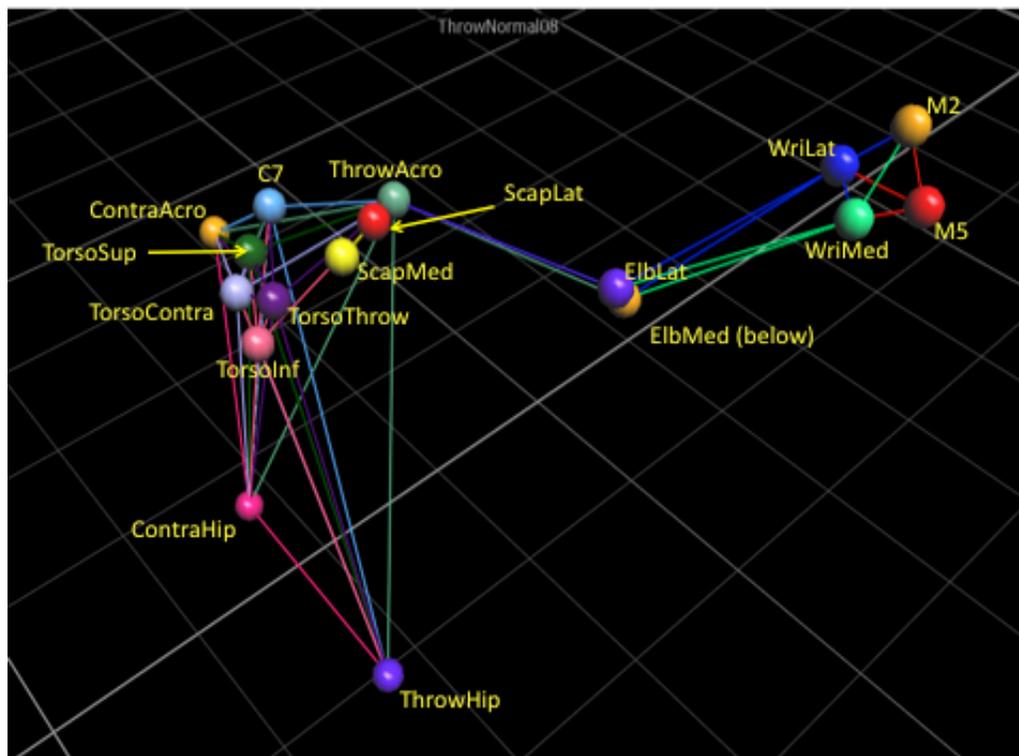


Figure S5 | Reflective markers on a subject at ball release. Note: there is no arm cluster in this trial.

Supplementary Note 19. *Experimental conditions* – All subjects performed both “slow” and “fast” throws in each of 5 conditions. During slow throws the subject was instructed to make a comfortable throw with no consideration of speed. During fast throws the subject was instructed to throw as fast as he felt comfortable throwing. The conditions were normal unrestricted kinematics and four brace restricted conditions (clavicular elevation, torso immobilization, shoulder rotation, and wrist extension). Condition order was randomized across subjects. The brace restrictions used commercially available therapeutic braces to limit range of motion at a specific joint. All brace conditions (except for torso immobilization) also included an intermediate sub-condition in which the brace was worn but no restriction was applied. During loaded brace conditions, subjects were instructed to attempt their normal throwing motion. In this paper, only data from the normal unrestricted and shoulder rotation restriction (Donjoy Shoulder Stabilizer - Donjoy Inc, Vista, CA) are used.

Supplementary Note 20. Filtering – Residual analysis was conducted following Winter²⁷⁴ on throwing trials from 5 randomly chosen subjects using a custom MATLAB script. The residual was calculated for 2nd, 4th and 6th order Butterworth lowpass filters with the cutoff frequency iterated between 1Hz and the Nyquist frequency of the data (500Hz). The residual was calculated for the ThrowHip, ThrowAcro, ElbLat, WristLat and MC2 markers using the formula;

$$\text{Equation S1: } R(f_c) = \sqrt{\frac{1}{N} \sum_{i=1}^N (X_i - \hat{X}_i)^2} \quad (\text{Eq. S1})$$

where R is the residual in meters, f_c is the cutoff frequency, X_i is the raw data of the i^{th} sample, and \hat{X}_i is the filtered data of the i^{th} sample. The full residual analysis was conducted twice; once with the full throwing trial (Figure S6) and once using only the critical period from the initiation of internal rotation of the humerus to ball release (Figure S7). Cutoff frequencies were manually chosen following Winter²⁷⁴.

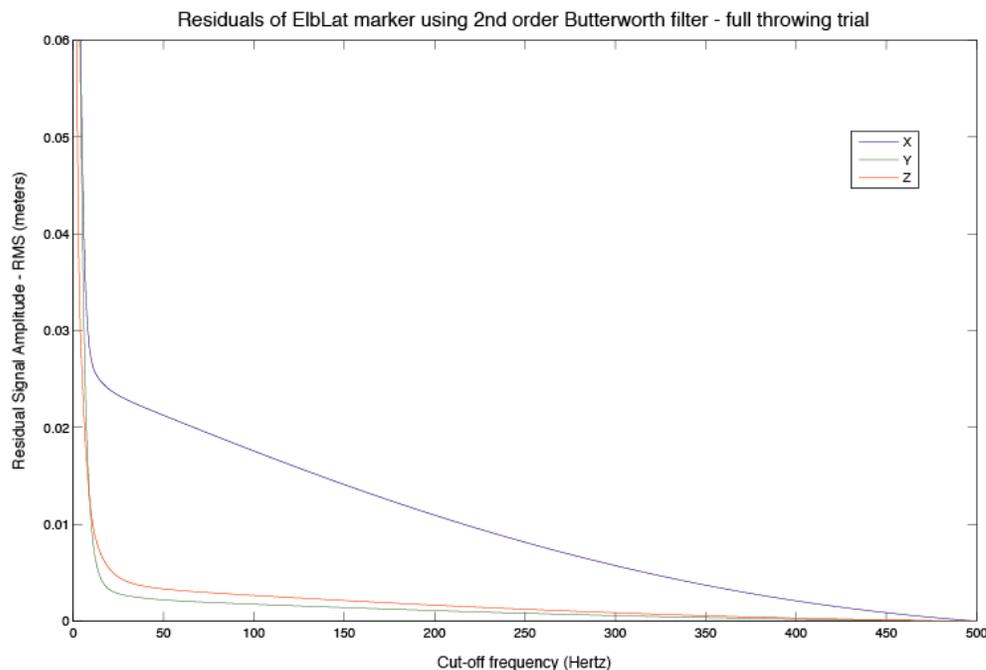


Figure S6 | Sample residual analysis data from the full trial. These data show the ElbLat marker data using a 2nd order Butterworth filter (Subject 006, trial 8).

A 2nd order filter was chosen as the best fit for the data because it consistently returned the lowest actual residuals across all markers. Full trial and critical period cutoff frequency means were statistically different ($p < 0.05$) using a matched pairs t-test (Table S4). The mean was calculated from the X, Y, and Z residuals from each marker and then again from all markers (all marker XYZ mean: 17.3 Hz – full data set; 36.7 Hz – critical period). For data processing, we split the difference between the full data period and the

critical period frequencies by using a 25 Hz cutoff frequency. As a final check on the sensitivity of our analyses, we added random noise (2mm width, zero mean) to all markers from a single subject's raw, unfiltered data. After filtering, no significant differences were detected in any kinetic measures.

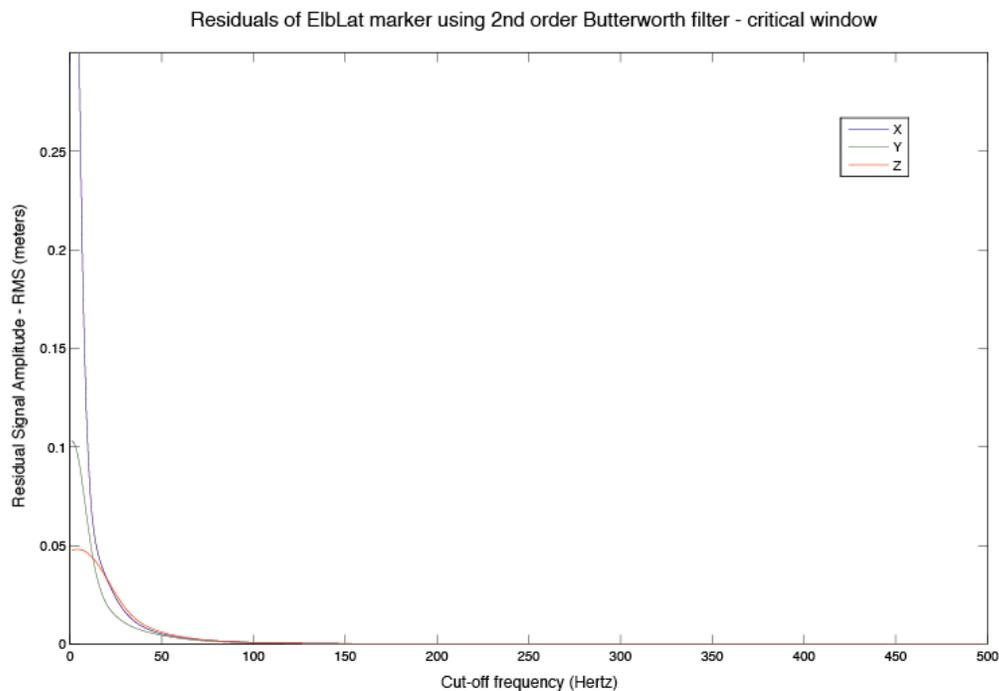


Figure S7 | Sample residual analysis data from the critical period. These data show the ElbLat marker data using a 2nd order Butterworth filter (Subject 006, trial 8).

Supplementary Table S4 - Cutoff frequency data (Hz) - 2nd order Butterworth filter					
<i>Marker</i>	<i>Data set</i>	<i>X</i>	<i>Y</i>	<i>Z</i>	<i>Mean XYZ</i>
ThrowHip	<i>full</i>	14.8(4.8)	12.2(3)	10.2(3.2)	12.4(3.7)
	<i>critical</i>	41(11.5)	35(7.8)	37.4(6.8)	37.8(8.7)
ThrowAcro	<i>full</i>	21(12.9)	12.8(4.4)	18(11.3)	17.3(9.5)
	<i>critical</i>	67.8(46.5)	58.4(45.7)	26.6(9.7)	50.4(34)
ElbLat	<i>full</i>	18.8(8.9)	15.2(3)	14.8(4.8)	16.3(5.6)
	<i>critical</i>	35.6(8.4)	34.2(8.5)	36.8(7.3)	35.5(8.1)
WristLat	<i>full</i>	30.2(15.7)	15.8(5)	13.2(1.6)	19.7(7.4)
	<i>critical</i>	41.8(11.9)	25(4.7)	25.2(4.3)	30.7(7)
MC2	<i>full</i>	34.4(10.9)	16(4.4)	12.4(1.8)	17.1(5.7)
	<i>critical</i>	25.2(9.4)	24.8(8.4)	24.2(7.5)	25.3(8.4)

Table S4 | Mean cutoff frequencies (and standard deviations). Data from 5 subjects using a 2nd order Butterworth filter.

Supplementary Note 21. *Throwing phase standardization* – Differences in timing between throws are controlled for in the kinematic and kinetic data by assigning portions of the motion to several standardized phases: windup, stride, arm-cocking, acceleration, and deceleration²⁷⁵, of which we focus here on arm-cocking and acceleration. Arm cocking is defined from the moment of leading foot contact with the ground at the end of stride (STR) to the maximum external rotation (MER) of the shoulder. Acceleration is defined from MER to the moment of release (REL). STR was defined using the minimum point of mid-pelvis linear velocity. MER was defined as the shoulder rotation angular velocity zero point following STR. Data from the entire internal rotation motion (including the full acceleration and deceleration phases) were further calculated from MER to DECEL, defined as the shoulder rotation angular velocity zero point following REL.

Because these phases often differ in duration between throws, further standardization is required in order to calculate mean values and variances for all parameters. Accordingly, all joint angles, angular velocities, torques and power values were processed in MATLAB by interpolating each phase 1000 fold and subsequently down sampling each throw to a set length. The acceleration phase was down sampled to 100 data points and the arm-cocking phase to 894 points (in keeping with the mean arm cocking/acceleration duration ratio). Note that the different throwing conditions did vary in this ratio (see Supplementary Note 10), but that in order to achieve comparable data between conditions the mean 8.94:1 ratio was used for all conditions.

Supplementary Note 22. Kinetics – The kinetic model was created using C-Motion Visual3D software. Segment definitions and rotational axes are described in Table S5. All segment masses, centres of mass, and radii of gyration were taken directly from Dempster²⁷⁶. A number of the markers used to define and track segments are virtual calculated markers. The markers midHip and midWrist represent the calculated midpoint between the hip and wrist markers respectively. The FuncSho marker is calculated as a functional joint from a movement trial. In this movement trial, the subject keeps his torso still, the arm is abducted 90 degrees and the elbow is fully extended. The subject then proceeds to slowly circumduct the arm keeping the elbow straight. The motion is tracked as two temporary segments (torso – ThrowAcro, ContraAcro, C7; arm – ThrowAcro, ElbMed, ElbLat). An optimization was performed to find the functional joint centre between the two segments with the lowest residual. A limitation of our model is that the shoulder is treated as a single joint, when in reality two joints are present (glenohumeral and scapulothoracic). This is common practice when modeling the shoulder (eg. ^{111,164,277-280}) due to the difficulty of accurately tracking scapular motion during high-speed movements^{100,101}. This simplified shoulder model does not affect our analysis as our inverse dynamics calculations are computed about the proximal end of the distal segment (eg. for the shoulder – the humeral markers are used).

The final calculated marker (RFA80) is both a marker and a joint (Figure S8). This marker is calculated as lying 80% of the distance towards the wrist along the chord from the calculated midElbow and midWrist markers. The marker was created to establish a virtual, independent segment in the forearm that allows for accurate measures of pro/supination and solves a tracking problem in the elbow. Because the humeroulnar and humeroradial joints have different joint centres, defining a single forearm segment requires choosing a joint centre that accurately represents one forearm motion but the other poorly or represents both poorly. This is evident when a single forearm segment model is loaded into the data as the forearm tracks very poorly at the elbow. To solve this problem, we created a two-segment forearm using the RFA80 marker. The proximal segment, ForearmUpper, contains 80% of the mass and length of the forearm, while the distal segment, ForearmLower, contains 20% of the mass and length. Due to the way both segments are defined, the motion at the joint between these two segments should be confined to movement around the Z axis.

Joint angle data from ForearmLower shows that this is largely the case, although there are minor angular changes around the X and Y axes (<6 degrees, approximately 4% of total angular motion at the joint). These minor movements likely represent slight deviations in the axis of pro/supination away from the estimated axis. The definition of these segments also prevents any problems with calculated moments as the lack of flex/extension motion at the ForearmPS joint and pro/supination motion at the elbow joint create non-independent masses for the entire forearm. The use of a two-segment forearm also resolves the model-tracking problem in the elbow.

Supplementary Table S5 - Segment Definitions				
Segment	Geometry	Defining Markers	Tracking Markers	Axes
Thorax/Pelvis	Cylinder	Proximal: ThrowHip, ContraHip Distal: ThrowAcro, ContraAcro	midHip (calc) ThrowAcro ContraAcro	X: axial flex/extension Y: lateral flex/extension Z: axial rotation
Arm	Cone	Proximal: FuncSho (calc), ThrowAcro Distal: ElbMed, ElbLat	FuncSho (calc) ElbMed EldLat	X: flex/extension Y: ab/adduction Z: int/external rotation
ForearmUpper	Cone	Proximal: ElbMed, ElbLat Distal: RFA80 (calc)	ElbMed ElbLat RFA80 (calc)	X: flex/extension
ForearmLower	Cone	Proximal: RFA80 (calc) Distal: WriMed, WriLat	RFA80 (calc) WriMed WriLat	Z: pro/supination
Hand	Sphere	Proximal: WriMed, WriLat Distal: MC5, MC2	midWrist (calc) MC5 MC2	X: flex/extension Y: ulnar/radial deviation
Ball	Sphere	Single marker: Ball Prox (calc)	midWrist (calc) MC5 MC2	No independent motion

Table S5 | Segment parameters using in the kinetic model. Segment length and diameter is obtained using the defining marker sets. Segmental movements are recorded using the tracking markers around the defined axes.

The most distal segment in the kinetic model is the ball. The ball segment is defined as a calculated marker, Ball, which is placed 130% of the distance along the chord from the WriLat to MC2 marker and 20% of the distance along the chord between the MC2 and MC5 markers. This places the ball between and slightly distal to the 2nd and 3rd metacarpal heads (a common placement for a standard split finger throw). The ball was given the appropriate mass (144g) and radius (3.68cm) of a standard baseball. The

ball segment was tracked using the same markers as the hand segment and therefore is non-independent. In all kinetic data from after the moment of release, the mass of the Ball segment is dropped to zero.

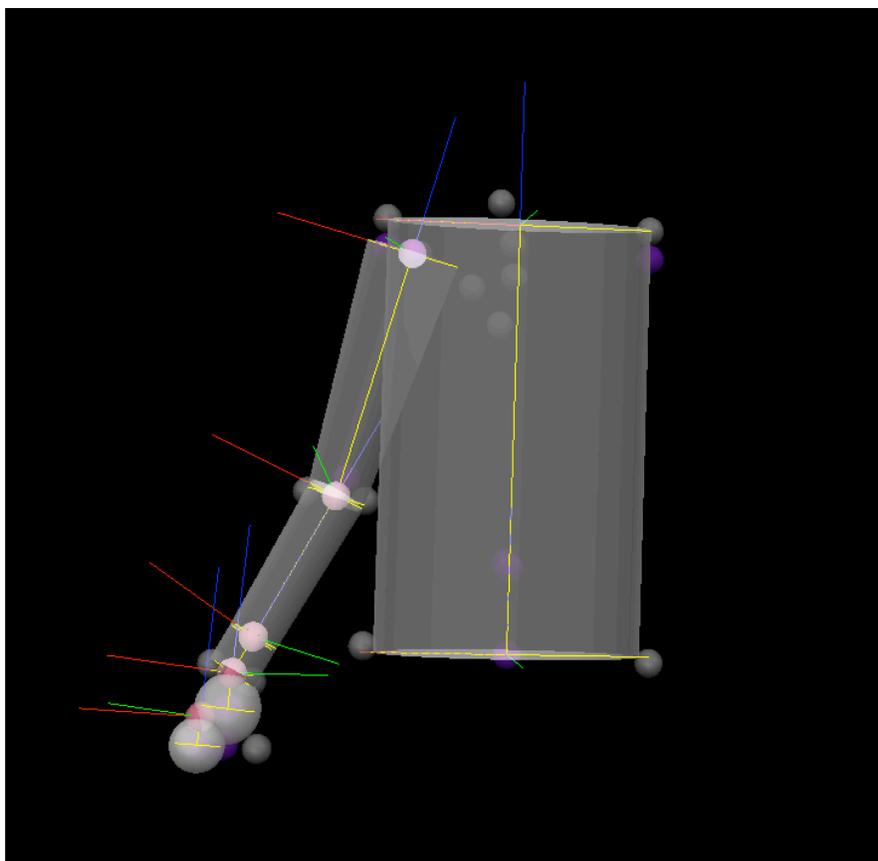


Figure S8 | Visual3D kinetic model showing the segments used in the inverse dynamics analysis. Note the distal ball segment as well as the location of the RFA80 and functional shoulder joints.

All defined joints in the kinetic model are described in Table S6. Note that all joint angles and velocities are defined using a X,Y,Z Cardan sequence of rotations and all joint measures are resolved relative to the proximal segment with the exception of the torso/pelvis, which is necessarily resolved relative to the lab global coordinate system, and the shoulder, which is resolved relative to its own axis to bring angular velocities and related measures in line with previously published data^{277,278}.

Supplementary Table S6 - Joint Definitions				
Joint	Segment	Reference Segment	Resolution Coordinate System	Cardan Sequence for Joint Angles
<i>Torso</i>	Thorax/Pelvis	Lab	Lab	X,Y,Z
<i>Shoulder</i>	Arm	Thorax/Pelvis	Arm	X,Y,Z
<i>Elbow</i>	ForearmUpper	Arm	Arm	X,Y,Z
<i>ForearmPS</i>	ForearmLower	ForearmUpper	ForearmUpper	X,Y,Z
<i>Wrist</i>	Hand	ForearmLower	ForearmLower	X,Y,Z

Table S6 | Joint parameters used in the kinetic model. The Cardan sequence is the series of rotations used to define both the joint Euler angles and the joint velocity, which is calculated using the instantaneous axis of rotation and not the first derivative of the Euler angles.

Supplementary Note 23. Comparison to previous estimates of power –

Although previous studies have not published data on power generation during throwing, we can directly compare the two measures from which mechanical power is derived: angular velocity and torque. Peak angular velocity for shoulder internal rotation in our subjects was 4290 ± 1127 °/sec, which is comparable to or below peak values reported elsewhere^{111,277,278,281}. Peak shoulder rotation torque in our sample was 206 ± 42 N/m. These torques fall squarely in the middle of previously reported values, with some previously published values being higher²⁷⁸, some approximately equivalent²⁷⁷, and still others lower^{111,282,283}. In the studies that reported lower torques, the filtering procedure was either not described²⁸² or used a lower, qualitatively chosen filtering cut-off frequency (13.4 Hz)^{111,283}. Our residual analyses suggest this low cutoff frequency will underestimate joint accelerations affecting the resulting torques, especially during the critical acceleration phase.

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