

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

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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

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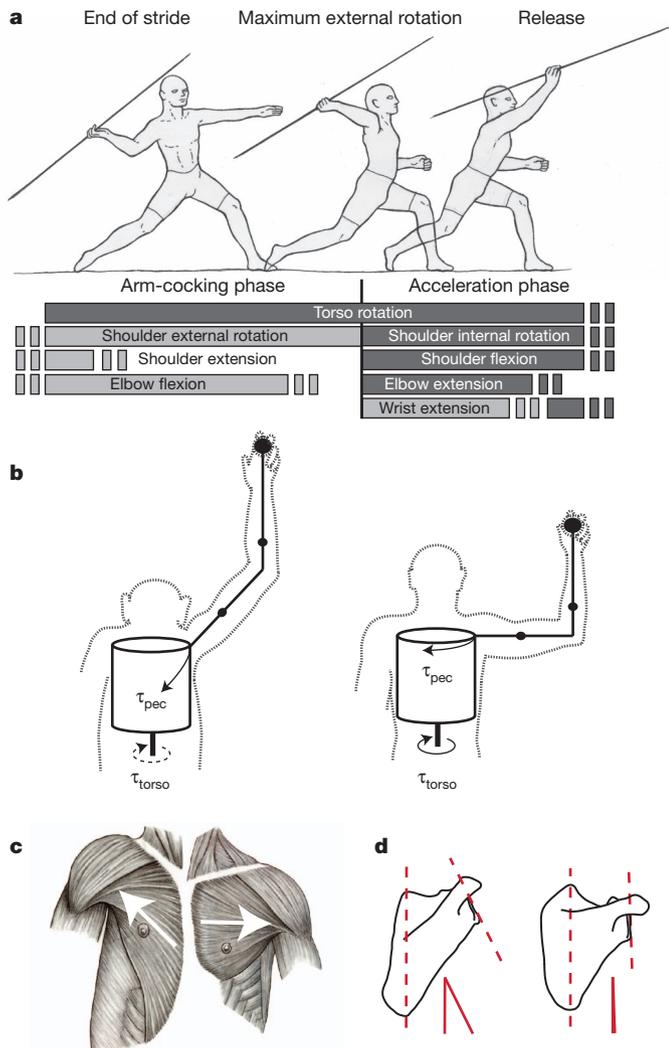


Figure 1 | Model of elastic energy storage. **a**, Arm-cocking and acceleration phases of the overhand throw. Light grey text boxes show the relative timing of the ‘cocking’ motions; dark grey boxes indicate the relative occurrence of the opposing ‘acceleration’ motions. Short boxes illustrate variation 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

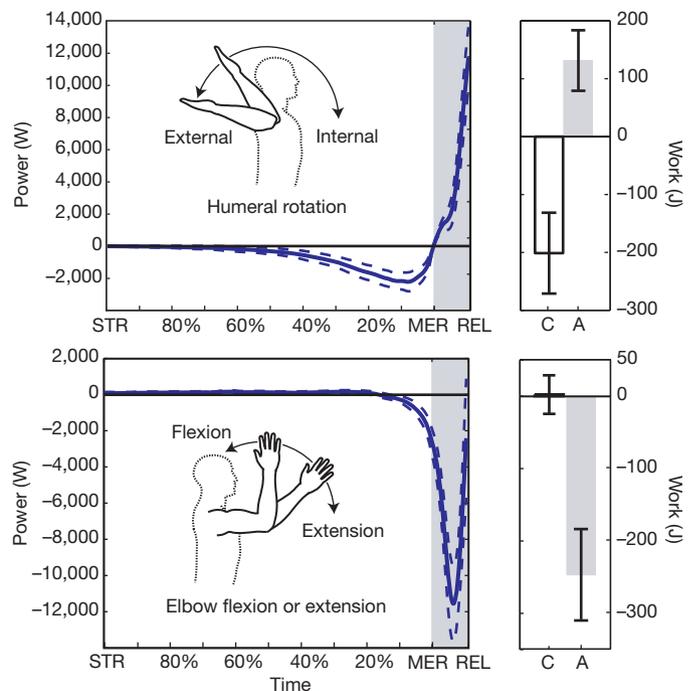


Figure 2 | Shoulder rotation and elbow flexion–extension power. Mean shoulder rotational power (solid blue line) with 95% confidence intervals (dotted blue lines) shows a sustained period (white) of negative power and work during arm-cocking (C), between stride (STR) and maximum external rotation (MER). 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.

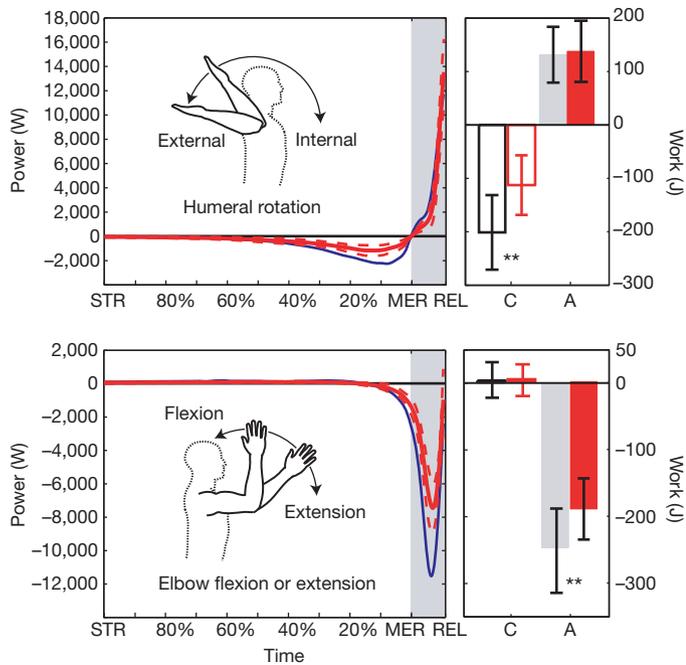


Figure 3 | Shoulder-brace restriction condition. Brace restricted mean power (solid red line) with 95% confidence intervals (dotted red lines) for shoulder rotation and elbow flexion-extension. Values for the unrestricted condition (no brace) are shown by the solid blue line. In the right panels, work 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.

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

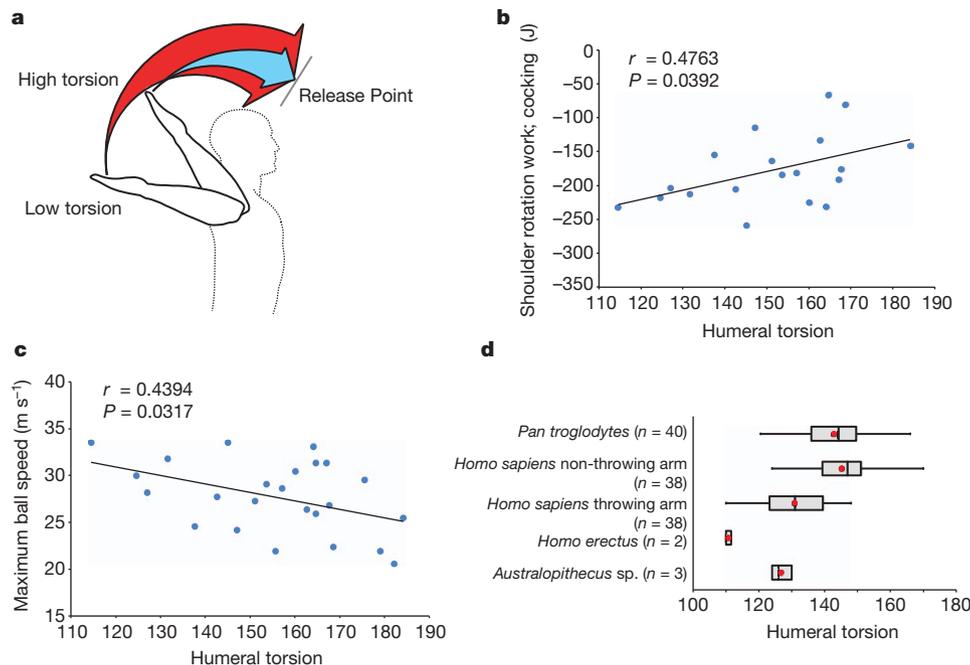


Figure 4 | Humeral torsion and throwing performance. a–c Low humeral torsion shifts the shoulder rotational ROM externally (a), enabling increased negative work during arm-cocking to be stored as elastic energy (b), and resulting in faster projectile speed (c). d, Humans and chimpanzees show comparable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

*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 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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