Control of Finger Grip Forces in Overarm Throws Made by Skilled Throwers

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INTRODUCTION

There is increasing evidence that certain tasks involving the hand are controlled by internal neural models of the hand and the interactions it has with expected external loads. However, the nature of the underlying neural mechanisms remains to be determined. For the precision (pinch) grip Johansson and Westling (1988b) proposed that anticipatory muscle responses generated when subjects dropped a ball into a cup held by the forefinger and thumb were best explained by an internal representation (internal model) that possessed knowledge about the dynamics of this situation. Similar conclusions about the existence of internal models of the hand that know dynamics have come from a variety of studies including catching a ball dropped from a height (Lacquaniti and Maioli 1989a,b), gripping and pulling a manipulandum subjected to different loads (Flanagan and Wing 1997), and controlling finger amplitudes in overarm throws (Hore et al. 1999). In the latter case, it was concluded that subjects adjusted the amplitude of finger opening by predicting the different back forces that occur on the fingers in throws with balls of different weights.

Hore, J., S. Watts, M. Leschuk, and A. MacDougall. Control of finger grip forces in overarm throws made by skilled throwers. J Neurophysiol 86: 2678–2689, 2001. In an overarm throw, as the hand opens and the ball rolls along the fingers, the ball exerts a back force on the fingers. Previous studies suggested that skilled throwers compensate for this back force by producing an appropriate finger flexor torque to oppose the back force, but it was unclear how this is controlled by the CNS. We investigated whether the increase in finger flexor torque is timed precisely to occur late in the throw as the fingers open or whether the increase occurs throughout the throw to anticipate the increase in hand acceleration. Recreational ball players threw balls of different weights and diameters at different speeds from both a sitting and standing position while arm joint rotations were recorded with the search-coil technique. Force transducers were taped to the distal and middle phalanges of the middle finger and subjects released the ball from this finger. Passive forces on the finger were also recorded in “fake” throws in which the ball was taped to the finger and subjects did not grip the ball. These skilled throwers correctly anticipated the magnitude of the back force from the ball on the finger because the mean amplitude of finger extension did not increase in throws made with a large range of increasing back forces. This was achieved by subjects gripping the ball during the backswing with a force proportional to ball weight and intended ball speed (acceleration) and progressively increasing the grip force throughout the backswing and forward throw. The magnitude of this grip force during the forward throw was not affected by ball texture. After ball release from the fingertip, the finger flexed in proportion to the peak force on the finger before ball release. It is concluded, in a skilled fast overarm throw where large, fast-changing forces on the fingers result from the sum of motions at all arm joints, that finger flexor torque is progressively increased throughout the throw in an anticipatory (predictive) fashion to counteract the progressively increasing back force from the ball.
forces from the ball on the fingers. To this end, we asked the following questions: is finger amplitude kept constant over a wide range of back forces produced by slow and fast throws and by balls of different diameters and weights? Is the increase in finger flexor torque timed precisely to occur late in the throw as the fingers open or does the increase occur throughout the throw to anticipate the increase in hand acceleration? And, is the grip of the fingers on the ball affected by the texture of the ball?

METHODS

General procedures

A variety of experiments were performed on a total of 18 right-handed males (ages 22–55) who gave their informed consent. In all cases, subjects were recreational ball players and all were instructed to throw with an overarm motion (i.e., with a backswing that took the hand behind the head and with a forward motion using shoulder adduction). In different experiments, subjects threw from a sitting position (so hand translation could be reconstructed) and from a standing position (so we could verify that results applied for a natural throw). In many cases, the same subject threw from both positions. In the sitting experiments, subjects sat on a wooden chair with the trunk fixed by means of straps over the shoulders. When standing, they stood with their left foot forward and feet stationary. In three of the five series of experiments (see following text), subjects threw five different balls: three tennis-sized balls (a light plastic ball with a hard surface, a tennis ball, and a tennis ball filled with concrete) and two hard-surfaced balls of larger diameter also filled with concrete. Weights and diameters were light ball (14 g, 70 mm), normal tennis ball (55 g, 65 mm), heavy tennis ball (196 g, 65 mm), 360 g ball (72 mm), and 715 g ball (92 mm). Subjects gripped the tennis-sized balls with the first three fingers and thumb. When throwing balls of larger diameter, the whole hand was used to grip the ball. In all cases, subjects were instructed to center the ball on the middle finger with the first and third fingers to the side of the ball. Subjects were instructed to throw with a normal motion but without gripping the ball. In the fifth series (does finger force change with different ball texture?), four subjects (Pe, Db, Iv, Ln) threw a different set of four balls that had the same hard, smooth plastic (slippery) surface and the same diameter (74 mm) but that were of different weights (20, 116, 242, and 416 g). Again, with force transducers taped to the middle finger, the ball was centered on the middle finger with the first and third fingers to the side of the ball. Subjects threw a particular (slippery) ball 15 times. The surface texture of the ball was then changed by taping it with black adhesive hockey tape (friction tape, Renfrew), which was sticky to the touch and added ~10 g to the weight of the ball. This tape is designed to wrap around the blade of an ice-hockey stick to produce increased puck control. Subjects made 15 throws with the taped (sticky) ball, the tape was removed, the ball cleaned, and the subject made a second 15 throws when the ball was slippery. This sequence was repeated for each ball.

Arm positions

Angular positions were obtained of the finger, hand, forearm, upper arm, and scapula using the magnetic-field search-coil technique. Subjects sat in orthogonal alternating magnetic fields of frequencies 62.5, 100, and 125 kHz with coil voltages sampled at 1,000 Hz. Search coils (Skalar) were securely taped to the distal phalanx of the middle finger, the back of the hand, the forearm proximal to the wrist, the lateral aspect of the upper arm, and the skin overlying the scapula. This configuration allowed the simultaneous recording of all five arm segments in three-dimensional space.

Data analysis

The angular position of each arm segment was computed off-line as previously (e.g., Hore et al. 1992, 1996; Tweed et al. 1990). Angular positions of the finger and hand in space were described as vertical rotations around a space-fixed horizontal axis. Finger opening was defined as the angular position of the distal phalanx of the middle finger with respect to the angular position of the hand. In this case, the horizontal axis rotated with the hand. Translational positions in the seated throws were reconstructed from coil signals by computer using the measured lengths of each arm segment and the space-fixed position of the sternum.

Statistics

The effect of two different throwing speeds on finger amplitude was analyzed with a t-test which assumed equal variance. To determine whether the amplitude of finger extension was different for throws with balls of five different weights, a one-way repeated-measures ANOVA was performed with Duncan’s multiple range test. Post hoc
regression analysis determined whether there was a finger amplitude increase or decrease with the balls of different weights. To determine whether there was a relation between any two further variables (e.g., amplitude of finger extension and time of ball release), 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 ANOVA procedure (\( F \) test of regression ANOVA).

RESULTS

Effect of a wide range of back forces on finger amplitude

In an overarm throw made from the sitting position, the hand rotates forward with a flattened arc trajectory. Figure 1A shows this rotation and arm segment positions every 5 ms over the last 60 ms of the throw to final ball release from the fingertips (time 0). The throw was made at a medium speed of 15 m/s. In such a throw, as the fingers accelerate forward and downward, they push on the ball and the ball pushes back on the fingers, i.e., there is a back force from the ball on the fingers. This is illustrated diagrammatically in Fig. 1B for a moment in the throw 5 ms before the ball rolled off the tip of the finger. The magnitude of the force on the finger at this moment is proportional to the acceleration of the finger and the mass of the ball. We previously found, when recreational ball players threw tennis-sized balls of different weights (14, 55, and 196 g) at \( \sim 15 \) m/s, that across subjects an increase in back forces produced by the heavier balls did not (as might have been expected) produce an increase in the amplitude of finger extension associated with releasing the ball (Hore et al. 1999). However, this result was for a relatively restricted set of throwing conditions that the subjects could have been familiar with and for which they could have learned specific motor patterns. That is, most subjects are familiar with light (14 g) plastic balls and tennis balls (55 g), and the heavy tennis ball at 196 g was not markedly different from the weight of a baseball (\( \sim 145 \) g). Would this previous result also apply for throws of different speeds and for balls of a wider range of weights and diameters?

The effect of different ball weights and speeds on the amplitude of finger extension is shown in Fig. 2. Figure 2A shows averages of finger extension (top) and of forces on the distal phalanx (bottom) for a subject \((Nv)\) who threw the 14-, 55-, and 196-g balls (which were of similar diameters) at a slow speed (thin line), medium speed (medium line), and fast speed (thick line) from a standing position using a grip such that during ball release the ball rolled along the middle finger. Records are averages of 15 throws aligned on the moment of ball release from the fingertips (vertical line). The peak force on the distal phalanx, which occurred just before ball release from the fingertip, was due to back force from the ball on the finger. This peak was markedly different for the different throws being larger for faster throws made with each ball and larger for throws of the same speed made with heavier balls. In spite of the markedly different back forces, the amplitude of finger extension did not increase for the different balls with an increase in back force. Figure 3A shows mean values of finger extension amplitude for 40 slow (S) and 40 fast (F) throws made from the standing position for each of the three different balls from a different experiment (without force transducers taped to the middle finger to avoid adding mass to the fingers) for this same subject \((Nv)\) and for five further subjects. Finger amplitude was measured from when onset of finger extension crossed a low-velocity threshold (200°/s) to the moment of final ball release from the fingertip. We have previously reported for these same fast throws (Hore et al. 1999) that an increase in back forces produced with balls of increasing weight did not increase finger amplitude (in fact finger amplitude was decreased with an increase in ball weight in subjects \(Nv, Dv, Jn,\) and \(Ak\)). A similar result was found for throws of slow and fast speeds. Although fast throws had larger back forces than slow throws (Fig. 2A), across subjects there was no increase in finger amplitude for fast throws compared with slow throws for any of the three balls, and there was a decrease for fast throws made with the 55-g ball (\( P < 0.05, \) t-test).

Considering balls of a wide range of weights (14–715 g) and diameters (65–92 mm), Fig. 2B (bottom) shows that when subject \( Ma\) was instructed to throw these balls at a medium speed while standing, peak forces on the distal phalanx of the middle finger just before final ball release from the fingertips (vertical line) were larger with balls of larger weight. In spite of this, the amplitude of finger extension (top) did not increase. Figure 3B shows for subject \( Ma\) and for five further subjects that the individual patterns of finger amplitude with balls of different weight were slightly different. For example, for the increase in ball weight from 14 to 360 g, there was no change in mean finger amplitude in subject \( Ma,\) a decrease in \( Dv\) and an increase in \( Ri\). However, across subjects, mean amplitudes of finger extension were not significantly different for the 14-, 55-, 196-, and 360-g balls and were decreased for the 715-g ball (1-way repeated-measures ANOVA with Duncan’s multiple range test). The same result was found for throws made...
from the sitting position. In summary, across subjects, an increase in back forces produced by either an increase in throwing speed or an increase in ball weight was associated with no change or a decrease in the amplitude of finger extension.

Forces recorded on the fingers throughout a throw

We have seen that during ball release the ball exerts a back force on the finger. This force recorded on the distal phalanx (e.g., Fig. 2A, bottom) increases during finger opening (extension) and peaks just before ball release. How is this force controlled by the CNS? At first sight, the records in Fig. 2A suggest that finger flexor force is timed to increase as the fingers open, i.e., it is timed to increase as the ball rolls along the fingers. However, examination of the forces recorded on the middle and distal phalanges throughout the throw and consideration of the mechanism of ball release revealed that this was not the case.

Figure 4 shows some hand and finger translational kinematic parameters together with forces recorded from the middle and distal phalanges from subject De, who threw with a slow backswing. Each trace is the mean of 10 throws made with a ball of a different weight (14–360 g) aligned on the moment of final ball release (time 0). This force recorded on the distal phalanx (Fig. 4E) also increased throughout the throw. However, ~60 ms before final ball release, they decreased before increasing again. The explanation for this pattern is illustrated in Fig. 4G, which is a diagrammatic representation of ball release from the fingers. Time periods in Fig. 4G are marked by vertical lines in Fig. 4, D–F. About 60 ms before final ball release (time 0) the distal phalanx begins to extend (Fig. 4F), thereby lifting the fingertip away from the ball (~60 to ~30, Fig. 4G). This causes a decrease in force on the distal phalanx (Fig. 4E) but not on the middle phalanx (Fig. 4D). As a result of this release of grip, the ball starts to roll up the finger (~30 to ~10, Fig. 4G), thereby rolling off the middle phalanx (decrease in force, Fig. 4D) and rolling on to the distal phalanx and reapplying a back force to it (increase in force, Fig. 4E). In summary, forces on the finger increase throughout the backswing and forward throw, but their recording on the distal phalanx is affected by lift-off of the distal phalanx from the ball during finger opening.

Two mechanisms by which subjects could compensate for increasing back forces from the ball are to increase finger flexor force or to strongly cocontract the fingers. In both situations, an increase in force would be recorded on the fingers during forward hand acceleration: in the first case because of finger flexor force and in the second because of inertial force pressing against a stiff segment. One way to distinguish between these possibilities is to instruct subjects to throw with a slow backswing and to examine forces at the end of the backswing where inertial forces are small or nonexistent. If cocontraction was exclusively occurring, one would expect a small grip force to hold the ball throughout the backswing (e.g., 1 N, Fig. 4, D and E, far left) and a ramp-like increase proportional to the gravitational force as the hand rotated backward and down. Figure 4 shows for subject De that at the
end of the backswing (dashed vertical line), the translational acceleration of the finger in both the backward-forward (Fig. 4B) and vertical direction (Fig. 4C) was close to zero. Contrary to the cocontraction hypothesis, the force on the middle finger was larger than could be accounted for by the initial grip force plus the gravitational force, e.g., for the 360-g ball at the end of the backswing the total force on the middle finger (middle phalanx plus distal phalanx) was −8 N, whereas the initial grip force (1 N) plus calculated maximal gravitational force [(360 g × 9.8) = 3.5 N] was only 4.5 N. Considering the balls of

### FIG. 3. Mean amplitudes of finger extension for all subjects for throws made under different conditions. Amplitude was measured from onset of finger opening to the moment the ball left the fingertip. 

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<tr>
<th>Ball Weight</th>
<th>Slow Speed</th>
<th>Fast Speed</th>
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<tbody>
<tr>
<td>14 g</td>
<td>30° ± 10°</td>
<td>35° ± 15°</td>
</tr>
<tr>
<td>55 g</td>
<td>32° ± 12°</td>
<td>37° ± 18°</td>
</tr>
<tr>
<td>196 g</td>
<td>34° ± 14°</td>
<td>39° ± 20°</td>
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<tr>
<td>360 g</td>
<td>36° ± 16°</td>
<td>41° ± 22°</td>
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<tr>
<td>715 g</td>
<td>38° ± 18°</td>
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### FIG. 4. Hand and finger translational kinematics and forces on distal and middle phalanges of middle finger for throws with balls of different weights. Throws made from sitting position. Ball weights were 14, 55, 196, and 360 g and diameters were 70, 65, 65, and 72 mm, respectively; subject De. Each trace is the mean of 10 throws aligned on final ball release from the fingertip (time 0). G: diagrammatic representation of hand and finger phalanx positions during ball release.
different weights, a strong relation was found between the magnitude of forces on the finger at the end of the backswing and the magnitude of the peak force recorded on the distal phalanx just prior to ball release. This is shown for the middle phalanx for two subjects in Fig. 5A and distal phalanx for two subjects in Fig. 5B. Again large forces occurred at the end of the backswing (start forward throw), e.g., for subject Ma, the value was ~15 N whereas the gravitational force for the 715-g ball was 7 N.

A second way to distinguish between the increase in finger flexor force hypothesis and the cocontraction hypothesis is to measure what happens at the moment of ball release. If there was a build-up of net finger flexor force to a large level, one would expect an abrupt flexion of the fingers at the moment of ball release. In contrast, if there was only cocontraction of the fingers, no finger flexion would be expected at ball release. We previously reported that immediately following ball release the fingers undergo a brief flexion (flick) whose amplitude is proportional to ball weight (Hore et al. 1999). This suggested that the flexion resulted from a finger flexor torque generated to counteract the back force, which at ball release suddenly became unopposed. According to this scenario, the larger finger flexions with the heavier balls would result from larger finger flexor torques produced during the throw. Figure 4 shows that indeed this was the case, i.e., the increase in peak distal phalanx force with balls of increasing weight before ball release (Fig. 4E) is accompanied by an increase in finger flexion amplitude after ball release (Fig. 4F). This relation is shown in Fig. 6A for subjects De and Ma, i.e., it shows the relation between mean values of peak force on the distal phalanx for each ball of different weight (14, 55, 196, and 360 g) and the corresponding mean values for the amplitude of finger flexion. Figure 6B shows the same relation for the individual throws. In both cases, there is a strong relation, which was seen in all subjects. Similarly, if peak force on the distal phalanx is plotted for individual trials against finger (flexion) position 10 ms after ball release (which is the optimal time for measuring finger flexion before the rebound of the finger toward extension), all skilled subjects showed a strong direct relation for throws made when standing (R² values were De, 0.78; Ma, 0.93; Ri, 0.91; Da, 0.78; and Me, 0.81).

![Graphs showing force comparison](http://jn.physiology.org/)

**Active and passive forces**

Although the results in Figs. 4 and 5 suggest that the back force from the ball is opposed by a progressive increase in finger flexor forces throughout the throw, it could be argued that for some subjects, a combination of initial grip, translational and gravitational forces could have caused the large forces at the end of the backswing (start of forward throw). To investigate the contribution of different forces and the possibility of cocontraction more rigorously, we recorded total forces (active, passive, and gravitational) on the middle finger in a normal throw with a slow backswing that was made with a tennis ball filled with concrete (228 g) to which was glued a flat surface that improved contact with the force transducers taped to the distal and middle phalanges. We ensured that forces were restricted to the middle finger by taping the other three fingers behind the middle finger. In a second experiment, only passive and gravitational forces were recorded. This was achieved by taping the ball to the fingers with the flat surface of the ball over the force transducers. The other three fingers were taped behind the middle finger so that neither they nor the thumb touched the ball. In addition, the fingers were splinted to the hand by means of a 14 × 7-cm sheet of wood that further restricted finger movement. Subjects were asked to make the same throwing motion as before and at the same speed without gripping the ball (fake throw). Figure 7 shows superimposed records of the average of 30 normal throws (thin lines) and 30 taped (fake) throws (thick lines) from one subject. The backward-forward component of hand translation (Fig. 7A) and the vertical component of hand angular position (Fig. 7B) were similar for the normal and taped throws. As expected, finger extensions were slightly different in the two throws (Fig. 7C).
In the normal throws, there was a small finger extension that released the ball, whereas in the taped throws, the fingers (although splinted) were pushed back a small amount by the back force from the ball. Forces recorded on the two phalanges were added together to give the total force on the finger (Fig. 7D). For the normal throws, total finger force started at a level of \( \approx 1 \) N during the backswing and increased progressively throughout the throw. The start of the hand in the forward translational direction is indicated by short vertical lines in Fig. 7, A and D. For the normal throws, \( \approx 35 \) ms before the hand was vertical in space (right vertical line) these forces decreased as the finger extended and the ball rolled off the finger. Forces on the finger for the taped throws (Fig. 7D) increased slightly toward the end of the backswing (due to gravity and deceleration of the hand). Their increase during the forward throw was associated with forward and downwards acceleration of the fingers (Fig. 4, B and C) as described previously (Hore et al. 1999).

Figure 7D shows that total force on the finger (thin line) for a normal throw had a different time course and magnitude than the passive/gravitational force (thick line). This is shown more clearly in Fig. 8A in which normal and taped throws for all subjects have been aligned on the start of hand forward translation (vertical line time 0). These records are not consistent with the cocontraction hypothesis. That is, if subjects were using a step-like increase in grip force to hold the ball and cocontraction to oppose the back force, one would expect a parallel increase in the two traces. However, for all subjects, the total force began earlier than the passive force and the separation between the two traces progressively increased throughout the throw. This difference between the two traces, which can only be attributed to active force, is shown in Fig. 8B. Contrary to the cocontraction hypothesis, which predicts a flat (horizontal) line, in all six subjects, there was a progressive increase in the difference between the traces throughout the throw which began during the backswing (on average, \( \approx 200 \) ms before the start of forward hand translation; dashed vertical line in Fig. 8B). In five subjects, the increase of total force over passive/gravitational force was associated with flexion of the finger prior to extension as shown for subject Pe in Fig. 7C, thin line. This occurred in spite of finger flexion being opposed by the thumb as the subject gripped the ball. These results are consistent with the hypothesis that there is an anticipatory progressive increase in active finger flexion force throughout the throw (with a large safety margin) to oppose the progressive increase in back force from the ball.

Influence of ball texture on finger force

In view of the importance of object friction in the precision grip (e.g., Cadoret and Smith 1996), the question arose whether similar effects occurred in throwing. There were two possibilities which made opposite predictions. The first was that subjects would grip the more slippery balls more tightly and would therefore show larger finger forces during the throw with the slippery balls. The second was that forces on the finger during the throw are dominated by the control of back forces and that finger forces would therefore be related to ball weight and speed (acceleration) and not to texture. Figure 4 shows that the second possibility appeared to be correct, i.e., throws with the
light plastic ball (14 g) that had a hard, smooth (relatively slippery) surface, had lower finger forces than throws made with the tennis ball (55 g) and heavy tennis ball (196 g), which had a similar diameter but had a fuzzy (higher-friction) surface. However, to investigate this more rigorously, four subjects threw four balls of the same diameter (74 mm) that had the same hard, smooth (slippery) plastic surface but which were of different weights (20, 116, 242, and 416 g). Subjects made 15 throws with a particular (slippery) ball, the surface texture of the ball was then markedly changed by covering it with tape that was sticky to the touch (see METHODS), and the throws were repeated. The tape was removed, the ball was cleaned, and another 15 throws were made when the ball was slippery again. Figure 9 shows the results from one representative subject. Force recorded from the middle phalanx is shown in Fig. 9A and from the distal phalanx in Fig. 9B. For each ball, the thin lines represent the averages of the 15 before and the 15 after throws with the normal (slippery) ball, whereas the thick line represents averages of the 15 throws with the taped (sticky) ball. Traces for the 242-g ball were omitted for clarity in Fig. 8B because they overlapped other traces. Forces on the finger were similar whether the ball was slippery or sticky. For example, 100 ms before ball release (dashed line during the forward throw), the 416-g sticky ball had a slightly smaller force on the middle phalanx but a slightly larger force on the distal phalanx, whereas this was reversed for the 116-g ball. This illustrates the point that the total grip force could be shared between the two finger phalanges. The finding that the taped (sticky) 20-g ball showed larger forces on both the middle and distal phalanges during the forward throw presumably occurred because the tape added 10 g to the weight of the ball, and this additional weight produced a relatively large (50%) increase in back forces on both phalanges. (Note that an addition of 10 g to the 416-g ball only increased its weight by 2.4%). To determine whether there was a statistically significant difference in force on the finger when the ball was slippery or sticky, we compared force in two ways. First, because total force was shared between the middle and distal phalanges, we added force on the two phalanges at an arbitrary point during the forward throw (100 ms before ball release) for individual throws with each ball. Simple linear regression lines for total finger force against ball weight were then obtained for the before throws with the slippery ball, throws with the sticky ball, and the after throws with the slippery ball (Fig. 8C). The
slopes and elevations (vertical positions on the graphs) of different pairs of lines were then compared with t-tests (Zar 1999). It should be noted that comparing lines in this way cancels out the effect of the additional 10 g due to the tape in the sticky ball condition. No statistical difference was found between any pair of lines. We also compared the peak force on the distal phalanx just before ball release for the slippery and sticky balls with the same procedure (Fig. 8D). Again no statistically significant difference was found between any pair of lines. We conclude that during the forward throw, forces on the finger were related to ball weight and not to ball surface texture.

DISCUSSION

Anticipatory control of the hand

Overarm throws made at different speeds with balls of different weights produce different back forces on the fingers. We previously proposed (Hore et al. 1999) that these back forces are compensated for by an internal model which scales finger flexor torques based on a prediction of hand dynamics. But it was unclear how this increase in finger flexor torque was controlled by the CNS. The present results show that in throws made with a slow backswing, back forces from the ball begin near the end of the backswing and increase progressively throughout the forward throw (Figs. 7 and 8). The results also show that the total flexor grip force developed by the fingers anticipated and counteracted the back forces by beginning earlier and also progressively increasing throughout the throw.

Many tasks involving the hand have now been found where muscle activity and the resulting forces are produced in an anticipatory fashion (Flanagan and Wing 1997; Hermsdörfer et al. 1999; Johansson and Westling 1998a,b; Lacquaniti et al. 1992; Serrien et al. 1999). These include tasks which are similar to throwing in that they required the subject to grip an object with the whole hand during rapid hand acceleration. For example, in one task subjects grasped a 400-g object with a four-fingers-and-thumb precision grip (Kinoshita et al. 1996). They then either shook the object in various directions or held it in front of them as they walked or ran on the spot (which also shook the hand). As in throwing, grip force was controlled in an anticipatory fashion, i.e., it increased and decreased in phase with hand acceleration. Similarly, grip force on a hand-held object was found to be modulated in phase with acceleration-dependent inertial loads in point-to-point arm movements (Flanagan and Wing 1993) and in brisk vertical cyclic arm movements (Flanagan and Wing 1995).

A consequence of anticipatory activity in throwing is that the total grip force throughout the throw was scaled in magnitude to the expected load. For example, the force on the finger at the end of the backswing was proportional to the peak force on the distal phalanx during ball rolling (Figs. 4 and 5). Similarly, in the precision grip, subjects scaled motor commands to the weight of familiar objects (Gordon et al. 1993; Westling and Johansson 1984). A relatively small safety margin ensured that slips did not occur and, at the same time, that large forces were

FIG. 9. Effect of ball texture on forces recorded on the middle finger. A and B: force recorded on the middle phalanx and distal phalanx, respectively. Each trace for each ball (20, 116, 242, and 416 g) is the average of 15 throws aligned on ball release (time 0) when the ball was sticky (thick lines) and before and after throws when it was slippery (thin lines). The tape added 10 g to the weight of the ball. C: relation between total force on the finger (obtained by adding forces on the middle and distal phalanges 100 ms before ball release) and ball weight for the slippery ball (thin lines) and sticky ball (thick lines). Open triangles, 1st (before) throws with slippery ball; filled squares, throws with taped (sticky) ball; open circles, 2nd (after) throws with slippery ball. D: relation between peak force on the distal phalanx just before ball release and ball weight for the slippery (thin lines) and sticky ball (thick lines). In both C and D each point gives the mean and SD of 15 throws. Lines of best fit were calculated on values for individual throws; subject Pe.
avoided that could crush fragile objects, cause unnecessary muscle fatigue, impoverish sensory feedback, or even damage the hand. In the hand-shaking task, subjects also scaled the magnitude of grip forces with the speed of shaking (Kinoshita et al. 1996), i.e., subjects increased and decreased grip force in proportion to the magnitude of hand acceleration, which ensured that a safety margin occurred to prevent slipping.

In throwing, the finding that total force on the finger began earlier and increased at a faster rate than the passive force (Figs. 7 and 8) is evidence for a progressively increasing grip force with a safety margin which ensured that the ball did not slip out of the hand. This additional grip force, beyond that necessary to oppose the back force, was necessary to overcome the force of gravity and forces associated with hand acceleration on a curved trajectory. It also allowed for continued grip in the face of a larger than expected back force arising from small errors in the estimation of ball weight or throwing speed. One possible reason that the safety margin was relatively large in the experiments shown in Figs. 7 and 8 was that the subjects were holding the ball in an unnatural way with only the middle finger and thumb and with force transducers on the gripping surface of the finger. Presumably smaller safety margins would occur when throwing naturally and gripping with the whole hand. Our recordings may also have overestimated the safety margin. In conclusion, anticipatory control is the normal mechanism by which the CNS controls potentially destabilizing loads in a variety of skilled tasks involving the hand including throwing.

Factors affecting grip force on the middle finger

In the precision grip, the force of finger grip is related to the texture or, more precisely, the surface friction of the object to be gripped (Cadoret and Smith 1996; Forssberg et al. 1995; Johansson and Westling 1984; Westling and Johansson 1984). Therefore at first sight it may have been expected that forces on the middle finger in throwing would be related to ball texture. However, as emphasized throughout this paper, the major variable that must be controlled in a throw is the back force from the ball, and this changes markedly in throws made at different speeds with balls of different weights (Figs. 2 and 4–6), irrespective of their surface texture. Consequently, forces on the finger during the forward throw were related to forces on the finger, and not to ball texture (Fig. 9).

The force recorded on the middle finger in experiments shown in Figs. 2–6 could have been affected by a different distribution of forces across the fingers with balls of different diameters. Although subjects were instructed to center the ball on the middle finger, it is likely that as ball weight and diameter increased, a relatively higher proportion of the total back force was applied to the first (index) and third fingers rather than to the middle finger. This is consistent with the finding (Fig. 2B) that forces recorded on the middle finger did not double with an almost doubling of ball weight (e.g., from 360 to 715 g). However, this finding could also have resulted from a decrease in magnitude of hand acceleration (and therefore back force) with the very heavy 715-g ball. In all likelihood, both factors contributed. If a change occurred in the distribution of back forces across the fingers, results from precision grip studies with thumb and several fingers indicate that this would be taken into account by the CNS (Birznieks et al. 1998; Burstedt et al. 1997; Edin et al. 1992; Flanagan et al. 1999; Li et al. 1998). That is, any changed distribution of back forces across the fingers would be counteracted by a compensatory redistribution of grip forces.

Control of the amplitude of finger opening

The results indicate that finger force in an overarm throw is controlled precisely to keep the amplitude of finger extension relatively constant from throw to throw (Figs. 2 and 3). The most obvious advantage of a constant finger amplitude is to ensure that injury does not occur to the fingers. For example, failure to anticipate the large back forces from the ball on the finger in fast throws made with a heavy ball could result in excessive finger extension and in finger injury. According to this scenario, the decreased amplitude of finger extension with the very heavy 715-g ball (Fig. 3B) occurred because subjects overcompensated for the very large back force (by producing excessively large finger flexor torques) to avoid any chance of finger injury.

A second possible reason for a constant amplitude of finger opening is to ensure that ball accuracy occurs. Although variability in finger amplitude has not been found to cause ball inaccuracy (Hore et al. 1999), failure to control finger amplitude could lead indirectly to changes in timing which is a major cause of ball inaccuracy. For example, very small amplitudes of finger opening could result in lack of precise timing in the initial uncoupling of the ball from the hand and thereby cause variable timing of ball release.

Although the results (Figs. 4–8) were not consistent with cocontraction of finger muscles being the sole mechanism by which back forces from the ball were opposed, they also do not rule out the possibility that some cocontraction was occurring. Such increased stiffness could potentially be of use as the first line of defense against any unexpected disturbing force. Further insight into this issue will require recording of finger flexor and extensor EMG activity.

Central neural mechanisms

The fact that anticipatory activity occurs in a variety of different tasks has led to the idea that the CNS creates an internal model (internal representation) of the motor apparatus, the load and their interaction. Based on this model, predictive commands are issued in advance of potentially destabilizing loads. This internal model is based on memory of previous experience (Gordon et al. 1993) and is updated on the basis of sensory information including vision (Ghez et al. 1995; Gordon et al. 1991), cutaneous information from handling the object (Gordon et al. 1993; Hore et al. 1999; Johansson and Westling 1984), and proprioception (Gordon et al. 1995). For the precision grip, the model is not innate but develops through childhood until adult-like anticipatory control is achieved at age 8–11 (Forssberg et al. 1991, 1992).

Two central structures that are likely involved in control of the grip force in throwing are cortical motor areas and the cerebellum. In a recent fMRI study of the power grip and the precision grip, Ehrsson et al. (2000) found, as expected, that both tasks were associated with activation of primary sensory and motor cortex and that activation was higher with the power grip. Interestingly, activation was higher in some cortical areas...
during the precision grip. Furthermore, in contrast to the contralateral representation for the power grip, the precision grip was associated with extensive activation of both contralateral and ipsilateral hemispheres. One interpretation of these results is that the precision grip is more demanding than the power grip in terms of neural control (Ehrsson et al. 2000). Since control of grip force in throwing is similar to that in the precision grip, it might be expected that both would involve control by the same cortical areas. However, cortical activation may be more widespread in throwing because it also requires precise control of timing and force of proximal muscles. The cerebellum is also likely involved in the control of grip force in throwing because disorders of anticipatory muscle activity occur with lesions of the cerebellum in a number of arm movement tasks including catching a ball (Läng and Bastian 1999), responding to limb perturbations (Hore and Vilis 1984) and generating EMG activity that predicts interaction torques in fast multijoint movements (Bastian et al. 1996). In keeping with these and other findings, motor theorists have proposed that the cerebellum is the site of internal models of the motor apparatus that generate predictive signals (Wolpert et al. 1998).

The role of the cerebellum in controlling finger position in overarm throws will be taken up in the accompanying paper.

Conclusion

The results show that back forces from the ball on the finger increase throughout an overarm throw, that they are opposed by a progressive increase in grip force that is scaled in magnitude to anticipate the back forces, and that during ball release, these forces are precisely balanced to allow a fairly constant amplitude of finger opening to occur from throw to throw. This anticipatory grip force is similar to the control found in a variety of hand tasks such as the precision grip, catching a ball and rapidly moving a hand-held object. The present results add to these previous findings by showing in a skilled fast movement where large, fast-changing forces on the fingers result from the sum of motions at other joints and where there is minimal time for proprioceptive feedback, that finger force is also controlled in an anticipatory (predictive) fashion.

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