Prediction and Compensation by an Internal Model for Back Forces During Finger Opening in an Overarm Throw

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Hore, J., S. Watts, and D. Tweed. Prediction and compensation by an internal model for back forces during finger opening in an overarm throw. J. Neurophysiol. 82: 1187–1197, 1999. Previous studies have indicated that timing of finger opening in an overarm throw is likely controlled centrally, possibly by means of an internal model of hand trajectory. The present objective was to extend the study of throwing to an examination of the dynamics of finger opening. Throwing a heavy ball and throwing a light ball presumably require different neural commands, because the weight of the ball affects the mechanics of the arm, and particularly, the mechanics of the finger. Yet finger control is critical to the accuracy of an overarm throw. We hypothesized that finger opening in an overarm throw is controlled by a central mechanism that uses an internal model to predict and compensate for movement-dependent back forces on the fingers. To test this idea we determined whether finger motion is affected by back forces, i.e., whether larger back forces cause larger finger extensions. Back forces were varied by having subjects throw, at the same fast speed, tennis-sized balls of different weights (14, 55, and 196 g). Arm- and finger-joint rotations were recorded with the search-coil technique; forces on the middle finger were measured with force transducers. Recordings showed that during ball release, the middle finger experienced larger back forces in throws with heavier balls. Nevertheless, most subjects showed proximal interphalangeal joint extensions that were unchanged or actually smaller with the heavier balls. This was the case for the first throw and for all subsequent throws with a ball of a new weight. This suggests that the finger flexors compensated for the larger back forces by exerting larger torques during finger extension. Supporting this view, at the moment of ball release, all finger joints flexed abruptly due to the now unopposed torques of the finger flexors, and the amplitude of this flexion was proportional to ball weight. We conclude that in overarm throws made with balls of different weights, the CNS predicts the different back forces from the balls and adjusts finger flexor torques accordingly. This is consistent with the view that finger opening in overarm throws is controlled by means of an internal model of the motor apparatus and the external load.

INTRODUCTION

Fast, goal-directed movements are often too brief to be controlled by sensory feedback. For overarm throwing, it has been proposed that finger opening could be triggered by proprioceptive feedback from elbow extension (Cordo 1990; Cordo et al. 1994). However, the time interval between the onset of elbow extension and onset of finger opening is ~20 ms for a fast throw, which does not leave sufficient time for feedback from elbow extension to enter the CNS and emerge again to trigger the finger extensors (Hore et al. 1999). In agreement, this previous study also showed that perturbations during throwing that blocked elbow extension did not block finger opening or change its timing.

If a movement is too fast for sensory feedback, what guides it to its goal? One possibility is a feedback system entirely within the CNS. The clearest example of this idea is perhaps Robinson’s (1975) internal-feedback theory of saccades, the rapid eye movements that shift the line of sight from object to object. In Robinson’s theory, a neural circuit called the oculomotor integrator monitors the neural commands being sent to the eye muscles and predicts the resulting changes in eye position before they happen. When the eye-position estimate from the integrator matches the desired eye position, the saccadic system switches off, and the eye comes to rest. As long as the integrator is accurate in its estimates, the saccade will stop on target.

Something similar may underlie fast arm movements: an internal predictor or model may monitor motor commands to the arm muscles and predict the resulting motion (e.g., Flanagan and Wing 1997; Jordan 1995; Kawato 1996; Windhorst 1996; Wolpert et al. 1995). Later occurring joint motions could then be triggered with respect to these central signals without reference to sensory feedback. In keeping with this idea Hore et al. (1999) proposed that the timing of finger opening in an overarm throw was likely controlled by means of an internal model that could predict hand trajectory.

The internal model for arm movements must be more complicated than the internal model for eye movements. For the case of the eye, any given neural command always produces the same motion, whereas for the arm, one and the same neural command will produce different motions depending on the load. If a pitcher threw a light ball and then a heavy ball, using the same neural activity both times, the flight paths of the two pitches would be very different. To maintain accuracy, the internal model would have to take into account the weight of the ball and adjust its predictions of arm and ball motion accordingly.

Our aim was to see whether the neural circuitry that controls finger opening in overarm throws takes into account the ball’s mass. We concentrated on the fingers, because they are the smallest, lightest parts of the motor apparatus, and therefore the parts most easily deflected by force from the ball. But at the same time, finger control is especially important for the accuracy of an overarm throw (Calvin 1983; Hore et al. 1996b). We proposed the hypothesis that finger opening is controlled by means of an internal model that predicts the movement-depen-
dent back forces on the fingers and adjusts the neural commands to the finger muscles to compensate for the differing loads. Without such correction, finger motion would be strongly affected by forces from the ball, with heavier balls producing larger finger extensions. To test the hypothesis, we therefore determined whether finger extension amplitude was larger in throws with balls of heavier weights.

METHODS

General procedures

Measurement techniques were similar to those used previously (e.g., Hore et al. 1996a–c). Experiments were approved by the local ethics review board, and all subjects gave informed consent. Subjects were right-handed male recreational ball players who were accurate throwers. Three series of experiments were performed: (1) to examine the mechanism of finger opening, (2) to determine whether back forces occurred on the fingers, and (3) to determine the kinematics of finger opening with balls of different weights. In each series, throws were made from the sitting position with the trunk fixed by straps so that hand translation could be computed (this required that the sternum was fixed in space), and from the standing position to verify that results applied for a more natural throw. In the first series, six subjects threw tennis balls while seated, and four subjects threw tennis balls from a standing position with the left foot forward without moving their feet. In the second series, six subjects threw balls of three different weights from the sitting and standing positions while back forces were recorded on the middle finger by means of a force transducer taped to the distal phalanx. And in the third series, six subjects threw balls of different weights from the sitting and standing position. In all experiments subjects were instructed to throw accurately at a medium to fast speed (~15 m/s) using an overarm style (i.e., with a motion involving horizontal adduction of the upper arm) and to grip the ball primarily with the middle finger (whose joint angles we measured) so that in the process of ball release the ball rolled along that finger. In the second and third series of experiments, balls were of different weights and diameters: a tennis ball (55 g, 65 mm), a tennis ball filled with concrete (196 g, 65 mm), and a hard hollow plastic ball (14 g, 70 mm). Subjects made a total of 40 throws with each ball in blocks of 20 throws in the order of normal tennis ball, light ball, and heavy ball, then repeated the sequence. They were instructed to throw these balls at the same speed at a grid of 6-cm, numbered target squares, and to aim for the central colored square, which was at eye level ~3.5 m away. Subjects were handed the balls that they then held on or above the right leg in anticipation of the command to throw. The weight of the ball was obvious to the subject, and when a change was made, e.g., from the light to the heavy ball, they usually commented that the weight of the ball was different. Subjects threw with a backswing that took the hand behind the head. Each throw was scored for accuracy by the subject calling out the square that was hit, which was verified by an experimenter.

Ball release was detected by offset of pressure switches attached to the proximal and distal phalanges of the middle finger (see Fig. 1A). If these signals were unavailable, e.g., because the ball rolled along the side of the finger, ball release was defined as the moment when the distal interphalangeal joint reversed its direction from extension to flexion, an event that coincides with departure of the ball from the finger tip (Fig. 1A). Throwing speed was monitored on-line as the peak angular velocity of the hand in space. In the experiments with seated throwers, this latter parameter was found to be strongly linearly related to ball speed (calculated from the flight distance and flight time to ball impact on the target measured by pressure detectors). For the standing throwers, because flight distance was uncertain, hand angular velocity was used as the measure of throwing speed.

Recording angular positions of arm segments

Angular positions of five arm segments were measured using a modification of Robinson’s (1963) search-coil technique (Tweed et al.
the palm forward. Arm horizontal and lateral, and forearm, hand, and fingers vertical with the hand. All joint angles were defined as being 0 when the arm was vertical. Angular positions (orientations) of arm segments in space were calculated directly from search-coil voltages. For the seated subjects, transnational positions were computed using these orientations and the measured lengths of the arm segments. Locations in space were expressed with respect to the sternal notch, which was held stationary by the straps over the shoulders.

Finger and hand configurations were also described in terms of joint angles. Flexion-extension at each finger joint was obtained from the angular positions of the corresponding phalanges, and for the metacarpophalangeal joint, the angular position of the proximal phalanx and the hand. All joint angles were defined as being 0 when the arm was in reference position, with the subject facing the target with the upper arm horizontal and lateral, and forearm, hand, and fingers vertical with the palm forward.

Statistics
To determine whether the amplitude of finger extension was different for throws with balls of different weights, a one-way 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.

Photography
To verify the accuracy of measurements computed from the coil signals, hand paths were also recorded with long-exposure photography (Fig. 1C). Six subjects threw from the seated position with a light-emitting diode attached to their hand. This diode was wired so that it went off for a few milliseconds at the time of offset of the switch on the proximal phalanx and went off permanently at the time of final offset of the switch on the distal phalanx, i.e., at final ball release. This latter signal was also used to trigger a stroboscope that flashed at final ball departure and 50 ms later, thereby giving the ball path.

Results
Ball release from the hand
In an overarm throw, ball release occurs by a mechanism that involves opening the fingers as the hand moves in a flattened arc underneath the ball (Hore et al. 1996a,b). Correspondingly, with respect to the hand, the ball rolls up the fingers and is released from the fingertips. The steps involved in this process are illustrated in Fig. 1A for a throw made by a seated thrower (Jn) at a medium speed (12.5 m/s). Zero angle for the finger joints indicates when the finger was in a straight line with the hand, and for the hand when it was vertical in space. At point 1, the start of the forward and upward angular motion of the hand in space, both distal and proximal switches (on the distal and proximal phalanges) are on as the hand grips the ball. At point 2, the distal switch goes off as the proximal and distal interphalangeal joints start to extend and the distal phalanx lifts off the ball. This early extension is clearly seen in the bottom trace, which shows the angle of the distal phalanx with respect to the hand. This finger extension is illustrated in Fig. 1B (point 2), which is a reconstruction of the finger and hand angular position in space. The switches are shown as small rectangles (filled shows switch on; open switch off). At point 3 the proximal switch goes off as the ball starts to roll up the finger, and at point 4 the distal switch goes on again as the ball rolls over it. At point 5 the distal switch goes off as the ball loses contact with the finger tip. The flattened arc of the hand is shown in Fig. 1C, a tracing from a long-exposure photograph of another throw from the same subject (see METHODS). The gap in the trace at point 3 indicates offset of the proximal switch, and the end of the trace indicates final offset of the distal switch at final ball release (point 5). At this point the direction of the hand path (dashed line) is not the same as the direction of the ball path (solid line).

Inspection of the individual finger-joint motions (Fig. 1A) reveals that in this sequence there is relatively little motion at the metacarpophalangeal joint and a relatively large extension at the proximal interphalangeal joint. The distal interphalangeal joint shows different components: an early small extension (which was not always present) followed by a faster extension whose timing was consistent with it occurring in part as a result of back force from the ball as it rolled up the finger. This was followed by a small flexion occurring after ball release, which was presumably due to the sudden loss of back force from the ball.

A back force from the ball occurs on the finger during finger opening
In an overarm throw, as the hand propels the ball forward, the ball exerts a back force on the hand. This force is described by Newton’s third law of motion: to every action there is an equal and opposite reaction, or in other words if the hand pushes on the ball, the ball pushes back equally hard on the hand. The push can be deduced from the ball’s mass and motion: the ball’s total translational acceleration, minus the acceleration due to gravity, equals the acceleration imparted by the hand. This acceleration, multiplied by the mass of the ball, is the force exerted by the hand on the ball. The same force vector, multiplied by −1, is the force exerted by the ball on the hand.

Is there any back force on the fingers while they are opening? The answer is not obvious because, in a fast throw, the ball rolls along the fingers only briefly (<20 ms, Fig. 1A), and it is not known whether the fingers undergo translational acceleration toward the ball during this period. Therefore we measured the translational acceleration of the fingers as the hand moved forward and the fingers opened. Subjects were asked to sit and throw balls of different weights at the same speed. Hand angular velocity was monitored on-line, and feedback was given to subjects if a throw was faster or slower than the predetermined speed.

Figure 2 shows averages from subject Jn of 10 throws with each of the 3 balls (light ball, thin line; normal tennis ball, medium line; heavy ball, thick line). Figure 2A shows computer reconstructions of the flattened-arc trajectory of the finger in space aligned on the moment the hand was vertical and viewed from the side (the same view as in Fig. 1C).
and C, shows the backward-forward and down-up components of the translational acceleration of the finger in space, and Fig. 2D shows the corresponding finger extension (motion of the distal phalanx with respect to the hand). Figure 2, B–D, was aligned on ball release so that finger acceleration occurring before ball release would not be confused with that occurring in association with the finger flexion that occurred after the ball left the finger tip. These traces show two important points. First, on average, the trajectories of the finger in space (Fig. 2A) are similar for throws with the different balls. This shows that the subject did not change his throwing style with the different balls. Second, finger translational acceleration occurs during the time of finger opening to ball release: as the fingers extend (Fig. 2D) they accelerate first forward (Fig. 2B) and then also downward (Fig. 2C). Our reconstructions overestimated the downward component of acceleration at the expense of the forward component because they were based on the angular position of the distal phalanx and assumed that the finger was straight. Nevertheless, it is clear that during the time of finger extension the finger underwent forward and downward translational acceleration, and therefore the ball exerted a back force on the finger. Further, because these accelerations were similar in magnitude for throws with the three balls, but the ball weights were markedly different (e.g., the heavy ball was 14 times as heavy as the light ball), it follows that the heavy ball exerted a larger back force on the fingers.

This result was confirmed in a separate series of experiments by direct measurement of forces on the distal phalanx during finger opening. Figure 3 shows averages of recordings from a force transducer taped to the distal phalanx of the middle finger as a subject made 10 throws with each of the 3 different balls from both sitting and standing positions. For both sets of throws, during the time of finger extension (Fig. 3A), there was first a decrease in force on the distal phalanx (Fig. 3B), followed by an increase, then a rapid decrease. This corresponds to the sequence in Fig. 1, in which the distal phalanx first lifts off the ball (force decrease), then the ball rolls up over it (force increase) before losing contact (rapid decrease). For both sitting and standing throws, the force on the finger was proportional to the weight of the ball, being largest with the heaviest balls. In summary, the ball pushes back on the finger during finger opening, the back forces are larger for the heavier balls, and they are similar for throws made from the sitting and standing positions.

**FIG. 2.** Translational acceleration of fingers during finger opening. All traces are averages of 10 throws made from the sitting position with either the light ball (thin line), normal tennis ball (medium line), or heavy ball (thick line). Traces in A aligned on the moment in the throw when the hand was vertical in space (vertical line) and in B–D on the moment the ball left the fingertips (ball release). A: translational trajectory of the distal end of the middle finger viewed from the side. B: backward-forward component of finger translational acceleration. C: down-up (vertical) component of finger translational acceleration. D: finger extension (motion of distal phalanx of middle finger with respect to the hand). Subject Jn.

**FIG. 3.** Forces on distal phalanx of middle finger during finger opening for throws with balls of different weights made from sitting or standing position. Each trace is the average of 10 throws with either the light, normal, or heavy tennis ball aligned on the moment of ball release from the finger tip (vertical line). A: averages of finger extension (angular position of distal phalanx of middle finger with respect to hand). B: averages of force recorded by a force transducer taped to the distal phalanx of the middle finger. Subject An.
Effect of back forces on finger extension amplitude

Do these larger back forces cause the fingers to open wider? We measured the amplitude of rotation at the different joints of the middle finger as 6 subjects stood and made 40 throws with each ball at the same speed. We concentrated on the proximal interphalangeal joint because it is largely responsible for finger opening (Fig. 1A). Figure 4 shows averages from two subjects of rotations at the three finger joints, and the distal phalanx with respect to the hand, aligned on the moment the ball left the fingertip (vertical line; see Fig. 1A, point 5). For subject Jn, inspection of the extensions at the proximal interphalangeal joint (Fig. 4A) shows that before ball release the traces overlap: on average, this joint moved much the same way regardless of the weight of the ball. For subject De (Fig. 1B), the average amplitude of extension of this joint decreased slightly with the heavy ball. For each subject we compared the amplitude of extension of both the proximal interphalangeal joint and the distal phalanx with respect to the hand. Figure 5A shows that for the proximal interphalangeal joint there was an increase in extension amplitude with ball weight in subject Co and a decrease in the other five subjects. This was statistically significant in all cases at the $P < 0.001$ level (see METHODS). For the amplitude of extension of the distal phalanx with respect to the hand, there was no increase with ball weight in any subject and a statistically significant decrease in four subjects (Jn, De, Nv, and Ak; $P < 0.001$).

FIG. 4. Effects of ball weight on the kinematics of extension at the different finger joints. Averages of 40 rotations (angular positions) at each finger joint for throws made from standing position at a medium-fast speed ($\sim 15$ m/s) with balls of different weights. All throws were aligned on the moment of ball departure from the fingertip (vertical line). A: subject Jn. B: subject De.

FIG. 5. Means ± SD of amplitudes of finger extensions for all 6 subjects for 40 throws of similar medium-fast speeds made from standing position with balls of different weights. A: amplitudes at the proximal interphalangeal joint. B: amplitudes of overall finger extension (distal phalanx with respect to hand). Start of extension was measured when velocity for each rotation crossed a threshold that was 30% of the mean peak velocity for all throws with the tennis ball; end of extension was the moment the ball left the fingertip.
In short, there was no overall increase in the amplitude of finger opening with heavier balls: increased back force did not increase finger extension.

**Indirect evidence that back forces were different**

Forces were not directly recorded during these latter experiments, but there was indirect evidence that the back forces were larger in throws with the heavy balls. This evidence came from inspection of finger motion after the ball left the hand. We have previously reported that, at the moment the ball leaves the fingertip, the finger flexes forward (Hore et al. 1995, 1996a) (see also Fig. 1A). The new finding is that the amplitude of this flexion movement is proportional to ball weight in throws of similar speeds. This can be seen in Fig. 4. Inspection of traces starting at the moment of final ball release (vertical line) reveals a flexion at the proximal interphalangeal joint that was larger for the throws with the heavier balls. Mean amplitudes of flexions of the proximal interphalangeal joint for all throws with the three balls of different weights from all subjects are shown in Fig. 6. In some subjects flexion did not occur for the light (14 g) ball, and this point is missing from the graph. In all subjects larger flexions occurred with the heavier balls. This flexion movement presumably resulted from offset of the back force as the ball left the fingertip, thereby leaving a finger flexor torque unopposed. The larger flexions with the heavier balls likely reflected increased torque from the finger flexors, which was required to oppose larger back forces in these throws.

**First throw with a ball of a new weight**

Was finger amplitude controlled precisely in the first throw with a ball of a new weight, or did it take a number of trials to adapt to the new back forces on the fingers? The unequivocal answer for all subjects is that for the first throw with a ball of a new weight (that had not been thrown previously), finger amplitude was adjusted to the new conditions. Figure 7 shows overplots from two representative subjects of finger amplitudes (Fig. 7A) and finger velocities (Fig. 7B) for the first throw with a heavy ball (thick line) and the next nine throws with this same ball (thin lines). Before throwing with heavy ball, subjects had made 10 throws with light ball.

**Does finger amplitude affect ball accuracy?**

Because in an overarm throw the ball is released from the fingers, the orientation of the fingers in space can affect the subsequent path of the ball. And because finger extension amplitude can affect finger orientation, it might be expected that the decrease in finger amplitude that occurred in four subjects with the heavy ball (Fig. 5) may have affected ball accuracy. In previous experiments with seated throwers, ball accuracy was related to the timing of finger opening and the
timing of ball release, but not to finger amplitude (Hore et al. 1996b). In the present experiments we asked whether this also applied to throws made with a normal tennis ball while standing, and whether it applied to those subjects who showed decreased overall finger amplitudes when standing and throwing with the heavy ball.

First, for standing throws with the normal ball, Fig. 8 shows a representative result (from subject Co). In spite of variability in the amplitude of finger opening (to ball release; Fig. 8A), there was no relation between this variability (over a range of ~25° for all 50 throws) and ball impact height on the target (Fig. 8B). In contrast, as before, a strong relation was found between ball impact height and timing of ball release (Fig. 8C). Similar results were found for all subjects who threw from the standing position. Second, for subjects who showed decreased finger amplitudes for throws with the heavy ball (Fig. 5), no relation was found between finger amplitude and ball accuracy. For example, Fig. 9 shows ball impact heights for all throws made with the light, normal, and heavy tennis balls in subject Nv, who showed decreased amplitudes of finger extension for throws with the heavy ball.

Presumably, the relation is absent because such a decrease in finger amplitude has a smaller effect on ball accuracy than does variability in timing, or alternatively, because this subject changed his timing to compensate for the decreased finger amplitude.
DISCUSSION

We have seen that in an overarm throw the weight of the ball affects the mechanics of its release. That is, for throws of a similar hand translational acceleration, larger back forces occurred on the fingers during finger opening for throws with heavier balls. Because the larger back forces did not produce larger finger extensions, we conclude that the CNS predicted the forces and compensated for them. This compensation appears to occur by the generation of larger finger flexor torques. This was deduced from the finding that the fingers flexed abruptly at the moment of ball release and the amplitude of this flexion was proportional to ball mass.

Presumably, this ability of recreational ball players to throw with small variability in finger amplitude and to adjust immediately to a ball of a new weight is a skill learned from considerable experience in throwing. In agreement, preliminary experiments on three unskilled throwers showed similar mean amplitudes of finger opening for the balls of different weights but larger variability from throw to throw (unpublished observations).

Are finger torques controlled by reflex mechanisms?

Could the compensation for different back forces be controlled by peripheral feedback? One way this could occur would be if larger back forces in throws with heavier balls produced larger initial velocities of finger opening, which in turn, would be signaled by changed kinesthetic feedback from the fingers. This would then generate, via spinal cord mechanisms, larger finger flexor activity. This proposal can be ruled out for two reasons. First, for the standing throwers, onset of finger opening (extension) occurred on average <40 ms before ball release (e.g., Figs. 4, 7, and 8). This does not leave sufficient time for signals from finger movement to pass to and from the spinal cord and for finger muscles to generate increased torque. Second, such a proposal predicts that the initial velocity of finger opening will be greater for throws with heavier balls. However, inspection of kinematic records of finger opening showed that this was not the case (Figs. 2–4). Similarly, changed kinesthetic feedback from wrist flexion and elbow extension in throws with heavier balls can be ruled out, again because there is insufficient time between onset of these joint rotations and onset of finger opening (4 ms for wrist flexion and 21 ms for elbow extension) (Hore et al. 1999). Although a contribution from changed feedback during the backswing cannot be ruled out, this possibility seems to be unlikely because subjects can throw accurately over short distances with balls of different weights with the arm starting from a stationary position at the end of the backswing, i.e., without any backswing motion at all (unpublished observations).

Possible mechanisms for compensation of back forces

Although the mechanism by which the CNS controls finger opening and compensates for back forces cannot be determined by these experiments, some possibilities can be proposed. First, a finger flexion contraction or cocontraction could have occurred that was precisely timed to counteract the back force from the rolling ball. Alternatively, presetting of finger stiffness (grip force) could have occurred at the start of the throw, or progressively throughout the throw, in anticipation of the increase in hand acceleration. The variable degrees of finger flexion after ball release seen in Fig. 6 may reflect intersubject differences in finger flexor activity versus cocontraction. Irrespective of how it is generated, this increase in finger flexor force would presumably be precisely related to the dynamics of the throw, but this remains to be shown.

Whatever the mechanism, finger opening appears to be an active process, i.e., it does not only occur as a result of back forces. Evidence for this can be seen in Fig. 1, A and B. Point 2 shows that during initial finger opening (~30 ms before final ball release) at a time when the hand was undergoing forward translational acceleration (Fig. 2), the fingertip lifted off the ball. This could not occur if finger extension was produced by back force from the ball on the finger. Exactly how the commands for finger stiffness and for timing finger opening, are generated and interact, remains to be determined by further experiments.

Evidence for an internal model

The idea that the CNS predicts and compensates for perturbations occurring during the throw fits with many observations of anticipatory responses to expected perturbations in a variety of different motor tasks. Perhaps the most relevant for throwing are the anticipatory actions involving the finger and hand that occur when gripping and lifting small objects (e.g., Johansson and Westling 1988a,b) and when catching a ball (e.g., Lacquaniti and Maioli 1989a,b).

An interesting conclusion of these finger and hand studies is that the central control mechanism knows dynamics, i.e., there is an internal representation that predicts the mechanical consequences of the perturbation. For example, Johansson and Westling (1988b) showed that prior knowledge of both the weight of an object dropped into a cup held by a subject, and the length of the drop, resulted in the generation of appropriate anticipatory muscle activation. They concluded that the central control processes possessed knowledge about the dynamics of the interactions between the held cup and the dropped weight and this led to anticipatory parameter setting of motor programs. In agreement, Flanagan and Wing (1997) concluded that, for a task involving gripping and moving a manipulandum subjected to a variety of different loads, the grip force anticipated the load force and that this occurred by means of an internal model of the loaded limb.

A similar conclusion came from studies of catching a ball dropped vertically (Lacquaniti and Maioli 1989a,b; Lacquaniti et al. 1992). By varying the height of the drop, it was found that anticipatory muscle activation was finely tuned to the expected properties of the ball’s impact with the hand. Again it was concluded that there was an internal model that took into account the time to contact, the momentum of the ball’s impact and the limb’s geometry. Studies of adaptation of arm movements to externally applied perturbing forces have also concluded that adaptive learning occurs by means of an internal model of the dynamics of the environment (Conditt et al. 1997; Goodbody and Wolpert 1998; Shadmehr and Mussa-Ivaldi 1994).

The concept of an internal model can be used to explain how subjects compensated for different back forces on the first throw with a ball of a new weight. According to this idea it
would arise from two mechanisms: first, an accurate internal
representation of the mechanics of throwing built up from
extensive previous experience of throwing, and second, an
updating (calibration) of the parameters of this model before
the first throw by means of information obtained from handling
the ball. This scheme is consistent with the finding of Jo-
hansson and Westling (1988b) that sensory information about
the weight of the ball dropped into the cup was obtained from
handling the ball prior to the drop. It is also consistent with the
finding that motor commands were scaled before lifting com-
mon objects on the basis of visual identification and an accu-
rate estimate of the object’s weight (Gordon et al. 1993).

Although internal models appear to be used in gripping and
lifting, in catching a ball and in throwing, the neural mecha-
nism for throwing would appear to be somewhat different. In
the lifting and catching tasks, contractions of proximal and
distal muscles occur together. In contrast, in throwing, there is
a proximal to distal sequence of joint rotations that occurs over
hundreds of milliseconds with finger opening being the last
rotation to occur. Because the back force that occurs on the
fingers from the ball as it rolls up the fingers is proportional to
the forward force produced by the hand on the ball, generation
of active finger force to oppose the back force requires knowl-
edge of the dynamics of the ongoing hand trajectory. Therefore
one possibility is that prediction of finger force in throwing is
based on an eff erence copy of the commands that generate the
hand trajectory.

Internal models for throwing

Motor theorists distinguish two types of internal model:
inverse and forward. An inverse model is a neural system that
“undoes” something that the muscles do. Perhaps the simplest
e xample is in Skavenski and Robinson’s (1973) theory of the
vestibulocu-ellar reflex (VOR). The VOR counterrotates the
eyes when the head turns, so as to keep the eyes stationary in
space. Its aim, therefore, is to make eye velocity equal 1 times
head velocity. It has sensors in the inner ear whose firing rates
are proportional to head velocity, but if it simply relayed this
sensory signal, times 1, to the motoneurons, the resulting eye
velocity would be wrong. The muscles, in transducing the
neural command, would distort it. Hence Skavenski and Rob-
inson proposed that the eye-velocity command passes to the
motoneurons both directly and through an integrator. This
combination of integrator and direct relay inverts, and hence
corrects for, the subsequent distortion by the muscles, produc-
ing a pattern of motoneuron activity that generates the desired
eye velocity.

A similar scheme could work for throwing: signals coding
the desired motion could pass through an inverse model of the
arm to generate an appropriate pattern of motoneuron firing.
But a major difference between the VOR and throwing is that
in the VOR the desired motion is easily computed: the desired
velocity of the eye is simply the head’s velocity times 1. For
a throw, considerable neural machinery would be needed to
device a suitable arm trajectory before this could be fed
through the inverse model: the model cannot be the complete
mechanism for generating throws. Another difference is that
the inverse model of the arm would have to contain an adjust-
able parameter representing the weight of the ball.

Forward models, in contrast to inverse models, do not undo
but rather mimic some aspect of muscle behavior. Feed a
pattern of motoneuron firing into a forward model of the arm
and it might compute the resulting joint velocities, or the
angles of the joints. As in Robinson’s model of saccades, a
forward model can be used in an internal feedback system:
nearal commands are fed through the forward model to yield
an estimate or prediction of body motion. This estimate is
compared with the desired motion, and any difference between
the two, called the motor error, is used to adjust the neural
commands.

With a complex linkage like the arm, however, it will take
some computation to figure out how to adjust the neural
commands, given a motor-error signal. For example, if the
forward model estimates that the hand is veering left of its
charted path, what is to be done? Should brachialis, for in-
estance, be more strongly activated or less? The brain needs
some device to transform an error signal into motoneuron
activity that will reduce the error. Such a device is a type of
inverse model: given a desired motor effect, it suggests a
neural command. In short, the brain would need an inverse
model of the arm to make use of a forward model for on-line
feedback control of throwing.

With this idea of a forward model and an inverse model
linked in a feedback loop, we have a rough picture of how a
complete throw generator could work, based on Robinson’s
scheme for saccades. Upstream centers set some parameters for
the throw: target location, speed of the throw, overarm or
sidearm technique, more or less elbow motion than last time,
and so on. They also estimate the weight of the ball, sending
this information to the forward and inverse models. Something
akin to a comparator collects information about the desired
parameters of the throw and, from the forward model, the
current state of the arm. This information is relayed to the
inverse model where it is transformed into a suitable neural
command. It is here, in the inverse model, that many of the
unconscious details of the throw are determined: the activation
pattern for brachialis, the precise arc of the hand, the moment
of finger opening and so on.

These internal models of the arm would have to be shaped in
early life, and kept calibrated thereafter, by learning mecha-
nisms such as those studied by Konczak et al. (1995, 1997) and
Shadmehr and Mussa-Ivaldi (1994). Such adaptation would
presumably affect all aspects of the internal models, including
our ability to adjust them based on an estimate of the weight of
a ball in the hand. Clearly a perfectly accurate, real-time
internal model of arm mechanics would need enormous com-
putational power, but this is not an objection to the hypothesis
of such models. For one thing, there surely is enormous com-
putational power in vast networks of neurons where each
neuron is a complex information processor in its own right.
And of course the neural computation consists of electrical and
chemical signals flowing through massively parallel networks
and therefore might proceed very quickly. Further, the internal
models need not be perfectly accurate, and of course we know
they are not, because if they were then every throw would
strike its mark. Presumably the networks in the brain, like
artificial neural networks, learn approximations. Their learning
is driven by error (i.e., teacher) signals, in this case perhaps the
visually judged errors in recent throws and the muscular effort
of the arm motion. Presumably the adaptation proceeds until
the error signals are reduced as far as possible, but not apparently to zero.

CNS structures

Two CNS structures that are likely components of the proposed internal model that controls finger force in overarm throwing are the motor cortex and cerebellum. The motor cortex is likely involved because of its special role in controlling precise finger movements and finger force (Porter and Lemon 1993). The cerebellum is likely involved, first, because of its role in the generation of anticipatory (predictive) mechanisms that control the arm, e.g., that brake single-joint elbow movements (Hore and Vilis 1984; Hore et al. 1991) and that control interaction torques in multijoint movements (Bastian et al. 1996), and second, because of its role in control of finger movements and finger force (Holmes 1922; Mai et al. 1988; Müller and Dichgans 1994). Although it is not known how these two CNS structures interact, a number of models have recently been put forward that make proposals (see Houk et al. 1996 for a recent review). For example, Kawato and Gomi (1992) specifically proposed that the lateral cerebellum functions as the inverse model of the limb’s controlled system. Most others view the cerebellum as the structure that through learning functions as a predictive controller for limb movement (e.g., Barto et al. 1996; Miall et al. 1993; Thach 1996; Thach et al. 1992).

Conclusion

Previous studies have shown that the CNS can predict 1) the mechanical consequence of external perturbations applied to the hand and 2) the forces required to produce relatively slow self-generated arm movements under different loads. The present findings add to this by showing in a fast skilled movement, where the fingers are likely entirely controlled by a central process, that finger force is also adjusted according to the mechanics of the movement. We previously proposed that timing of finger opening in an overarm throw is most likely the mechanics of the movement. We previously proposed that finger force is also adjusted according to the mechanics of the movement. We previously proposed that timing of finger opening in an overarm throw is most likely controlled by means of an internal model that can predict the trajectory (kinematics) of the throw. The present results are best explained if finger force is also controlled by an internal model that can predict the dynamics of the throw.

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