Skilled Throwers Use Physics to Time Ball Release to the Nearest Millisecond

Jon Hore*, Sherry Watts

Department of Physiology and Pharmacology, University of Western Ontario, London, Ontario N6A 5C1, Canada

*To whom correspondence should be addressed. Email: jon.hore@schulich.uwo.ca
ABSTRACT

Skilled throwers achieve accuracy in overarm throwing by releasing the ball on the handpath with a timing precision as low as one millisecond. It is generally believed that this remarkable ability results from a precisely timed command from the brain that opens the fingers. Alternatively, precise timing of ball release could result from a backforce from the ball that pushes the fingers open. The objective was to test these hypotheses in skilled throwers. Angular positions of the hand and phalanges of the middle finger were recorded with the search-coil technique. In support of the backforce hypothesis, we found that when subjects made a throwing motion without a ball in the hand (i.e., without a backforce) they could not open the fingers rapidly, and they had lost the ability to time finger opening in the 1-2 millisecond range. In addition, relationships were found between the magnitude and timing of hand angular acceleration and finger (joint) extension acceleration. The results indicate that although a central command produced initial hand opening, precise timing of ball release came from a mechanism involving Newtonian mechanics, i.e., hand acceleration produced a backforce from the ball on the fingers that pushed the fingers open. In this mechanism, given the appropriate finger force/stiffness, correction for errors in hand acceleration occurs automatically because hand motion causes finger motion. We propose that skilled throwers achieve ball accuracy by computing finger force/stiffness based on state estimation of hand acceleration, and that ball inaccuracy occurs when this computation is imprecise.
INTRODUCTION

Intuitively, finger opening in overarm throwing motions, like ball throwing and dart throwing, appears to be controlled by a command from the brain. In keeping with this it might be expected that throwing inaccuracy would be caused by lack of precision in the timing of the central command to the fingers. Such evidence has been found in overarm ball throwing where modeling and experimental studies have shown that ball high/low inaccuracy could be caused by variability in the timing of finger opening on the handpath (Calvin 1983a, b; Chowdhary and Challis 1999; Hore et al. 1996). However, in dart throwing, inaccuracy has been associated with errors in hand trajectory speed (Smeets et al. 2002).

For overarm ball throwing, two pieces of evidence have recently caused us to question this view of a central timing command for finger opening (timing command hypothesis), at least for the case of skilled throwers. First, studies on throws made fast and accurately revealed that timing windows for ball release were surprisingly low, e.g., 5 ms for skilled subjects throwing from a standing position (Jegede et al. 2005), and 2-3 ms for two competitive baseball players (Hore et al. 2002). Although timing of finger opening and ball release have been measured with respect to different kinematic parameters (e.g., Jegede et al. 2005) most previous studies, and the present study, measured them to the moment on the handpath when the hand was vertical in space. Extrapolating previous results to baseball revealed that to consistently hit the strike zone required a timing precision of 1-2 ms (Hore et al. 2002). It would be surprising if a command from the brain to the finger muscles could time finger opening from throw to throw with a precision of 1-2 ms. Second, in experiments on recreational players, some of whom had been competitive baseball players, we noticed that there appeared to be two phases of opening at the
proximal interphalangeal (PIP) joint. The first phase, which occurred early in the forward throw, consisted of a variable pattern of extension or flexion at the PIP joint from subject to subject. In contrast, the second phase of finger opening which occurred as the ball rolled along the finger, always involved a rapid extension at the PIP joint. Given that backforces occur on the fingers during a throw (Hore et al. 1999b, 2001) the possibility arose that precise timing of finger opening and ball release resulted from Newton’s third law of motion. That is, as the hand pushed on the ball to accelerate it forward, the ball pushed back on the hand, and this backforce pushed the fingers open (backforce hypothesis).

The objective was to test in skilled subjects whether finger opening occurs by means of a central timing command, or from the backforce from the ball. In experiments on relatively skilled recreational subjects we tested the central timing command hypothesis by determining the relation between ball high/low accuracy on the target and the timing of opening at the PIP joint with respect to the handpath (this was not possible in highly skilled subjects because they make few throwing errors). Having found that ball accuracy was related to the second rapid phase of PIP joint opening, we wondered whether this second phase could have been produced by the backforce from the ball. This was tested in university-level baseball players where forces on the fingers were larger. The results show that two mechanisms of finger opening are involved. First, a central signal produces initial hand opening. However, this does not time ball release from the hand. Second, a backforce from the ball produces the finger opening which can time ball release to the nearest millisecond.
METHODS

General procedures

The experiments, which were approved by the local ethics review board, were performed on a total of 30 male adults aged 20-24 who gave their informed consent. All threw with their dominant arm. We investigated throwing in two situations. In the first experiment, 20 recreational baseball players (right-handed strong throwers) made 30 throws with a baseball from a seated position with the trunk fixed by straps over the shoulder. This enabled us to compare results with previous experiments from our laboratory which used this constrained throwing position. In the second experiment, 10 highly skilled baseball players from the University of Western Ontario baseball team (7 were pitchers, one was left-handed) threw with baseballs from a standing position in which the left foot was ~45 cm in front of the right foot, and both feet were kept relatively stationary, i.e., there was no baseball wind-up. In both experiments, subjects threw with a natural arm motion that involved forward horizontal motion of the upper arm. After practice throws for acclimatization they made 30 throws with a baseball (150gm) at a central target square (6 x 6 cm) at about eye height that was 3.1 m from the sternum in the sitting throws and about the same distance away at ball release in the standing throws. The central (aimed) target was on a grid of numbered squares (each 6 x 6 cm), 9 squares wide x 27 high. Each throw was scored for accuracy by the subject calling out the number of the square that was hit. In the data analysis, on-target throws were those that struck the aimed target row (level) and one 6 cm row above and one below this level; high throws were any row above the 3 on-target rows; low throws were any row below the on-target rows. Subjects were instructed to throw fast and accurately. Ball speed was measured with a radar gun (Stalker Professional Sports Radar –
sampling rate 100/s). For the recreational throwers, ball release was measured by two pressure-
sensitive microswitches (triggers) that were attached to the front of the distal and proximal
phalanges of the middle finger. Subjects were instructed to grip the ball so that they applied
pressure to the proximal switch. However, the university players threw without the proximal
microswitch in order to eliminate any effect of this switch on ball release from the hand. Both
recreational and university players were instructed to release the ball from the middle finger so
that the ball rolled over the distal microswitch. The accuracy of the distal microswitch was
verified by comparing it with the time of the start of rapid finger flexion after finger extension,
which is a moment that is known to correlate with departure of the ball from the fingertip (e.g.,
Hore et al. 1999b).

The university team players made three sets of throws. In the first set, they made 30
throws with a baseball from a standing position (as previously described). In the second set they
were instructed to make the same throwing motion from the standing position, with a baseball
and without a baseball in the hand. Subjects made 60 throws alternating between a throw with a
baseball, and a throw without a baseball, both at the same aimed throwing speed. For the throws
without a baseball, subjects were instructed to open the fingers as in the normal throws. In the
third set of throws the university players made 30 fast throws with a light (3g) hollowed-out
styrofoam ball, then 30 throws with a heavy baseball (340g), and finished with 30 throws with a
baseball (150g).

Recording angular positions of arm segments

Angular positions of finger and arm segments were measured using the search-coil
technique as described previously (e.g., Hore et al. 1992, 1996). Although the search-coil
technique records angular motions of arm segments robustly and with great precision, it does not
record translational motion. Search coils were securely taped to the back of the three phalanges
of the middle finger, the back of the hand, the back of the forearm proximal to the wrist, the
lateral aspect of the upper arm, and the sternum. Subjects sat or stood in three orthogonal
alternating magnetic fields of frequency 62.5, 100 and 125 kHz generated by 3 x 3 x 4-m
Helmholtz coils. Coil voltages, sampled at 1,000 Hz, were used to calculate the simultaneous
angular positions of each segment in three-dimensional space by means of algorithms described
in Tweed et al. (1990). Hand and finger kinematics were low-pass filtered at 170 Hz with a
second-order Butterworth filter using Matlab (The Mathworks). A 170 Hz filter was used to
minimize attenuation of the signals associated with the rapid motions of the finger joints. For
illustrative purposes, records in Fig. 1B (single trials) and Fig. 2 (averages) show unfiltered data.
At the start of each experiment a calibration of the search-coils was performed in which the
upper arm was horizontal and lateral, and the forearm, hand and fingers were vertical in a line
with the palm forward. Hand position in space, and angular positions of each joint were defined
as being 0° at this position, i.e., finger joints were 0° when the hand and fingers were in a straight
line.

Coordinate systems

Two coordinate systems were used to describe arm motion measured with the search-coil
technique. First, for the hand in space, we used a space-fixed coordinate system in which
motions were described as components of rotations around axes aligned with the magnetic fields.
In this system, we measured the vertical component of hand angular position in space which was
the component of rotation that occurred around the medial-lateral horizontal axis. Second, finger
segment motions were also described in terms of joint rotations by computing angular positions of finger segments with respect to the adjacent proximal segment. In this case, the axes were imbedded in the proximal segment and rotated with it. It must be emphasized that joint motions do not represent a component of motion around a space-fixed axis. Rather, joint motions were computed as normal joint rotations. Overall finger extension, was motion of the distal phalange with respect to the hand irrespective of hand orientation. Figure 1A shows the three finger joints and their abbreviations (DIP, PIP, MCP) at the moment in the throw when the ball started to roll with respect to the fingers.

Timing Windows

As previously (e.g., Hore et al. 2002) the timing of ball release and finger opening were measured with respect to the moment on the handpath when the hand was vertical in space. This point was chosen because it occurs within a few milliseconds of ball departure from the fingertip which was signaled by the distal microswitch. For both ball release and finger opening, a mean time and SD was obtained for each subject. The timing variability was expressed statistically as a timing window for 95% of the throws (SD of the mean time x 3.92). When measuring the minimum timing window for finger opening in the baseball throws made by the university players we used a high threshold value of 50% peak finger velocity. This was because the results showed that the kinematic parameter associated with ball accuracy was the late second phase of PIP joint opening. However, because subjects showed low finger peak velocities in the no-ball throws (throws without a ball), this threshold value was sometimes higher than the maximal no-ball finger velocity. Consequently, for measuring the timing of finger opening for the no-ball throws and the balls of different weights we chose a threshold separately for each subject that
was between 20% - 30% of the magnitude of the mean peak finger velocity for the baseball throws, and used this threshold value for all ball conditions.
RESULTS

_Two phases of finger opening_

The starting point for this study was the observation in seated throws made by recreational subjects that ball release in overarm throwing was associated with two phases of finger opening (mean throwing speed across subjects was 53.2 km/h, SD 4.3). These phases are shown for a single throw from one subject in Fig. 1B. In the first phase (phase 1), the fingers gripped the ball and pushed against the backforce from the ball during the backswing and initial part of the forward throw. This was associated in this subject with both metacarpophalangeal (MCP) joint flexion and proximal interphalangeal (PIP) joint extension. This finger joint motion caused the knuckle of the PIP joint to move forward (Fig. 1A, up-right arrow) thereby pushing on the ball and producing initial hand opening, i.e., in some recreational subjects the fingertip lifted off the ball (Fig. 1A, down-left arrow). Most subjects showed MCP joint flexion to various degrees, but sometimes it occurred together with distal interphalangeal (DIP) joint extension and PIP joint flexion, which is an alternative way to uncouple the ball. The second phase of finger opening (Fig. 1B phase 2) started at the onset of rolling of the ball with respect to the fingers as measured by the proximal microswitch. This second phase was associated with a rapid extension at the PIP joint, and a slightly later extension at the DIP joint as the ball rolled over it. In summary, there are two phases of finger opening: in the first phase the ball is uncoupled from the hand, and in the second phase the ball rolls along the finger.
**Ball accuracy is associated with the second rapid phase of PIP joint opening**

Inaccuracy in throwing occurs because of errors in the relation between finger opening and handpath. A prediction of the timing command hypothesis is that onset of finger opening for high throws (which hit above the target) and low throws (which hit below the target) will occur at different places on the forward handpath with high throws occurring early on the handpath and low throws late. We tested this by measuring the point on the handpath when finger opening occurred. Figure 1C shows the PIP joint velocity-hand angular position relation for 4 high and 4 low throws from the representative recreational subject (shown in Fig 1B). Contrary to the prediction of the timing command hypothesis, there is no difference in hand position for the high and low throws at onset of PIP joint extension (low threshold) when PIP joint velocity crossed 0.

To determine across subjects whether there was a difference in place on the handpath for the high and low throws at onset of PIP joint extension, we measured hand angular position at the zero PIP joint velocity threshold (Fig. 1C, dashed vertical line). We then divided throws into 3 groups: high throws, on target throws, and low throws based on the level struck by the ball on the target. Figure 1D, low (zero) threshold, shows that across subjects there was no difference between the 3 groups of throws at the low threshold level (repeated measures ANOVA, $F_{(2, 19)} = 2.321, P = 0.112$). This result does not support the prediction of the timing hypothesis that there will be different finger opening points on the handpath for the high and low throws. However, when hand angular position was measured at a high level threshold that was 50% of mean peak PIP joint velocity (Fig. 1C), i.e., during the second ball rolling phase of finger opening, there was a difference between the 3 groups of throws (Fig. 1D, high threshold). ANOVA values were $F_{(2, 19)} = 31.26, P < 0.0001$; Tukey’s multiple comparison test showed that all groups were different from each other (low-on target $P < 0.001$; low-high $P < 0.001$; on target-high $P < 0.01$). In
summary, ball high/low inaccuracy was associated with differences in the finger opening–hand path relation for the second (ball rolling) phase of finger opening phase, but not for the first initial hand opening phase. That is, the second phase of finger opening timed the ball release that determined accuracy.

*Testing the backforce hypothesis*

Could the second rapid (ball rolling) phase of PIP joint extension result from a backforce from the ball? If so it would be expected to be more obvious in fast standing throws made by highly skilled throwers than in seated throws made by recreational throwers because of the greater forces on the hand in the highly skilled throwers. Considering the first 30 throws with a baseball made by the university players, across subjects the mean ball speed was 93.6 km/h (SD 6.0). The university players had high ball accuracy on the target (see later) and low variability in the timing of ball release and finger opening. The exact value for the timing precision for ball release and finger opening depends on the criterion used to define them. For the university team players the mean timing window for ball release (see Methods) from the first set of 30 baseball throws was 3.1 ms SD 0.5, and for finger opening (high threshold) 3.3 ms SD 0.9. Yet over a short series of throws each subject threw more precisely than this. For example, all subjects showed a series of successive throws where the timing differed by only 1 ms. Across subjects the mean value for the largest number of successive throws which differed by 1 ms was 12 successive throws for ball release, and 11 successive throws for finger opening. That is, these very skilled subjects timed finger opening and ball release from throw to throw with a variability of one millisecond.
Three predictions of the backforce hypothesis are 1) that in fast throws with a ball that produces a large backforce, e.g., a baseball, a rapid second phase of PIP joint extension will occur, 2) that in the absence of a backforce from the ball, the rapid second phase of PIP joint extension will not occur, and 3) without a rapid second phase of PIP joint extension, precise timing of ball release will be lost. To test these predictions, the university team players were instructed to make the same throwing motion, and the same finger opening, with and without a baseball in the hand. Across subjects the angular velocities of the hand in space, which is one measure of throwing speed, were within 10% of each other for the two sets of throws: baseball 4483°/s SD 112, no-ball 4071°/s SD 159 [t test, t(18) = 2.11; P = 0.049]. Figure 2A shows averages at the DIP, PIP and MCP joints for 30 throws made with a baseball, and without a ball (no-ball) by pitcher Pa; Fig. 2B, C, D shows extension at the PIP joint for baseball and no-ball throws made by pitchers (Mn, Ch, Ck). Throws were aligned on the moment when the hand was vertical in space (time 0; solid vertical line) which in each case for throws with the baseball was within 3 ms of the time of ball release. In keeping with the first prediction, throws with a baseball showed a second phase of rapid extension at the PIP joint (Fig. 2A middle panel, B, C, D). In agreement with the second prediction, in the no-ball throws there was no rapid second increase in PIP joint velocity. Instead, PIP joint opening occurred but it was relatively slow. At the DIP joint (Fig. 2A top panel) the later rapid extension observed in the baseball throws was absent in the no-ball throws.

The university players all showed a rapid flexion (mean 13.1° SD 3.9) at the MCP joint after ball release when throwing with a baseball. This can be seen for subject Pa in the baseball throws in Fig. 2A, bottom panel (the moment of ball release occurs 2 ms after the moment of hand vertical). In the present experiments 9 of 10 subjects did not show a marked flexion at the
PIP joint at ball release for the baseball throws (mean across all subjects 1.8° SD 3.2), e.g., Fig. 2A middle panel, B, C, D.

In the analysis of results across university players we measured overall finger opening, i.e., the sum of all finger joint rotations, which is given by rotation of the distal phalanx (fingertip) with respect to the hand. We did this for two reasons: 1) because one subject timed ball release primarily by motion at the DIP joint rather than the PIP joint, and 2) because across subjects timing windows were smaller and relationships were stronger with the overall finger movements. Inspection of 10 trials of overall finger joint velocity for the baseball throws made by pitcher Pa (Fig. 3A) and no-ball throws (Fig. 3B), shows the same slower rate of rise of finger extension velocity for the no-ball throws (decreased finger angular acceleration) as in Fig. 2. Similar results were found across subjects. In agreement with the second prediction, Fig. 3C shows that the peak magnitude of finger extension acceleration for the no-ball throws was much smaller than that for the baseball throws \( t(18) = 5.08, P < 0.0001 \). In agreement with the third prediction, for the no-ball throws (Fig. 3B) there was loss of timing precision, i.e., there was increased variability in the time that finger velocity crossed a threshold that was 20% - 30% of the peak velocity in the baseball throws (increased timing window – see Methods). For pitcher Pa the finger opening timing window for the 30 baseball throws at the chosen threshold was 2.6 ms (Fig. 3A), and for the 30 no-ball throws 12.0 ms (Fig. 3B). Figure 3D shows that across subjects the precision of finger timing with the baseball (mean timing window 4.0 ms SD 2.2) was lost in the no-ball condition (mean 27.1 ms SD 17.6) \( t(18) = 4.10, P = 0.0003 \). In summary, the data supported the three predictions of the backforce hypothesis.
Throws with a very light ball

A possible criticism of the previous experiment is that the throws without a ball were not a natural throwing motion. To address this criticism we asked the university players to make 30 fast throws with the lightest hard-surfaced ball that we could find. This was a baseball-sized hollowed-out styrofoam ball with a weight of 3g. This minimized, but did not eliminate a backforce from the ball. Subjects also made 30 fast throws with a heavy baseball (340g) and a baseball (150g). The prediction from the backforce hypothesis was that throws with the light (3g) ball will have a decrease in finger opening velocity and acceleration (because this is an unfamiliar throwing situation with an abnormally low backforce). Surprisingly, 4 subjects maintained similar finger opening kinematics for the light ball and one other ball, e.g., subject Ha (Fig. 4A). Note that finger extension peak velocity was similar for the light ball (2,673 °/s) and heavy ball (2,865 °/s), and that variability in the time of finger opening at threshold was not greater for the light ball (light 3.0 ms, baseball 2.6 ms, heavy 5.3 ms). Presumably, as previously shown for balls of different weights (Hore et al. 1999b, 2001), this subject was able to adjust his finger opening appropriately for the backforce from the 3g ball. However, as predicted, 6 subjects showed decreased finger extension velocities and increased finger timing variability for the light 3g ball. For example, subject Pa (Fig. 4B) showed a decreased peak velocity for the light ball (1,918 °/s) compared to the baseball (3,557 °/s) and heavy ball (3,276 °/s), and an increased finger timing window for the light ball (7.6 ms) compared to the baseball (2.6 ms) and heavy ball (3.5 ms). Across subjects, comparison of throws with the 3 balls revealed that there was a difference for finger extension peak acceleration (Fig. 4C) (repeated measures ANOVA \( F_{(2, 9)} = 14.36, P = 0.0002 \)). Tukey’s test showed that the throws with the light ball were different from throws with the baseball \( (P < 0.001) \) and the heavy ball \( (P < 0.01) \). There was
also a difference for the finger extension timing windows (Fig. 4D) (repeated measures ANOVA $F_{(2, 9)} = 5.454, P = 0.014$). Tukey’s test showed that finger timing windows with the light ball (mean 7.0 ms SD 2.6) were different from windows with the baseball (mean 4.0 SD 2.2) ($P < 0.05$). Throws with the light ball went very low, often hitting the floor a few metres in front of the thrower. The likely reason was that this occurred because the wrist joint, and thereby the hand in space, underwent a larger amplitude of flexion before ball release. In summary, as expected, across subjects throws with the light ball had smaller finger extension peak accelerations and increased finger extension timing windows compared to throws with the baseball.

Relationships between kinematic parameters

The backforce hypothesis states that in baseball throws hand acceleration produces finger extension acceleration. A fourth prediction of the backforce hypothesis is that relationships will occur between these two kinematic parameters. In agreement, a relationship was found in university players between the magnitude of hand angular acceleration (in the vertical plane) and the magnitude of finger extension acceleration. Figure 5A, B shows records from 10 throws made by pitcher Pa throwing a baseball. In both cases throws are aligned on the moment when the hand in the vertical plane started to move forward (hand onset). Note that hand acceleration (Fig. 5B) starts before hand onset because hand deceleration during the backswing, when the hand is rotating backwards, is in the same direction as hand acceleration in the forward direction. For both finger extension acceleration and hand angular acceleration, variability occurred in the peak magnitude. Figure 5C shows that across subjects, when results were normalized by aligning the relations for each subject on mean magnitude of hand acceleration and mean
magnitude of finger acceleration (these mean values were defined as 0), a statistically significant
relation was found (generalized least squares estimation using elementwise regression, $F_{(1,9)} =
48.69, P < 0.001$).

A second relation was found between the time (from hand onset) when hand angular
acceleration crossed a high threshold of 50% peak mean value (Fig. 5B) and the time when
finger extension acceleration crossed a high threshold of 30% of its peak mean value (Fig. 5A).
Because the mean finger and mean hand acceleration times were different in different subjects,
we normalized both values across subjects by taking their mean value and calling it 0. Figure 5D
shows the scatter plot for all 300 throws for the time of finger acceleration at the high threshold,
and the time of hand acceleration at its high threshold. A mixed model analysis showed that the
relation was statistically significant ($F_{(1,9)} = 68.77, P < 0.001$). In summary, these findings
support the backforce hypothesis.

According to the backforce hypothesis, differences in high and low throws arise from a
failure to match finger flexor force, or finger stiffness, to the hand acceleration. For example,
low throws will have too much finger flexor force, or too much stiffness, for a given hand
acceleration. Consequently, for low throws, onset of PIP joint extension will be delayed until
hand acceleration reaches a higher value. For the university players the two populations of high
and low throws are shown in Fig. 5E. However, there were insufficient high and low throws to
enable a mixed model analysis to be performed. For the less accurate recreational players (Fig.
5F) the mixed model analysis revealed that the high and low populations were significantly
different ($F_{(1,17)} = 91.59, P < 0.0001$). The difference between the two lines at the mean time of
hand acceleration (time 0) was 2.8 ms for the recreational players (Fig. 5F) and 1.4 ms for the
university players (Fig. 5E). That is, on average high and low throws were associated with a
finger timing difference (error) of about 3 ms in recreational players and 1-2 ms in university
players.
How, in skilled overarm throwing, does the CNS time finger opening and ball release to the nearest millisecond? We previously found evidence that ball accuracy in throwing resulted from the timing of ball release on the handpath which, in turn, was determined by the timing of finger opening. Given that finger opening was not driven by proprioceptive feedback (Hore et al. 1999a), we assumed that PIP joint extension was caused by a central command to the finger muscles (Hore et al. 1996; Hore and Watts 2005; Timmann et al. 1999). The present results show that this view needs to be modified. Specifically, the new evidence suggests that there are two phases of finger opening. The first, in which finger flexor torque is progressively increased throughout the throw in anticipation of the progressively increasing backforce from the ball, produces initial hand opening. This first phase, that has been observed as an early lift-off of the distal phalanx from the ball, and as an early decrease in force on the distal phalanx (Hore et al. 2001), was previously suggested to be evidence for a central timing command (Hore et al. 2002). However, in recreational subjects this first phase does not determine ball accuracy, i.e., it does not time ball release from the hand. This first phase is presumably generated by the CNS because finger pushing (MCP joint flexor muscle torque) must occur by active muscle contraction. The new evidence supports the idea that the second (ball rolling) phase of finger opening, which determines ball accuracy, is produced when backforce from the ball overcomes PIP joint flexor force/stiffness. That is, hand acceleration times the finger opening that causes ball release.
Mechanisms for timing ball release in the 1-2 ms range

The evidence indicates that a number of different factors contributed to the millisecond timing precision in the university players. The first factor is that, compared to the recreational players, there was low variability from throw to throw in the joint motions and accompanying handpath in space (unpublished results) as previously reported for high level pitchers (Fleisig et al. 2009). A second factor is that errors in the time domain are decreased in faster throws, and these subjects threw extremely fast. For example, if the same angular position error occurred when matching onset of finger opening to handpath in throws of different speeds, then in the time domain, the faster the throw the smaller will be the timing error. The third, and most important, factor is the mechanism in which the backforce from the ball pushes the fingers open (backforce hypothesis). Previous work has demonstrated, that in throws with a baseball, large backforces occur on the finger during the ball rolling phase of finger opening (Hore et al. 1999b, 2001). The present results suggest that these backforces affect the kinematics of finger opening (Figs. 2, 3C, 4C, 5C). One feature of this backforce mechanism is that, given the appropriate finger force/stiffness based on state estimation (see later), correction for errors in the timing of hand acceleration occurs automatically. For example, if wrist flexion (which contributes to hand angular acceleration in space) is delayed, then finger opening, which is driven by hand acceleration, will also be delayed. This present result appears to be an exquisite example of the long-standing and generally accepted idea (Bernstein 1967; Lashley 1951) that the CNS takes advantage of the physical properties of the arm in achieving its motor objectives, in this case precision in the timing of ball release.
Some subjects may have also used passive forces, rather than finger muscle contraction, to open the fingers in the throws without a ball. The results show that in the no-ball throws, there was loss of timing precision in finger opening (mean values changed from 4 ms to 27 ms, Fig. 3D). Figure 3D also shows for the no-ball throws, that across subjects there was a large variability (large SD) in timing precision, e.g., three subjects had mean windows for finger opening of 46-55 ms, whereas another three subjects had mean windows of 11-13 ms. We speculate that subjects with the long timing windows opened their fingers by a central neural command to the finger muscles, whereas subjects with the short windows (including subject Pa, Fig 2A) used interaction torques from hand acceleration to extend the fingers.

One possibility is that the increased variability in throws with the 3g ball and in the no-ball throws is due to lack of familiarity (lack of practice). Extensive training with the 3g ball would not give definitive information because it is likely that subjects would learn to use the small backforce from this ball. However, training in the no-ball situation might be informative: the backforce hypothesis predicts that even after training, subjects will be unable to consistently open the fingers rapidly and with a timing precision of 1-2 milliseconds.

Finger force/stiffness

According to the backforce hypothesis for finger opening, ball high/low errors are due to a failure to precisely adjust finger force/stiffness to hand acceleration. For example, for low throws, the delay in finger opening for a given hand acceleration (Fig. 5F) would be due to finger flexor force/stiffness that is too large for that throw. It is likely that skilled throwers used a combination of finger flexor muscle torque (force) and finger stiffness (produced by coactivation of flexor and extensor muscles) to oppose backforces and control finger opening (cf. Milner and
We have previously proposed that the rapid flexion which occurs at the MCP joint at ball release (e.g., Fig. 2A bottom panel) results, at least in part, from a finger flexor torque which suddenly becomes unopposed (Timmann et al. 2001). The finding that at ball release there was rapid flexion at the MCP joint but not at the PIP joint (e.g., Fig. 2A) suggests that flexor torque predominated at the MCP joint and stiffness predominated at the PIP joint. One possibility is that ball inaccuracy in throwing could be caused by failure to precisely match stiffness at the PIP joint to hand acceleration.

We agree with the view (Loeb et al. 2002; Nichols 2002) that a full understanding of a complex movement (like skilled throwing) can only come when the nature of the underlying biomechanics is revealed. However, there are major experimental challenges associated with investigating the proposed finger force/stiffness mechanism. It will be difficult to distinguish between effects at individual finger joints because their motion is influenced by both extrinsic (forearm) finger muscles and intrinsic (hand) finger muscles in a complex way. For example, there is no one muscle whose sole function is to produce extension at the PIP joint. This is because the extrinsic finger extensor muscle (extensor digitorum communis) acts simultaneously at all 3 finger joints, as in opening the hand from a clenched position. Similarly, the extrinsic finger flexors either act simultaneously at all 3 finger joints (flexor digitorm profundus), or simultaneously at the PIP joint and MCP joint (flexor digitorum superficialis). Although the intrinsic finger muscles extend the interphalangeal joints, they also simultaneously flex the MCP joint. One last point is that because of their small size it will be difficult to record from the intrinsic finger muscles in fast overarm throws.
Central mechanisms

The present and previous results have led to two principles by which the CNS controls wrist and finger joint rotations in skilled fast overarm throws. The first principle is that there is a fixed (constant) relation between finger opening (joint position) and hand angular path (position) in space in the vertical plane for throws of different speeds (Hore and Watts 2005). That is, for these two parameters a fast throw is the same as a slow throw sped-up. This does not apply for the relation between finger opening and proximal joint rotations, because proximal joints have different patterns of joint rotations in fast and slow throws which are associated with the variable exploitation of interaction torques at distal joints (Hore et al. 2005). This first principle occurs because wrist joint and finger joint rotations have constant amplitudes under a wide variety of throwing conditions where backforces at the wrist and finger are different (Debicki et al. 2004; Hore et al. 1999b, 2001). In the present experiments (Fig. 4C) finger opening peak acceleration was also constant in magnitude when going from the baseball to the heavy ball. It was only when an extremely light (3 g) ball was used, that was outside the weight range of balls normally experienced by these subjects, that there was a decrease in finger extension peak acceleration.

The second principle is that increased wrist and finger joint velocities in very fast throws, which are necessary to keep the wrist and finger opening amplitudes constant, occur by exploitation of passive forces. For the wrist, Hirashima et al. (2007) showed that in fast standing throws made by skilled throwers, an assistive interaction torque occurred in the flexion direction. For the fingers, the present results suggest that in fast throws, the torque from the ball rolling along the fingers was utilized to rapidly open the fingers, thereby maintaining the constant amplitude of finger opening. Given that fast and accurate throws are made with the dominant
arm, the proposed hand-finger force scheme fits with the proposal that the mechanisms that control the dominant arm are specialised for exploiting limb dynamics in feedforward situations (Sainburg and Kalakanis 2000; Sainburg 2002; Bagesteiro and Sainburg 2003; Heuer 2007).

We have previously described how internal models could be employed in a feedforward situation to generate an overarm throw (Hore et al. 1999b). Internal models are sensorimotor maps that transform a desired action (represented as limb kinematics) into motor commands (represented as joint torques). One structure that may be involved in the formation of internal models and their expression is the motor cortex. To enable the motor cortex to function as an internal model it would need to know the current kinematic state of the limb. In keeping with this, early studies showed that motor cortex neurons responded to rapid limb perturbations with neural discharge that encoded position, velocity, acceleration and jerk (Bedingham and Tatton 1985; Flament and Hore 1988). Given the proposed importance of hand acceleration in throwing, it is of interest to know whether internal models which control limb dynamics learn by means of a representation that is optimal for control of inertial objects, i.e., by means of basis elements that are exclusively sensitive to acceleration. In a study on reaching in acceleration-dependent fields Hwang et al. (2006) found that these elements were not optimized for control of inertial objects, i.e., they were sensitive to both acceleration and velocity, and that velocity dominated (like proprioceptive feedback).

One interpretation of these principles is that the planning of finger and arm movements occurs by state-space coordination in which information about the state of the arm is used in the control of finger opening (Haggard and Wing 1998; Thach et al. 1992). A recent extension of this idea is optimal feedback control theory (Diedrichsen et al. 2010) which predicts that
finger/arm coordination is based on higher-level state estimates of task-relevant variables. We previously proposed (Hore and Watts 2005) that finger opening results from a central spatial controller that matches angular positions of finger opening to a positional representation of the handpath. The present results suggest that at the level where force is implemented the task-relevant variables are hand acceleration in space, the finger flexor muscle torque that opposes the initial backforce from the ball, and the finger stiffness that sets the force threshold for timing finger opening.

One structure that is implicated in state-dependent motor control is the cerebellum (Bo et al. 2008; Miall et al. 1993; Paulin 1997). This has been studied in a number of tasks that involve arm-hand coordination. In a task that involved an arm movement and thumb press, Diedrichsen et al. (2007) found that there was cerebellar activation when the brain used an estimate of the state of the arm for coordinating the thumb press (state estimation), but not when it used an internal estimate of time. Disorder in cerebellar function may disrupt state estimation. In a further study Miall et al. (2007) found that transmagnetic stimulation of the cerebellum produced errors in a reach-to-target movement which were interpreted as being due to disruption in the state estimate of hand position. Similarly, patients with lesions of the cerebellum show disorder in matching grip force, between the thumb and index finger, to arm lift force (Müller and Dichgans 1994; Nowak et al. 2007). And in throwing, cerebellar patients (like unskilled subjects) showed large variability from throw to throw in the amplitude of finger opening that was due to an inability to control finger force precisely and consistently (Hore et al. 2001). Such results fit with the idea of loss of state estimation with lesions of the cerebellum. In short, we propose that ball accuracy in throwing requires precise computing of finger force/stiffness by the
cerebellum based on state estimation of hand acceleration, and that ball inaccuracy occurs when
this computation is imprecise.

Conclusion

In overarm throws made by highly skilled subjects no evidence was found to support the
idea that timing to the nearest millisecond was achieved by a timing command to the finger
muscles from the CNS. Rather, the results suggest that timing of finger opening occurred by
feedforward computation of finger force/stiffness, and Newtonian mechanics involving the ball
and finger.
ACKNOWLEDGEMENTS

We thank Leopold van Cleeff for technical assistance. Larry Stitt from the Department of Epidemiology and Biostatistics, UWO performed the mixed model analyses.

GRANTS

The work was funded by a Canadian Institute of Health Research Grant to J Hore.
REFERENCES


Fig. 1 (A) Finger joints, ball and microswitches (rectangles) for timing ball release shown at onset of ball rolling. (B) Two phases of finger opening. A second rapid phase of PIP joint extension occurs at onset of ball rolling signaled by proximal microswitch. Finger joint rotations for a single throw made by recreational subject Ry. (C) Hand angular position in space –PIP joint velocity records for 4 throws that hit high on the target and 4 throws that hit low from subject Ry. Low threshold: zero PIP joint velocity, high threshold: 50% of mean peak PIP joint velocity. (D) Hand angular positions (means and SDs) across 20 recreational seated subjects for low, on-target and high throws at the low threshold, and at the high level threshold, as in C.

Fig. 2 Average finger joint rotations for 30 throws with a baseball, and for 30 throws without a ball in the hand (no-ball) made by 4 university pitchers (Pa, Mn, Ch, Ck) from a standing position. Throws aligned on moment when hand was vertical in space (time 0; solid vertical line). (A) Rotations at DIP, PIP and MCP joints for subject Pa. (B, C, D) Rotations at PIP joint for subjects Mn, Ch, Ck. Dashed lines indicate onset of rapid increase in PIP joint velocity, i.e., onset of second phase of PIP joint opening.

Fig. 3 (A, B) 10 single trials from university pitcher Pa of overall finger extension velocity (distal phalanx with respect to hand) for throws made with and without a baseball. Traces aligned at moment when hand was vertical. Threshold was when velocity in baseball throws reached 22% mean peak finger velocity. (C) The mean and SD across 10 university players, who each made 30 throws, of the magnitude of peak finger extension acceleration during finger
opening with and without, a baseball (no ball). (D) The mean timing window for finger opening across 10 university players with and without a baseball (no ball).

Fig. 4  Kinematics of finger opening with balls of 3 different weights. (A, B) Finger extension velocity (distal phalanx with respect to hand) for 30 throws aligned on moment in throw near ball release when hand was vertical in space (0 time). Threshold was when velocity reached a value of 20% - 30% of mean peak velocity for baseball throws (see Methods). A, Subject Ha; B, Subject Pa. (C) Mean across subjects and SD of finger extension peak acceleration. (D) Mean across subjects and SD of finger extension timing window (see Methods).

Fig. 5. (A, B) 10 single trials of finger extension acceleration and hand angular acceleration in space in the vertical plane in throws made by university pitcher Pa. Throws aligned at moment when hand first moved forward in the vertical plane (hand onset). Thresholds: finger – 30% of mean peak extension acceleration; hand – 50% of mean peak angular acceleration in space. (C) Relation between magnitude of peak finger extension acceleration and peak hand angular acceleration in space for all 300 throws made by 10 university players. (D) Relation between time when finger extension acceleration and hand acceleration in space crossed a high threshold (as in A, B) for throws aligned on hand onset. (E) Relations as in D for the few high and low throws made by university players. (F) Relations as in D for high and low throws made by recreational throwers.
Hand Position at PIP Joint Vel
Angular Joint Position

Low threshold
High threshold

High throws
Low throws

Ext
Flex
Backswing
Forward

Hand Angular Position in Space

PIP Joint Velocity

C

D

Low threshold
High threshold

Low On High Low On High

Onset Ball Rolling
Ball Release
A Subject Pa Baseball

Finger Exten Velocity

Threshold

Ext

Flex

-40ms -20 0

Hand vertical

B Subject Pa No-ball

Finger Exten Velocity

Threshold

Ext

Flex

-40ms -20 0

C All Subjects

Finger Exten Peak Accel

Baseball No-ball

6.0x10^6 g/s^2

4.0x10^5

2.0x10^5

D All Subjects

Finger Exten Timing Window

Baseball No-ball

40

30

20

10

***