Overarm Throws With the Nondominant Arm: Kinematics of Accuracy

J. HORE, S. WATTS, D. TWEED, AND B. MILLER
Physiology Department, University of Western Ontario, London, Ontario N6A 5C1, Canada

SUMMARY AND CONCLUSIONS

1. Overarm throws made with the nondominant arm are usually less accurate than those made with the dominant arm. The objective was to determine the errors in the joint rotations associated with this inaccuracy, and thereby to gain insight into the neural mechanisms that contribute to skill in overarm throwing.

2. Overarm throws from both left and right arms were recorded on different occasions as six right-handed subjects sat with a fixed trunk and threw 150 tennis balls at about the same speed at a 6-cm square on a target grid 3 m away. Joint rotations at the shoulder, elbow, wrist, and finger, and arm translations, were computed from recordings of arm segment orientations made with the magnetic-field search-coil technique.

3. All subjects threw less accurately in this task with the left (nondominant) arm. For throws made with the left arm, the height of ball impact on the target grid was related to hand trajectory length and to hand orientation in space at ball release, but not to hand trajectory height.

4. Two hypotheses were proposed to explain the decreased ball accuracy in the high-low direction during throwing with the nondominant arm: that it was caused by increased variability in the velocity or timing of onset of rotations at proximal joints (which determine the path of the hand through space) or increased variability in the velocity or timing of onset of finger extension (which determine the moment of ball release).

5. A prediction of the first hypothesis was that proximal joint rotations should be more variable in throws with the left arm. This was the case for the majority of proximal joint rotations in the six subjects when variability was examined in joint space. However, some proximal joint rotations were more variable in the right arm.

6. The first hypothesis was directly tested by determining whether hand angular position in space (which represents the sum of all proximal joint rotations) was related to ball impact height on the target grid at a fixed translational position in the throw. No relation was found between these variables for throws with the left arm in four subjects, whereas a weak relation was found for two subjects. It was concluded that, considering all subjects, the first hypothesis could not explain the results.

7. In contrast, in agreement with the second hypothesis, a strong relation ($P < 0.001$) was found in all subjects between ball impact height on the target grid and time of ball release for throws with the left arm, and with time of onset of finger extension.

8. Across all six subjects the timing precision (windows) for 95% of the throws was (for ball release) right arm, 9.3 ms; left arm, 22.5 ms; (for onset of finger extension) right arm, 13.7 ms; left arm, 26.7 ms.

9. Timing of onset of finger extension was no less accurate than timing of onset of other joint rotations for both left and right arms. However, simulations of throws showed that, for the same error in timing, finger extension had twice as large an effect on ball direction as any other joint rotation. Timing errors at the fingers have a greater effect than errors at other joints because finger errors are scaled by the higher angular velocity of the hand in space rather than by the smaller angular velocities of the individual joints.

10. It is concluded that although rotations were in general more variable at both proximal and distal joints of the nondominant (left) arm, the major cause of its decreased throwing accuracy was increased variability at the distal joints, i.e., in the timing of onset of finger extension. This may be due to a lack of precision in the commands from the right hemisphere to the left fingers in right-handed throwers.

INTRODUCTION

Most humans favor one hand, usually the right, for skilled unimanual tasks. Studies have looked at many aspects of handedness—its heritability and development in children, its traces in human prehistory, and its analogues in other species—but little work has been done on its kinematics, i.e., on the quantitative differences in the timing and velocity of rotations at various joints that distinguish the more or less graceful movements of one arm from the clumsiness of the other. We addressed this question by measuring the three-dimensional rotations of the shoulder, elbow, wrist, and finger joints during overarm throwing, looking for differences between the two arms and for the consequences of these differences in terms of throwing accuracy.

It is common experience that right-handers usually throw better with the right hand. Because each hand is controlled by the contralateral cerebral hemisphere, right-handed skill has been attributed to the superior performance of the left hemisphere (e.g., Annett 1985; Harrington and Haaland 1991; Kimura 1977). But although the distal muscles of each arm are activated by the contralateral hemisphere, the proximal muscles are under more bilateral control (Brinkman and Kuypers 1973; Gazzaniga 1970). Thus one may expect that the differences between the kinematics of the right and left arms will be less marked for the proximal joints.

Proximal and distal joints play rather different roles in throwing. Proximal joints (shoulder, elbow, and wrist) determine the trajectory of the hand in space, whereas distal joints (the fingers) grip and release the projectile. As long as the fingers are closed around it, the projectile, which in our experiments was a tennis ball, must share the hand's motion; but when the fingers open, the ball is free to fly off. It flies roughly tangentially to the path of hand translation, but its motion is also influenced by finger orientation because it rolls along the fingers during the process of release (Hore et al. 1996a). Thus the job of the proximal joints is to bring the hand's location, velocity, and orientation to the correct
values for an accurate launch, at which instant the distal joints must release the ball. Errors in either part can cause inaccuracy: the fingers may open too soon or too late, or the proximal joints may fail to provide adequate conditions for an accurate launch. For throws with the dominant (right) arm, the major factor in ball high and low inaccuracies was errors in finger timing (Hore et al. 1996b).

In this study we compare the three-dimensional kinematics of right and left arm throwing. How much less accurate is the nondominant arm? What are the quantitative differences between the arms as regards the timing and amplitude of rotations at various joints? Are these differences more marked for distal than for proximal joints? And which differences are most responsible for the relative inaccuracy of the nondominant arm?

**METHODS**

**General procedures**

Experiments were performed on six right-handed male university students who gave informed consent. All had played recreational baseball or softball and were good throwers. Subjects sat in a low chair with the trunk fixed by straps over the shoulder so that translational position (hand trajectory) could be computed (see later). Each subject performed the entire experiment with the left (nondominant) arm, and then, on a later date, with the right (dominant) arm. Subjects were allowed ~10 practice throws to warm up. In each experiment, subjects throw 150 tennis balls at a 168-cm-high × 54-cm-wide grid of numbered squares, each 6 cm across (about the size of a tennis ball). Subjects aimed for a central square that was 3 m from the chest and at about eye level. They were instructed to throw fast and accurately with the use of an overarm motion. The experimenter, seated behind the subject, scored each throw for accuracy by noting the number of the square that was struck. Subjects threw on a verbal command given approximately every 10 s. Hand angular velocity in space (which correlates with ball speed) was monitored on-line. During the second (right arm) experiments, subjects were asked to increase or decrease the speed of the throws as necessary to approximate the speed of the previously recorded (left arm) throws, so that speed did not become a factor influencing accuracy.

**Ball release and ball speed**

Ball release was signaled by microswitches (triggers) taped to the proximal and distal phalanges of the middle finger. If these switches malfunctioned, additional kinematic criteria for final ball
release were: the distal phalanx trigger followed the proximal phalanx trigger by 20–30 ms, hand position in space reached vertical near the time of the distal trigger, and the distal trigger occurred near the time of a deflection or a peak in finger extension, which was a point that was previously found to correlate reliably with ball release (Hure et al. 1995).

Ball speed was calculated from the ball flight horizontal distance and ball flight time. Flight distance was obtained by subtracting the amplitude of hand forward translation at ball release from the distance from chest to target. The start of ball flight time was signaled by ball release, whereas the end was the time at which the ball hit the target grid, as indicated by an impact detector.

Recording angular and translational arm position

Arm segment orientations were measured with the use of a modification of Robinson’s (1963) magnetic-field search-coil technique (Tweed et al. 1990). Subjects sat within three orthogonal, high-frequency (62.5, 100, and 125 kHz) alternating magnetic fields, each generated by four field coils 3 m diam. Arm movements were monitored by a pair of orthogonal search coils taped to each arm segment: scapula (acromion process), upper arm, forearm, hand, and tip of the middle finger. During the experiment the composite induced signal was sent from the coil to an electronic circuit that separated the signal into its three components. These signals were then amplified and sent to the computer for sampling at 1,000 Hz and storing. With the use of this technique the orientation of each arm segment was determined with respect to a coordinate system that was fixed in space. At the beginning of each experiment, a reference arm position was recorded in which the upper arm was held horizontal and the forearm and fingers were held vertical as in Fig. 1A. Rotation matrices were calculated that indicated the magnitude of rotation of the search coils from this reference position. In all figures, finger and hand angular position in space is the amplitude of vertical rotation from the reference position around the space-fixed horizontal (pitch) axis. Calculations were also performed to obtain joint rotation (angular) positions of the wrist, elbow, and shoulder joints, and of the finger tip with respect to the hand. As shown in Fig. 1B, motions at the shoulder were described in terms of shoulder azimuth (horizontal rotation of the upper arm, i.e., adduction-abduction), shoulder elevation (up-down rotation of the upper arm irrespective of azimuth), and shoulder roll (rotation of the upper arm around its own axis). Measurements with coils attached to the distal, middle, and proximal segments of the middle finger confirmed that finger opening during ball release was associated with extension at the distal and middle finger joints and relatively little movement at the proximal joint (cf. Hore et al. 1996a).

The translational position of the end of each arm segment was computed with the use of its measured length and its angular position with respect to the distal end of the adjacent proximal segment. For this computation, the first segment (scapula) must rotate with respect to a point that is fixed in space, and therefore the sternum was fixed by straps over the shoulder attached to the chair.

Statistics

To determine whether there was a relation between any two variables, a scatter diagram was plotted and the slope of the regression line and the correlation coefficient r were computed. The null hypothesis, that the slope of this line was 0, was tested by an analysis of variance procedure (F test of regression analysis of variance) (Campbell 1992; Zar 1984).

RESULTS

Accuracy of throws with the left and right arms

We first confirmed that all our subjects threw more accurately with the right arm than the left. As in Hore et al. (1996b), we reduced accuracy to a one dimensional variable for simplicity by considering only the vertical dimension, i.e., accuracy was scored in terms of the height of ball impact on the target grid. Subjects aimed for a target square at the center of the grid, near eye level, and we counted how often, of 150 throws, the ball hit the central row of squares. The percentage of accurate throws for each subject was (right arm %, left arm %) 51, 13; 46, 13; 25, 8; 46, 15; 34, 23; and 33, 23, i.e., all subjects scored better with the right arm. Across all subjects, the average accuracy was right arm 39%, left arm 16%.

Another way to assess accuracy was to calculate the mean impact height of the ball and to use the SD as a measure of throwing variability and thereby accuracy. Figure 2 shows the mean impact height and the SD for ~150 throws made with the right and left arms for all subjects. For every subject, the SD for the left arm was 2–6 times that for the right arm. This difference was significant at the P < 0.001 level in all subjects by the variance ratio test (Zar 1984). Thus both our accuracy measures showed that all the subjects were less accurate when throwing with the left arm.

Variability in hand trajectory

Each subject displayed a different throwing motion and a slightly different hand trajectory shape for the left arm compared with the right arm. Figure 3 shows a side view of one right arm throw and one left arm throw from subject Gt.
The hand trajectory is indicated by the curved line for each throw, i.e., it gives the path of the distal end of the middle metacarpal through space from the start of forward hand translation until final ball release (distal trigger). Although both throws hit the target, the configuration of the arm at ball release was different for the two throws. Nevertheless, shapes of trajectories of left and right arms appeared to be more similar between arms of one subject than between subjects. This can be seen in Fig. 4, which shows the side view of the hand trajectories for 10 consecutive throws made with the right and left arms in all six subjects.

In general, throws with the left arm were slightly more variable in height and much more variable in length than throws with the right arm. This variability can be seen in Fig. 4 and in Table 1, which shows means ± SD for hand trajectory heights and lengths at ball release from the sternal notch for all throws. For five of six subjects, the height of hand trajectory at ball release was slightly more variable (as measured by the SD) for the left arm than the right arm. In contrast, in all cases, the SD of the mean length of hand trajectory was much larger for the left arm.

How do these features of left arm throws affect accuracy, i.e., is ball impact height on the target grid related to hand trajectory height or length? One problem with answering this question is that, because the hand trajectory is curved, hand height at ball release depends on hand trajectory length, i.e., the longer the throw, the lower the hand at release. To avoid this problem, we measured hand height at a fixed location along the trajectory, 0.2 m forward of the sternum. Measured this way, left hand trajectory height was not related to ball impact height for any of the six subjects at the $P < 0.05$ level. Plots for three subjects are shown in Fig. 5A. In contrast, all six subjects showed a significant relation at the $P < 0.001$ level between ball impact height and left hand trajectory length (e.g., Fig. 5B), hand angular position in space at ball release (Fig. 6A), and finger angular position in space (Fig. 6B). As previously found for the right arm (Hore et al. 1996b), ball impact height and ball speed were unrelated, presumably because the target was so near that gravity had little time to bend the ball’s path.

**Proximal joint variability**

What causes the greater variability in hand trajectory height and length in left arm versus right arm throws? One possibility is that it is due to increased variability in the velocity, or timing of onset, of rotations at proximal joints (shoulder, elbow, wrist). This implies that rotations of these joints should have larger variability in left arm throws.

To test this idea, we compared variability of joint rotations in the two arms. There are many ways to compare variability, and we sought a method that would identify specifically those sources of variability that cause inaccuracy. For example, we did not compare joint angles at a fixed time in the throw because variation there can be caused by different speeds of throws, and speed per se does not cause inaccuracy over the speed range in this study. Further, we needed a comparison that was not biased toward any one joint motion. Thus joint angles were not compared at a fixed orientation in space of any arm segment, because each segment’s orientation is largely determined by a particular joint rotation, e.g., the moment at which the forearm is vertical in space is largely determined by elbow extension.

To avoid these problems, errors in joint rotations were measured as variability in joint space. That is, variability of rotation for a particular joint was determined with respect to a fixed angle of another joint. This fixed angle was taken, e.g., the moment at which the forearm is vertical in space, as the average angle for all throws when the hand was 35° backward from its vertical position, which always occurred

**TABLE 1.** Hand trajectory height and length at ball release for throws with right and left arms

<table>
<thead>
<tr>
<th>Subject</th>
<th>Right Height</th>
<th>Right Length</th>
<th>Left Height</th>
<th>Left Length</th>
</tr>
</thead>
<tbody>
<tr>
<td>Gt</td>
<td>31.0 ± 2.9</td>
<td>27.2 ± 4.1</td>
<td>63.7 ± 1.8</td>
<td>64.6 ± 7.2</td>
</tr>
<tr>
<td>Mr</td>
<td>40.0 ± 3.1</td>
<td>33.3 ± 3.1</td>
<td>54.9 ± 3.2</td>
<td>36.6 ± 6.1</td>
</tr>
<tr>
<td>Ax</td>
<td>33.6 ± 3.2</td>
<td>34.7 ± 4.8</td>
<td>52.1 ± 2.3</td>
<td>54.4 ± 5.8</td>
</tr>
<tr>
<td>Bs</td>
<td>31.1 ± 1.9</td>
<td>27.8 ± 2.9</td>
<td>37.3 ± 3.7</td>
<td>53.5 ± 8.5</td>
</tr>
<tr>
<td>Tw</td>
<td>12.4 ± 3.0</td>
<td>27.3 ± 3.7</td>
<td>21.9 ± 1.6</td>
<td>29.8 ± 3.5</td>
</tr>
<tr>
<td>Sk</td>
<td>41.7 ± 2.6</td>
<td>31.1 ± 3.9</td>
<td>45.0 ± 2.2</td>
<td>52.6 ± 7.3</td>
</tr>
</tbody>
</table>

Values are means ± SD, in cm. Translational positions were measured with respect to the sternum. n ~ 150 throws.
before ball release. Figure 7 shows, for subject Gt, that when measured in joint space, joint rotations were more variable for the left arm than for the right. In this figure, angular positions of each joint are plotted against those of the adjacent joint for 10 consecutive throws. Dashed lines represent the fixed angles. It can be seen for a fixed elbow angle that the amplitude of rotation was more variable in the left arm for shoulder roll (Fig. 7B), shoulder elevation (Fig. 7C), and wrist flexion (Fig. 7D). For simplicity, in the following, variability of joint amplitudes is taken with respect to the fixed angle of one adjacent joint, but results were similar whenever proximal joint was taken for the fixed angle.

Variability of joint rotation was defined as the SD of the mean amplitude of rotation for 150 throws at the fixed angle. Figure 8 shows that for subject Gt, SDs were higher for the left arm at all joints. Statistical difference at the P < 0.05 level is indicated by asterisks (for left > right) and by filled circles (for right > left). Considering all subjects, rotations at proximal joints (not including finger extension) were more variable for the left arm in 17 of 30 cases, and for all joints in 22 of 36 cases. Each subject showed more variability in the left arm in at least one proximal joint, but all subjects except subject Gt had at least one proximal joint where the left arm was not significantly more variable, and in three cases, proximal joint rotations were less variable in the left arm (Fig. 8). And there was no one proximal joint for which all subjects were significantly more variable with the left arm. Thus greater variability in the proximal joints of the nondominant arm was a tendency, but was far from a universal rule.

**Proximal joint coordination and throwing accuracy**

The proximal joint variability was examined further by means of the following hypothesis: that the decreased ball accuracy of the left arm was caused by increased variability in the velocity or the timing of onset of rotations at proximal joints. Because, as noted above, the tendency for increased variability at proximal joints of the left arm cannot be attributed to any one joint, we looked at the correlation between throwing accuracy and two kinematic variables that reflect the summed rotations of all proximal joints: hand translation in space and hand orientation in space. The values and rates of change of these variables at ball release are the ultimate determinants of ball path, and so if the proximal joints are responsible for throwing inaccuracy, then their failure should
show up in these variables, e.g., plots of hand orientation versus hand location should show separation, describing separate curves for accurate, for high and for low throws. This is illustrated in Fig. 9 for one of many possible cases, i.e., for joint rotations at the elbow and wrist that were faster or began earlier than normal (low throws) or were slower or
later (high throws). It is assumed in this figure that all throws had the same time to ball release.

The hypothesis was tested by plotting hand orientation in space (i.e., hand vertical rotation around a space-fixed horizontal axis) against hand translation in the backward-forward direction for 10 high throws (Fig. 10A, ——) and 10 low throws (Fig. 10A, ○) in subject Gt. Traces end at ball release. Contrary to the prediction of the hypothesis, traces for high and low throws overlapped. For any fixed hand location (before the earliest ball release), no difference was seen in hand orientation in space for high and low throws. Similarly, when all throws were considered, plots of ball impact height on the target grid versus hand orientation in space at a fixed hand location were unrelated at the P < 0.05 level (Fig. 10B). The same result was found for all of the six subjects. Two subjects showed a weak relation. For P < 0.05, F1,140(2) = 5.13. F values for the six subjects were 1.28, 0.08, 5.23, 1.60, 3.43, and 8.01. Thus in the majority of subjects the evidence was not consistent with the hypothesis that ball inaccuracy was due to variability in the motions of proximal joints.

Time of ball release and throwing accuracy

To test a second hypothesis—that the relative inaccuracy of the left arm is due to mistimed ball release, caused by mistimed finger opening—we first looked at all left arm throws to see whether ball impact height was related to time of ball release. As before (Hore et al. 1995, 1996b), time was measured with respect to the moment in the throw that the hand was vertical in space. Figure 11 shows plots of ball impact height on the target grid against time of ball release for all left arm throws in each subject. Throws released early hit above the target (0), whereas throws released late hit below. In all cases, F tests confirmed the significance of the relation at the P < 0.001 level. F values were 356.1, 237.3, 139.8, 545.5, 509.5, and 256.9.

Variability of finger opening

Because ball release is related to finger opening, it is likely that variability in some parameter of finger opening results in variability in timing of ball release. Figure 12 shows tracings of finger opening from 10 consecutive throws for both the right and left arms in four representative subjects. Each trace represents the angular position of the distal phalanx of the middle finger with respect to the hand, synchronized to the time of vertical hand position (°). Time of onset of finger opening was defined as the moment when finger extension crossed a set threshold (Fig. 12, top left, ——) that was about one third of the average finger amplitude at ball release (marked by arrow).

Three major differences occurred for throws made with the left arm: there was increased variability in the time of onset of finger extension, increased variability in the amplitude of finger extension, and increased variability in the velocity of finger extension. To determine which of these errors played the major role in causing ball throwing inaccuracy, the relation between ball impact height on the target grid and each of the three finger parameters was determined for throws with the left arm. Plots for subject Gt are shown in Fig. 13. All subjects showed a strong relation between ball impact height and the time of onset of finger extension, all significant at the P < 0.001 level, with F values of 138.4, 110.9, 108.2, 296.5, 154.6, and 311.5. In contrast, five of the six subjects showed no significant relation (P < 0.05) between ball impact height and finger amplitude, with F values of 2.0, 0.9, 6.9, 0.1, 2.0, and 0.1. Peak finger extension
velocity was usually reached just before ball release. For four subjects the relation between ball impact height and peak velocity of finger extension was significant at the $P < 0.05$ level, with $F$ values of 5.43, 0.35, 0.08, 49.69, 10.92, and 11.53. Thus throwing accuracy was strongly related to the timing of onset of finger extension in all subjects and was relatively weakly related to peak finger velocity in four subjects and to finger amplitude in one subject.

Precision of timing for left and right arms

How precise was the timing of ball release in throws with the left arm compared with that in throws with the right arm? For each subject, the mean time of ball release (with respect to time of hand vertical position) and the SD were calculated. Variability as measured by the SD was consistently higher for the left arm than the right. In a normal distribution, 95% of observations occur in the interval defined by the mean ± 1.96 × SD (Sokal and Rohlf 1987). Considering 95% of the throws (3.92 × SD), ball release windows for the right arm for the six subjects were 6.2, 9.6, 10.8, 15.0, 7.2, and 6.9 ms (mean 9.3 ms). For the left arm, windows were 25.8, 24.5, 19.5, 27.7, 12.2, and 25.3 ms (mean 22.5 ms).

Variability in the time of onset of finger extension (with respect to time of hand vertical position) was also higher for left arm throws than right arm throws. Considering 95% of the throws, finger opening windows for the right arm for the six subjects were 9.9, 11.5, 17.4, 20.9, 13.7, and 8.8 ms (mean 13.7 ms). For the left arm, finger opening windows were 29.7, 27.7, 22.4, 35.2, 17.2, and 27.9 ms (mean 26.7 ms).

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Why are throws made with the nondominant arm less accurate than throws made with the dominant arm? The results show four major findings: 1) for throws made with the nondominant arm, ball accuracy was less accurately than rotations at other joints. We tested this idea by measuring the variability in onset time for all joint rotations for both left and right arms. Onset was defined as the moment when each joint rotation crossed a set high threshold (Fig. 14A), with times measured relative to time 0, the time when the hand was vertical. Variability was measured as the SD of the mean onset time for 150 throws. Figure 14B shows the mean SD across all subjects for each joint rotation. SDs for finger extension for both right and left arms were not larger than those for other joint rotations of the same arm. Similarly, when timing was measured at a similar point in the throw near ball release, SDs were not larger for the finger (Fig. 14C). Thus no evidence was found that finger extension was less accurately timed than rotations at other joints.

**DISCUSSION**

Why are throws made with the nondominant arm less accurate than throws made with the dominant arm? The results show four major findings: 1) for throws made with the nondominant arm, hand trajectories and rotations at all joints were, in general, more variable than those of the dominant arm, 2) the decreased ball accuracy in the high-low direction was not primarily caused by variability in the proximal joints affecting hand trajectory; instead, 3) this decreased accuracy was primarily caused by increased variability in the timing of onset of finger extension, and thereby in the timing of ball release, and 4) timing of finger extension for both dominant and nondominant arms was no less accurate than timing of other joint rotations.

**Cause of ball inaccuracy for the nondominant arm**

Over 90% of people favor the right hand for many tasks (Annett 1972; Oldfield 1971), and they continue to do so even after extensive practice with the left hand, particularly for actions that involve temporal sequencing of movements (Annett et al. 1974, 1979; Peters 1976). The superiority of the dominant arm has been measured in several exacting tasks including reaching to a target (Fisk and Goodale 1985), placing pegs in a board (Annett et al. 1979), tapping (Kimura and Davidson 1975), and dart throwing (Watson and Kimura 1989).

For overarm throwing, we found that right-handers hit the target height ~1.5–4 times more often with the right arm than with the left. But this is not a good way to quantify relative throwing accuracy because it depends on an arbitrary definition of target size. A better general measure of accuracy is plotted in Fig. 2, which shows that the SD of ball impact heights was 2–6 times larger with the left arm.

The present results also demonstrate the cause of the decrease in throwing accuracy in the high-low direction. For throws with the nondominant arm, ball inaccuracy was related to variability in hand and finger angular position in space at ball release, which, in turn, was caused by variable timing of onset of finger extension.

This result fits with the principle of a proximal-to-distal shift in the focus of motor control as skill is achieved (Gesell 1947). Increased involvement of distal limb segments in skilled action has also recently been reported in a writing task (Newell and van Emmerik 1989) and in a ball striking task (Southard 1989). It remains to be determined whether...
this principle will apply for throwing accuracy in the left-right direction. Intuitively it might be expected that left-right accuracy would be associated with disorders in control of proximal joints (e.g., shoulder azimuth), although it is possible that the amplitudes of shoulder rotations at ball release are related to the timing of ball release and thus are also controlled by distal joints.

As previously discussed (Hore et al. 1996b), the relation between finger and hand orientation at ball release and ball direction is complex. One reason is that in a throw the hand moves in a flattened arc (Hore et al. 1995) and therefore ball direction will be affected by the changing direction of the velocity vector of the hand. Second, in the process of release, the ball rolls along the fingers while being transported by the hand. Consequently its velocity vector is not the same as those of the hand or the fingertip, but also depends on finger orientation. Thus our observed correlation between throwing accuracy and finger and hand orientation was probably due to two factors: finger and hand orientation are indirectly related to ball path because they are correlated with hand translational velocity (cf. Fig. 3), and finger orientation also influences ball direction directly, through its effect during rolling.

The finding that ball inaccuracy was related to timing of onset of finger extension both in the dominant arm (Hore et al. 1996b) and the nondominant arm (present results) suggested that control of timing of the fingers was less precise than that of other joints. However, timing of finger extension for both the dominant and nondominant arm was no less accurate than timing for other joints (Fig. 14).

**Effect of the fingers on ball accuracy**

Why then is it only timing of the fingers that is significantly related to ball throwing accuracy? One factor is that hand orientation at ball release is more sensitive to finger timing than to other joint motions. For example, suppose that at ball release the angular velocity of the hand in space is 2,400°/s, with shoulder roll, elbow extension, and wrist flexion each contributing 800°/s. Note that a 10-ms error in finger timing will result in a 24° error in hand orientation at ball release, whereas the same timing error at any one of the proximal joints will cause an error of only 8°. Thus errors in finger timing are more critical, because their consequences for projectile motion are scaled by the higher velocity of the hand in space.

To estimate this effect more realistically, we can use the computer to decompose a throw into the contributions of separate joints and then manipulate these contributions to see which ones have the greatest effect on the flight path of the ball in simulated throws. Figure 15A shows the final 100 ms of a real throw by a typical subject, with individual computer snapshots of the arm at 2-ms intervals. In the final snapshot, which is actually taken 10 ms before the distal trigger signaled final ball release, the translational velocity of the metacarpophalangeal joint is drawn as an arrow. We know that metacarpophalangeal motion at this moment accurately reflects ball velocity, better than metacarpophalangeal motion at final release, because the hand releases its grip on the ball before final contact is lost at the finger tips (Hore et al. 1996a). The angle between the hand and the distal phalanx of the middle finger is 57.4° at this instant, and so we take this value as the criterion for effective ball release in the simulated throws in Fig. 15, B–D.

Figure 15B shows a throw constructed by the computer, in which the motion of the finger relative to the hand is delayed 10 ms, but all other joint motions (shoulder azimuth, elevation, and roll; elbow and wrist extension) are exactly as in Fig. 15A. We assume that the ball is effectively released when the finger angle equals its threshold value of 57.4° and that ball flight velocity equals metacarpophalangeal velocity at this instant. Because of the delay, the finger angle reaches 57.4° 10 ms later than in Fig. 15A, with the result that the ball flies off on a downward trajectory. The angle Θ between the ball velocity in the altered throw (Fig. 15B) and the actual throw (Fig. 15A) is 20.3° in this case.

To compare the influences of different components of the throw, we shifted each component (shoulder azimuth, elevation, and roll; elbow and wrist extension; and finger opening) while leaving all other components unchanged, and measured the effects on Θ. Figure 15, C and D, shows the effects of delaying roll and elbow extension by 10 ms. When quantifying Θ, we delayed the components by the more realistic interval of 1 ms. Thus, if we start with the normal throw in Fig. 15A, a 1-ms delay in finger motion causes a change in ball direction (Θ) of 2.2°, whereas equal delays in shoulder roll and elbow extension caused changes of 1.1° and 0.9°, and all other components of the throw changed ball direction by <0.2°. Thus finger delay had twice the effect of shoulder roll or elbow extension, and ≈10 times the effect of any other component. To get a feel for these numbers, note that a 2.2° change in the direction of ball flight away from horizontal results in a 250 × tan(2.2°) = 9.7-cm change in the point of impact of the ball on a vertical screen 250 cm away from the point of release. This is the accuracy cost of a 1 ms error in finger timing, assuming a ball speed of ~12 m/s, as in the throw in Fig. 15A. Actual measurements for all throws of the timing of ball release and the associated spread of ball impact heights on target (Fig. 11) indicate that a 1-ms difference in ball release caused a 4- to 6-cm difference on the target. For a baseball pitcher or an ice age hunter, throwing 3 times as fast and
>8 times as far, the cost might exceed 1–2 m, i.e., one to two strike zones or half a mammoth (cf. Calvin 1983). These simulations support the idea that the projectile’s flight path is especially sensitive to finger timing, and this may explain the correlations between accuracy and finger motion.

Control of proximal joints

Although ball inaccuracies resulted from errors in timing of the fingers, we also found evidence for less precise control of rotations at proximal joints of the left versus the right arm. Thus hand trajectory heights were more variable (Table 1) and there was greater variability of rotations at proximal joints (Fig. 8). Presumably this reflects decreased precision in the neural commands to the proximal muscles.

The more variable hand trajectories and joint rotations of the nondominant arm could result from lack of practice. In other situations, practice resulted in more consistent trajectories in a dart throwing task (Higgins and Spachte 1972), in elbow flexion and extension movements in humans (Darling and Cooke 1987), and in an arm aiming task in monkeys (Georgopolous et al. 1981).

Variability of the hand trajectory is produced by variability in joint rotations, but the relation between the two is complex. Although it might be expected that increased variability in one would be directly associated with increased variability in the other, many examples have been found for motor equivalence, i.e., a fixed hand trajectory is associated with variable patterns of joint rotations. For example, in skilled marksmen, wrist and shoulder rotations covaried to produce low end point variability (Arutunyan et al. 1968, 1969). Similarly, in dart throwing, practice produced changes in joint relations whereas trajectories stayed relatively constant (McDonald et al. 1989). For throwing, greater accuracy of the dominant arm is associated with a general reduction but not abolition of variability in rotations at all joints (Fig. 8). Achievement of accuracy may depend not only on a reduction in variability, but also on refinement of mechanisms whereby variability at proximal joints is corrected for by adjustments in rotations at distal joints (cf. Cordo 1990).

Differences in hemispheric control

The differences in performance between the right and left arms may result from differences in control by the left and right hemispheres. Insight into hemispheric differences has come from studies of patients with unilateral brain damage (e.g., Goodale 1988). To control for natural hand asymmetries, hemiparesis, and hemisensory loss, performance of the limb ipsilateral to the lesion is compared with that of controls using the same limb. Such studies have provided evidence that each hemisphere has a specialized role in the control of goal-directed movements of both arms. The right hemisphere has a preferential role in visual guidance both before and during movement (Fisk and Goodale 1988; Goodale et al. 1990; Haaland and Harrington 1989a,b; Weinstein and Pohl 1995), whereas the left hemisphere has a preferential role in programming the ballistic aspects of movement, in particular timing and sequencing (Harrington and Haaland 1991; Kimura 1977; Weinstein and Pohl 1995).

These behavioral specializations may be associated with anatomic and physiological differences between the two hemispheres. In the squirrel monkey, Nudo et al. (1992) found that distal forelimb representations in motor cortex were larger and had a more complex organization contralateral to the preferred hand. Similarly in humans, Wasserman et al. (1992), using magnetic stimulation, found a larger cortical representation for the abductor pollicis brevis muscle on the dominant hemisphere, and Triggs et al. (1994), using magnetic stimulation of the vertex of the scalp, found lower thresholds for excitation of arm and hand muscles of the dominant arm. These stimulation differences could reflect differences between the hemispheres in the density, excitability, or synaptic efficacy of synaptic inputs to corticospinal neurons or in the corticospinal neurons themselves. Such differences could reflect intrinsic organizational differences between the hemispheres or result from the effects of training and experience (Kaas 1991; Karni et al. 1995; Pascual-Leone and Torres 1993; Pascual-Leone et al. 1995; Recanzone et al. 1992).

The classic studies of Gazzaniga (1970) and Brinkman and Kuypers (1973) demonstrated two important points. First, they showed that proximal muscles of the arms are controlled from both hemispheres. This may explain the apparent similarity of the hand trajectory in left and right arms of the same subject (Fig. 4). Second, they found that hand and fingers are controlled from separate (contralateral) hemispheres. Furthermore, it is clear that the hand and fingers receive strong inputs from the corticospinal tract (e.g., Palmer and Ashby 1992; Porter and Lemon 1993), particularly from corticomontoneuronal cells (Fetz and Cheney 1980; Lemon et al. 1986). Given that the left hemisphere is specialized for timing of movement sequences in right-handers, it follows that the disorder in timing of finger opening of the left hand in overarm throwing may result from either inadequate interhemispheric transfer of timing information from the left to the right hemisphere or from inadequate intrinsic timing ability of the right hemisphere. Either way it is likely that the inferior timing of the left fingers in overarm throwing in right-handers results from imprecise timing of the commands from the right hemisphere to the left fingers by way of corticomontoneuronal cells.

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