

RESEARCH ARTICLE

Upper body contributions to power generation during rapid, overhand throwing in humans

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ABSTRACT

High-speed and accurate throwing is a distinctive human behavior. Achieving fast projectile speeds during throwing requires a combination of elastic energy storage at the shoulder, as well as the transfer of kinetic energy from proximal body segments to distal segments. However, the biomechanical bases of these mechanisms are not completely understood. We used inverse dynamics analyses of kinematic data from 20 baseball players fitted with four different braces that inhibit specific motions to test a model of power generation at key joints during the throwing motion. We found that most of the work produced during throwing is generated at the hips, and much of this work (combined with smaller contributions from the pectoralis major) is used to load elastic elements in the shoulder and power the rapid acceleration of the projectile. Despite rapid angular velocities at the elbow and wrist, the restrictions confirm that much of the power generated to produce these distal movements comes from larger proximal segments, such as the shoulder and torso. Wrist hyperextension enhances performance only modestly. Together, our data also suggest that heavy reliance on elastic energy storage may help explain some common throwing injuries and can provide further insight into the evolution of the upper body and when our ancestors first developed the ability to produce high-speed throws.

KEY WORDS: Throwing, Biomechanics, Elastic energy storage, Kinetic chain, Human evolution

INTRODUCTION

The human forelimb is derived relative to other hominoids and to earlier hominins (Larson, 1993; Larson, 2007). One reason the human shoulder may be so different is selection for humans' unique ability to throw objects overhand with both accuracy and high velocity. Today, most high-speed throwing occurs during sports, but in the past throwing was probably crucial for hunting, defense against predators, and aggressive interactions. Regardless of their purpose, high-speed overhand throws are produced using a stereotypic, whip-like motion involving the whole body.

The throw begins with movement of the legs and progresses quickly up the trunk and arm, ending with rapid movement of the throwing hand as the projectile is released. There has been considerable inquiry into how this complex motion generates high projectile velocities, and which joints and joint-specific angular motions are primarily responsible (Dillman et al., 1993; Fleisig et al., 1995; Hirashima et al., 2007; Hirashima et al., 2008; Hong et al.,

2001; Pappas et al., 1985; Putnam, 1993). Previous work has shown that large angular velocities of torso rotation, shoulder internal rotation, elbow extension and wrist flexion all occur at the moment of release and significantly contribute to projectile speed (Fig. 1) (Fleisig et al., 1995; Fleisig et al., 1996; Hirashima et al., 2007; Pappas et al., 1985). This study focuses on how these large angular velocities are produced in the upper body.

Angular movements are produced when torques act across joints, generating mechanical work and power. Muscles are the source of most torques and are thus key contributors to joint power production and angular velocity. As expected, electromyography (EMG) patterns of muscle activity during throwing show sequential activation of muscles mirroring the progression of the throwing motion (Hirashima et al., 2002). However, muscle activation patterns alone cannot fully explain how throwing power is generated. For example, an individual with a paralyzed triceps brachii can still achieve rapid elbow extension during throwing, indicating that the triceps does not power rapid elbow extension on its own (Roberts, 1971). In addition, although EMG recordings of shoulder internal rotator muscles indicate high activity during internal rotation (DiGiovine et al., 1992; Gowan et al., 1987), experimental data on shoulder power show that these muscles only generate approximately 50% of the power for this rapid motion (Roach et al., 2013). A further problem with using EMG to evaluate the roles of muscles in generating torques in the upper body is the lack of any simple relationship between EMG intensity and muscle force production (Bell, 1993; Gans, 1992).

Previous research has suggested that additional sources of torque to power large angular velocities during throwing come from movements generated in adjacent, connected body segments, which can be transferred from joint to joint via a 'kinetic chain' (Atwater, 1979; Fleisig et al., 1996; Hirashima et al., 2008; Hore et al., 2005; Ben Kibler and Sciascia, 2004). These interaction torques can result directly from muscular actions at other joints or from velocity-dependent, centrifugal or Coriolis forces (Hirashima et al., 2008). Mathematical decomposition of throwing kinematics using equations of motion has shown that high angular velocities observed at the elbow and wrist joints at release are largely due to these interaction torques (Feltner, 1989; Hirashima et al., 2007; Hirashima et al., 2003; Hong et al., 2001; Putnam, 1993). Induced acceleration analyses of these interaction torques further show that elbow extension during throwing is driven primarily by velocity-dependent forces generated by torso rotation and shoulder internal rotation (Hirashima et al., 2008). The same study also found that wrist flexion during throwing is mostly driven by velocity-dependent forces generated by elbow extension. These data strongly support the hypothesis that power generated at more proximal joints (such as the hips, torso and shoulder) is transferred to the throwing arm, producing very rapid, 'whip-like' accelerations of the arm and hand (Alexander, 1991; Atwater, 1979; Feltner, 1989; Putnam, 1993). However, like all kinetic analyses, these studies estimated only the

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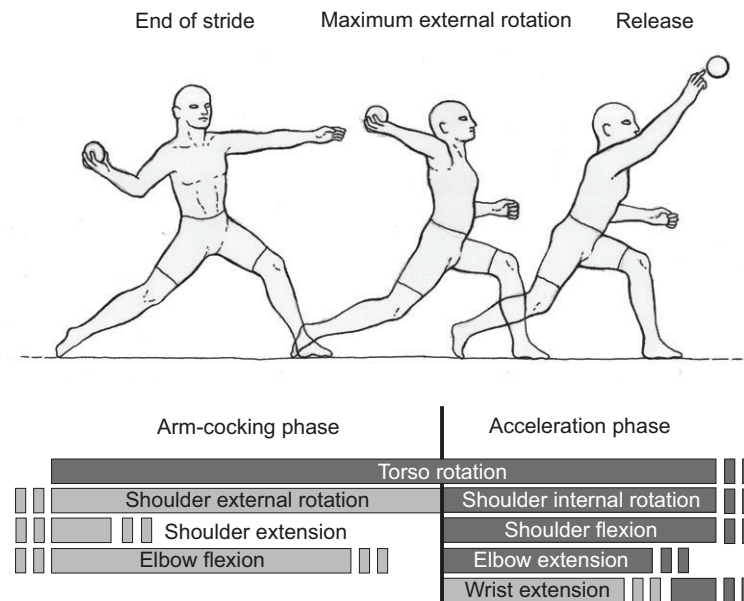


Fig. 1. The arm-cocking and acceleration phases of the throw.

Arm cocking begins with the contralateral foot touching the ground at the end of a large stride in the target direction. During the cocking phase, the humerus externally rotates until it reaches maximum external rotation. Following maximum external rotation, the very brief acceleration phase occurs in which the humerus rapidly internally rotates, the elbow extends and the wrist is flexed. Acceleration ends with the release of the projectile. Light gray bars indicate the relative timing of 'cocking' motions, while the dark gray bars indicate the timing of 'acceleration' motions.

contributions of joint rotational motions (i.e. shoulder internal/external rotation) without measuring how much energy was produced by particular muscles or by elastic energy storage mechanisms.

Several studies have suggested that the storage and release of elastic energy also plays a role in power enhancement during throwing. Wilk et al. (Wilk et al., 1993) argued that throwing athletes enhance torque production by 'pre-stretching' numerous throwing muscles just prior to their activation, resulting in elastic energy storage in the muscle itself. In addition, Roach et al. (Roach et al., 2013) found that the posture of the 'cocked' arm (externally rotated) just prior to the rapid shoulder internal rotation motion passively stretches elastic elements crossing the shoulder. By comparing actual power production during throwing to modeled maximum power values for all muscles potentially involved, they inferred that passive stretching results in significant amounts of elastic energy being stored and released, powering the rapid internal rotation of the humerus that follows. Although power amplification is well known and well studied in the human lower limb (e.g. Anderson and Pandy, 1993; Komi and Bosco, 1978), understanding the workings of such amplification mechanisms in humans is complicated by the difficulty of collecting direct strain measurements (Finni et al., 2000; Komi et al., 1987; Lewis et al., 1982; Pourcelot et al., 2005) and the inability to use invasive methodologies, such as sonomicrometry. Accordingly, the present study combines inverse dynamics analysis with experimental perturbations of the throwing motion using therapeutic braces. These restrictions allow us to non-invasively examine how muscular force, kinetic transfer and elastic energy storage interact and power the throwing motion.

Here, we test how the upper body contributes to power generation during throwing by experimentally manipulating four key motions hypothesized to be responsible for projectile speed (torso rotation, shoulder internal rotation, elbow extension and wrist flexion; Fig. 2). We used therapeutic braces that limit joint range of motion (ROM) or modify joint position to induce variation in throwing kinematics. Note that these braces are not intended to fully remove these movements, as this would make throwing difficult or impossible. They are instead designed to induce modest perturbations that help

illuminate the effects each motion has on overall performance and upon the other critical motions in the upper body. Further, these restrictions allowed us to test the effects of morphological variations associated with performance in a study group where all individuals have comparable, high skill levels. The braces used also served to recreate evolutionarily relevant chimpanzee-like and hominin-like joint positions and ROM, as apes throw poorly and with very different kinematics (Goodall, 1964; Goodall, 1986; Kohler, 1925; Sugiyama and Koman, 1979) and intermediate morphologies are found solely in extinct fossil taxa.

Hypotheses

Hypothesis 1: the hip rotator muscles generate the majority of the torso rotation power during throwing

Previous studies have shown that hip rotation is an important component of the throwing motion that correlates with throwing performance (Matsuo et al., 2001; Stodden et al., 2001; Wight et al., 2004). We propose that by stabilizing the torso relative to the pelvis through bilateral contraction of the intrinsic spinal rotator muscles, the large hip rotators power the rapid rotation of the torso and pelvis together. Both the medial hip rotators (gluteus medius and minimus, and tensor fasciae latae) and the lateral hip rotators (gluteus maximus, quadratus femoris, both gemelli, both obturators, piriformis and sartorius) can be active at the same time during the throwing motion at the contralateral and ipsilateral hips, respectively. Additional contributions from the large hip flexor and extensor muscles in the thighs may also increase pelvic rotation power as the body is vaulted over the legs during the throw. We therefore predict that by limiting intervertebral rotation with a brace, most torso/pelvic rotation will occur at the hip. This should significantly reduce torso rotation angular velocity, torque, power and work. These reductions, however, are expected to be modest because we are limiting rotational motion only between the vertebrae and not at the hips.

Hypothesis 2: torso rotation primarily powers the storage of elastic energy at the shoulder

Roach et al. (Roach et al., 2013) proposed that by abducting the shoulder and flexing the elbow as torso rotation reaches its peak

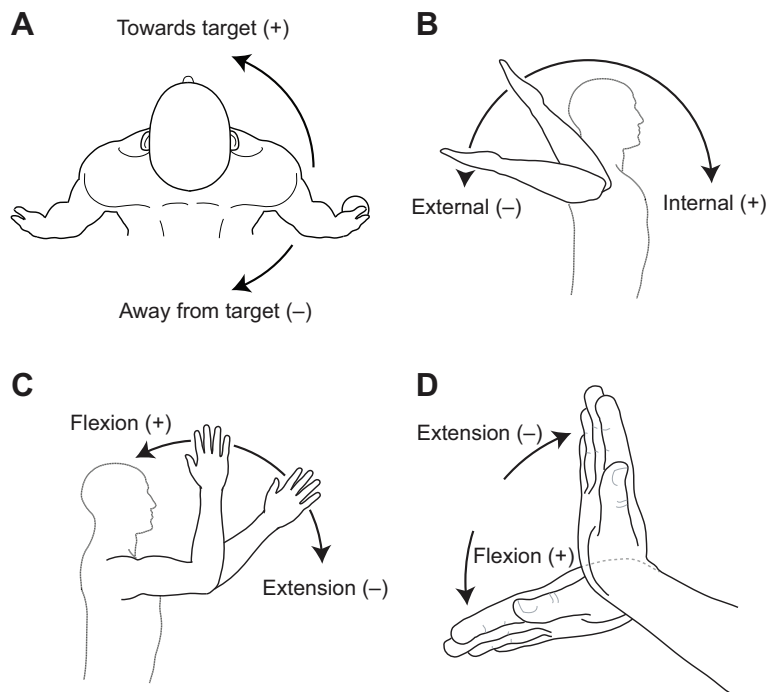


Fig. 2. The four critical upper body motions examined in this study. (A) Torso rotation; (B) shoulder rotation; (C) elbow flexion/extension; (D) wrist flexion/extension. The + and – senses in the diagram show the convention used to describe the directionality of the angular velocities and torques. Note: the torso rotation senses are dependent upon handedness, as the description is relative to the throwing side.

angular velocity, the forelimb's mass is positioned away from the shoulder, increasing its moment of inertia, and causing the forelimb to lag behind the accelerating torso. This lag causes further external rotation of the shoulder beyond the active ROM achieved by the external rotator muscles and into the passive range (Miyashita et al., 2008a; Miyashita et al., 2008b; Roach et al., 2013). We therefore predict that using a brace to limit torso rotation will reduce the amount of negative work done at the shoulder during the cocking phase. This reduction in shoulder rotation work should further reduce shoulder rotation angular velocity, torque, power and work during acceleration.

Hypothesis 3: the pectoralis major also powers the storage of elastic energy at the shoulder

We propose that when the forelimb is maximally cocked (Dillman et al., 1993), muscular action by the largest horizontal flexor of the shoulder, the p. major, will also generate substantial torque around the same shoulder axis as the torso rotation torque, causing the forelimb's mass to lag, thus stretching elastic elements that cross the shoulder. We therefore predict that using a brace to abduct the shoulder should cause a suboptimal realignment by cranially rotating the p. major's major line of action. We expect that this will significantly reduce the amount of negative work done at the shoulder during cocking, and thus reduce shoulder rotation angular velocity, torque, power and work during acceleration.

Hypothesis 4: rapid elbow extension and wrist flexion at the end of the throw are largely generated passively

Previous research has suggested that the work and power necessary to achieve rapid angular movements in the elbow and wrist are derived from the kinetic transfer of power generated at more proximal joints (Feltner, 1989; Hirashima et al., 2007; Hirashima et al., 2003; Hirashima et al., 2008; Putnam, 1993). We therefore predict that braces restricting more active proximal joints (torso and shoulder) will cause significant decreases in angular velocity in more passive distal joints (elbow and wrist).

Hypothesis 5: wrist hyperextension allows release to occur later in the throwing motion, enabling the shoulder internal rotation and elbow extension motions to attain higher angular velocities

Kinematic data on the overhand throwing motion have shown that while the arm is cocking, the wrist slowly hyperextends and then rapidly flexes as the arm accelerates towards the target (Fleisig et al., 1995; Hirashima et al., 2007). This wrist hyperextension could enable other more proximal joint actions (e.g. elbow flexion) to continue to accelerate prior to release and still achieve an accurate release trajectory. We therefore predict that when a brace is used to restrict wrist hyperextension, there will be a significant decrease in the duration of the final acceleration phase of the throw, as well as significant reductions in wrist flexion, elbow extension, and shoulder internal rotation angular velocities and work.

RESULTS

Normal unrestricted

During normal throwing, the maximum ball speed was $27.7 \pm 3.8 \text{ m s}^{-1}$ (mean \pm s.d. of all subject means), with the ball striking the target on average $0.3 \pm 0.2 \text{ m}$ from the center or bullseye. While considerable variation exists between subjects in overall performance and the timing and duration of the throwing phases, there was little variation in kinematic patterns across subjects (Fig. 3). The angular velocity of torso rotation peaked ($848 \pm 160 \text{ deg s}^{-1}$) during the latter half of the cocking phase, before producing an opposing braking torque during the brief acceleration phase. This opposing torque resulted in a short period of power absorption during acceleration, generating net negative work ($-74 \pm 44 \text{ J}$). During the cocking phase at the shoulder, the humerus was externally rotated while simultaneously generating a large opposing internal rotation torque. This resulted in a sustained period of negative work ($-201 \pm 70 \text{ J}$) at the shoulder. As the acceleration phase began with the initiation of internal shoulder rotation, the shoulder rotation torque and angular velocity became in-phase, resulting in very high angular velocities ($4290 \pm 1127 \text{ deg s}^{-1}$) and peak power ($11,838 \pm 4170 \text{ W}$). The elbow continued to flex as the cocking phase began and as a moderate flexion torque was

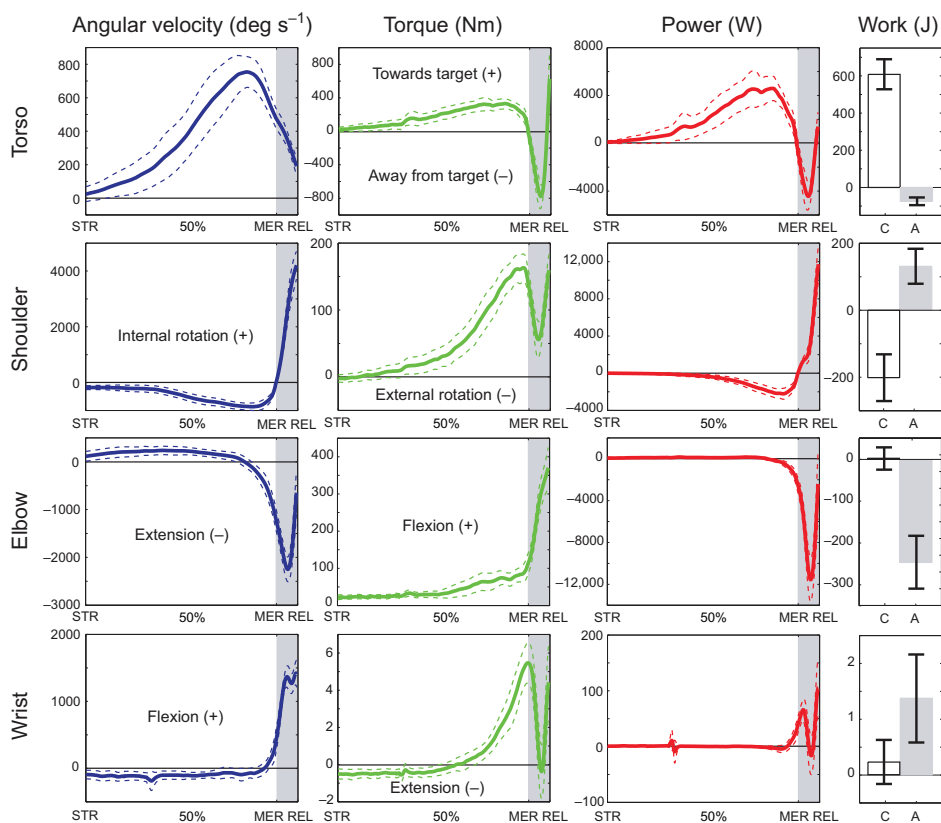


Fig. 3. Joint kinematic and kinetic data from the four critical joint axes during normal throwing. Mean data of all individual subject means are shown as bold lines, while 95% confidence intervals are shown as dashed lines. Differences in phase timing between individuals were standardized by interpolating each phase 1000-fold and subsequently down-sampling each throw to a standard length. The length ratio of the two phases was kept proportional to the mean normal, unrestricted phase duration ratio. The arm-cocking phase [between stride (STR) and maximum external rotation (MER)] is shown in the white field and labeled C in the work plots, while the acceleration phase [between MER and release (REL)] is shown in a gray field and labeled A in the work plots. Note: peak values shown here differ from mean peak values reported in Tables 1–4. This results from each subject's peak performance occurring at slightly different times relative to the normalized phases of the throw.

produced. However, during the last quarter of the cocking phase the elbow began to extend rapidly ($-2434 \pm 552 \text{ deg s}^{-1}$), peaking midway through the acceleration phase. During this rapid extension, the opposing flexion moment at the elbow intensified, resulting in large amounts of negative work ($-246 \pm 63 \text{ J}$). Finally, at the wrist, a sustained extension occurred until the very end of the cocking phase, when the wrist began to rapidly flex, continuing through the acceleration phase. A small flexion moment was produced (peak: $7 \pm 3 \text{ Nm}$) at the end of the cocking phase, which then dropped to near zero and again increased during the acceleration phase. This oscillating power generated a small, net positive amount of work ($1 \pm 2 \text{ J}$) during the acceleration phase.

Torso restriction

The torso restriction brace provided near-complete restriction of intervertebral rotation between the clavicles and the pelvis, allowing only the hip rotators to rotate the trunk. Given the design of the torso brace, no sham condition was possible. Contrary to expectations, there were no significant reductions in torso rotation peak power, angular velocity or torque (Table 1). However, there was a significant drop in torso rotation work during cocking ($-11 \pm 18\%$, $P=0.005$). As expected, there were significant reductions in shoulder rotation power ($-14 \pm 20\%$, $P=0.012$), and work during the cocking phase ($-8 \pm 11\%$, $P=0.004$). A reduction also occurred in elbow extension peak angular velocity ($-6 \pm 7\%$, $P=0.001$). No significant reductions in angular velocity, torque, power or work were measured at the wrist. As hypothesized, when the torso restriction brace was applied, maximum ball speed dropped moderately ($-5 \pm 6\%$, $P<0.001$).

Clavicle restriction

The clavicle brace cranially rotated the scapula $7 \pm 4 \text{ deg}$ and also limited scapular protraction. The clavicle sham produced no

significant effects on joint motion relative to the unbraced condition. However, data from the sham trials (Table 2) indicate some perturbation of the normal throwing motion as evident from reductions in: mean maximum ball speed ($-3 \pm 5\%$, $P=0.029$), phase duration (cocking $-12 \pm 27\%$, $P=0.028$; acceleration $-16 \pm 27\%$, $P=0.010$), torso rotation work acceleration ($-42 \pm 42\%$, $P<0.001$), elbow extension work acceleration ($-10 \pm 17\%$, $P<0.001$), shoulder rotation work acceleration ($-56 \pm 25\%$, $P<0.001$) and shoulder rotation angular velocity ($-11 \pm 12\%$, $P<0.001$). When the restriction was added, maximum ball speed dropped by a further $3 \pm 6\%$ ($P=0.031$). Reductions in shoulder rotation peak torque ($-13 \pm 31\%$, $P<0.001$) and work during cocking ($-9 \pm 10\%$, $P=0.002$) were recorded relative to normal values. Elbow work during acceleration dropped by $8 \pm 13\%$ ($P<0.001$) relative to the reduced sham values. No statistically significant changes were observed in wrist performance.

Shoulder restriction

The shoulder brace reduced shoulder external rotation by $24 \pm 9 \text{ deg}$. However, the shoulder brace also restricted external rotation by $11 \pm 7 \text{ deg}$ in the sham condition, much like wearing a tight jacket. During the sham trials, there were also slight reductions in mean maximum ball speed ($-3 \pm 5\%$, $P=0.026$) and shoulder rotation work during the cocking phase ($-9 \pm 13\%$, $P<0.001$), and a slight shortening of the duration of the acceleration phase ($6 \pm 10\%$, $P=0.045$; Table 3). For each significant change in the sham condition, a further significant reduction occurred when the restriction was employed. The restricted trials caused an $8 \pm 6\%$ reduction in maximum ball speed relative to the sham trials ($P<0.001$). The duration of the cocking phase of the restricted trials shortened ($-9 \pm 14\%$, $P=0.032$), while the acceleration phase lengthened ($38 \pm 56\%$, $P=0.013$). Reductions in torso rotation work

Table 1. Kinematic and kinetic performance measures for the four critical joint axes during normal and torso restriction conditions

Performance measure	Normal	Torso restriction
Performance		
Max. ball speed (m s ⁻¹)	27.7±3.8	26.3±4*
Accuracy (m from bullseye)	0.3±0.2	0.4±0.3
Timing		
Duration of cocking (ms)	387±182	303±122*
Duration of acceleration (ms)	40±12	37±12
Torso rotation (+ throw arm towards target, – away from target)		
Peak angular velocity (deg s ⁻¹)	848±160	835±158
Peak torque (Nm)	828±437	773±424
Peak power (W)	6207±2190	5968±2166
Work – cocking (J)	609±171	536±149*
Work – acceleration (J)	-74±44	-79±40
Shoulder rotation (+ internal, – external)		
Peak angular velocity (deg s ⁻¹)	4290±1127	3970±1226§
Peak torque (Nm)	206±42	178±42
Peak power (W)	11,838±4170	9872±4005*
Work – cocking (J)	-201±70	-184±73*
Work – acceleration (J)	132±52	100±56§
Elbow flexion/extension (+ flexion, – extension)		
Peak angular velocity (deg s ⁻¹)	-2434±552	-2284±582*
Peak torque (Nm)	392±116	357±121
Peak power (W)	2028±3983	2473±4498
Work – cocking (J)	2±27	-1±22
Work – acceleration (J)	-246±63	-218±53§
Wrist flexion/extension (+ flexion, – extension)		
Peak angular velocity (deg s ⁻¹)	1593±336	1645±280
Peak torque (Nm)	7±3	6±3
Peak power (W)	138±90	155±109
Work – cocking (J)	0.2±1	0.3±1
Work – acceleration (J)	1±2	1±2

Given that no sham was possible for this condition, restricted values that statistically differ from normal values are indicated with asterisks (* $P<0.05$); values that met the $P<0.05$ threshold but did not survive multiple testing correction are indicated with §. Bold values indicate hypothesized reductions from normal values, while italic values indicate unexpected changes.

were recorded for both phases (cocking $-14\pm 20\%$, $P=0.006$; acceleration $-41\pm 57\%$, $P<0.001$). Although shoulder rotation work during the cocking phase dropped significantly ($-45\pm 17\%$, $P<0.001$) from normal values, no further significant reductions occurred in shoulder rotation peak angular velocity, torque, power or work during acceleration. As predicted, there were significant reductions in elbow extension angular velocity ($-21\pm 10\%$, $P<0.001$) and elbow work during acceleration ($-20\pm 21\%$, $P<0.001$). Wrist flexion peak angular velocity remained unchanged, but a significant reduction in wrist work during the cocking phase ($P=0.020$) was followed by a significant increase in wrist work during the acceleration phase ($P=0.003$).

Wrist restriction

The wrist brace reduced wrist extension ROM by 62 ± 7 deg, but there was no significant reduction in the sham condition. However, the wrist restriction sham trials showed numerous significant reductions in the measured performance variables (Table 4). Although the restricted condition produced significant reductions in ball speed and phase duration from normal values, these reductions were not significantly different from the sham condition. Restricted shoulder rotation peak angular velocity dropped by $6\pm 8\%$ ($P<0.001$) from sham conditions, while shoulder rotation peak power ($P<0.001$) and work during acceleration values ($P<0.001$) both dropped relative to normal and increased relative to sham trials. Restricted elbow work during acceleration dropped by $19\pm 14\%$ ($P<0.001$) from sham levels. The wrist flexion peak angular velocity dropped by $34\pm 37\%$ ($P<0.001$) relative to the sham trials, while

wrist flexion/extension peak power ($P<0.001$) and work during acceleration ($P<0.001$) increased relative to the sham trials.

DISCUSSION

Hypothesis testing

We proposed (H1) that by restricting rotational movement between the vertebrae, measures of throwing performance would decrease. However, despite the restriction of intervertebral motion, torso rotation work decreased significantly only during the cocking phase and all other measures remained unchanged. This result suggests that during normal throwing, most ($\sim 90\%$) of the work required to achieve high projectile velocity is generated at the hips (Matsuo et al., 2001; Stodden et al., 2001; Wight et al., 2004). The reduction in torso rotation work during the cocking phase may be driven by a substantial ($-19\pm 22\%$) reduction in the duration of this phase ($P=0.006$). However, the fact that other brace conditions result in similar changes in phase duration without affecting the amount of torso rotation work performed suggests otherwise. Further study is necessary to determine which hip rotator muscles generate this power.

Although the torso restriction caused mostly minor, non-significant reductions in angular velocity, torque and power at the torso, the effects of this brace are amplified at the shoulder. We hypothesized (H2) that if torso rotation helps power the elastic storage mechanism at the shoulder (Roach et al., 2013), even minor reductions in torso rotation performance should result in less elastic energy storage and, consequently, large reductions in shoulder rotation performance. The data from the torso restriction trials

Table 2. Kinematic and kinetic performance measures for the four critical joint axes during normal and clavicle brace restriction conditions

Performance measure	Normal	Clavicle sham	Clavicle restriction
Performance			
Max. ball speed (m s ⁻¹)	27.7±3.8	27±4.2*	26.3±4.1*‡
Accuracy (m from bullseye)	0.3±0.2	0.4±0.2	0.4±0.2
Timing			
Duration of cocking (ms)	387±182	300±72*	306±93*
Duration of acceleration (ms)	40±12	32±9*	34±11
Torso rotation (+ throw arm towards target, – away from target)			
Peak angular velocity (deg s ⁻¹)	848±160	862±144	870±155
Peak torque (Nm)	828±437	580±167	588±240
Peak power (W)	6207±2190	6869±2617	6492±2159
Work – cocking (J)	609±171	638±177	607±174
Work – acceleration (J)	-74±44	-109±53*	-107±63*
Shoulder rotation (+ internal, – external)			
Peak angular velocity (deg s ⁻¹)	4290±1127	3852±1175*	3778±1126*
Peak torque (Nm)	206±42	180±38	169±37*‡
Peak power (W)	11,838±4170	8431±4455§	8958±4552§
Work – cocking (J)	-201±70	-188±60	-173±63*‡
Work – acceleration (J)	132±52	54±35*	58±32*
Elbow flexion/extension (+ flexion, – extension)			
Peak angular velocity (deg s ⁻¹)	-2434±552	-2326±517	-2220±517§
Peak torque (Nm)	392±116	357±80	336±84§
Peak power (W)	2028±3983	631±1050	630±1064
Work – cocking (J)	2±27	4±21	5±22
Work – acceleration (J)	-246±63	-225±58*	-206±59*‡
Wrist flexion/extension (+ flexion, – extension)			
Peak angular velocity (deg s ⁻¹)	1593±336	1505±255	1510±276
Peak torque (Nm)	7±3	6±2	6±2
Peak power (W)	138±90	113±80	107±73
Work – cocking (J)	0.2±1	0.4±1	0.3±1
Work – acceleration (J)	1±2	1±1	1±1

Restricted and sham values that statistically differ from normal values are indicated with asterisks (* $P<0.05$), while restricted values that statistically differ from the sham are shown with ‡. Values that met the $P<0.05$ threshold but did not survive multiple testing correction are indicated with §. Bold values indicate hypothesized reductions from normal values, while italic values indicate unexpected changes.

support this hypothesis. Negative shoulder rotation work during the cocking phase, a proxy for elastic energy storage, decreased by more than 10% during the torso brace trials. Further reductions in shoulder rotation power accompany this reduction in work during the cocking phase. While a reduction in cocking phase duration may again be partly responsible for these changes, data from other conditions in which this phase shortened without affecting these measures make this unlikely. Furthermore, no change is seen in acceleration phase duration when peak shoulder rotation angular velocity and power are achieved. By assuming that the performance reductions the braces caused reflect the overall contribution of the hips to downstream motions, and combining our data with forward dynamics induced acceleration data (Hirashima et al., 2008), we estimate that the hip rotators account for ~30% of the power/work generated for the rapid internal rotation of the shoulder. These results therefore provide additional support for the hypothesis that torso rotation significantly contributes to elastic energy storage in the shoulder during the arm-cocking phase.

The secondary source of power proposed (H3) to contribute to elastic energy storage at the shoulder is the p. major. By holding the shoulder complex in a superiorly abducted position, we sought to change this muscle's major line of action, effectively excluding contributions from the inferior fibers to horizontal flexion at the shoulder. Although the sham had no effect on static shoulder ROM, significant changes in performance during sham trials suggest that the unloaded brace did cause some restriction, potentially by limiting scapular protraction at release. While reductions in shoulder

rotation torque and work during cocking and elbow extension work during acceleration confirm the role of the p. major in loading the elastic elements in the shoulder, the lack of significant shifts in the other performance measures (e.g. shoulder rotation angular velocity, power and work during acceleration) leaves this hypothesis only partially supported. It is possible that the brace caused too little superior rotation to yield a large enough effect on these performance measures.

As hypothesized (H4), work during both the cocking and acceleration phases of a normal throw is very low at the wrist and either low or negative at the elbow. This suggests that both motions are generated less by muscles crossing each distal joint, but rather by passive forces transmitted from more proximal joints. Furthermore, when examining all conditions (torso, clavicle and shoulder) in which proximal joint actions (torso and/or shoulder rotation) were affected, significant performance reductions were seen at the elbow, but not the wrist. These data reinforce previous evidence that the elbow is likely powered primarily by kinetic transfer from upstream joints (Feltner, 1989; Hirashima et al., 2007; Hirashima et al., 2008; Putnam, 1993). This kinetic chain may also apply to the wrist, although the lack of response to the restrictions at the wrist suggests that some compensatory action by the wrist flexors is possible. Given the brevity of the acceleration phase, having multiple passive components in the shoulder, elbow and wrist could simplify the difficult neural control problem that rapid throwing poses. Such reduced complexity would allow the throwing motion to be more easily, effectively and consistently produced.

Table 3. Kinematic and kinetic performance measures for the four critical joint axes during normal and shoulder brace restriction conditions

Performance measure	Normal	Shoulder sham	Shoulder restriction
Performance			
Max. ball speed (m s ⁻¹)	27.7±3.8	27±4*	24.9±4*‡
Accuracy (m from bullseye)	0.3±0.2	0.4±0.3	0.4±0.3
Timing			
Duration of cocking (ms)	387±182	392±167	<i>354±196*‡</i>
Duration of acceleration (ms)	40±12	38±14*	<i>55±27*‡</i>
Torso rotation (+ throw arm towards target, – away from target)			
Peak angular velocity (deg s ⁻¹)	848±160	859±161	833±156
Peak torque (Nm)	828±437	827±404	890±453
Peak power (W)	6207±2190	6111±2036	5559±2000
Work – cocking (J)	609±171	587±152	<i>513±154*‡</i>
Work – acceleration (J)	-74±44	-78±42	<i>-42±57*‡</i>
Shoulder rotation (+ internal, – external)			
Peak angular velocity (deg s ⁻¹)	4290±1127	4261±1106	4038±1141
Peak torque (Nm)	206±42	206±45	198±45
Peak power (W)	11,838±4170	12,145±4628	13,566±6141
Work – cocking (J)	-201±70	-181±63*	<i>-113±57*‡</i>
Work – acceleration (J)	132±52	124±63	138±58
Elbow flexion/extension (+ flexion, – extension)			
Peak angular velocity (deg s ⁻¹)	-2434±552	-2341±505	<i>-1923±471*‡</i>
Peak torque (Nm)	392±116	355±88	326±100
Peak power (W)	2028±3983	1229±2050	1180±2383
Work – cocking (J)	2±27	3±20	4±24
Work – acceleration (J)	-246±63	-236±58	<i>-190±46*‡</i>
Wrist flexion/extension (+ flexion, – extension)			
Peak angular velocity (deg s ⁻¹)	1593±336	1549±490	1515±332
Peak torque (Nm)	7±3	6±2	6±2
Peak power (W)	138±90	128±74	127±70
Work – cocking (J)	0.2±1	0.4±1	<i>-0.1±1*‡</i>
Work – acceleration (J)	1±2	1±2	2±1*‡

Restricted and sham values that statistically differ from normal values are indicated with asterisks (* $P<0.05$), while restricted values that statistically differ from the sham are shown with ‡. Bold values indicate hypothesized reductions from normal values, while italic values indicate unexpected changes.

We also hypothesized (H5) that wrist hyperextension allows throwers to delay projectile release, enabling additional acceleration of the proximal joints prior to release. Although the wrist brace restriction did reduce the duration of the acceleration phase relative to the normal condition, this reduction does not differ from that of the sham trials. In fact, unlike responses to the other brace's sham conditions, the performance effects of the wrist sham were pervasive and severe. Significant performance reductions were seen in all segments analyzed during the wrist sham condition. Given that no measurable effect of wrist ROM was noted with the sham, it is possible that the addition of the brace itself altered proprioception at the hand and wrist, resulting in timing changes and a cascade of performance reductions. However, we would expect a major proprioceptive perturbation to also result in differences in accuracy between brace and non-brace conditions, which was not the case. Alternatively, it is possible that the effects seen during the sham trials were due to the addition of the brace's mass to the distal forelimb. Although the mass of the brace was only ~165 g, this additional mass more than doubles the previously added mass of the ball at the hand. These sham results suggest that the elastic storage mechanism at the shoulder could be quite sensitive to changes in projectile or distal forearm mass. Without postural adjustments, such a change in mass could significantly increase the forelimb's moment of inertia during the critical cocking phase and disrupt a system finely tuned for passive action.

The wrist brace restriction did cause significant performance effects relative to the wrist sham where expected (shoulder rotation angular velocity, elbow extension work acceleration, and wrist

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

Limitations

Our experimental approach can be an effective way to address how different regions of the upper body contribute to the complex throwing motion, but this approach has limitations. For example, our subjects threw only overhand baseball-type pitches, as this throwing style is known to produce the fastest throws. However, further study of other throwing kinematic patterns such as windmill-type cricket bowls could provide important insights into differences in the underlying mechanisms of power generation. We also collected data only from the upper body, as previous studies have shown that leg contributions to projectile velocity are minimal (Hirashima et al., 2007; Hirashima et al., 2008). Additionally, although all brace restrictions (except for the wrist) led to significant reductions in ball speed relative to both their sham and normal trials, these reductions were relatively minor (0.5–9%). Such minor reductions highlight the ability of the subjects – all accomplished throwers – to compensate for minor to moderate disruptions of their normal throwing motion.

Table 4. Kinematic and kinetic performance measures for the four critical joint axes during normal and wrist brace restriction conditions

Performance measure	Normal	Wrist sham	Wrist restriction
Performance			
Max. ball speed (m s ⁻¹)	27.7±3.8	26.1±3.9*	25.8±4*
Accuracy (m from bullseye)	0.3±0.2	0.4±0.2	0.4±0.2
Timing			
Duration of cocking (ms)	387±182	309±72*	311±95*
Duration of acceleration (ms)	40±12	34±9*	33±10*
Torso rotation (+ throw arm towards target, – away from target)			
Peak angular velocity (deg s ⁻¹)	848±160	838±175	831±188
Peak torque (Nm)	828±437	431±96*	409±101*
Peak power (W)	6207±2190	5488±1670	5676±2149
Work – cocking (J)	609±171	541±136*	550±155*
Work – acceleration (J)	-74±44	-69±42	-62±39§
Shoulder rotation (+ internal, – external)			
Peak angular velocity (deg s ⁻¹)	4290±1127	3799±1237*	3579±1217*‡
Peak torque (Nm)	206±42	191±53	185±53
Peak power (W)	11,838±4170	3534±1415*	4852±2614*‡
Work – cocking (J)	-201±70	-181±66§	-192±68§
Work – acceleration (J)	132±52	33±27*	49±31*‡
Elbow flexion/extension (+ flexion, – extension)			
Peak angular velocity (deg s ⁻¹)	-2434±552	-2308±587§	-2261±588§
Peak torque (Nm)	392±116	351±116	276±81*‡
Peak power (W)	2028±3983	537±466	354±178
Work – cocking (J)	2±27	15±19*	-0.5±24‡
Work – acceleration (J)	-246±63	-215±63*	-174±61*‡
Wrist flexion/extension (+ flexion, – extension)			
Peak angular velocity (deg s ⁻¹)	1593±336	1406±331*	881±243*‡
Peak torque (Nm)	7±3	3±2*	6±2‡
Peak power (W)	138±90	24±28*	47±29*‡
Work – cocking (J)	0.2±1	0.5±1	0.5±0.4
Work – acceleration (J)	1±2	-3±2*	1±1‡

Restricted and sham values that statistically differ from normal values are indicated with asterisks (* $P<0.05$), while restricted values that statistically differ from the sham are shown with ‡. Values that met the $P<0.05$ threshold but did not survive multiple testing correction are indicated with §. Bold values indicate hypothesized reductions from normal values, while italic values indicate unexpected changes.

Brace restrictions can also lead to unintended responses, such as limiting scapular protraction (clavicle brace) or causing compensatory flexion action at the wrist (shoulder brace). Our experimental design targeted key motions responsible for projectile speed, but the effects of these braces were not restricted to only the motions reported here. Furthermore, even when tasked to throw as hard as possible in all brace-restricted conditions, some subjects tended to fight through the restrictions in order to throw as fast and accurately as possible, contributing to variation among trials and diminishing the effects of the restrictions. Despite these experimental drawbacks, the consistent accuracy and kinematic patterns maintained across all conditions confirm that the normal throwing motion was mostly preserved.

Conclusions

The results of this study confirm the importance of power generation during throwing via both the kinetic chain (Atwater, 1979; Feltner, 1989; Fleisig et al., 1996; Higgins, 1977; Hirashima et al., 2008) and elastic energy storage at the shoulder (Roach et al., 2013; Wilk et al., 1993). The hip rotators account for most of the torso rotation power and work produced during throwing. Through a kinetic transfer of power, torso rotation passively loads the elastic elements in the shoulder during the cocking phase. Much of the energy absorbed at the shoulder during cocking is then recovered in the acceleration phase, resulting in faster shoulder internal rotation and elbow extension just prior to release. The p. major also contributes to energy absorption (negative work) at the shoulder during the cocking phase and helps power elbow

extension. It is likely that kinetic power transfers from proximal to distal segments also help drive the rapid elbow extension and wrist flexion motions at the end of the throw (Feltner, 1989; Hirashima et al., 2007; Hirashima et al., 2008; Putnam, 1993). These effects are confirmed by the lack of positive work produced by the wrist and elbow during either the cocking or acceleration phases. The effects of wrist hyperextension on the throwing motion remain unclear. While there are some performance benefits to hyperextension, the unexpected effects of adding mass at the wrist cloud interpretation of these results.

Implications

Throwing mechanics and power generation have implications for understanding both the etiology of common throwing injuries as well as the evolution of the human upper body. Three of the most common injuries in throwing athletes occur at the shoulder (shoulder labrum tears and shoulder instability) and elbow (medial epicondylitis) (Altkchek and Dines, 1995; Anz et al., 2010; Badia and Stennett, 2006; Fleisig et al., 2011; Fleisig et al., 1995; Fleisig et al., 1996; Jobe et al., 1996; Meister, 2000; Rizio and Uribe, 2001). The amount of passive external rotation at the shoulder during the arm-cocking phase (when elastic energy is stored) is known to be correlated with such injuries (Miyashita et al., 2008a; Miyashita et al., 2008b). Damage to the shoulder labrum at the biceps attachment site [a superior labrum extending from anterior to posterior (SLAP) lesion/tear] likely results from this high degree of passive humeral external rotation (Burkhart et al., 2000; Burkhart et al., 2003). In order to maintain a flexed elbow, which is vital to increase the

forelimb's moment of inertia for elastic energy storage (Roach et al., 2013), the biceps are activated during cocking (Hirashima et al., 2002). However, the combination of biceps flexion and passive external rotation of the humerus causes high concentrations of stress at the biceps' tendinous insertion on the labrum. The flexed elbow position also results in very high valgus torques at the elbow during both the arm-cocking and early acceleration phases (Fleisig et al., 1995; Loftice et al., 2004; Sabick et al., 2004; Werner et al., 1993). This high torque, which is aligned differently from the plane of the joint, stretches the ulnar collateral ligament that stabilizes the elbow, potentially leading to painful inflammation or tearing from many repeated throws (Fleisig et al., 1995; Fleisig et al., 1996; Rizio and Uribe, 2001). Similarly, shoulder instability and the problems it can cause [e.g. anterior ligament laxity, increased likelihood of dislocation (Meister, 2000)] may be driven by use of the capsular ligaments to store elastic energy. While these injuries directly result from forelimb positioning necessary to maximize elastic energy storage, it may be possible to protect against such injuries by limiting the frequency of high-speed throwing (Feltner and Dapena, 1986; Fleisig et al., 2011; Fleisig et al., 1996; Gainor et al., 1980; Rizio and Uribe, 2001; Sabick et al., 2004) or wearing mildly restrictive garments (such as a compression shirt) to prevent over rotation.

Finally, morphological shifts known to occur in hominins may affect the performance of each of the motions targeted in this study. The torso brace restriction, which mimics the reduced torso mobility of apes (Bramble and Lieberman, 2004), shows that torso rotation is vital to generating elastic energy storage in the shoulder. Similarly, the clavicle brace restriction highlights how a more ape-like cranially oriented shoulder complex reduces elastic energy storage and throwing performance. The torso restriction data also implicate the hip rotators in powering much of the torso rotation motion and thus helping to power many of the rapid motions of the forelimb. These data suggest that the reorganization of the pelvis and hip musculature seen in *Australopithecus* (e.g. Lovejoy, 1988; Stern and Susman, 1983) and especially the expansion of the gluteus maximus in *Homo erectus* (Lieberman et al., 2006; Marzke et al., 1988; Stern, 1972) may have substantially improved throwing performance. Additionally, the hypothesis that adding mass to the distal forelimb (e.g. via the wrist brace) perturbs the elastic energy storage mechanism, reducing throwing performance, bears further investigation. If supported, selection for throwing would provide a functional explanation for the relative shortening of the forearm that

occurred in the genus *Homo* (e.g. Richmond et al., 2002; Ruff and Walker, 1993; White, 2002). In sum, these data support the hypothesis that *H. erectus* could have produced fast, accurate throws and may have used this ability to hunt, protect themselves and expand into new habitats both in and out of Africa nearly 2 million years ago (Roach, 2012; Roach et al., 2013).

MATERIALS AND METHODS

Subjects

Data were collected from 21 male subjects (ages 19–23) who fulfilled several predetermined inclusion criteria designed to exclude poor throwers. First, they needed to be able to hit a 1×1 m square target from 10 m away at 22.4 m s⁻¹ (50 mph) or higher within five tries. In addition, at least one throw across all conditions had to reach 22.4 m s⁻¹ or higher. One subject was excluded because his kinematic patterns were more than two standard deviations away from mean performance measures in all brace conditions. Female subjects were excluded from the study as CT imaging of relevant skeletal traits was deemed a heightened breast cancer risk by the Harvard University and Massachusetts General Hospital Human Subjects Committees.

Data collection

Kinematic data were collected at 1000 Hz using an eight-camera Vicon T10s 3D infrared motion capture system (Vicon Inc., Centennial, CO, USA). Each subject had 21 passive reflective markers taped on the throwing arm and torso (Fig. 4; supplementary material Table S1). Subjects were given the opportunity to warm up and then asked to throw a 144 g baseball at a 1 m radius target positioned 10 m from the subject. Each subject threw approximately 10–20 baseball-type pitches in each of five randomly ordered experimental conditions. Ball speed was measured using a Sports Radar Model 3600 radar gun, and accuracy was calculated using ImageJ software (v1.41) from digital video collected with a 30 Hz Canon Vixia HV30 digital video camera (Canon Inc., Tokyo, Japan) recording the ball impacting the target. Ball release was timed using a synched FlexiForce A201 force sensor (Tekscan Inc., Boston, MA, USA) collecting at 1000 Hz taped to the palmar side of the distal phalanx of the third digit.

Experimental treatments

Five different experimental treatments were used: normal unrestricted, torso restricted, clavicle restricted, shoulder restricted and wrist restricted. All restricted conditions were repeated with sham trials in which the brace was applied but not tightened to test the effect of the brace independently of the restriction (except for the torso condition, for which this was not possible). Subjects were given *ad libitum* practice throws to acquaint themselves with both the sham and restricted portions of each condition. The torso restriction condition employed a DonJoy Dual TLSO back brace (DonJoy Inc., Vista,

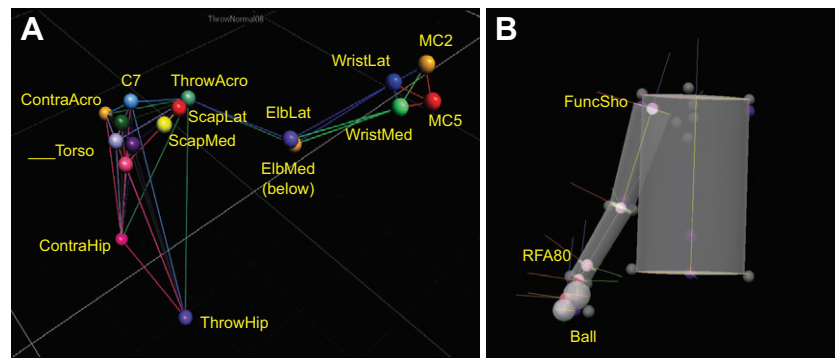


Fig. 4. Reflective markers (A) and kinetic model (B) used in data collection and analysis. Note: The markers labeled __Torso are a rigid cluster of four markers (SupTorso, ContraTorso, InfTorso and ThrowTorso). A second rigid __Arm cluster is missing from this trial. In B, the light gray kinetic model shows the segments used in the inverse dynamics analysis. The ball segment was a non-independent point mass added to the hand segment at the approximate ball position of a split-finger throw. This mass was dropped to zero in the analyses after the ball was released. The FuncSho marker highlighted is the functional joint center of the shoulder joint defined using a conical motion trial. RFA80 refers to another functional joint used to solve a tracking problem resulting from the different joint centers for flexion/extension and pronation/supination in the elbow (Roach et al., 2013).

CA, USA) to limit intervertebral motion from the T2/T3 vertebrae to the sacrum. This brace fastens rigid plastic plates to both the dorsal and ventral sides of the torso and fixes a steel bar against the clavicles to restrict rotational motion in the torso. The clavicle restriction condition used a DonJoy Clavicle Posture Support brace to hold the shoulder in a superiorly rotated, 'shrugged' posture. This brace runs two straps over the shoulders and under the armpits, joining in the back. The subject was requested to shrug his shoulders as the brace was tightened, preventing relaxation. For the shoulder restriction condition, a DonJoy Shoulder Stabilizer brace was used to limit external rotational ROM at the shoulder. This brace is a tight, elastic vest with a single, elastic half-sleeve on the throwing arm. To restrict external rotation of the humerus, the arm was internally rotated and a Velcro strap was affixed from the ventral side of the vest to the dorsal side of the sleeve. The wrist restriction condition employed an Allsport Dynamics IMC Wrist brace (Allsport Dynamics Inc., Nacogdoches, TX, USA) with the 0 deg extension stop either employed (restricted) or absent (sham). When the extension stop was screwed into place, the plastic sleeve contacts a dorsal hand plate and prevents the wrist from hyperextending.

Analysis

Marker data were identified using Vicon Nexus software (v1.7.1) and exported to C-Motion Visual3D software (v4) for analysis. A Butterworth second-order low-pass filter with a cut-off frequency of 25 Hz was applied after a residual analysis of the data was conducted (Roach et al., 2013; Winter, 1991). Marker gaps of up to 100 frames were interpolated. Joint Euler angles were calculated and inverse dynamics analyses performed using mass distribution ratios from Dempster (Dempster, 1955). Joint angular velocities, moments and power were calculated using each joint's instantaneous axis of rotation. The Cardan sequence of rotations at each joint was XYZ. Joint work was calculated in MATLAB (v7.11.0) using the trapz function.

Statistics

Statistical inquiry was limited to the arm-cocking and acceleration phases as positive projectile velocity is generated only during these phases (Fig. 1). Individual subject means from a number of performance measures were compared across experimental conditions using repeated-measures ANOVA or MANOVA when variances were not equal (Mauchly's sphericity chi-square, $P < 0.05$). Corrections for multiple comparisons were applied using the Holm–Bonferroni method with each experimental condition treated as a family and a maximum alpha threshold of < 0.05 (Holm, 1979). *Post hoc* matched pairs *t*-tests were used to determine which condition (sham and/or restricted) accounted for the significance in multivariate tests. Because the torso restriction condition did not have a sham, all reported statistics for this condition are matched pairs *t*-tests.

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Competing interests

The authors declare no competing financial interests.

Author contributions

N.T.R. and D.E.L. designed the study, N.T.R. collected and analyzed the data, N.T.R. wrote the paper, and N.T.R. and D.E.L. edited the manuscript.

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Supplementary material

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References

- Alexander, R. M. (1991). Optimum timing of muscle activation for simple models of throwing. *J. Theor. Biol.* **150**, 349–372.
- Altciek, D. W. and Dines, D. M. (1995). Shoulder injuries in the throwing athlete. *J. Am. Acad. Orthop. Surg.* **3**, 159–165.
- Anderson, F. C. and Pandy, M. G. (1993). Storage and utilization of elastic strain energy during jumping. *J. Biomech.* **26**, 1413–1427.
- Anz, A. W., Bushnell, B. D., Griffin, L. P., Noonan, T. J., Torry, M. R. and Hawkins, R. J. (2010). Correlation of torque and elbow injury in professional baseball pitchers. *Am. J. Sports Med.* **38**, 1368–1374.
- Atwater, A. E. (1979). Biomechanics of overarm throwing movements and of throwing injuries. *Exerc. Sport Sci. Rev.* **7**, 43–86.
- Badia, A. and Stennett, C. (2006). Sports-related injuries of the elbow. *J. Hand Ther.* **19**, 206–227.
- Bell, D. G. (1993). The influence of air temperature on the EMG/force relationship of the quadriceps. *Eur. J. Appl. Physiol. Occup. Physiol.* **67**, 256–260.
- Ben Kibler, W. and Sciascia, A. (2004). Kinetic chain contributions to elbow function and dysfunction in sports. *Clin. Sports Med.* **23**, 545–552, viii.
- Bramble, D. M. and Lieberman, D. E. (2004). Endurance running and the evolution of *Homo*. *Nature* **432**, 345–352.
- Burkhart, S. S., Morgan, C. D. and Kibler, W. B. (2000). Shoulder injuries in overhead athletes. The 'dead arm' revisited. *Clin. Sports Med.* **19**, 125–158.
- Burkhart, S. S., Morgan, C. D. and Kibler, W. B. (2003). The disabled throwing shoulder: spectrum of pathology Part I: pathoanatomy and biomechanics. *Arthroscopy* **19**, 404–420.
- Dempster, W. T. (1955). *Space Requirements for the Seated Operator*. Wright-Patterson Air Force Base, OH: Wright Air Development Center.
- DiGiovine, N. M., Jobe, F. W., Pink, M. and Perry, J. (1992). An electromyographic analysis of the upper extremity in pitching. *J. Shoulder Elbow Surg.* **1**, 15–25.
- Dillman, C. J., Fleisig, G. S. and Andrews, J. R. (1993). Biomechanics of pitching with emphasis upon shoulder kinematics. *J. Orthop. Sports Phys. Ther.* **18**, 402–408.
- Feltner, M. E. (1989). 3-dimensional interactions in a 2-segment kinetic chain. Part II. Application to the throwing arm in baseball pitching. *Int. J. Sport Biomech.* **5**, 403–419.
- Feltner, M. and Dapena, J. (1986). Dynamics of the shoulder and elbow joints of the throwing arm during a baseball pitch. *Int. J. Sport Biomech.* **2**, 235–259.
- Finni, T., Komi, P. V. and Lepola, V. (2000). In vivo human triceps surae and quadriceps femoris muscle function in a squat jump and counter movement jump. *Eur. J. Appl. Physiol.* **83**, 416–426.
- Fleisig, G. S., Andrews, J. R., Dillman, C. J. and Escamilla, R. F. (1995). Kinetics of baseball pitching with implications about injury mechanisms. *Am. J. Sports Med.* **23**, 233–239.
- Fleisig, G. S., Barrentine, S. W., Escamilla, R. F. and Andrews, J. R. (1996). Biomechanics of overhand throwing with implications for injuries. *Sports Med.* **21**, 421–437.
- Fleisig, G. S., Andrews, J. R., Cutter, G. R., Weber, A., Loftice, J., McMichael, C., Hassell, N. and Lyman, S. (2011). Risk of serious injury for young baseball pitchers: a 10-year prospective study. *Am. J. Sports Med.* **39**, 253–257.
- Gainor, B. J., Piotrowski, G., Puhl, J., Allen, W. C. and Hagen, R. (1980). The throw: biomechanics and acute injury. *Am. J. Sports Med.* **8**, 114–118.
- Gans, C. (1992). Electromyography. In *Biomechanics – Structures and Systems: A Practical Approach* (ed. A. A. Biewener), pp. 123–147. Oxford: Oxford University Press.
- Goodall, J. (1964). Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature* **201**, 1264–1266.
- Goodall, J. (1986). *The Chimpanzees of Gombe: Patterns of Behavior*. Cambridge: Harvard University Press.
- Gowan, I. D., Jobe, F. W., Tibone, J. E., Perry, J. and Moynes, D. R. (1987). A comparative electromyographic analysis of the shoulder during pitching. Professional versus amateur pitchers. *Am. J. Sports Med.* **15**, 586–590.
- Higgins, J. R. (1977). *Human Movement: an Integrated Approach*. St Louis, MO: Mosby.
- Hirashima, M., Kadota, H., Sakurai, S., Kudo, K. and Ohtsuki, T. (2002). Sequential muscle activity and its functional role in the upper extremity and trunk during overarm throwing. *J. Sports Sci.* **20**, 301–310.
- Hirashima, M., Ohgane, K., Kudo, K., Hase, K. and Ohtsuki, T. (2003). Counteractive relationship between the interaction torque and muscle torque at the wrist is predestined in ball-throwing. *J. Neurophysiol.* **90**, 1449–1463.
- Hirashima, M., Kudo, K., Watarai, K. and Ohtsuki, T. (2007). Control of 3D limb dynamics in unconstrained overarm throws of different speeds performed by skilled baseball players. *J. Neurophysiol.* **97**, 680–691.
- Hirashima, M., Yamane, K., Nakamura, Y. and Ohtsuki, T. (2008). Kinetic chain of overarm throwing in terms of joint rotations revealed by induced acceleration analysis. *J. Biomech.* **41**, 2874–2883.
- Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scand. J. Stat.* **6**, 65–70.
- Hong, D. A., Cheung, T. K. and Roberts, E. M. (2001). A three-dimensional, six-segment chain analysis of forceful overarm throwing. *J. Electromyogr. Kinesiol.* **11**, 95–112.
- Hore, J., O'Brien, M. and Watts, S. (2005). Control of joint rotations in overarm throws of different speeds made by dominant and nondominant arms. *J. Neurophysiol.* **94**, 3975–3986.
- Jobe, C. M., Pink, M. M., Jobe, F. W. and Shaffer, B. (1996). Anterior shoulder instability, impingement, and rotator cuff tear: theories and concepts. In *Operative Techniques in Upper Extremity Sports Injuries* (ed. F. W. Jobe), pp. 164–176. St Louis, MO: Mosby.

- Kohler, W.** (1925). *The Mentality of Apes*. New York: Harcourt and Brace.
- Komi, P. V. and Bosco, C.** (1978). Utilization of stored elastic energy in leg extensor muscles by men and women. *Med. Sci. Sports* **10**, 261-265.
- Komi, P. V., Salonen, M., Järvinen, M. and Kokko, O.** (1987). *In vivo* registration of Achilles tendon forces in man. I. Methodological development. *Int. J. Sports Med.* **8 Suppl. 1**, 3-8.
- Larson, S. G.** (1993). Functional morphology of the shoulder in primates. In *Postcranial Adaptation in Non-human Primates* (ed. D. L. Gebo), pp. 45-69. Chicago, IL: Northern Illinois University Press.
- Larson, S. G.** (2007). Evolutionary transformation of the hominin shoulder. *Evol. Anthropol.* **16**, 172-187.
- Lewis, J. L., Lew, W. D. and Schmidt, J.** (1982). A note on the application and evaluation of the buckle transducer for the knee ligament force measurement. *J. Biomech. Eng.* **104**, 125-128.
- Lieberman, D. E., Raichlen, D. A., Pontzer, H., Bramble, D. M. and Cutright-Smith, E.** (2006). The human gluteus maximus and its role in running. *J. Exp. Biol.* **209**, 2143-2155.
- Loftice, J., Fleisig, G. S., Zheng, N. and Andrews, J. R.** (2004). Biomechanics of the elbow in sports. *Clin. Sports Med.* **23**, 519-530, vii-viii.
- Lovejoy, C. O.** (1988). Evolution of human walking. *Sci. Am.* **259**, 118-125.
- Marzke, M. W., Longhill, J. M. and Rasmussen, S. A.** (1988). Gluteus maximus muscle function and the origin of hominid bipedality. *Am. J. Phys. Anthropol.* **77**, 519-528.
- Matsuo, T., Escamilla, R. F., Fleisig, G. S., Barrentine, S. W. and Andrews, J. R.** (2001). Comparison of kinematic and temporal patterns between different pitch velocity groups. *J. Appl. Biomech.* **17**, 1-13.
- Meister, K.** (2000). Injuries to the shoulder in the throwing athlete. Part one: Biomechanics/pathophysiology/classification of injury. *Am. J. Sports Med.* **28**, 265-275.
- Miyashita, K., Urabe, Y., Kobayashi, H., Yokoe, K., Koshida, S., Kawamura, M. and Ida, K.** (2008a). Relationship between maximum shoulder external rotation angle during throwing and physical variables. *J. Sports Sci. Med.* **7**, 47-53.
- Miyashita, K., Urabe, Y., Kobayashi, H., Yokoe, K., Koshida, S., Kawamura, M. and Ida, K.** (2008b). The role of shoulder maximum external rotation during throwing for elbow injury prevention in baseball players. *J. Sports Sci. Med.* **7**, 223-228.
- Pappas, A. M., Zawacki, R. M. and Sullivan, T. J.** (1985). Biomechanics of baseball pitching. A preliminary report. *Am. J. Sports Med.* **13**, 216-222.
- Pourcelot, P., Defontaine, M., Ravary, B., Lemâtre, M. and Crevier-Denoix, N.** (2005). A non-invasive method of tendon force measurement. *J. Biomech.* **38**, 2124-2129.
- Putnam, C. A.** (1993). Sequential motions of body segments in striking and throwing skills: descriptions and explanations. *J. Biomech.* **26 Suppl. 1**, 125-135.
- Richmond, B. G., Aiello, L. C. and Wood, B. A.** (2002). Early hominin limb proportions. *J. Hum. Evol.* **43**, 529-548.
- Rizio, L. and Uribe, J. W.** (2001). Overuse injuries of the upper extremity in baseball. *Clin. Sports Med.* **20**, 453-468.
- Roach, N. T.** (2012). *The Biomechanics and Evolution of High-Speed Throwing*. PhD thesis, Department of Anthropology, Harvard University, Cambridge, MA, USA.
- Roach, N. T., Venkadesan, M., Rainbow, M. J. and Lieberman, D. E.** (2013). Elastic energy storage in the shoulder and the evolution of high-speed throwing in *Homo*. *Nature* **498**, 483-486.
- Roberts, E. M.** (1971). Cinematography in biomedical investigation. In *Selected Topics in Biomedical Investigation. Proceedings of the C.I.C. Symposium on Biomechanics* (ed. J. M. Cooper), pp. 71-81. Chicago, IL: The Athletic Institute.
- Ruff, C. and Walker, A.** (1993). Body size and body shape. In *The Nariokotome Homo Erectus Skeleton* (ed. A. Walker and R. E. Leakey), pp. 234-272. Cambridge, MA: Harvard University Press.
- Sabick, M. B., Torry, M. R., Lawton, R. L. and Hawkins, R. J.** (2004). Valgus torque in youth baseball pitchers: A biomechanical study. *J. Shoulder Elbow Surg.* **13**, 349-355.
- Stern, J. T., Jr** (1972). Anatomical and functional specializations of the human gluteus maximus. *Am. J. Phys. Anthropol.* **36**, 315-339.
- Stern, J. T., Jr and Susman, R. L.** (1983). The locomotor anatomy of *Australopithecus afarensis*. *Am. J. Phys. Anthropol.* **60**, 279-317.
- Stodden, D. F., Fleisig, G. S., McLean, S. P., Lyman, S. L. and Andrews, J. R.** (2001). Relationship of pelvis and upper torso kinematics to pitched baseball velocity. *J. Appl. Biomech.* **17**, 164-172.
- Sugiyama, Y. and Koman, J.** (1979). Tool-using and making behavior in wild chimpanzees at Bossou, Guinea. *Primates* **20**, 513-524.
- Werner, S. L., Fleisig, G. S., Dillman, C. J. and Andrews, J. R.** (1993). Biomechanics of the elbow during baseball pitching. *J. Orthop. Sports Phys. Ther.* **17**, 274-278.
- White, T. D.** (2002). Earliest hominids. In *The Primate Fossil Record* (ed. W. C. Hartwig), pp. 407-417. Cambridge, UK: Cambridge University Press.
- Wight, J., Richards, J. and Hall, S.** (2004). Influence of pelvis rotation styles on baseball pitching mechanics. *Sports Biomech.* **3**, 67-84.
- Wilk, K. E., Voight, M. L., Keirns, M. A., Gambetta, V., Andrews, J. R. and Dillman, C. J.** (1993). Stretch-shortening drills for the upper extremities: theory and clinical application. *J. Orthop. Sports Phys. Ther.* **17**, 225-239.
- Winter, D. A.** (1991). *The Biomechanics of Motor Control of Human Gait: Normal, Elderly and Pathological*. Waterloo, ON: University of Waterloo Press.

Supplementary Information

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 S1. Segment parameters used in the kinetic model. Segment length and diameter is obtained using the defining marker sets. Segmental movements are recorded using the tracking markers around the defined axes.