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RESEARCH ARTICLE

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Kinematics of wrist joint flexion in overarm throws made by skilled subjects

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Abstract Previous studies of multijoint arm movements have shown that the CNS holds arm kinematics constant in different situations by predictively compensating for the effects of interaction torques. We determined whether this was also the case for wrist joint flexion in natural overarm throws performed by skilled subjects in 3D, a situation where large passive torques can occur at the wrist. Specifically, we investigated whether wrist flexion amplitudes are held constant in throws of different speeds. Joint rotations were recorded at 1,000 Hz with the search-coil technique. Contrary to a previous study on constrained 2D throwing, indirect evidence was found that in fast throws passive torques associated with forearm deceleration were exploited to increase wrist flexion velocity. This increase in wrist flexion velocity was associated with constant wrist flexion amplitudes at ball release (mean 27°) for throws of different speeds. Furthermore, final wrist flexion positions after ball release were similar for a particular subject irrespective of the speed of the throw. This was associated in faster throws with increased magnitudes of wrist flexor and wrist extensor EMG activity which damped passive torques associated with forearm angular deceleration. It is concluded that wrist flexion in overarm throws of different speeds is produced by central signals which precisely control net joint torque by both exploiting and damping passive torques during different parts of the throw to keep wrist joint angular position parameters constant. As such the results show that control strategies for natural 3D throwing are different from those for constrained 2D throwing.

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Introduction

Although interaction torques which occur in multijoint movements have the potential to influence motion at adjacent joints (e.g., Hollerbach and Flash 1982; Hoy and Zernicke 1986) and could therefore cause unwanted movement, a number of studies have shown that the CNS can keep arm kinematics constant in different situations by predictively compensating for the effect of these passive torques (Shadmehr and Mussa-Ivaldi 1994; Flanagan and Wing 1997; Gribble and Ostry 1999; Sainburg et al. 1999; Koshland et al. 2000). Similarly, in skilled overarm throwing, subjects kept the amplitude of finger opening relatively constant by predictively compensating for different back forces from the ball on the fingers (Hore et al. 1999, 2001). In contrast, Bernstein (1967) proposed that the high degree of coordination needed in skilled movement would involve exploitation of interaction torques. In agreement, Schneider et al. (1989) found in a fast arm movement task, that with practice subjects used muscle forces to complement the interaction torques, i.e., these passive forces were exploited for movement control. Similarly, it has been proposed that passive torques resulting from motion of the proximal thigh play a role in producing motion of the distal leg (Phillips et al. 1983; Ulrich et al. 1994; but see Putnam 1991, 1993).

Another situation where interaction torques may assist the desired motion is wrist flexion in skilled overarm throwing. Here the CNS may take advantage of a whip-like effect associated with forearm deceleration (cf. Hollerbach and Flash 1982; Smith and Zernicke 1987) to generate faster wrist flexion for faster throws without the need for increases in wrist muscle activation. Such a passive increase in wrist flexion velocity could be accompanied by an increase in wrist flexion amplitude. Alternatively, these passive increases in wrist flexion velocity could be damped by wrist muscle activation. In a recent study of a constrained throwing motion in 2D, Hirashima et al. (2003) demonstrated that at the wrist joint, muscle torque always counteracted the interaction torque. Whether this applies for natural throws in 3D is not known.

The objective was to determine in natural 3D overarm throws made by skilled subjects whether wrist flexion amplitudes are held constant in throws of different speeds. This was achieved by investigating, for the first time, the kinematics of wrist joint motion at high resolution (1,000 Hz), together with EMG activity of wrist flexors and extensors. Although it was not technically possible to compute limb dynamics for the standing throws (see "Materials and methods"), the kinematic and EMG results provide evidence that wrist angular positions were held constant using muscle activation patterns that both assisted and opposed passive torques during different phases of the movement. The results demonstrate that control strategies for natural 3D throwing are different from constrained, 2D throwing tasks. More generally, they suggest that complex, multijoint 3D movements such as throwing are achieved using neural control strategies that both exploit and damp passive torques to keep kinematic patterns constant.

Materials and methods

Subjects

A total of 12 male subjects participated. All were right-handed for overarm throwing and had played on recreational (Cr, Sr, Ls, Bl, Fr, Pc) or competitive (Db, St, Mg, Ps, Ch, Vt) baseball teams. The study was approved by the University of Western Ontario Ethics Review Board and all subjects gave informed consent.

Two series of experiments

Angular positions were recorded of arm segments with the search-coil technique as before (e.g., Hore et al. 1996, 2001). There were two limitations for these particular experiments with our existing version of this technique. First, because the technique directly records angular position, arm translations had to be calculated, and this could only be done for throws made from the sitting position where the sternum remained stationary in space. Thus subjects performed both sitting and standing throws. Second, we could not record in the same experiment angular positions of five arm segments and EMG activity from four muscles. This was because our data collection system only allowed us to record simultaneously 32 channels at 1,000 Hz, and each search coil (which consists of two orthogonal coils) required six channels. Thus two series of experiments were performed: a "kinematic" series for which angular positions from all five arm segments were recorded, and an "EMG" series for which angular positions of the four distal arm segments were recorded concurrently with EMG activity from four muscles of the wrist joint. In both cases throws were made from the sitting and standing position. The EMG experiments were performed some time after the kinematic experiments and only two of the original subjects were still available.

General procedures

In the kinematic experiments 8 subjects were instructed to make 30 accurate throws with a tennis ball at a slow, medium and fast speed from both a sitting and standing situation (total 180 throws). In the sitting experiments subjects sat on a wooden chair with the trunk fixed by straps over the shoulders; in the standing experiments, subjects stood with their left foot forward and feet stationary. In all experiments they were instructed to make the same natural overarm throwing motion using upper arm adduction, and to release the ball from the middle finger. Ball release was detected by a microswitch taped to the distal phalanx of the middle finger. Timing of ball release was verified by observation of the moment when the finger (with respect to the hand) reversed direction from extension to flexion, which is an event that coincides with the departure of the ball from the fingertip. Throws were made at a central 6-cm target on a vertical grid consisting of 6-cm numbered squares with the central target square located at eye height 3.1 m from the sternum. Each throw was scored for accuracy by the subject calling out the square that was struck.

In the EMG experiments 6 subjects (including 2 from the kinematic experiments) made 30 slow, 30 medium speed and 30 fast throws with a tennis ball, and 30 fast throws with a baseball, from both the sitting and standing positions. For the fast throws subjects were instructed to throw accurately at a speed that was fast, to fast as possible, bearing in mind that they had to make a total of 120 throws at this fast speed. Subjects also made 30 fast as possible wrist flexions from a position of maximum wrist extension to the neutral position (where hand and forearm were in a straight line) and 30 fast as possible wrist extensions from a position of maximum wrist flexion to the neutral position.

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 wrist flexors and extensors based on anatomical landmarks. EMG activity was recorded during isotonic and isometric (resisted) wrist flexions and extensions and radial-ulnar deviations 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 (1) to activate maximally the wrist flexors then wrist extensors, and (2) to make some fast practice throws with the baseball. The largest amplitude EMG activity inevitably occurred during the fast throws. The gains of the amplifiers were adjusted based on the maximum values. However, during the experiment some subjects threw faster which resulted in different maximal EMG levels. Consequently, in order to compare the EMGs across subjects it was necessary to normalize EMG activity. This was done by assuming that maximal activity of all muscles occurred at some point during the fast, standing throws made with the baseball. This maximum point was found by taking 25-ms blocks of EMG activity for each muscle, integrating and taking the mean value. This 25-ms period was staggered every 5 ms throughout the throw and the maximal mean value obtained. This value for each muscle was then taken as 100. To compare the relative muscle activation across throwing conditions the amplitude of EMG activity for each muscle was integrated over a 100-ms time window spanning movement onset. For wrist flexor muscles, the window used for integration started at 75 ms before onset of wrist flexion and ended at 25 ms after onset of wrist flexion. For wrist extensor muscles, this window went from 50 ms before to 50 ms after the onset of wrist flexion. Two different time windows were used for flexor and extensor muscles in order to include as much of the burst of EMG activity as possible across subjects.

Throwing speed

In the kinematic experiments average ball speed for the sitting throws was calculated from the flight distance and flight time (time of ball impact on the target was measured by impact detectors). For the standing throws, exact flight distance was unknown and therefore ball speed could not be calculated. However, after the completion of the kinematic experiments a radar gun was obtained (Stalker Professional Sports Radar—sampling rate 100/s) and ball speed was measured with it in the six EMG experiments. Strong correlations were found (in all cases r^2>0.94) between measured ball speed with the radar gun and (1) calculated ball speed in the sitting experiments, and (2) forearm angular velocity in space at ball release for throws made from both the sitting and standing positions. A strong relation occurs between ball speed and forearm angular velocity, in part because most ball speed comes from forearm motion (unpublished observations). Consequently, in the analysis of the kinematic experiments, forearm angular velocity in space at ball release was used as a measure of throwing speed. Across subjects values of forearm angular velocity of 1,000, 2,000, 3,000°/s correspond approximately to ball speeds of 30, 55, 80 km/h, respectively.

Recording angular positions of arm segments

Angular positions of five arm segments in the kinematic experiments, and four arm segments in the EMG experiments, were measured using the search-coil technique as described previously (e.g., Hore et al. 1996). 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, and, in the kinematic experiments, the acromion process. Subjects sat or stood in three orthogonal alternating magnetic fields of frequency 62.5, 100 and 125 kHz generated by 3×3×4-m Helmholtz coils. Coil voltages, sampled at 1,000 Hz, were used to calculate the simultaneous angular positions of each arm segment in 3D space.

Coordinate systems

Three coordinate systems were used to describe arm motion: angular motions around space-fixed axes, joint rotations and translations (e.g., see Fig. 1, which gives examples of motions for the three coordinate systems). When considering angular positions of arm segments 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 (Hore et al. 1996). Horizontal angular motion of an arm segment was the motion which occurred around a space-fixed vertical axis, vertical motion occurred around a space-fixed medial-lateral horizontal axis and torsion around a space-fixed torsional axis. In all cases in the text forearm angular velocity in space refers to the vertical component around the horizontal axis. Second, arm motions were also 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. It is important to appreciate that wrist motion (on which the quantitative analyses were performed) does not represent a component of vertical motion around a space-fixed horizontal axis. If it had been represented this way it would have varied with forearm orientation. Rather, wrist motion was computed as a joint rotation, i.e., hand motion with respect to forearm motion irrespective of forearm orientation. All joint angles were defined as being 0 when the arm was in a reference position, with the subject facing the target with the upper arm horizontal and lateral and with the forearm, hand and fingers vertical in a straight line with the palm forward. And, third, translational positions, velocities and accelerations of arm segments were computed for the sitting throws from the angular positions, and the measured lengths of arm segments with the origin at the sternal notch, which was held stationary by the shoulder straps.

Limb dynamics

Limb dynamics were not computed in either series of experiments. It was not technically possible to calculate the equations of motion of the arm for standing throws because of the absence of arm translational data for this set of throws (due to the limitation of the search-coil technique). Therefore we could not explain the differences observed in kinematics between sitting and standing throws by differences in dynamics because the calculation of dynamics was not possible for the standing throws. Nevertheless, the analysis of wrist joint kinematics coupled with the analysis of wrist muscle activation patterns has enabled us to gain insight into how the CNS deals with interaction torques during natural, unconstrained overarm throwing.

Results

Kinematics of forward portion of an overarm throw

We investigated wrist motion in throws made from both a sitting and standing position. Subjects threw from the sitting position because the search-coil technique, although having many advantages, has the disadvantage that translations of arm segments can only be calculated from the angular positions, with the origin of the arm fixed in space. Consequently, translations were only available for the sitting experiments. To determine whether findings on wrist flexion for the sitting throws applied for the standing throws, we also had subjects throw from the standing position.

Some kinematic parameters of a representative throw (from subject St) made fast and accurately from the sitting position are shown in Fig. 1. Figure 1A shows a reconstruction of the forward portion of the throw every 2 ms based on recorded angular and calculated translational positions of arm segments. The throw is viewed from the side with the finger represented as a straight line segment and having the orientation of the distal phalanx. This made the finger appear more flexed than it really was. This subject threw with a partly side arm motion which resulted in shorter arm segments from the side view. Figure 1B–F shows a variety of kinematic parameters for the same throw aligned on the time of ball release (time 0). Note that Fig. 1B and C show parameters of arm segments in space around space fixed axes (see "Materials and methods"), whereas Fig. 1D, E, and F show joint rotations (at elbow and wrist). In the last 20 ms before ball release the upper arm was relatively stationary in the horizontal plane (Fig. 1C—horizontal) having completed its forward-left motion, but was undergoing downward motion in the vertical plane (Fig. 1C—vertical). Consequently, in the last 20 ms before ball release hand translational motion in the forward direction resulted primarily from elbow extension (Fig. 1D), and wrist flexion (Fig. 1E), though there was also some downwards (vertical) motion of the upper arm (Fig. 1C) and shoulder humeral rotation (not shown).

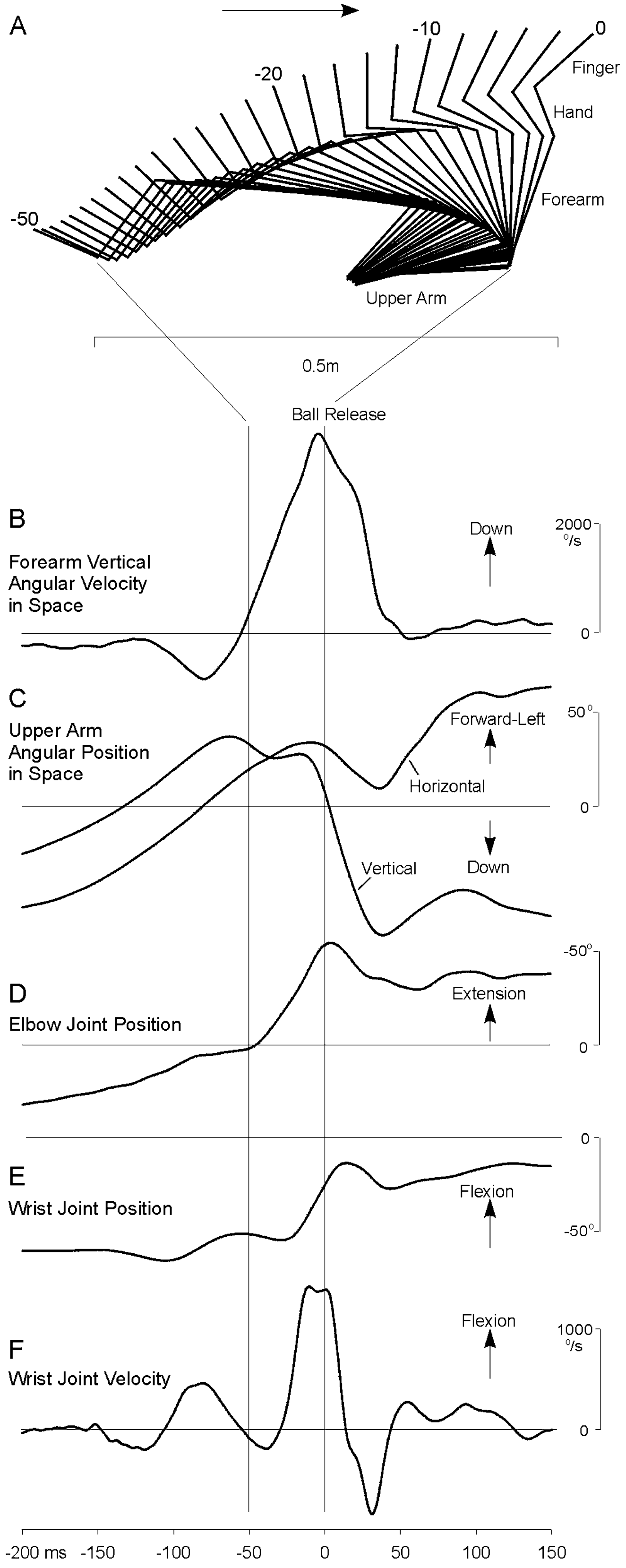

Fig. 1A–F Kinematics of forward portion of a single, fast, overarm throw made from sitting position. **A** Reconstruction of last 50 ms of throw shown every 2 ms to ball release (time 0) viewed from the side. *Right pointing arrow* gives direction of throw. **B** Vertical component of angular velocity of forearm in space around a space-fixed horizontal axis. *Vertical line* at time 0 gives time of ball release. **C** Vertical and horizontal components of upper arm angular position around space-fixed horizontal and vertical axes, respectively. **D, E** Rotations at elbow and wrist joints. **F** Wrist joint velocity. Zero for angular and joint positions occurred when arm was in reference position (see "Materials and methods"). Subject St

Wrist positions and amplitudes to ball release in throws of different speeds

Figure 1E shows that, in this sitting throw, motion at the wrist consisted of extension during the early portion of the throw, flexion followed by a second period of extension and then final flexion starting about 25 ms before ball release. At the moment of ball release from the fingertip (vertical line at time 0) the wrist had only flexed by about 30°. Furthermore, at this point the wrist was still in an extended position with respect to the neutral position where hand and forearm were in a straight line (marked by the horizontal line at 0° in Fig. 1E).

In a series of throws of the same speed wrist flexion to ball release was relatively similar from throw to throw. This is shown for wrist flexions from ten consecutive fast throws in Fig. 2A made by subject St. Traces have been aligned on the onset of wrist flexion defined when wrist flexion velocity crossed a low threshold of 200°/s. The moment of ball release is marked by horizontal lines. Figure 2B (lower) shows wrist flexion positions at the onset of wrist flexion with respect to the neutral position (0°) for all slow (triangles), medium (squares) and fast throws (circles) from this subject plotted against forearm angular velocity (which is a measure of throwing speed—see "Materials and methods"). For all throwing speeds there is a very narrow distribution of wrist onset positions. Mean wrist onset positions and SDs for all subjects are indicated by the lower end of the bars in Fig. 2C (for sitting throws) and in Fig. 2D (for standing throws). For each subject the bars from left to right give these values for the 30 slow (S), 30 medium-speed (M) and 30 fast (F) throws. For each subject there were fairly similar wrist onset positions for sitting throws (Fig. 2C) and for subjects Cr, Sr, Ls, Bl and St for standing throws (Fig. 2D). This likely occurred because the wrist was at its maximally extended position at the onset of wrist flexion, though this does not explain the more flexed positions in the fast standing throws made by subjects Db, Mg and Ps (Fig. 2D). Across subjects the mean wrist extension position at onset of wrist flexion in degrees is shown in Table 1A.

A surprising finding for all throws made by all subjects was that at ball release the wrist had flexed by only a small amount and was still in a position of extension. This can be seen for the fast throws in Fig. 2A (to the small horizontal lines) and for all throws made by this subject in Fig. 2B—upper points. Mean wrist positions at ball release for all subjects are given by the upper end of the bars in

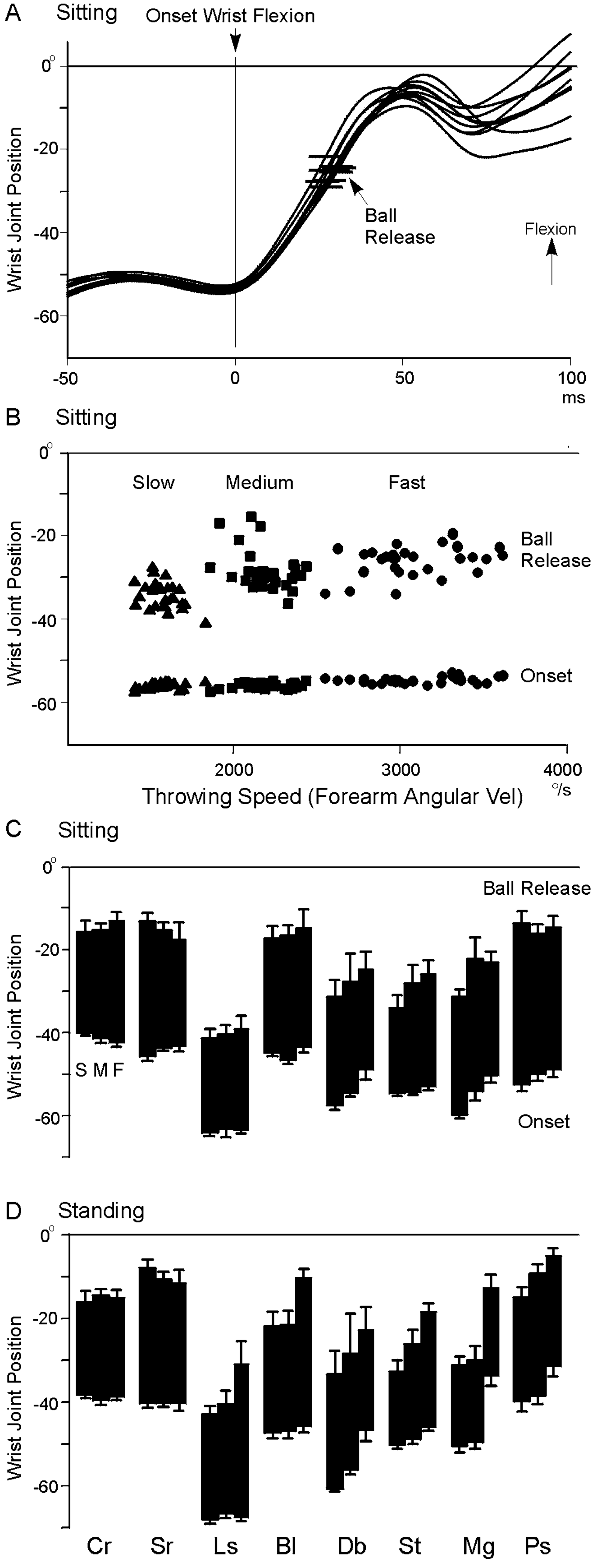

Fig. 2A–D Wrist flexion (joint) positions in an overarm throw. **A** Superimposed traces of ten wrist flexions for fast throws made by subject St from sitting position aligned on onset of wrist flexion (200°/s). *Short horizontal lines* indicate ball release. Zero is when hand was in a straight line with forearm. **B** Angular positions of the wrist joint at the onset of wrist flexion (*lower points*) and at ball release (*upper points*) for all slow throws (*triangles*), medium-speed throws (*squares*) and fast throws (*circles*) made from sitting position by subject St. Forearm angular velocity at ball release gives a measure of throwing speed. **C** Means and SDs of wrist angular position at onset of wrist flexion (*lower end of bars*) and at ball release (*upper end of bars*) for slow (*S*), medium (*M*) and fast (*F*) throws made from sitting position in all subjects. Thus *filled bars* represent the amplitude of wrist flexion. **D** Same for standing throws

Fig. 2C, D and across subjects in Table 1B. In all cases ball release occurred when the wrist was extended (0° gives the neutral position).

A consequence of these wrist positions was that wrist flexion amplitude to ball release (the length of the bars in Fig. 2C, D) was similar for throws of different speeds made from both the sitting and standing situations (Table 1C). A two factor repeated measures ANOVA showed that the amplitude was not significantly affected by throwing speed, throwing situation, or any interaction between these two factors ($P>0.05$ for each main effect analysis). In summary, in throws of different speeds made from both the sitting and standing situations, wrist joint positions and wrist flexion amplitudes to ball release were similar (i.e., they were the same or differed by only a few degrees).

The magnitude of wrist joint velocity in throws of different speeds

We investigated the characteristics of wrist joint velocity because this parameter could be affected by passive torques and could influence ball speed. Figure 3B–E shows average kinematic parameters of 30 fast throws made from the sitting position from a second subject (Ps) aligned on forearm peak vertical angular velocity in space (vertical line, time 0). We chose to align data on this point because it marks the onset of forearm angular vertical deceleration (which would be expected to affect wrist motion) and because the search-coil technique accurately measures angular positions in space (from which angular velocities in space were calculated). Figure 3B shows that wrist joint velocity in the flexion direction increased about 50 ms before time 0, peaked, and then decreased in the last 10 ms before forearm peak angular velocity. A decrease in wrist flexion velocity prior to forearm vertical peak angular velocity occurred in five of the eight subjects (Cr, Ls, Db, Mg, Ps) when making fast throws from the sitting position and in four subjects (Cr, Ls, Bl, Db) when making fast throws from the standing position.

Why did wrist flexion decrease? Over the last 20 ms to forearm vertical peak angular velocity there were two accelerations which would be expected to be associated with forces which would push the wrist towards extension: forearm angular downward acceleration (Fig. 3C) and

Table 1 Wrist joint position parameters. Wrist joint position parameters for throws made from sitting and standing positions at a slow medium and fast speed. Values are means from eight subjects in degrees ± SD. Negative indicates a wrist angular position in extension from the neutral position (0°) where wrist and forearm were in a straight line

			Slow	Medium	Fast
A	Wrist onset position	Sit	−52±8.3	−51±7.1	−49±7.0
		Stand	−50±10.5	−48±9.6	−44±11.1
B	Wrist position at ball release	Sit	−25±11.0	−23±9.0	−22±8.6
		Stand	−25±11.8	−23±10.7	−16±8.1
C	Amplitude of wrist flexion at ball release	Sit	28±5.8	28±3.6	28±3.3
		Stand	24±4.6	26±3.3	28±5.6

forearm translational downward acceleration (Fig. 3E). In contrast, forearm translational forward deceleration (Fig. 3D) would be expected to push the wrist towards flexion. According to this scenario, the decrease in wrist flexion velocity resulted from a failure of active contraction of wrist flexors to completely compensate for the summation of all the passive torques due to forearm angular and translational acceleration/deceleration (see later EMG section).

This decrease in wrist flexion (joint) velocity during forearm acceleration had an effect on wrist flexion velocity at ball release. Intuitively, it was expected that wrist flexion velocity would be faster in the fast throws than in the slow throws. However, when wrist flexion velocity was measured at ball release, this was not the case for the sitting throws. Figure 4A shows averages of wrist flexion velocity from subject Ps of 30 slow, 30 medium and 30 fast throws made from the sitting position aligned on the time of ball release. Mean throwing speed (forearm angular velocity at ball release) for the three sets of throws is shown in Fig. 4C. For each subject in Fig. 4B, C (and Fig. 5B, C), the order of the bars from left to right is slow (S), medium-speed (M), and fast (F) throws. Contrary to the expectation, average wrist flexion velocity at ball release (Fig. 4A) was actually smaller in the fast throws than the slow throws. Similarly, considering all subjects throwing from the sitting position (Fig. 4B), there was no statistical difference at the $P<.05$ level in wrist flexion velocity for the slow, medium and fast throws (repeated measures ANOVA, $P = 0.127$).

In contrast, a different pattern was observed in standing throws. For subject Ps, the average wrist flexion velocity at ball release (Fig. 5A) increased from the slow to the medium to the fast throws. Mean throwing speed is shown for the three speeds of throws for each subject in Fig. 5C. Considering all subjects (Fig. 5B), a repeated measures ANOVA showed significant differences in wrist flexion velocity for the different ball speeds at $P<0.01$. Regression analysis showed a statistically significant increase in wrist flexion velocity with an increase in throwing speed for all eight subjects ($P<0.003$) (cf. Fig. 5B).

The increase in wrist flexion velocity associated with forearm angular deceleration does not make a major contribution to ball speed

The greater wrist flexion velocity in the fast standing throws than in the fast sitting throws could have been due to an increase in passive torques associated with an increase in forearm translational deceleration or an increase in forearm angular deceleration, or could have been the result of an increase in wrist flexor EMG activity. Due to the nature of the recording technique we could not measure forearm translation in the standing throws. However, it was possible to measure the contribution of the other two parameters.

With respect to forearm angular deceleration, there was often a brief second increase in wrist flexion velocity during this period (e.g., Fig. 3B). This could have resulted from a whip-like effect due to forearm angular or translational deceleration or from a reactive force associated with ball release (cf. Hore et al. 1999). Given that the second increase in wrist flexion velocity may have resulted from forearm angular deceleration, the question arose whether this increase was exploited to increase ball speed. If the second increase in wrist flexion velocity contributed to an increase in ball speed, then ball release must have occurred during this period. This did not consistently happen. Across subjects more than half of all fast throws were released before the time of forearm peak angular velocity. Furthermore, for the fast throws made when standing, 95% of balls for each subject were released no more than 7 ms after forearm peak angular velocity.

However, because in some throws ball release occurred during forearm angular deceleration, we calculated the increase in wrist flexion velocity during this period that was potentially used by each subject in medium-speed and fast throws made from the standing position. This was done by measuring the difference between wrist flexion velocity at forearm peak angular velocity and at ball release as shown by the double-headed vertical arrow in Fig. 6A. Throws that occurred before forearm peak angular velocity were not included in the calculation. Figure 6B shows the mean magnitude of wrist flexion velocity for each subject at the time of forearm peak angular velocity (filled bars) and the mean across subjects (hatched bar); Fig. 6C shows the magnitude of the change in wrist flexion velocity from the time of forearm peak

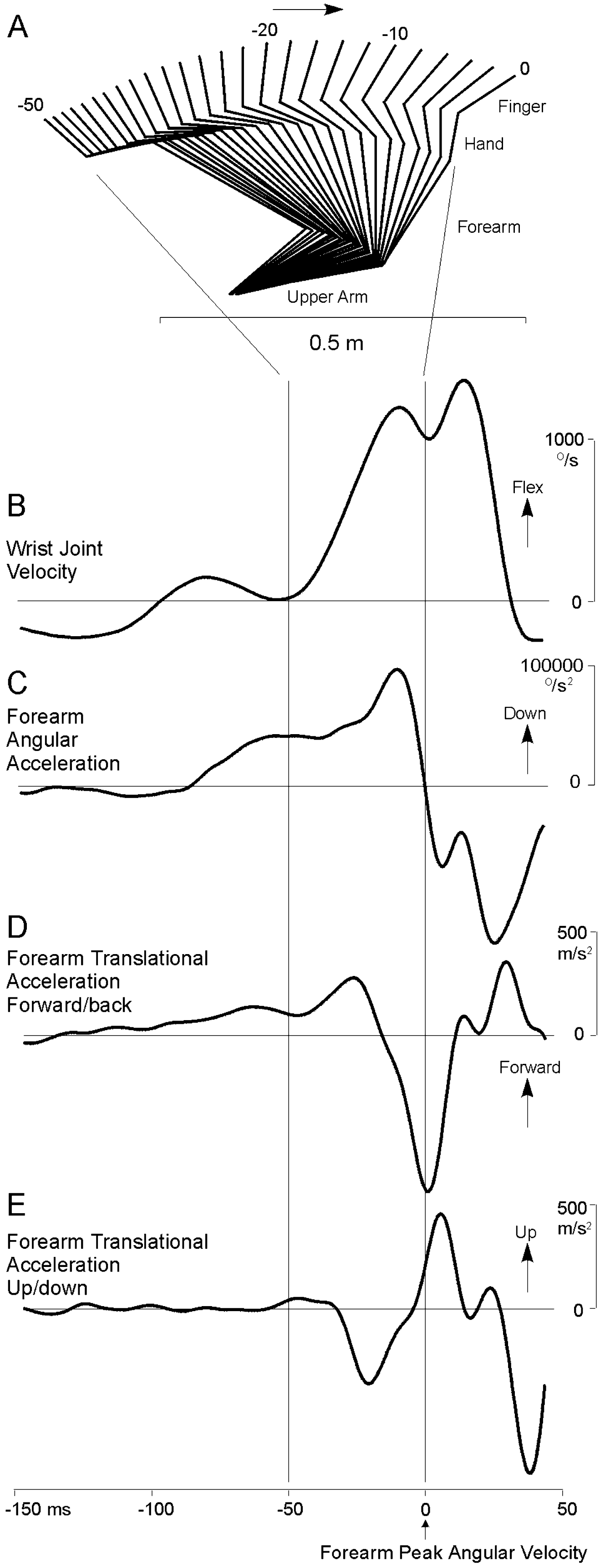

Fig. 3A–E Forearm angular and translational accelerations and wrist angular velocity during forward portion of overarm throw. **A** Average reconstruction of last 50 ms of 30 fast throws to ball release made from sitting position. **B–E** Average kinematic parameters of

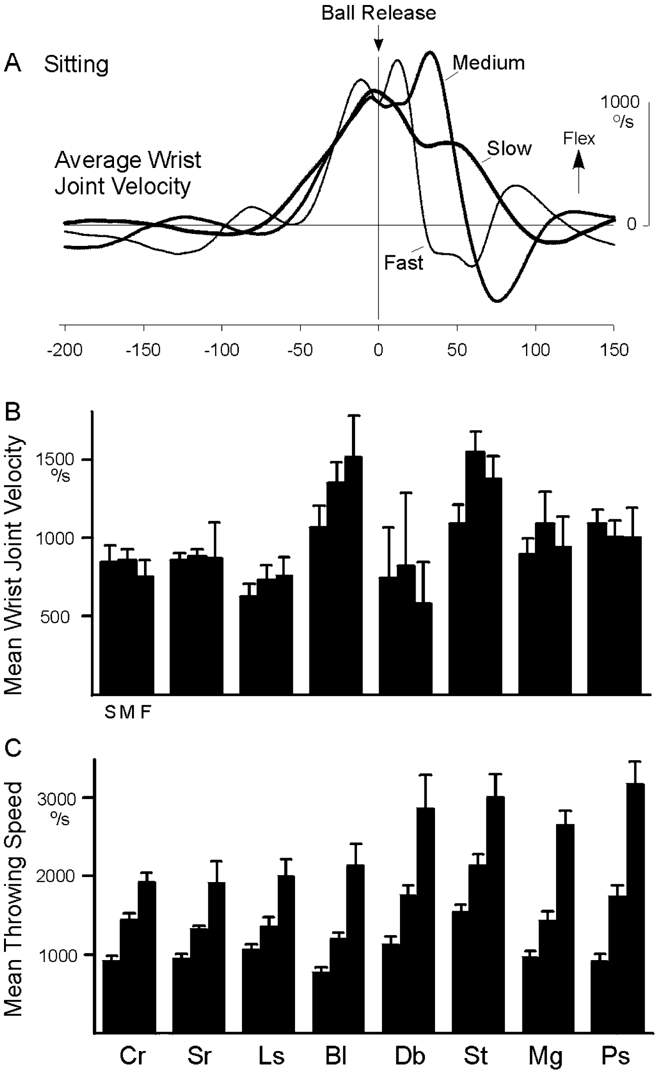

Fig. 4A–C Wrist flexion velocity for throws made from sitting position. **A** Average of wrist flexion velocity for 30 slow, 30 medium-speed and 30 fast throws aligned on ball release. Subject Ps. **B** Means and SDs of wrist flexion velocities at ball release for all subjects for 30 slow, 30 medium-speed and 30 fast throws. **C** Means and SDs of throwing speed (forearm angular velocity at ball release) for throws in **B**

angular velocity to ball release. It is clear, for both medium-speed and fast throws, that apart from fast throws in subject Mg, the second increase in wrist flexion velocity to ball release was small (means across all subjects were medium-speed 39°/s ± 151; fast 90°/s ± 186, whereas mean wrist flexion velocities at forearm peak angular velocity were 834°/s and 1,233°/s respectively). This suggests across subjects the second increase in wrist flexion velocity that was actually exploited would have had little effect on ball speed.

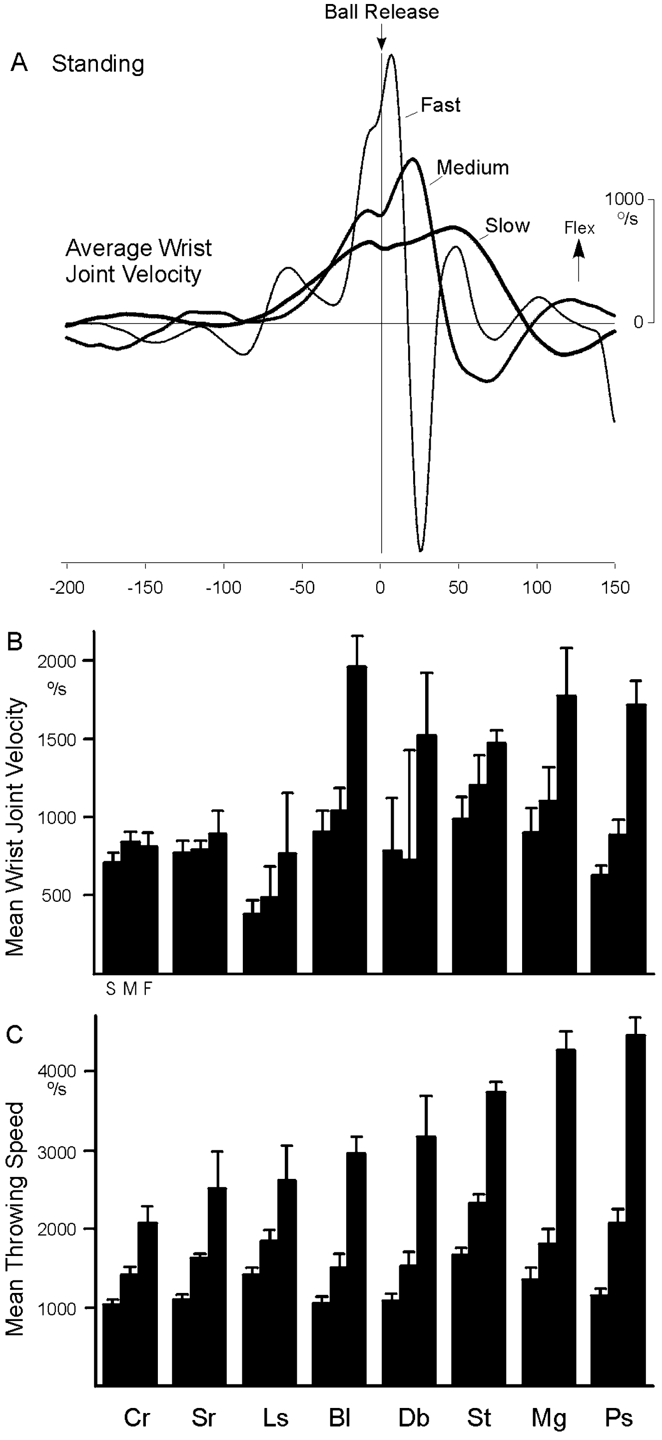

Fig. 5 Wrist flexion velocity for throws made from standing position. Same format as Fig. 4. Subject Ps

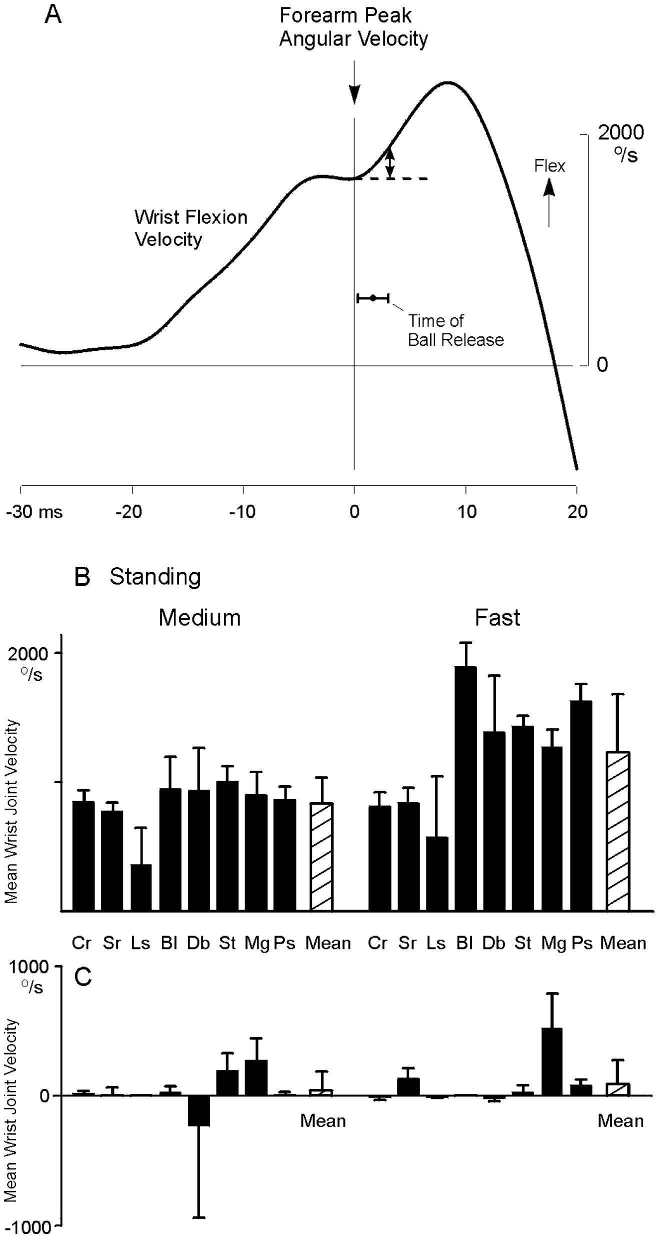

Fig. 6A–C Lack of exploitation of change in wrist flexion velocity during forearm angular deceleration. **A** Wrist flexion velocity for a single fast throw from subject Ps aligned on forearm peak angular velocity in space (*vertical line*). Time of ball release shows mean and timing window (SD × 3.92) which gives the range for 95% of throws. **B** Mean and SD of wrist velocities at forearm peak angular velocity for each subject for standing throws made at a medium and a fast speed. *Crosshatched bars* give means across subjects. **C** Magnitude of change in wrist flexion velocity from time of forearm peak angular velocity to ball release as shown by *double-headed arrow in* **A** (for those throws released after peak forearm angular velocity)

Braking of wrist flexion

At around the time that the ball is released in throws made by skilled subjects the forearm starts to undergo rapid angular deceleration which presumably produces large torques at the wrist in the direction of wrist flexion. It is possible that an important aspect of central control in a throw is to prevent excessive wrist flexion and thereby to prevent injury. This was investigated by determining the point of maximum wrist flexion associated with the wrist flexion movement in each throw. Figure 7A shows for the fastest thrower when standing (Ps), 30 consecutive fast throws made from the standing position aligned on onset of wrist flexion (at 200°/s). Maximum wrist flexion occurred about 25° past the neutral position (0° on the vertical axis).

We expected that maximum wrist flexion position would be greater (more flexed) for faster throws, but this was not the case. Instead maximum wrist flexion position was similar for throws of different speeds made by each subject. For subject Ps, Fig. 7B shows that although there was more variability for the slow and medium-speed throws when standing, mean maximum wrist flexion positions differed by about 15° (slow 40° into flexion, medium 35°, fast 26°). Figure 7D shows that mean flexion positions were similar for the slow, medium and fast throws made by each subject when standing. Comparison of Fig. 7C and D shows a second finding, i.e., each subject had strikingly similar maximum wrist flexion positions for the sitting and standing throws. Although mean maximum wrist flexion positions were similar for all throws made by each subject, these positions were different between subjects. Maximum wrist flexion positions varied from about 20° into extension (subject Db) to about 80° into flexion (subject Sr). Across subjects maximum wrist position was not significantly affected by throwing speed, throwing situation or by interaction between these two factors ($P>0.05$, two factor repeated-measures ANOVA).

A further finding about maximum wrist flexion position was that its variability was often low. This can be seen in the fast throws made by subject Ps in Fig. 7A and B (circles) and in the SDs for the standing fast throws in all subjects in Fig. 7D. Across subjects the mean SD for standing fast throws was 7°. However, for the five fastest throwers (Bl, Db, St, Mg, Ps) the mean SD for fast standing throws was 4°.

Wrist flexor and extensor EMG activity

The fact that onset of wrist flexion (Fig. 3B) occurred during the period of forearm angular acceleration (Fig. 3C) and forearm forward translational acceleration (Fig. 3D), when the wrist would be expected to be subjected to torques that push it towards extension, suggests that initial wrist flexion was produced by active wrist flexor muscle activity. And the finding that there was relatively small variability from throw to throw in the maximum wrist flexion angular position for each subject especially for fast standing throws (Fig. 7D) indicates that wrist flexion was precisely braked. The role of active wrist muscle activity in the onset and braking of wrist flexion was investigated in a second series of experiments by recording EMG activity in two situations: first, during single joint wrist flexions made as fast as possible from the maximal wrist extension position to the neutral position (where hand and forearm were in a straight line), and, second, in slow, medium-speed and fast throws made with a tennis ball and in fast throws made with a baseball. This investigation was performed so that we could compare braking of wrist flexion in situations where there would be expected to be different magnitudes of passive torques. Figure 8A shows averages from subject Pc of voluntary single joint wrist flexions (thick line) made on command to the neutral position and averages of wrist flexions during the four throwing conditions. Each trace is the average of 30 trials aligned on the moment of onset of wrist flexion (when wrist flexion velocity crossed a threshold of 200°/s) which is indicated by the solid vertical line. The small horizontal bar (Fig. 8A) aligned with the dashed vertical line gives the timing window for ball release for the fast baseball (FB) throws. Figure 8B–E shows EMG activity from the two flexor and two extensor wrist muscles for the same voluntary movements (thick lines) and for standing throws: slow (S), medium (M), fast (F) tennis ball and fast baseball (FB). These averages show the four major findings that were found across subjects. First, wrist flexor EMG activity was slightly larger in the fast throws made with both the tennis ball and baseball than in the voluntary wrist flexions made as fast as possible. This can be seen in Fig. 8B, C and in Fig. 9A, B for all subjects. The magnitude of the bars in Fig. 9 was obtained by first normalizing EMG activity (see “Materials and methods”) then integrating activity for a 100-ms period. For the flexors this was from 75 ms before onset of wrist flexion to 25 ms after (because in some subjects wrist flexor EMG began as early as 75 ms before onset), and for the extensors from 50 ms before to 50 ms after wrist onset. Across subjects the magnitude of integrated flexor carpi radialis activity (Fig. 9A) was larger for fast tennis (F) (sitting) and fast baseball (FB) (sitting and standing) than for voluntary single joint wrist flexion, and for flexor carpi ulnaris (Fig. 9B) it was larger for fast baseball (sitting) ($P<0.05$, Tukey test). Second, wrist flexor EMG activity progressively increased in magnitude from the slow to the fast throws made with the tennis ball, and was larger still for the fast throws made with the baseball. This can be observed in the records in Fig. 8B, C and in the means across all six subjects in Fig. 9A, B (across subjects there was a main effect of throwing speed, $P<0.05$, two factor repeated-measures ANOVA). Third, whereas in the single joint (voluntary) wrist flexions, wrist extensor muscle EMG activity was largely reciprocal, i.e., it was initially inhibited during wrist flexor EMG activity (Fig. 8D, E, thick lines), in throws there was an increased magnitude and earlier onset of wrist extensor EMG activity. This resulted in an increased period of coactivation, e.g., in Fig. 8 during the period from onset of wrist flexion (vertical line) to 100 ms after this moment. For all subjects, Fig. 9 shows that EMG activity of the extensors was larger for the throws with the tennis ball (S, M, F) and baseball (FB) made from the sitting or standing position than for the fast voluntary wrist flexions [activity of extensor carpi radialis was larger for medium (M) and fast throws (F, FB) sitting and standing, and extensor carpi ulnaris was larger for all throwing conditions, $P<0.05$, Tukey test].

A fourth finding is with respect to the question raised earlier, namely, are wrist flexion velocities larger in the fast standing throws (Fig. 5B) than in the fast sitting throws (Fig. 4B) because of increased flexor muscle

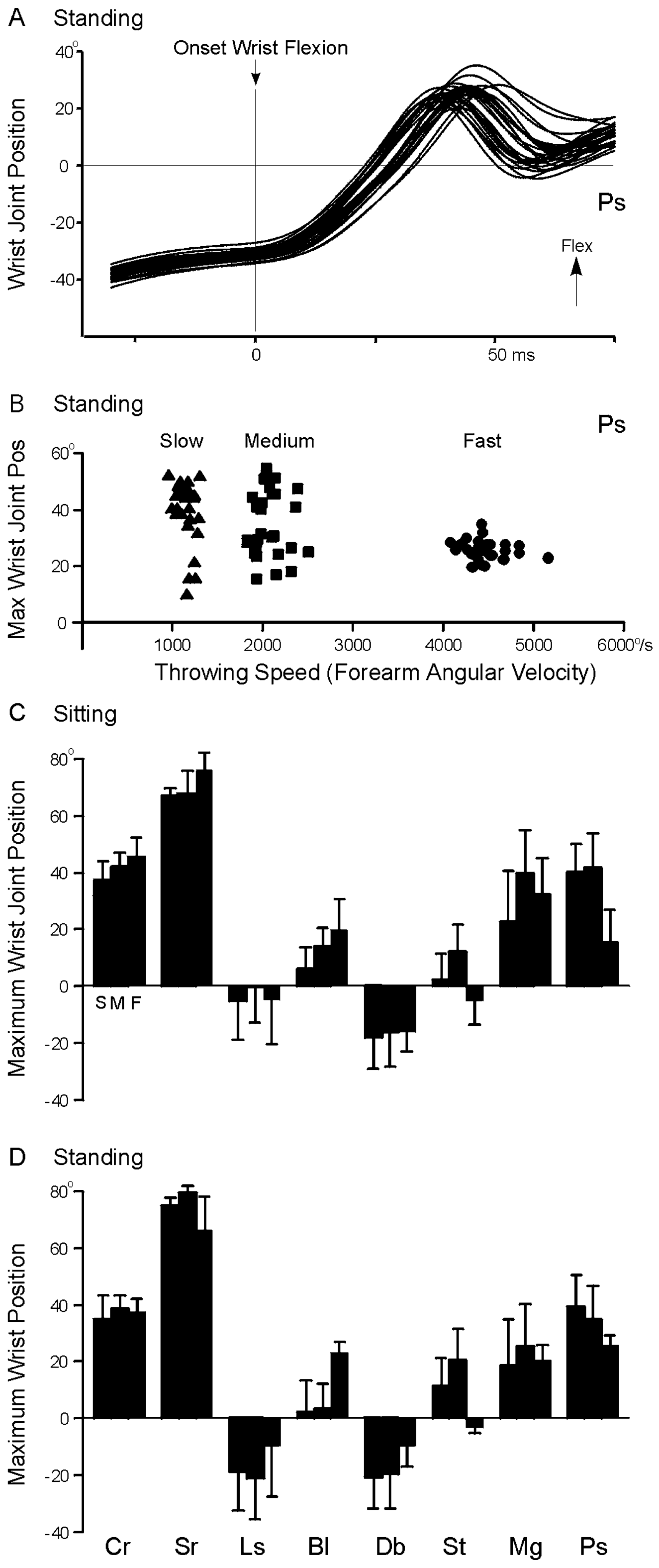

Fig. 7A–D Maximum wrist flexion positions associated with the wrist flexion movement after ball release. **A** Thirty superimposed traces of wrist flexion (angular position) aligned on onset of wrist flexion (200°/s) for throws from standing position made by subject Ps. **B** Maximum wrist flexion positions for all slow, medium and fast throws made from standing position by subject Ps. **C** Mean maximum wrist flexion position and SD for all slow (*S*), medium (*M*) and fast (*F*) throws made from sitting position by all subjects. **D** Same as **C** but for standing throws

activity? Inspection of the fast throws made with a tennis ball (F) in Fig. 9A, B reveals that flexor EMG was not increased in the fast standing throws compared to the fast sitting throws (across subjects there was no main effect of throwing situation, $P>0.05$, two factors repeated measures ANOVA). Given that no evidence was found for a major role for passive effects on wrist flexion velocity associated with forearm angular deceleration (Fig. 6) the tentative conclusion is that the third parameter, forearm translational deceleration, was the main factor causing the increase in wrist flexion velocity in the fast standing throws.

Discussion

We investigated the kinematics of wrist motion in overarm throws to determine whether wrist flexion amplitudes are held constant in throws of different speeds. Although whip-like effects occurred at the wrist, they were not accompanied by larger wrist flexion amplitudes in faster throws. Instead, throws of different speeds had constant wrist flexion amplitudes at ball release. Furthermore, final wrist joint flexion positions after ball release were similar for a particular subject irrespective of the speed of the throw. The results indicate that the CNS achieved these constant wrist flexion positions in part by exploiting passive torques associated with forearm translational deceleration, and by damping those associated with forearm angular deceleration.

Exploiting passive torques

Exploiting passive dynamics that arise during limb movements has long been proposed as a central mechanism to make movement efficient (Bernstein 1967). For the case of 3D overarm throws, the present results suggest that the CNS exploited passive interaction torques arising from the forward translational deceleration of the forearm in both the sitting (chest fixed) and standing (unconstrained) throws.

For the sitting throws, kinematic records showed that forearm translational deceleration began about 25–35 ms before ball release (e.g., Fig. 3D where ball release occurred within a few milliseconds of forearm peak angular velocity). This would have produced a passive torque in the direction of wrist flexion (e.g., Hollerbach and Flash 1982). EMG records (Fig. 8A, B) showed that during this time there was large wrist flexor EMG activity. The muscle torques resulting from this EMG activity would have added to the passive torques resulting from forearm translational deceleration. The net effect was that wrist flexion velocity was maintained fairly constant at ball release in throws of different speeds (Fig. 4B).

For the standing throws, although it was not possible to measure forearm translational deceleration directly, indi-

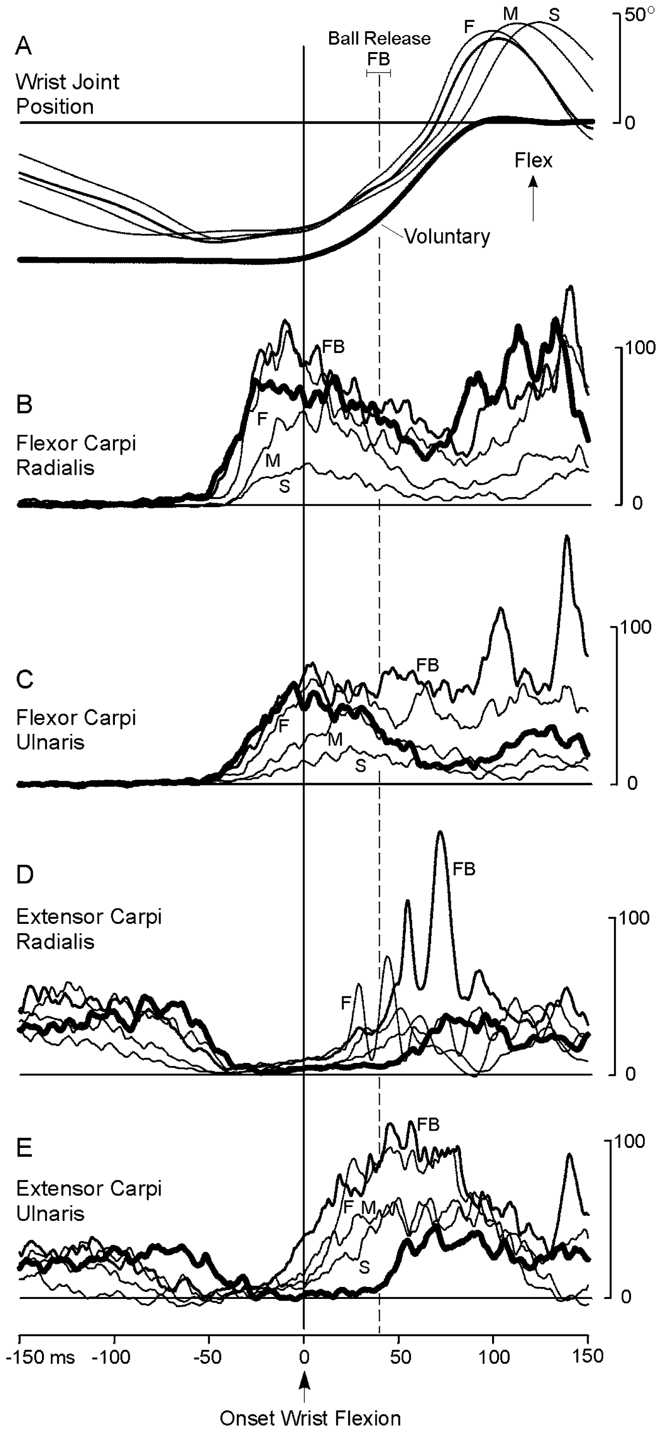

Fig. 8A–E Wrist flexor and extensor EMG activity during fast voluntary wrist flexions and standing throws. **A** Averages of 30 wrist flexions during voluntary wrist flexions (*thick lines*); slow (*S*), medium (*M*) and fast (*F*) throws made with a tennis ball (*thin lines*); fast throws made with a baseball (*FB*) (*medium line*). In all cases averages were aligned on onset of wrist flexion velocity (200°/s). **B–E** Corresponding average EMG activity. Subject Pc

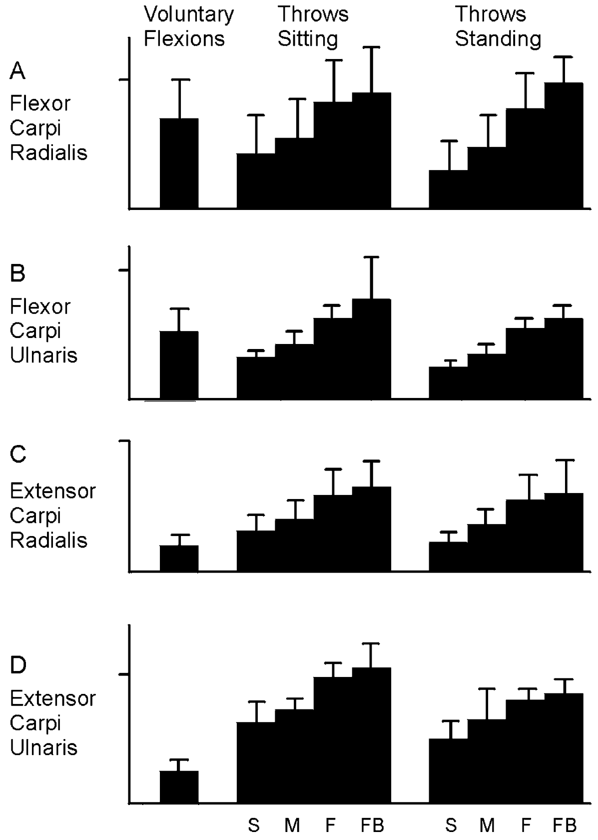

Fig. 9 Means and SDs across six subjects of integrated EMG activity from wrist flexors and extensors during voluntary wrist flexions and throws (see text)

rect evidence suggested that it contributed to increasing wrist flexion velocity, i.e., wrist flexion velocity was larger in the fast standing throws (Fig. 5B) than in the fast sitting throws (Fig. 4B). No other factor was able to explain this increase in wrist flexion velocity. For example, it could not be explained by an increase in forearm angular deceleration because the rapid increase in wrist flexion velocity in the fast standing throws (Fig. 5A) occurred about 25 ms before onset of forearm angular deceleration. Similarly, it could not be explained by an increase in wrist flexor EMG activity because this activity was not larger in fast standing throws than in the fast sitting throws (Fig. 9A, B). This whip-like effect from forearm translational deceleration did not result in significantly larger wrist flexion amplitudes at ball release in faster throws (Table 1). In keeping with this finding others have reported that in baseball pitches wrist angular positions at ball release are near the neutral position (Vaughn 1985; Elliott et al. 1986; Barrentine et al. 1998; Sakurai et al. 1993). It is concluded for fast standing throws that a whip-like effect associated with forearm translational deceleration was exploited to increase wrist flexion velocity, which in turn kept wrist flexion amplitude constant.

In contrast, in a study of a throwing motion in 2D, Hirashima et al. (2003) found no evidence that interaction torques were exploited at the wrist. One feature of their results was that wrist angular velocity at ball release was kept relatively constant in throws of different speeds. This is the same result we found in the sitting throws (Fig. 4B) and in subjects Cr and Sr in the standing throws (Fig. 5B). The calculations of Hirashima et al. revealed that for the

2D throws the wrist flexion muscle torques counteracted the wrist extension interaction torques produced as the arm underwent forward acceleration. Although at first sight the results of the two studies appear to be different, they are in fact compatible if the following assumption is made: that no large forward translational deceleration of the forearm occurred in 2D throwing motions, in sitting throws with the chest fixed (Fig. 4B) and in the two least skilled subjects who made unconstrained throws from the standing position (note that subjects Cr and Sr had the lowest fast ball speeds of the eight subjects in Fig. 5C). Put another way, it is suggested that exploitation of interaction torques to increase wrist flexion velocity only occurred in skilled subjects making unconstrained 3D throws. The difference between the 2D and 3D studies emphasizes the importance of studying natural, skilled, multijoint tasks in order to understand fully how the CNS controls arm dynamics.

Damping interaction torques after ball release

The explanation for the absent or small increase in wrist flexion velocity due to passive effects associated with forearm angular deceleration (Fig. 6) is that skilled throwers damp interaction torques at the wrist due to forearm angular deceleration to various degrees. Analysis of wrist extensor EMG activity in both voluntary single joint wrist flexions and in throws of different speeds showed that the magnitude of extensor activity was scaled with the expected increase in the interaction torque effect. For example, in voluntary wrist flexions (for which there were no interaction torques at the wrist) the typical triphasic pattern of EMG activity was recorded. This is consistent with past studies of single joint movements in which centrally controlled phasic antagonist activity was primarily responsible for braking the movement (e.g., Wierzbicka et al. 1986; Karst and Hasan 1987; Mustard and Lee 1987; Hoffman and Strick 1990, 1993; Pfann et al. 1998). In the present study, the EMG activity of wrist extensors near ball release became progressively earlier and larger as the throws became faster (Fig. 8). This resulted in coactivation with the flexors (Fig. 8) and in larger integrated areas of extensor EMG activity (Fig. 9) which would have resulted in damping of interaction torques. The central control of this EMG activity is likely to be complex because there is evidence that reciprocal activation and coactivation commands are independently controlled (Yamazaki et al. 1994, 1995; Suzuki et al. 2001).

The end result of damping interaction torques was the strikingly precise braking of wrist flexion such that maximum wrist positions were similar for a particular subject irrespective of the speed of the throw and the throwing situation (Fig. 7C, D). It is noteworthy that for the five fastest throwers the SDs of maximum wrist position were lowest for the fast throws made from the well practiced standing position (Fig. 7D). Since for seven of the eight subjects the maximum wrist position was within 50° of the neutral wrist position, braking could not be attributed to visco-elastic forces. This finding of damping adds to reports of a number of situations where unwanted motions resulting from interaction torques were suppressed, e.g., in multijoint elbow and shoulder movements (Gribble and Ostry 1999; Galloway and Koshland 2002), in cyclic elbow-wrist movements (Dounskaia et al. 1998), and in single joint movements at the fixed joint (Almeida et al. 1995; Latash et al. 1995; Gribble and Ostry 1999).

CNS control of wrist angular position

The constant wrist flexion amplitudes at ball release and the constant maximum wrist flexion positions in throws of different speeds suggests that wrist joint angular position may be a variable which is specifically controlled in throws. Indeed, it has been proposed that voluntary movement and the associated time varying patterns of muscle forces may be produced by central commands which directly specify equilibrium positions of the limb (Feldman et al. 1990; Feldman and Levin 1995). In contrast, others have suggested that the CNS specifies more directly the muscle forces and joint torques necessary to produce a given limb trajectory (Gottlieb 1998). According to this class of direct force control model, either agonist/antagonist EMG bursts (Hoffman and Strick 1993; Pfann et al. 1998) or time-varying muscle forces and/or joint torques (Schweighofer et al. 1998a, 1998b) are computed in advance of movement and directly specified in descending control signals to muscles. In principle, the present data do not distinguish between force or positional control models. Nevertheless, the constant wrist flexion positions are evidence that the CNS was able to fully account for the limb dynamics which occurred during the throw. This ability to compensate appropriately for interaction torques depends on the availability of proprioceptive information (Sainburg et al. 1995) and the integrity of the cerebellum (Bastian et al. 1996; Topka et al. 1998; Cooper et al. 2000; Timmann et al. 2001).

Conclusion

The results show that in 3D throws of different speeds the CNS deals with different passive torques at the wrist by generating active torques which first contribute to and then brake wrist flexion, thereby keeping maximum wrist flexion position constant. As such these results in a natural skilled task performed at extremely fast speeds are consistent with other demonstrations that limb movement kinematics are preserved in the face of perturbing forces arising from limb dynamics. Together they fit with the notion that skilled multijoint movements are produced by central signals which precisely control net joint torque. However, the striking constancy of wrist angular position parameters observed in throws with different dynamics suggests that wrist joint position (or amplitude) is also an important controlled variable.

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