Exp Brain Res (2011) 208:115–125
DOI 10.1007/s00221-010-2465-2

RESEARCH ARTICLE

Wrist muscle activation, interaction torque and mechanical properties in unskilled throws of different speeds

Derek B. Debicki · Paul L. Gribble · Sherry Watts · Jon Hore

Received: 13 August 2010 / Accepted: 12 October 2010 / Published online: 28 October 2010

Abstract An unexpected property of unskilled overarm throws is that wrist flexion velocity at ball release does not increase in throws of increasing speed. We investigated the nature of the interaction torques and wrist mechanical properties that have been proposed to produce this property. Twelve recreational throwers made seated 2-D throws, which were used as a model for unskilled throwing. Joint motions were computed from recordings made with search coils; joint torques were calculated from inverse dynamics. Wrist flexion velocity at ball release was actually smaller in fast throws than in slow throws. This was associated in fast throws with the decrease in a large wrist flexor muscle torque (i.e., a calculated residual torque) in the last 40 ms before ball release, and its reversal to an extensor torque. Consequently, wrist flexor muscle torque was unable to oppose a small maintained wrist extensor interaction torque that arose from continuing elbow extension acceleration. The decrease in wrist flexor muscle torque was not associated with a decrease in wrist flexor EMG activity, nor with an increase in wrist extensor EMG activity. These findings support the hypothesis that the smaller wrist flexion velocity at ball release in fast 2-D throws results from a wrist extensor interaction torque and from a large wrist extensor viscoelastic torque. We propose that in fast 3-D throws skilled subjects decelerate elbow extension before ball release to help overcome these wrist extensor torques.

Keywords Throwing · Interaction torque · Viscoelastic · Wrist · Human · Speed

D. B. Debicki · P. L. Gribble · S. Watts · J. Hore (✉)
Department of Physiology and Pharmacology,
Medical Science Bldg., University of Western Ontario,
London, ON N6A 5C1, Canada
e-mail: jon.hore@schulich.uwo.ca

P. L. Gribble
Department of Psychology,
The University of Western Ontario,
London, ON, Canada

Introduction

The objective of the present study was to investigate a property of wrist flexion velocity in unskilled throws that involves control of interaction torques at the wrist. The property is that in many unskilled throwing situations (2-D throws, 3-D seated throws, 3-D standing throws with the nondominant arm), wrist flexion velocity at ball release does not increase in throws of increasing speed, i.e., slow and fast throws have similar wrist flexion velocities (Hirashima et al. 2003a; Debicki et al. 2004; Gray et al. 2006). The current explanation for this property comes from the pioneering work of Hirashima et al. (2003a, b). They found in three-joint 2-D throws (vertical overarm throws, constrained to the parasaggital plane) that there was a wrist flexor muscle torque that increased with throwing speed, but that it was counteracted (opposed) by a wrist extensor interaction torque that also increased with throwing speed. In a computer simulation, Hirashima et al. (2003b) concluded that, in addition to the extensor interaction torque at the wrist, the counteractive relation was also due to other mechanical properties of the wrist, i.e., to a short hand length and a considerable viscoelastic torque. They suggested that these mechanical properties would keep the wrist stable in multijoint movements, e.g., this stability would prevent excessive motion at the wrist that might cause injury and would provide a stable base for control of finger force. For throwing, they argued that the mechanical properties of the wrist made the wrist joint unsuitable for receiving an assistive (i.e., flexor) interaction torque that would increase ball speed.

However, it has since been shown that wrist flexion velocity at ball release in skilled unconstrained (standing) 3-D throws increases in proportion to throwing speed (Debicki et al. 2004; Gray et al. 2006; Hirashima et al. 2007). Furthermore, contrary to the finding in 2-D throws that the interaction torque did not assist wrist flexion (Hirashima et al. 2003a, b), these authors found in skilled 3-D throws that an increase in wrist flexion velocity occurred by utilization of a wrist flexor interaction torque (Hirashima et al. 2007).

In light of the recent findings in skilled 3-D throwing, the objective of the present experiments was to examine in greater depth the cause of the failure in 2-D throws to increase wrist flexion velocity at ball release in fast throws. 2-D throwing was used as a model of unskilled throwing. This was because 2-D throwing with the dominant arm has similarities to 3-D throwing with the unskilled nondominant arm: in both, there is a decrease in wrist velocity and a progressive increase in elbow extension velocity before ball release, neither of which occur in skilled dominant arm 3-D throwing (Gray et al. 2006). We extended the findings of Hirashima et al. (2003a, b) in two ways. First, we determined the origin of the wrist interaction torque, which was achieved by parceling out its components. Second, we investigated the role of wrist agonist and antagonist contractile activity by recording EMG activity. In their computer simulation, Hirashima et al. (2003b) simplified the model by leaving out antagonist muscles. In the present study, we determined whether changes in wrist flexor or wrist extensor muscle contractile activity could have caused the decrease in wrist velocity in fast throws.

Methods

Subjects and procedures

The study was approved by the University of Western Ontario Ethics Review Board, and all subjects gave informed consent. Twelve male subjects participated whose age was 21–24 years. All were right-handed skilled recreational throwers. Subjects made 2-D throws from a sitting position with the chest constrained from moving forward by straps pulled tightly over the shoulders. This minimized but did not eliminate forward chest motion. The participants were instructed to throw accurately using a baseball (150 g). Two-dimensional throws were made in the following order: 20 slow, 20 medium, 20 fast and 20 medium. Only the first 3 sets of throws were analyzed in detail. For the medium speeds, subjects were instructed to use a 2-D overarm motion (keeping the elbow in the vertical plane), to throw at a comfortable speed, and to throw accurately; for the slow throws, the instruction was the same, but to throw more slowly than the medium speeds (which had been established in practice throws). For the fast throws, subjects were instructed to throw as fast as possible and accurately and that they were free if they wished to increase the amplitude of shoulder motion by increasing the backswing (shoulder flexion). Subjects were allowed practice throws until they were comfortable at all instruction speeds. Subjects were instructed to keep the arm in a parasagittal (vertical) plane. An experimenter standing behind the subject reported if the elbow came out of the plane and these throws were excluded. Planarity was also verified by off-line analysis of each throw. Throws were also excluded if their speed or accuracy for a particular condition was markedly different from the mean for that subject, i.e., were outside the range for 95% of throws, which is given by SD $\times$ 3.92. On average, 2 slow, 2 medium and 4 fast throws/subject were deleted. Throws were made on command about every 30 s at a vertical grid of 6 $\times$ 6 cm numbered squares (9 squares across and 27 high). The target was a square of 6 $\times$ 6 cm at about eye level and 3.1 m from the chest. Each throw was scored for accuracy by the participant calling out the number on the square that was struck.

The timing of ball release from the tip of the middle phalanx was measured with a pressure-sensitive microswitch that was attached to the distal phalange of the middle finger. The participants were instructed to grip the ball so that it rolled over the distal switch. The timing accuracy of the distal microswitch was verified by comparing it with the time of onset of finger flexion after finger extension, which is a moment that coincides with release of the ball from the fingertip (e.g., Hore et al. 1999, 2001). Ball speed was measured with a radar gun (Stalker Professional Sports Radar, sampling rate 100 Hz), which was located about 4 m behind the target curtain (i.e., about 7 m from the participants).

Recording angular positions of arm segments

Angular positions of five arm segments and the trunk were measured using the magnetic-field search-coil technique as described previously (Hore et al. 1999). Search coils were securely taped to the back of the distal phalanx, the back of the hand, the back of the forearm proximal to the wrist, the lateral aspect of the upper arm, the acromion process of the scapula and the sternum. The participants sat in 3 orthogonal alternating magnetic fields of frequency 62.5, 100 and 125 kHz generated by 3 $\times$ 3 $\times$ 4 m Helmholtz coils. Coil voltages, sampled at 1,000 Hz, were used to calculate the simultaneous angular positions of each arm segment and the trunk in three-dimensional space (Tweed et al. 1990).

Arm motions were described in terms of joint rotations by computing angular positions of arm segments with respect to the adjacent proximal segment. In this case, the axes were embedded in the proximal segment and rotated with it. Joint angular velocities and accelerations were obtained by differentiation. Shoulder, elbow and wrist joint kinematics were low-pass filtered using a second-order Butterworth filter at 20, 30 and 45 Hz respectively using Matlab (The Mathworks). At the start of each experiment, a calibration was performed in which the upper arm was rotated 90° to the front and the forearm pronated such that the forearm, hand and fingers were in a vertical line with the palm facing forward. This position was used as the reference position in the kinematic figure (Fig. 1). For the equations of motion, we used the convention described by Hirashima et al. (2003a).

Joint dynamics

Shoulder, elbow and wrist torques were computed using inverse-dynamics equations of motion for a 2-D (vertical plane) 3-joint planar link-segment model of the human arm as described by Hirashima et al. (2003a). Shoulder joint angles were defined relative to the vertical axis passing through the shoulder joint, elbow joint angles were defined relative to the long axis of the upper arm, and wrist joint angles were defined relative to the long axis of the forearm. Positive joint angles were in the counter-clockwise (upwards) direction (shoulder flexion, elbow flexion and wrist extension). The arm model included translations of the origin in a parasagittal plane in vertical (*Y*) and horizontal (*X*) directions. Translational movements of the origin were recorded using Optotrak at 500 Hz. Translations were linearly interpolated and resampled at 1,000 Hz off-line and were temporally aligned with the angular search coil data using an analog step signal that was sampled from a channel common to both motion acquisition systems. Translation positions were subsequently low-pass filtered at 15 Hz and differentiated to obtain linear velocities and accelerations of the origin. Anthropometric variables were computed for each individual subject based on constants defined by Winter (2005). The mass of the ball was incorporated into the model. The equations of motion were used to compute the net torque (NET), the muscle torque (MUS), the interaction torque (INT) and the torque due to gravity (GRA) for each of the shoulder, elbow and wrist joint. Torque variables were defined according to previous studies (e.g., Hollerbach and Flash 1982; Gribble and Ostry 1999; Bastian et al. 1996, 2000; Cooper et al. 2000; Hirashima et al. 2003a; Debicki and Gribble 2004) where the NET torque is defined as the sum of the other components (NET = MUS + INT + GRA) and where the MUS torque parameter is computed as a residual value

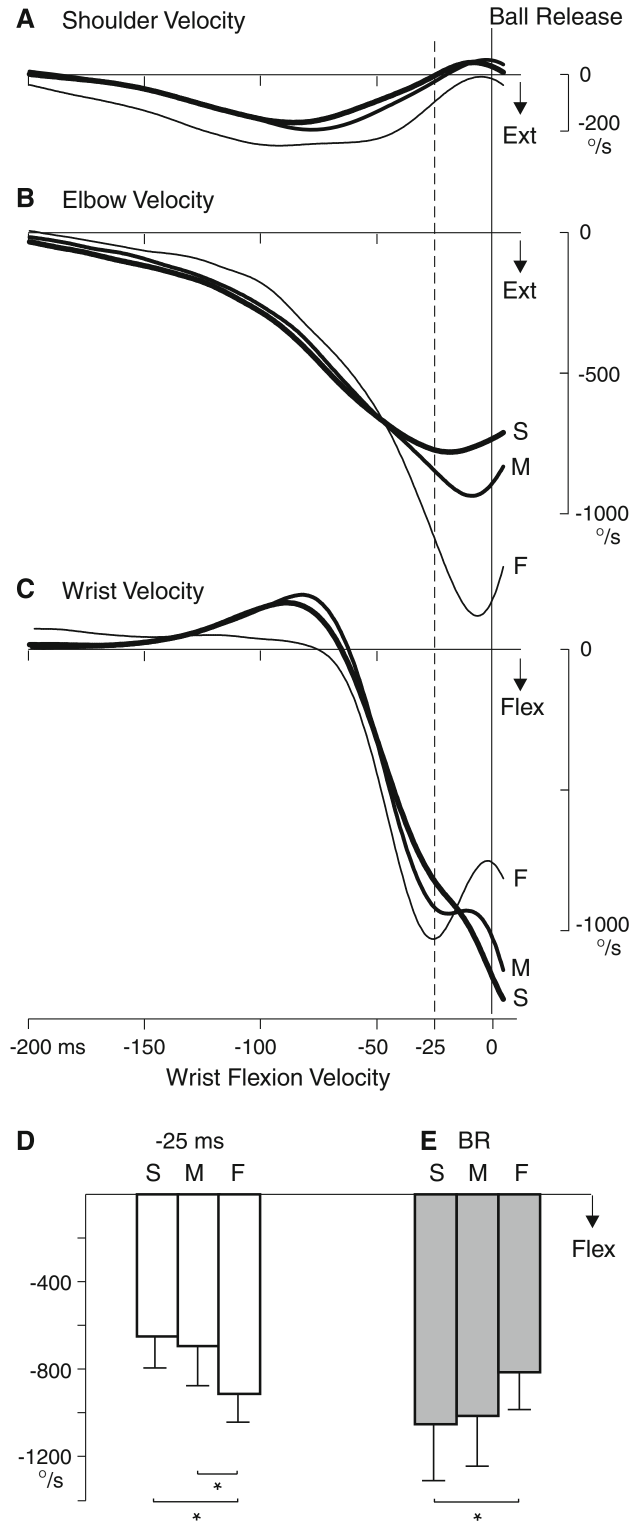

Fig. 1 **a**, **b**, **c** Average angular kinematics of joint rotations from 2-D throws made at a slow (*S*), medium (*M*) and fast (*F*) speed by representative subject Pr. Each trace is the average of about 20 throws aligned on the time of ball release. *Vertical arrows* indicate direction of rotation for each joint. *Dashed line* indicates 25 ms before ball release. **d**, **e** Means and SDs across subjects for magnitude of wrist flexion velocity for slow (*S*), medium (*M*) and fast (*F*) throws. *Open bars* at 25 ms before ball release (*BR*), *Gray bars* at ball release. * $P < 0.05$ (post hoc Tukey test)

(MUS = NET – INT – GRA). Thus, the MUS torque is a generalized muscle torque that includes both torque generated from muscle activation and torque generated from the passive properties of the muscle and other joint tissues. To quantify the computed joint dynamics, net, muscle, interaction and gravity torques were obtained at certain times for each individual throw then averaged across throwing speeds and across subjects.

EMG activity

EMG activity was recorded at 1,000 Hz with surface electrodes from flexor carpi radialis, flexor carpi ulnaris, extensor carpi radialis and extensor carpi ulnaris. Electrodes were placed over the muscle bellies of the wrist flexors and extensors based on anatomical landmarks. EMG activity was recorded during isometric (resisted) wrist flexions and extensions, and during finger movements, to verify electrode placement functionally and to ensure that there was no cross talk. These signals were amplified, filtered (30–200 Hz) and full-wave rectified. The magnitude of EMG activity was established as follows. At the start of each experiment, subjects were asked to activate maximally the wrist flexors, then the wrist extensors, and to make some fast practice 2-D throws. The gains of the amplifiers were adjusted to achieve the same levels of maximal EMG activity in all muscles.

Statistics

Unless otherwise specified, statistical analysis was completed with two-way repeated-measures ANOVA. Post hoc analysis was performed with the Tukey test where appropriate, with statistical significance set at $P < 0.05$, which is shown by asterisks in the figures.

Results

Wrist joint velocity

The first objective was to determine whether, for this population of throwers, wrist flexion velocity was similar at ball release in throws of slow, medium and fast speeds as found by Hirashima et al. (2003a). The mean values for ball speeds were 28.1 km/h (SD 2.7) for slow, 33.8 (1.8) for medium and 44.6 (4.0) for fast throws. There was a main effect of instruction on throwing speed (repeated-measures ANOVA, $P < 0.001$). A post hoc Tukey test showed significant differences between each throwing speed at the $P < 0.05$ level.

Figure 1a, b, c shows kinematic averages aligned on ball release from 20 slow (thick traces), 20 medium speed (medium traces) and 20 fast 2-D throws (thin traces), made by a representative subject. Compared to the slow and medium throws, the fast throws were associated with a slightly larger peak shoulder extension velocity before ball release (Fig. 1a). Elbow extension velocity (Fig. 1b) was considerably larger in the fast throws and peaked near ball release. At the wrist, in the slow throws (Fig. 1c), wrist flexion velocity increased until ball release. In the medium speed throws, wrist flexion velocity plateaued about 25 ms before ball release and then increased. In contrast, in the fast throws, about 25 ms before ball release, there was a rapid decrease in wrist flexion velocity. In some subjects (not shown), this decrease was followed by an increase to ball release. Nevertheless, in the representative subject, and in 11 of 12 subjects, at ball release, the fast throws had a smaller wrist flexion velocity than the slow or medium throws.

The data across subjects are shown in Fig. 1d, e. Wrist flexion velocity is given at two points: at 25 ms before ball release (−25 ms) (Fig. 1d, open bars) and at ball release (BR) (Fig. 1e, gray bars). A two-factor repeated-measures ANOVA showed that there was a significant interaction between throwing speed and measurement time on wrist flexion velocity [$F(1,14) = 37.9$; $P < 0.001$]. There was a simple effect of throwing speed on wrist flexion velocity at −25 ms [$F(2,22) = 36.6$; $P < 0.001$], i.e., wrist velocity for fast throws at −25 ms (Fig. 1d) was larger than that found for slow and medium speed throws. At ball release (Fig. 1e), there was also a significant simple effect of throwing speed on wrist flexion velocity [$F(1,14) = 7.984$; $P = 0.009$]. But in this case, fast throws were significantly smaller than slow throws.

In summary, wrist flexion velocity continued to increase to ball release for both slow and medium throws. In contrast, for fast throws, it peaked about 25 ms before ball release then decreased, such that it had a lower value than slow throws at ball release.

Torques at the wrist

To determine why wrist flexion velocity decreased before ball release in the fast throws, torques at the wrist were calculated using equations of motion (see "Methods"). Figure 2 shows average wrist flexion velocities for about 20 slow (S), 20 medium (M) and 20 fast (F) throws (the same as Fig. 1c) together with torques aligned on ball release. For all speeds, the initial increase in wrist flexion velocity (down-going trace in Fig. 2a) was associated with a wrist net torque in the direction of flexion (Fig. 2b). The net torque in the flexion direction peaked at about the same time before ball release for all speeds of throw. The time of peak wrist flexor net torque for the fast throws (T1, dashed line, which was at −45 ms for this subject), was used as a

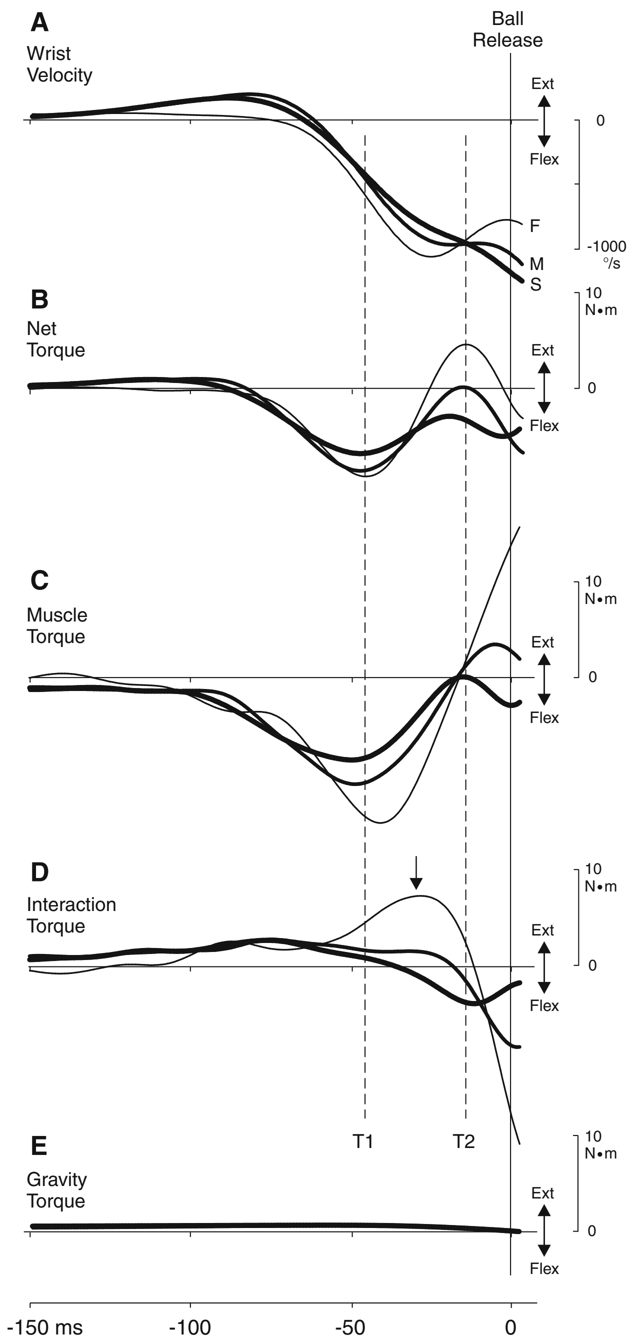

Fig. 2 Wrist flexion velocity and computed torques from representative subject Pr. Each trace represents the average of about 20 throws for slow (*S*), medium speed (*M*) and fast throws (*F*) aligned on time of ball release (*solid vertical line*, 0 ms). *T1* time of average peak net flexor torque for fast throws; *T2* time of average peak net extensor torque for fast throws

measurement point in subsequent analysis. The peak net flexor torque for all speeds was due to a flexor muscle torque (Fig. 2c), which was larger for fast throws. It was not due to an interaction torque (Fig. 2d) because at this time, the interaction torque was acting in the direction of wrist extension. The torque due to gravity was relatively small and was also in the direction of wrist extension until ball release (Fig. 2e).

After the peak in net flexor torque (Fig. 2b), the pattern of its decrease was related to throwing speed. For slow and medium throws, the net flexor torque approached zero but did not become extensor before ball release. For fast throws, the net torque changed direction and became an extensor torque before ball release. This change in direction in fast throws from a flexor, to an extensor net torque, was the cause of the decrease in wrist flexion velocity in fast throws (Fig. 2a). For all throwing speeds, the decrease in the magnitude of the wrist flexor net torque (Fig. 2b) was associated with a decrease in the magnitude of the wrist flexor muscle torque (Fig. 2c). By the time the net torque for the fast throws reached its extensor peak (Fig. 2b, T2, dashed line, which was at −15 ms for this subject), the muscle torque for all three speeds of throw was near zero. One difference between throwing speeds was that over this time period (T1–T2), the interaction torque for fast throws (Fig. 2d, arrow) was at its largest value and in the extensor direction, whereas it was small or reversed to the flexor direction for medium and slow throws.

A similar pattern was observed across subjects. Figure 3 shows histogram bars that represent the values for the wrist of net torque, muscle torque, interaction torque and gravity torque at the time of the flexor and extensor peaks in net torque in fast throws for each subject (T1, open bars, and T2, gray bars) averaged across subjects for slow (S), medium (M) and fast (F) throws. The time points (peak net flexor torque, T1, and peak net extensor torque, T2) were chosen because they were robust kinetic parameters that were easily discernible in the fast throws for all subjects. Furthermore, they were relevant points in the throw because we were interested in determining the factors associated with the decrease in the net wrist flexor torque (peak at T1), and for fast throws, the factors associated with its reversal to an extensor torque (peak at T2). When comparing the different torques at the 3 speeds and 2 time points, we first performed a two-factor repeated-measures ANOVA. This showed that there were significant speed–time interaction effects for the net torque [$F(2,22) = 71.8$; $P < 0.001$], the muscle torque [$F(1,14) = 13.2$; $P = 0.001$] and for the interaction torque [$F(2,22) = 7.7$; $P = 0.003$]. The values of gravity torque at T1 and T2 were small and will not be considered further. The following results involve the analysis of simple effects.

Figure 3a shows that across subjects, net torque in fast (F) throws reversed from a flexion direction (T1) to an extension direction (T2) but not in slow and medium speed throws. There were two reasons for this. First, muscle torque for all speeds of throws (Fig. 3b) fell from speed-related values at T1 to close to zero at T2: slow [$F(1,11) = 27.4$; $P < 0.001$], medium [$F(1,11) = 40.4$;

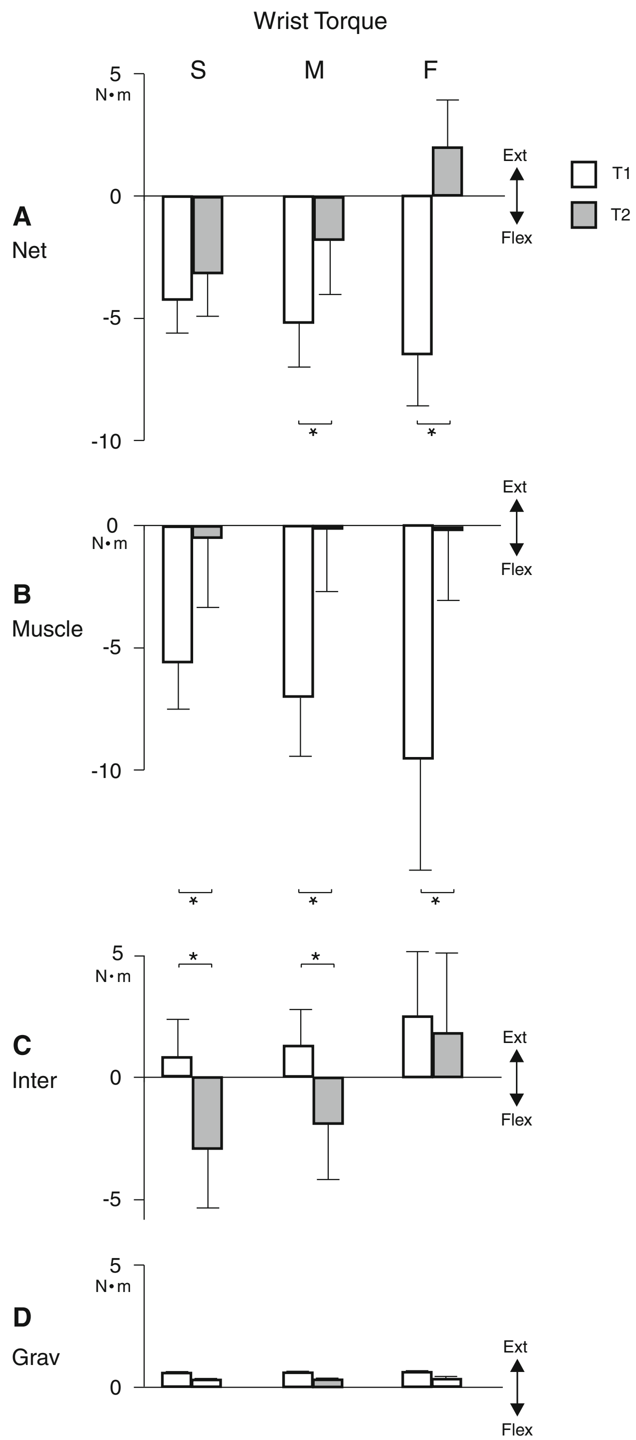

Fig. 3 Means and SDs of wrist net (**a**), muscle (**b**), interaction (**c**) and gravity (**d**) torque across subjects for slow (*S*), medium (*M*) and fast (*F*) throws measured at T1 (*open bars*) and T2 (*gray bars*). * $P < 0.05$ (post hoc Tukey test)

$P < 0.001$] and fast [$F(1,11) = 60.4$; $P < 0.001$]. Second, whereas the interaction torque changed significantly from T1 to T2 (Fig. 3c) for slow [$F(1,11) = 49.5$; $P < 0.001$] and medium [$F(1,11) = 22.3$; $P = 0.001$] from values in the extensor direction at T1 to values in the flexor direction at T2, the value for fast throws did not change [$F(1,11) = 1.1$; $P = 0.324$].

In summary, the decrease in wrist flexion velocity prior to ball release in fast throws was due to a wrist net torque that changed from the flexion direction to the extension direction. This, in turn, was due to two factors: a decrease in wrist flexor muscle torque, which occurred for all speeds of throw, and the presence of an extensor interaction torque that was only maintained in fast throws.

Interaction torques parceled out

To determine why the interaction torque in fast throws remained in the direction of wrist extension at T2, the wrist interaction torques across subjects measured at T1 and T2 were parceled out (Fig. 4). The total interaction torque at T1 (Fig. 4a), which was in the extension direction for all speeds of throw, was primarily due to the component associated with the effects of elbow extension acceleration (Fig. 4c), which was larger for fast throws than for the slow and medium throws [$F(1,13) = 16.5$; $P = 0.001$]. All other components at T1 were either small in magnitude (Fig. 4b, d, e, f) or were acting in the direction of wrist flexion (Fig. 4g, h).

Figure 4i shows that at time T2, the total interaction torques for the slow and medium throws were in the flexor direction and that the total interaction torque for the fast throws was still in the extensor direction. The change in the direction of the interaction torque for slow and medium throws was associated with a significant decrease in the magnitude of the effect associated with elbow extension acceleration at T2, compared to T1 (cf. Fig. 4c, k), slow [$F(1,11) = 25.3$; $P < 0.001$] and medium speed [$F(1,11) = 4.9$; $P = 0.048$]. In contrast, for fast throws, the effect associated with elbow extension acceleration increased at T2 compared to T1 [$F(1,11) = 7.4$; $P = 0.020$]. This corresponded with a late increase in elbow acceleration associated with shoulder deceleration (Fig. 1a). The elbow acceleration-dependent increase in the interaction torque was countered by a shoulder deceleration-dependent torque in the direction of wrist flexion (cf. Fig 4b, j), which was larger at T2 than at T1 for slow [$F(1,11) = 10.7$; $P = 0.007$], medium [$F(1,11) = 19.4$; $P = 0.001$] and fast throws [$F(1,11) = 14.6$; $P = 0.003$]. It was also countered by an elbow centripetal effect that increased in magnitude from T1 to T2 for medium [$F(1,11) = 8.0$; $P = 0.016$] and fast [$F(1,11) = 31.7$; $P < 0.001$] but not for slow throws [$F(1,11) = 0.0$; $P = 0.897$]. Any changes in the other torque components between the two time points were either small or were not significant.

In summary, the decrease in wrist velocity in fast throws was due to two factors: a decrease in wrist flexor muscle torque to zero and a maintained wrist extensor interaction

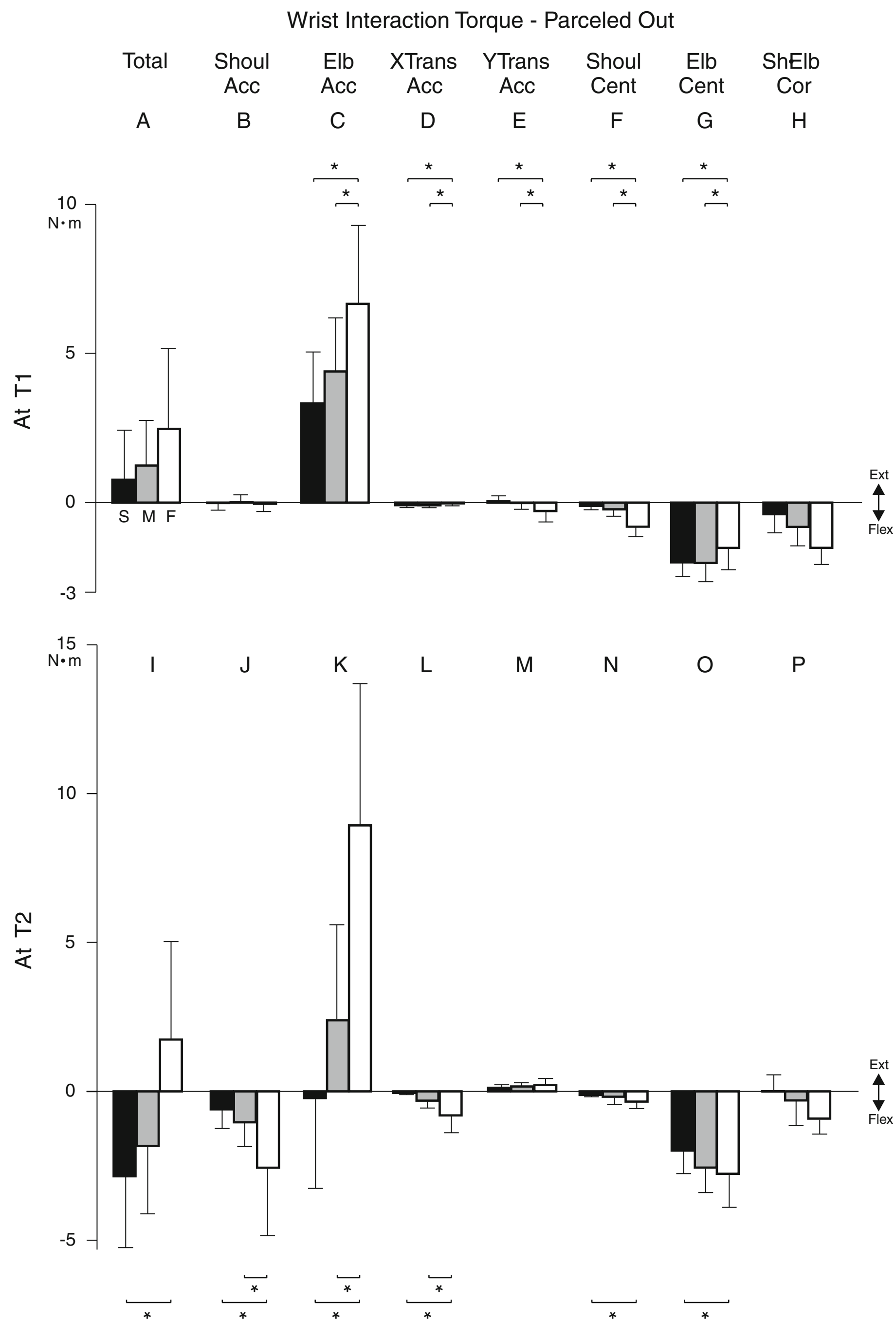

Fig. 4 Parceled out wrist interaction torque at T1 and T2. *A*, *I* total interaction torque (from Fig. 4). Parceled out torques were associated with parameters as follows: *B*, *J* shoulder acceleration, *C*, *K* elbow acceleration, *D*, *L* horizontal translation acceleration of origin of arm model, *E*, *M* vertical translation of the origin, *F*, *N* centripetal effects from shoulder angular velocity *G*, *O* centripetal effects from elbow angular velocity, *H*, *P* Coriolis effects from elbow and wrist angular velocities. *Arrows* indicate direction of torque at elbow joint

torque arising from the continuing elbow extension acceleration.

Wrist EMG activity

The remaining question is: why in all subjects did wrist flexor muscle torque in fast throws begin to decrease about 40–50 ms before ball release (Fig. 2c, 3b)? One possibility is that the decrease in muscle torque was due to a change in wrist flexor or extensor muscle contractile activity, i.e., to a decrease in wrist flexor muscle activity, to a reciprocal increase in wrist extensor muscle activity or to coactivation. This was investigated in fast throws by averaging wrist flexor and wrist extensor EMG activity with respect to averaged peak wrist flexor muscle torque. Figure 5 shows average EMG activity across all 12 subjects from flexor carpi radialis (FCR), flexor carpi ulnaris (FCU), extensor carpi radialis (ECR) and extensor carpi ulnaris (ECU). To allow for the electrical–mechanical coupling time, the EMG activity in Fig. 5 was shifted 25 ms to the right (cf. Hoffman and Strick 1999). With this shift, records of muscle torque and EMG activity can be directly compared on

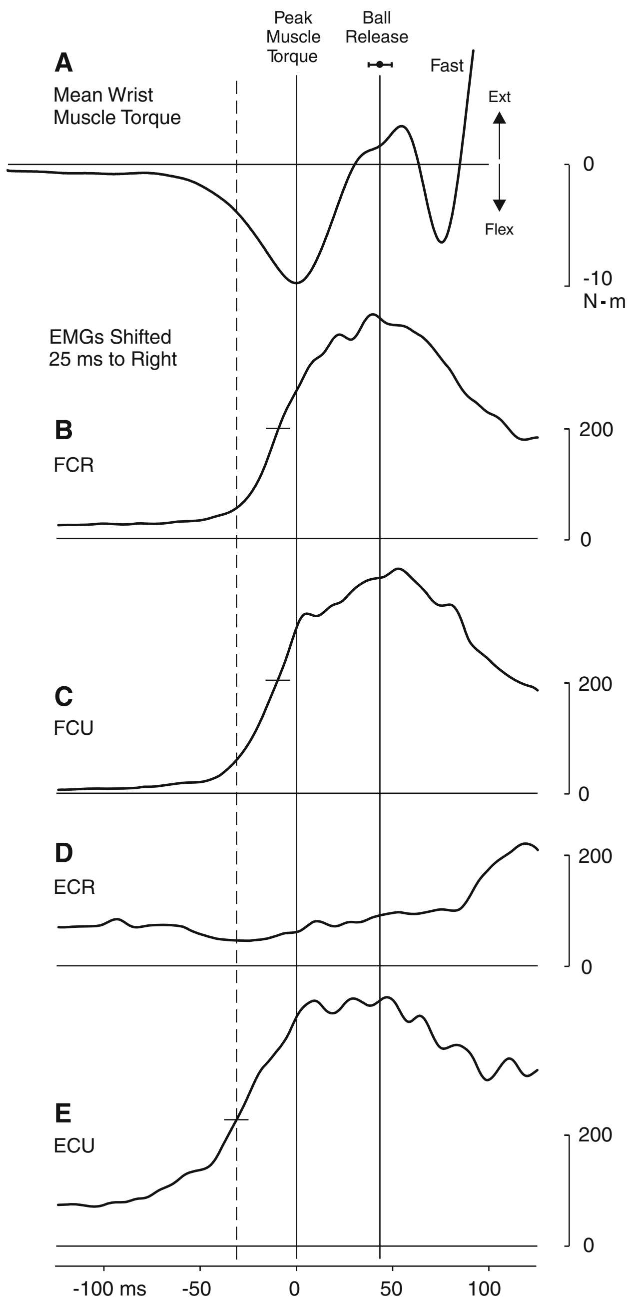

Fig. 5 Average wrist muscle EMG activity across subjects for fast throws. EMG traces averaged with respect to time of peak wrist flexor muscle torque. To allow for electrical–mechanical coupling time, EMG traces were shifted 25 ms to right. *Short horizontal line* on EMG traces gives 50% of peak EMG activity. *Dashed vertical line* is at 50% peak value for ECU. *Filled circle* and *horizontal bar* mean ± SD time ball release. *FCR* flexor carpi radialis, *FCU* flexor carpi ulnaris, *ECR* extensor carpi radialis, *ECU* extensor carpi ulnaris. Units for EMG are arbitrary

the same time scale. Surprisingly, during the period of the rapid decrease in wrist flexor muscle torque (Fig. 5a, between solid vertical lines), there was an increase in EMG activity in the wrist flexor muscles FCR (Fig. 5b) and FCU (Fig. 5c). Considering amplitudes of shifted EMG activity, at peak flexor muscle torque (time 0, solid vertical line) and at the mean time of ball release (+43 ms, solid vertical line), the values for both FCR and FCU were significantly larger at mean ball release (2-tailed *t*-test, FCR $P < 0.001$; FCU $P < 0.01$). Larger differences occurred if the EMG traces were shifted to the right by larger amounts. Thus, the decrease in wrist flexor muscle torque was not caused by a decrease in wrist flexor muscle contractile activity.

No evidence was found that the decrease in wrist flexor muscle torque was associated with an increase in wrist extensor muscle activity. An influence from ECR (Fig. 5d) is unlikely for two reasons: first, during the period of the rapid decrease in wrist flexor muscle torque, the level of activity of ECR was very small, and second, 6 of 12 subjects did not show any increase in shifted EMG activity during this period (not shown), yet all showed a decrease in wrist flexor muscle torque (Fig. 5a). For ECU, there was coactivation with FCR and FCU for all speeds of throw. However, there was no evidence that this coactivation had any effect on wrist flexor-extensor muscle torque. For example, for the fast throws, Fig. 5e shows that 100 ms before peak flexor muscle torque (time 0), there was tonic ECU EMG activity (baseline at 0), which then increased before onset of FCR and FCU. The short horizontal line on all EMG traces represents the point where EMG activity reached 50% of its peak value (from 0 to peak). If ECU activity was responsible for the rapid decrease in wrist flexor muscle torque, it would be expected that, when its early tonic activity and early increase were largely unopposed (before dashed vertical line in Fig. 5), muscle torque in the direction of wrist extension would be produced. However, this did not occur as muscle torque was in the flexor direction (Fig. 5a). Furthermore, during the period of the rapid decrease in wrist flexor muscle torque, when activity of FCR and FCU was increasing, activity of ECU was not increasing but had plateaued. Again, this is not consistent with a role for ECU in producing the rapid decrease in wrist flexor muscle torque.

Discussion

Role of interaction torque

The finding that wrist flexion velocity at ball release did not increase in fast 2-D throws is consistent with previous studies of 2-D overarm throwing (Hirashima et al. 2003a). In the present fast 2-D throws, wrist flexion velocity was not held constant compared to slow and medium speed throws, but showed a rapid decrease in the last 25 ms before ball release (Fig. 1). We investigated whether the decrease in wrist flexion velocity at ball release in fast throws occurred because subjects could not adequately compensate for a large wrist extensor interaction torque. In natural speed reaching movements, wrist musculature compensated for interaction torques by a predictive feedforward mechanism such that perturbations in the movement trajectory were minimized (Koshland et al. 2000). However, in other very fast arm movements, muscle torque was not large enough to compensate for the large interaction torque at the wrist (Virji-Babul and Cooke 1995; Dounskaia et al. 1998). In this case, the net torque at the wrist was dominated by the interaction torque. Similarly, in the present case, over the last 25 ms before ball release muscle (residual), torque was not large enough to compensate for the interaction torque. The decrease in muscle (residual) torque in the fast throws and the maintained extensor interaction torque resulted in the reversal in direction of the net torque and the decrease in wrist flexion velocity prior to ball release.

Why did wrist flexor muscle torque decrease?

Why did the wrist flexor muscle torque decrease at such an early point in the throw? The EMG results (Fig. 5) showed that the decrease in wrist flexion muscle torque was not due to a decrease in activity of FCR or FCU. This fits with previous results (Debicki et al. 2004) where EMG activity in the wrist muscles was close to maximal in fast sitting 3-D throws. These results suggest that subjects cannot compensate for large wrist extensor torques by increasing wrist flexor muscle contractile activity. In the following, we consider four possible explanations for the decrease in wrist flexor muscle torque. The first deals with finger opening, the next two deal with coactivation of extensor carpi ulnaris, and the last one deals with wrist viscoelastic torques.

The first explanation is that the decrease in wrist flexor muscle torque was associated with the activity of finger muscles, which occurs during finger opening to release the ball. Finger flexor muscles, which are used to grip the ball during the throw, also cross the wrist joint and can contribute to wrist flexor torque. Similarly, the finger extensor muscles, extensor digitorum communis, can also contribute to wrist extensor torque. Given that for fast 2-D throws onset of finger opening occurs at about the time of the decrease in wrist flexor muscle torque, it could be argued that finger opening to release the ball involves a decrease in finger flexor torque and an increase in finger extensor torque, both of which would decrease wrist flexor muscle torque. However, this effect is highly unlikely because the finger muscles exert only a weak effect at the wrist, and any finger effect in the last 43 ms before ball release occurs at a time when wrist flexor muscle contractile activity is at a high level (Fig. 5). Furthermore, finger opening does not involve a large decrease in finger flexor torque. In an overarm throw, subjects have an anticipatory progressive increase in finger flexor force, both during gripping and during the period when the ball rolls along the finger (Hore et al. 1999, 2001). This finger force occurs to oppose the progressive increase in back force from the ball (because the ball accelerates until ball release). Compared to the magnitude of these active finger flexor forces, the change in finger force to extend the fingers would be extremely small. Consequently, we believe that changes in wrist torque associated with finger opening cannot cause the large and rapid decrease in wrist flexor muscle torque.

The second explanation for the early decrease in wrist flexor muscle torque is that it was associated with the coactivation of extensor carpi ulnaris (ECU), which occurred to stabilize the wrist after ball release by increasing joint stiffness (cf. De Serres and Milner 1991; Milner et al. 1995; Milner and Cloutier 1998; Burdet et al. 2001; Milner 2002). This may be necessary in fast throws to avoid injury from a sudden wrist flexion acceleration after ball release caused by the rapid deceleration of elbow extension (which occurred at about the time of ball release) and from a sudden decrease in the mass of the hand-ball due to ball departure. However, there are two results that do not fit with this scheme. First, extensor carpi radialis (ECR) was not strongly coactive (Fig. 5). Second, in fast standing 3-D throws, where it would be expected that greater wrist stiffness would be needed, coactivation occurs for FCR and FCU with both ECR and ECU, but primarily after ball release rather than before it, when allowance is made for the electrical–mechanical coupling time (see Debicki et al. 2004, Fig. 8). Thus, it is unlikely that the observed coactivation of ECU was associated with a strategy of generating stiffness at the wrist before ball release to prevent wrist motion occurring after ball release.

The third explanation for the early decrease in wrist flexor muscle torque is that it was related to coactivation of ECU, which was required to orient the hand during the throw. One difficulty in performing 2-D throws in which motion is confined to a parasagittal plane is to have the palm facing forward while keeping the wrist, elbow and shoulder joints in vertical alignment. This involves pronating the forearm, which likely resulted in the requirement, when flexing the wrist, to produce an active torque at the wrist in the direction of ulnar deviation to prevent the hand from deviating radially. This could potentially have had the unwanted effect of ECU acting as a wrist flexor antagonist. Insight into wrist muscle function has come from the work of Hoffman and Strick (1999) who found that the preferred direction of activation of a wrist muscle in a voluntary wrist movement differs from its pulling direction produced by electrical stimulation. This occurs because many movement directions cannot be produced by the actions of one muscle alone. Consequently, certain movement directions were associated with coactivation of wrist muscle pairs that are usually considered to be antagonist muscles (see also Fagg et al. 2002; Haruno and Wolpert 2005). However, in monkeys, in the arm pronated position, the pulling direction of ECU is pure ulnar deviation (Fagg et al. 2002). This is consistent with the present results in humans (Fig. 5) where no evidence was found for an effect of ECU activity on wrist flexor-extensor muscle torque. Together, these findings suggest that in the pronated forearm position in 2-D throws, ECU is not a wrist flexor antagonist whose activity contributes to wrist extensor muscle torque. In conclusion, we think it unlikely that coactivation of ECU was responsible for the rapid decrease in wrist flexor muscle torque; however, we cannot rule out that it exerted some effect.

The last, and likely most important, contributor to the decrease in wrist flexor muscle torque is the viscoelastic properties of the wrist. It is important to emphasize that the muscle torque which is calculated by inverse dynamics (e.g., Hirashima et al. 2003a) is a residual torque that represents the sum of torque generated both by contractile activity of muscles surrounding the joint and by structural viscoelastic properties of tissue associated with the joint (from muscles, tendons, ligaments, articular capsule and other connective tissue). Hirashima et al. (2003b) demonstrated in a two-joint simulation that for wrist flexion velocities of about 500°/s, viscosity at the wrist produces an extensor torque that is comparable in size to both the active wrist flexor muscle torque (due to muscle contractile activity) and the wrist extensor interaction torque. In this simulation, the decrease in wrist flexor muscle torque was due to an increase in viscous and elastic torques in the wrist extension direction. Given that viscosity increases with joint angular velocity, it would be expected that the high wrist joint velocities of 600–1000°/s in fast throws, that we observed 40–25 ms before ball release (Fig. 1c, d), would produce a large viscoelastic torque at the wrist in the extensor direction prior to ball release. In agreement, in natural fast 3-D throws made by skilled subjects (Hirashima et al. 2007) where wrist flexion velocity was high, a representative subject showed the same rapid decrease in wrist flexor muscle torque, and reversal to a large wrist extensor muscle torque, as we (Fig. 2c) and Hirashima et al. (2003b, Fig. 4d) observed in 2-D throws. The likely interpretation of this evidence is that the most important factor responsible for the decrease in wrist flexor muscle residual torque is the viscoelastic properties of the wrist.

Conclusion

The inverse dynamics analysis confirmed the results of Hirashima et al. (2003a) by showing that two factors contributed to the failure of wrist flexion velocity to increase in fast 2-D throws: a rapid decrease in wrist flexor muscle residual torque about 40 ms before ball release and its reversal to a wrist muscle extensor torque, and a wrist extensor interaction torque that was only maintained in fast throws. Furthermore, our EMG recordings demonstrated that the decrease in wrist flexor muscle residual torque was not caused by a decrease in wrist flexor muscle contractile activity, nor by an increase in wrist extensor contractile activity. We conclude that the smaller wrist flexion velocities at ball release in fast 2-D throws is not an intended effect at the wrist (based on EMG patterns of wrist muscles). Rather the present results and those of Hirashima et al. (2003a, b) suggest that it likely results in fast throws from an inability of wrist flexor muscle contractile activity to counteract two torques: a wrist extensor interaction torque and a wrist extensor viscoelastic torque. These findings suggest that there are three reasons why 2-D throwers (and presumably unskilled subjects throwing naturally) are not successful at increasing wrist flexion velocity at ball release in throws of increasing speed. First, wrist flexor muscle contractile activity is large and cannot be increased much further. Second, the throwing pattern of continuing elbow acceleration to ball release in 2-D throws (cf. Debicki et al. 2010) results in a maintained wrist extensor interaction torque that slows wrist velocity. The continued elbow extension acceleration to ball release also occurred in unskilled 3-D throws (Gray et al. 2006). Third, the faster the wrist flexion velocity becomes, the more it will be opposed (and slowed) by wrist viscoelasticity. We propose that skilled throwers overcome these inherent mechanical constraints by changing their interjoint throwing pattern so that they produce a large elbow extension deceleration before ball release, which produces an assistive wrist flexor interaction torque (Hore et al. 2005a, b; Gray et al. 2006; Hirashima et al. 2007, 2008).

Acknowledgments L. van Cleeff provided technical assistance during experiments. The work was funded by a Canadian Institutes of Health research grant to J. Hore and P. Gribble.

References

Bastian AJ, Martin TA, Keating JG, Thach WT (1996) Cerebellar ataxia: abnormal control of interaction torques across multiple joints. J Neurophysiol 76:492–509

Bastian AJ, Zackowski KM, Thach WT (2000) Cerebellar ataxia: torque deficiency or torque mismatch between joints? J Neurophysiol 83:3019–3030

Burdet E, Osu R, Franklin DW, Milner TE, Kawato M (2001) The central nervous system stabilizes unstable dynamics by learning optimal impedance. Nature 414:446–449

Cooper SE, Martin JH, Ghez C (2000) Effects of inactivation of the anterior interpositus nucleus on the kinematic and dynamic control of multijoint movement. J Neurophysiol 84:1988–2000

De Serres SJ, Milner TE (1991) Wrist muscle activation patterns and stiffness associated with stable and unstable mechanical loads. Exp Brain Res 86:451–458

Debicki DB, Gribble PL (2004) Inter-joint coupling strategy during adaptation to novel viscous loads in human arm movement. J Neurophysiol 92:754–765
Debicki DB, Gribble PL, Watts S, Hore J (2004) Kinematics of wrist joint flexion in overarm throws made by skilled subjects. Exp Brain Res 154:382–394
Debicki DB, Watts S, Gribble PL, Hore J (2010) A novel shoulder-elbow mechanism for increasing speed in a multijoint arm movement. Exp Brain Res 203:601–613
Dounskaia NV, Swinnen SP, Walter CB, Spaepen AJ, Verschueren SM (1998) Hierarchical control of different elbow-wrist coordination patterns. Exp Brain Res 121:239–254
Fagg AH, Shah A, Barto AG (2002) A computational model of muscle recruitment for wrist movements. J Neurophysiol 88:3348–3358
Gray S, Watts S, Debicki D, Hore J (2006) Comparison of kinematics in skilled and unskilled arms of the same recreational baseball players. J Sports Sci 24:1183–1194
Gribble PL, Ostry DJ (1999) Compensation for interaction torques during single- and multijoint limb movement. J Neurophysiol 82:2310–2326
Haruno M, Wolpert DM (2005) Optimal control of redundant muscles in step-tracking wrist movements. J Neurophysiol 94:4244–4255
Hirashima M, Kudo K, Ohtsuki T (2003a) Utilization and compensation of interaction torques during ball-throwing movements. J Neurophysiol 89:1784–1796
Hirashima M, Ohgane K, Kudo K, Hase K, Ohtsuki T (2003b) 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, 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, Ohtsuki T (2008) Kinetic chain of overarm throwing in terms of joint rotations revealed by induced acceleration analysis. J Biomech 41:2874–2883
Hoffman DS, Strick PL (1999) Step-tracking movements of the wrist. IV. Muscle activity associated with movements in different directions. J Neurophysiol 81:319–333
Hollerbach MJ, Flash T (1982) Dynamic interactions between limb segments during planar arm movement. Biol Cybern 44:67–77
Hore J, Watts S, Tweed D (1999) Prediction and compensation by an internal model for back forces during finger opening in an overarm throw. J Neurophysiol 82:1187–1197
Hore J, Watts S, Leschuk M, MacDougall A (2001) Control of finger grip forces in overarm throws made by skilled throwers. J Neurophysiol 86:2687–2689
Hore J, Debicki DB, Watts S (2005a) Braking of elbow extension in fast overarm throws made by skilled and unskilled subjects. Exp Brain Res 164:365–375
Hore J, O'Brien M, Watts S (2005b) Control of joint rotations in overarm throws of different speeds made by dominant and nondominant arms. J Neurophysiol 94:3975–3986
Koshland GF, Galloway JC, Nevoret-Bell CJ (2000) Control of the wrist in three-joint arm movements to multiple directions in the horizontal plane. J Neurophysiol 83:3188–3195
Milner TE (2002) Adaptation to destabilizing dynamics by means of muscle cocontraction. Exp Brain Res 143:406–416
Milner TE, Cloutier C (1998) Damping of the wrist joint during voluntary movement. Exp Brain Res 122:309–317
Milner TE, Cloutier C, Leger AB, Franklin DW (1995) Inability to activate muscles maximally during cocontraction and the effect on joint stiffness. Exp Brain Res 107:293–305
Tweed D, Cadera W, Vilis T (1990) Computing three-dimensional eye position quaternions and eye velocity from search coil signals. Vision Res 30:97–110
Virji-Babul N, Cooke JD (1995) Influence of joint interactional effects on the coordination of planar two-joint arm movements. Exp Brain Res 103:451–459
Winter D (2005) Biomechanics and motor control of human movement. Wiley, Hoboken