Dynamic Coordination of Body Parts During Prism Adaptation

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Martin, Tod A., Scott A. Norris, Bradley E. Greger, and W. Thomas Thach. Dynamic coordination of body parts during prism adaptation. J Neurophysiol 88: 1685–1694, 2002; 10.1152/jn.00305.2002. We studied coordination across body parts in throwing during adaptation to prisms. Human subjects threw balls at a target before, during, and after wearing laterally shifting prism eyeglasses. Positions of head, shoulders, arm, and ball were video-recorded continuously. We computed body angles of eyes-in-head, head-on-trunk, trunk-on-arm, and arm-on-ball. In each subject, the gaze-throw adjustment during adaptation was distributed across all sets of coupled body parts. The distribution of coupling changed unpredictably from throw to throw within a single session. The angular variation among coupled body parts was typically significantly larger than angular variation of on-target hits. Thus coupled body parts changed interdependently to account for the high accuracy of ball-on-target. Principal components and Monte Carlo analyses showed variability in body angles across throws with a wide range of variability/stereotypy across subjects. The data support a model of a dynamic and generalized solution as evidenced by the distribution of the gaze-throw adjustment across body parts.

INTRODUCTION

With practice, humans are able to hit targets with thrown objects with a remarkable degree of accuracy. The ease with which this is accomplished belies the challenges faced by the nervous system. Among these are sighting of the target, determination of the target’s position relative to the body, and compensation for irregularities in the physical world (e.g., ground surface, wind velocity). The nervous system must also determine how the motor system will use different means to similar ends (“motor equivalence”) (Bernstein 1967; Lashley 1930). Variations in motor equivalence occur either at the level of strategy selection (e.g., Field and Stein 1997) or at the level of inter-joint coordination of component body parts within a single form of a movement (cf. Abbs and Cole 1987). In the present study, we have examined throw adaptation to laterally shifting wedge prisms, focusing on the range of parametric covariance across moving body components.

Wearing laterally shifting prisms while throwing at visual targets has been used to study motor coordination, motor adaptation, and motor learning (Martin et al. 1996a, b). Initially, gaze centers on the target prior to throw (Vickers 1994), and the throw is made in the direction of gaze. Donning base-right prism eyeglasses causes the eyes to deviate to the left to foveate the target. The first throw is in the direction of gaze, to the left of the target. In subsequent throws, the gaze-throw angle widens and the hits fall closer to the target (motor adaptation). When the subject doffs prisms, the first throw shows the storage of the gaze-throw angle: the first throw is to the right of the target (the negative aftereffect), and the subject must un-adapt to baseline levels. However, with repeated practice with prisms over weeks, subjects learn to hit a target on first donning or doffing the “known” prisms (motor learning).

Prism-adapted throwing requires a compound coordinated movement that is made toward a specific goal and is performed in a specific context. Adaptation of right-hand throws does not carry over to left-hand throws; adaptation of overhand throws does not usually carry over to underhand throws (Martin et al 1996b). The adaptation occurs gradually through practice. The process itself is not altogether conscious; it can occur in parallel with volitional corrections. One has little or no insight as to when the process is operating. Finally, it requires the use of errors for subsequent modifications of the gaze-throw calibration (Kohler 1964).

We have therefore sought to use prism adaptation of throwing as an experimental paradigm to study the mechanisms underlying the coordination and adaptation of compound movements. The main question that we address here is “does the widened gaze-throw angle during adaptation consist of a fixed relation among body parts or instead a changing and interdependent relation among body parts?”

Portions of this work have been presented previously in brief (Greger et al. 1996).

METHODS

Subjects

Subjects were unpaid, healthy, adult volunteers with no history of neurologic injury and were naive to the purpose of the experiments. We recorded data from eight subjects (mean age 25.5 ± 5.0 yr; range 20–33; 6 female, 2 male) in the motor adaptation paradigm. All subjects were right-handed and threw with their dominant arm. All had participated in recreational softball or baseball, but none was highly trained.

The study was approved by the Human Studies Committee of Washington University School of Medicine. All subjects gave informed consent.

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Task

Prism adapted throwing has been described previously (Martin et al. 1996a, 2001). In brief, subjects stood and threw small, plastic balls (2 cm diam., ~10 g) at a 1.80 m wide \( \times 1.15 \) m high Plexiglas board divided into 5-cm numbered squares. Each square was further divided into four quadrants, allowing a resolution of 2.5 cm for locations of ball hits. The target was indicated by a \( 15 \times 15 \) cm box drawn on the board’s surface, 2.5 m from the subject and at shoulder level. The subject’s head was unrestrained, and no directions were given about trunk, shoulder, or head/neck posture. After ~10 warm-up throws, subjects threw at the target before, during, and after (50 throws each) wearing prism eyeglasses. After each throw, an observer called out the square and quadrant number of the hit location, which was then recorded. To ensure reliability of scoring, a second observer marked the hit location with a piece of colored tape (1 color was used for each block of 50 throws). Throwing occurred approximately once every 5 s with ~1 min between each block. Subjects were instructed to make an overhand throw (from behind the ear, out of view) rather than a dart-like throw.

As a baseline performance measure, subjects threw the balls at the target before donning prisms. After donning prisms, the subjects were instructed to throw with the same arm “where you see the target,” and the results were marked as described in the preceding text. When donning prisms, subjects viewed the target binocularly through 30 diopter (~17.2’), Fresnel 3 M Press-On plastic lenses (3 M Health Care, Specialties Division) mounted base-right on safety eyeglasses. After doffing prisms, the subjects threw again with the same arm. Subjects had an unobstructed view of the target during the entire session but were instructed not to look down at their hands as they were handed the balls or during the throws. The locations of the hits were then plotted sequentially by trial number (abscissa) versus horizontal displacement (in degrees) from an imaginary drawn-in vertical line passing through the target center (ordinate), with hits to the left of the target plotted as negative values and those to the right as positive values. The adaptive process was modeled by fitting an exponential decay curve to the data (see following text).

Quantification of performance and adaptation

We have previously shown how performance and adaptation can be distinguished (Martin et al. 1996a). During the prism control period, the scatter of the hits around the mean baseline reflected how consistently the subject threw. In all cases, the horizontal errors (distance from each hit location to a vertical line passing through the target) of the subject’s 50 throws before donning prisms served as the baseline performance. The SD of these errors (in degrees) was called the performance coefficient (PC).

A mathematical model of each subject’s adaptation data quantified the rate of adaptation. During normal adaptation, the hit locations were plotted against the trial number and were fitted by an exponential decay function. The rate of change of slope of the exponential decay curve was taken as a measure of the rate of adaptation (Keating and Thach 1990). This rate constant was called the adaptation coefficient (AC). It is the number of throws required to reach a point \( (1 - e^{-1}) \) or ~63.2% of the way through the adaptation.

All curve fits were generated using Microcal Origin software (Microcal Software; Northampton, MA) and were fit to the regression equation

\[
y = y_A + A_0 e^{-r (x - x_0)}
\]

where \( y_A \) is the asymptote of the exponential decay function, \( A_0 \) is the magnitude of the adaptation required from the first throw to the value \( y_A \), and \( r \) (the time constant) represents the rate at which adaptation takes place (AC). This method gave objective, independent, and quantitative measures of adaptation and performance (Martin et al. 1996a).

Kinematics of gaze-throw coordination during motor adaptation

We evaluated the kinematics of throwing for the individuals undergoing motor adaptation. We focused on the horizontal angles of the eyes-in-head, head-on-trunk, trunk-on-arm, and direction of ball translational velocity with respect to arm (arm-on-ball). Each subject was videotaped from overhead at 60 fields/s while throwing before, during, and after donning prisms. Reflective markers marked the major axes in the horizontal plane of head (sagittal) and shoulders (transverse). Reflective markers were placed on the front and back of the head and on the acromion process of both shoulders. The thrown balls were also reflective. In addition, reflective markers were placed on a normal line passing through the center of the target (above the subject’s head) to calibrate the video image to the direction of the target. The videotape was digitized and analyzed using a peak-performance motion-analysis system (Englewood, CO).

During each throw, when the hand was near its most anterior position and the ball had just been released (viewed as the 1st field on the videotape when the ball was no longer touching the fingers), these axes were measured and used to calculate three of the angles—eyes-in-head, head-on-trunk, and trunk-on-arm—while throwing before, during, and after wearing prisms (see Fig. 1). Knowing the angle of the head-in-space with respect to the target at the time of ball release, the angular deviation of the optic path by the prisms (with subjects foveating the target), and the lateral shift of the calculated head-shoulder center in space and assuming that the subject was foveating...
the target as instructed, we could calculate the horizontal positions of the eyes-in-head before, during, and after prism use. A straight-ahead eyes-in-head angle was assigned a value of 0°, with deviations of the eyes to the left relative to the head assigned positive values and deviations to the right assigned negative values. The head-on-trunk angle was calculated from the intersection of the line connecting the two head markers and the line connecting the two shoulder markers. A 90° angle between these two lines was normalized to a 0° value for the head-on-trunk angle. Deviations of the shoulders to the right with respect to the head were assigned positive values and deviations to the left assigned negative values. The trunk-on-arm angle was calculated between a line connecting the left shoulder and the calculated head-shoulder center in space and a line connecting the head-shoulder center and the ball position at the time of release. A value of 90° of this angle was normalized to 0°, with deviations of the ball release location to the right assigned positive values and deviations to the left assigned negative values. The direction of ball translational velocity with respect to the arm (arm-on-ball) was calculated from the line connecting the calculated head-shoulder center and ball location at release and the line connecting the ball location at release and the ball at the edge of the video image. The calculation of this angle allowed for mathematical translation so that its vertex was the same as the other angles, the center of the head. There was a minimum of four to five fields of videotape in which the ball was in free flight (67–83 ms; ~40–50 cm of ball flight distance) before it exited the viewing field of the camera.

Because of the manner in which the angles were measured and defined, they could be added to give an independent predictive value of the ball-hit location. A calibration factor was calculated for each subject from the subject’s before prisms throws to correct for incorrect marker placements. The intercept of the linear regression of the calculated ball-hit locations (from the additions of the 4 body angles) and of the actual ball-hit locations was used as an offset and added as a constant (“calibration factor”) to each of the subject’s throws before, during, and after prism use.

**ANCOVA and motor equivalence**

**MONTE CARLO ANALYSIS.** We used standard statistical measures to test for relationships between variables (linear regression and ANCOVA). To obtain a graphical representation of the degree to which a subject coordinated the four body angles determining ball-hit location in the 50-throw block before donning prisms, we used a modified Monte Carlo analysis based on a model of linear summation of the angles previously described. Each Monte Carlo simulation (5,000 per subject) generated a ball-hit location by selecting a value for each body angle from the mean and SD of that angle (each angle was assumed to have a normal Gaussian distribution) and summing the four angle values. This sum was stored for each simulation and used to create a population of simulated ball-hit locations that could be compared directly to the actual sums of the angles (actual ball-hit locations).

**COORDINATION INDEX.** We used the relationship between the SD of the actual ball-hit locations and the SD of the simulated ball-hit locations from the Monte Carlo analysis as a means to quantify the extent of coordination across joints in a subject (coordination index, CI). The SD of actual ball-hit locations is an estimation of throwing accuracy, equivalent to the PC discussed earlier. The SD of simulated ball-hit locations is an indication of angular variability or the potential amount of joint space available to the subject on a single throw. A ratio between the two values normalizes the subject’s actual throws to the amount of available joint space the subject traverses. A value of 1.0 indicates that the relationship between angles was no better than a random coupling of the body parts. Values <1.0 indicate complementarity across body angles: the lower the number, the tighter the covariance of the angles relative to the available joint space. A subject may decrease the CI by having either a smaller SD of hits or a larger SD of the individual body angles. Thus the value also can be thought of as a measure of motor equivalence normalized to the subject’s throwing accuracy. A value >1.0 would imply that the subjects were coordinating actions across joints but in such a manner as to intentionally hit different areas around the target. Finally, this method requires that there be variability at more than one joint, and this proved to be the case.

**PRINCIPAL COMPONENTS ANALYSIS.** To probe further the covariance among angles, we used a principal components analysis on the kinematic data for each subject. Principal components analysis is used to look for inter-related variables in a multi-variable system. It is a common method of data reduction and is used to search for correlations between variables that would suggest that they could be considered as a single variable. As a general example, consider the case of two measured variables. A regression line can be drawn on a plot of one variable versus the other. A new variable is defined to approximate the regression line and this variable (often called a “factor” or a “principal component”) captures the essence of the two variables. This factor is calculated to capture the maximum variance in the two variables, and the amount of variance extracted by the factor is represented by an eigenvalue. Successive factors are calculated iteratively to account for the variance in the variables not accounted for by the preceding factor.

In our study, we analyzed the trial-by-trial body angles across throws before and during prism use. Correlation matrices of the variables were calculated and eigenvalues computed. Only eigenvalues >1.0 were retained (representing 25% of the total variance of the angles; thus only new factors that accounted for more variance than 1 original variable were retained). Loadings of variables on principal components are only reported for factor loadings >0.7 (factor loadings are correlations between each of the body angle variables and the computed factors). Because only factors with eigenvalues >1 are retained, the final factors do not necessarily account for the total variance of all four body angle variables. Factors with eigenvalues less than one account for the remaining small percentages of the total angle variance. To obtain the clearest pattern of factor loadings, a varimax (variance maximizing) rotational strategy was employed. All principal components analyses were performed using Statistica software (Tulsa, OK).

**RESULTS**

Figure 2 shows the results of a throwing experiment with one subject (Fig. 2A, subject DL) and the results of the throwing experiments averaged across seven of the eight subjects [Fig. 2B, subject SH excluded (see following text)]. For each throw in Fig. 2B, the hit location is averaged across the 7 subjects, and the mean ± 1 SD is plotted. The individual and average data show that subjects’ baseline throws were around the center of the target (0°). The results of a throwing experiment with one subject (Fig. 2A, subject DL) and the results of the throwing experiments averaged across seven of the eight subjects [Fig. 2B, subject SH excluded (see following text)]. For each throw in Fig. 2B, the hit location is averaged across the 7 subjects, and the mean ± 1 SD is plotted. The individual and average data show that subjects’ baseline throws were around the center of the target (0°). The results of a throwing experiment with one subject (Fig. 2A, subject DL) and the results of the throwing experiments averaged across seven of the eight subjects [Fig. 2B, subject SH excluded (see following text)]. For each throw in Fig. 2B, the hit location is averaged across the 7 subjects, and the mean ± 1 SD is plotted. The individual and average data show that subjects’ baseline throws were around the center of the target (0°).
participating in the motor adaptation paradigm. One of the eight subjects (SH) had an unusual adaptation curve that could not be fit with an exponential decay function. The residuals of the curve fits for the remaining seven subjects were normally distributed, validating the curve fitting procedure. The average PC value was 2.7°/H11006 1.0°, and the average AC was 4.4°/H11006 4.6°/H11006 4.6 throws. There was no significant correlation between the AC and PC values [r = 0.29, p(r = 0) = 0.53].

Calculation of body angles

To investigate the kinematics of the throw during baseline performance and adaptation, we analyzed each throw as a combination of four body angles: eyes-in-head, head-on-trunk, trunk-on-arm, and arm-on-ball. These four angles gave an independent measure of ball-hit location. A comparison of calculated and actual ball-hit locations tested the validity of the system of angle calculations. Figure 2C shows a graph of calculated ball-hit location versus actual ball-hit location for a single subject (subject KZ) for throws before, during, and after prism use. The correlation coefficient (r) for this subject’s 150 throws was 0.98, and the slope of the regression line was 0.99. The correlation coefficient for the remaining subjects were: SB, 0.97; DL, 0.95; JF, 0.96; KK, 0.96; TM, 0.98; GS, 0.97; SH, 0.96. The mean correlation coefficient for the eight subjects was 0.97 ± 0.01, and the mean slope was 0.98 ± 0.04. Thus the four angles provide a reliable measure of actual ball-hit location, and any discrepancies in geometric addition have been overcome by the calibration factor. The calibration factor (see METHODS) for this and all subjects was <5°.
TABLE 2.

The ball angle itself. The exception was the eyes-in-head angle, larger degree of variability in individual body angles than in trial-by-trial basis. Body angles across a 50-throw block of trials as well as on a PC value is produced. We investigated the variability of these PC value; the other with relatively little variability in each throw. Two subjects with the same PC value could show variability of the angles (motor equivalence) comprising the ball-hit location (it is the SD of the ball hits in degrees measured as an angle with its vertex at the center of the head). However, the PC gives no indication of the relative variability of the angles (motor equivalence) comprising the throw. Two subjects with the same PC value could show distinctly different angle distributions: the one with a high degree of variability spread across single/multiple angles coupled with a precise combination of angles to produce a certain PC value; the other with relatively little variability in each angle distributed on a trial-by-trial basis such that an equivalent PC value is produced. We investigated the variability of these body angles across a 50-throw block of trials as well as on a trial-by-trial basis.

Within a block of 50 throws, subjects generally showed a larger degree of variability in individual body angles than in the ball angle itself. The exception was the eyes-in-head angle, which was always less variable than the ball-hit location. Figure 2D shows the SDs of each angle during 50-block throws before, during, and after prism use for a single subject (subject DL). The subject’s head-on-trunk, trunk-on-arm, and arm-on-ball angles are more variable than the ball-hit angular position in the “before” condition. The relative variability among these angles stays fairly constant across prismatic conditions (e.g., arm-on-ball angle is always less variable than head-on-trunk and trunk-on-arm angles) as was true in all eight subjects.

Table 2 lists the mean and SD of each of the four angles for each subject before donning prisms. The calibration factor has not been added to these data (see METHODS). The sum of the four angular means plus this calibration factor equals the mean of ball-hit locations.

A Monte Carlo analysis provides a graphical representation of these data and gives an indication of the degree of coordination among joints. A linear summation model of the four body angles was used in which the input data to the Monte Carlo analysis were the means and SDs of the angles (Table 2, each assumed to have a normal distribution as was the case statistically). The analysis simulates a throw by choosing a value from each angle population (with the chance of any particular value being selected based on its distribution) and summing them to give a ball-hit location. The population of ball-hit locations calculated from this simulation is then compared with the actual ball-hit locations. Figure 3 shows this analysis for three subjects. Each graph contains the normal distribution of the actual angle summations (— in Fig. 3: additions of actual body angles for each of the 50 throws; by this technique, equivalent to the ball-hit location or hit accuracy). In addition, each graph contains the results of the Monte Carlo analysis (□ in Fig. 3: this plotted as a normal distribution based on the mean ± SD of the simulation). Thus □ are simulations where the combination of angles for each simulated trial is made up of a weighted random selection based on the distribution of variation of each angle. The calibration factor has been added to each plot in the graphs. The results of Table 2 lists the mean and SD of each of the four angles for each subject before donning prisms.

The means ± SD of each of the four body angles before donning prisms are listed for each subject. In addition, the means ± SD of the actual ball hit locations (ball angle) are listed. The results of the Monte Carlo analysis are listed as well (simulated ball angle). The coordination index (CI) is a ratio of the last two values (ball angle and simulated ball angle; see text).

**TABLE 1. Prism performance and adaptation results for subjects in the motor adaptation study**

<table>
<thead>
<tr>
<th>Subject</th>
<th>Sex</th>
<th>Age, yr</th>
<th>Baseline PC</th>
<th>Prisms, °</th>
<th>Adapted, °</th>
<th>Negative After-effect, °</th>
<th>AC (Threws)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SB</td>
<td>F</td>
<td>23</td>
<td>−0.4 ± 2.1</td>
<td>2.1</td>
<td>−11.5</td>
<td>−2.0</td>
<td>8.6</td>
</tr>
<tr>
<td>DL</td>
<td>M</td>
<td>22</td>
<td>0.1 ± 1.5</td>
<td>1.5</td>
<td>−11.5</td>
<td>−1.1</td>
<td>6.5</td>
</tr>
<tr>
<td>JF</td>
<td>F</td>
<td>33</td>
<td>0.7 ± 3.3</td>
<td>3.3</td>
<td>−11.0</td>
<td>−1.5</td>
<td>5.9</td>
</tr>
<tr>
<td>KK</td>
<td>F</td>
<td>20</td>
<td>0.0 ± 1.9</td>
<td>1.9</td>
<td>−6.5</td>
<td>−1.7</td>
<td>5.9</td>
</tr>
<tr>
<td>TM</td>
<td>F</td>
<td>22</td>
<td>−0.8 ± 3.8</td>
<td>3.8</td>
<td>−8.6</td>
<td>−4.0</td>
<td>4.0</td>
</tr>
<tr>
<td>GS</td>
<td>F</td>
<td>31</td>
<td>−0.1 ± 4.3</td>
<td>4.3</td>
<td>−9.6</td>
<td>−3.4</td>
<td>6.9</td>
</tr>
<tr>
<td>SH</td>
<td>M</td>
<td>23</td>
<td>−0.2 ± 3.0</td>
<td>3.0</td>
<td>−5.7</td>
<td>−2.8</td>
<td>6.1</td>
</tr>
<tr>
<td>KZ</td>
<td>F</td>
<td>30</td>
<td>−0.3 ± 1.8</td>
<td>1.8</td>
<td>−10.6</td>
<td>−3.0</td>
<td>7.38</td>
</tr>
</tbody>
</table>

The SD of the subject’s 50 before-prisms throws (baseline) serves as the performance coefficient (PC), which is listed separately. The average of the first 3 throws after donning prisms (prisms) serves as an indication of the initial deviation of the subject. The average of the last 3 throws while wearing prisms (adapted) approximates the location to which the subject had adapted after 50 throws while wearing prisms. The average of the first 3 throws after donning prisms (negative after-effect) is a measure of the stored adaptation. The time constant of the exponential decay function fitting the throws while wearing prisms serves as the adaptation coefficient (AC), a measure of the rate of adaptation. Baseline values are means ± SD in degrees. * An exponential decay function could not be fitted to the throws of subject SH (see text).

**Overall variability**

Subjects showed relatively good throwing performance as indicated by low PC values. The PC value is a measure of the variability of the ball-hit location (it is the SD of the ball hits in degrees as an angle with its vertex at the center of the head). However, the PC gives no indication of the relative variability of the angles (motor equivalence) comprising the throw. Two subjects with the same PC value could show distinctly different angle distributions: the one with a high degree of variability spread across single/multiple angles coupled with a precise combination of angles to produce a certain PC value; the other with relatively little variability in each angle distributed on a trial-by-trial basis such that an equivalent PC value is produced. We investigated the variability of these body angles across a 50-throw block of trials as well as on a trial-by-trial basis.

Within a block of 50 throws, subjects generally showed a larger degree of variability in individual body angles than in the ball angle itself. The exception was the eyes-in-head angle, which was always less variable than the ball-hit location. Figure 2D shows the SDs of each angle during 50-block throws before, during, and after prism use for a single subject (subject DL). The subject’s head-on-trunk, trunk-on-arm, and arm-on-ball angles are more variable than the ball-hit angular position in the “before” condition. The relative variability among these angles stays fairly constant across prismatic conditions (e.g., arm-on-ball angle is always less variable than head-on-trunk and trunk-on-arm angles) as was true in all eight subjects.

**TABLE 2. Body angles before donning prisms**

<table>
<thead>
<tr>
<th>Subject</th>
<th>Eyes-in-Head</th>
<th>Head-on-Trunk</th>
<th>Trunk-on-Arm</th>
<th>Arm-on-Ball</th>
<th>Ball Angle</th>
<th>Simulated Ball Angle</th>
<th>Coordination Index</th>
</tr>
</thead>
<tbody>
<tr>
<td>SB</td>
<td>3.5 ± 1.1</td>
<td>−23.2 ± 3.7</td>
<td>36.8 ± 2.4</td>
<td>−12.4 ± 2.0</td>
<td>−0.4 ± 2.1</td>
<td>−0.3 ± 5.0</td>
<td>0.42</td>
</tr>
<tr>
<td>DL</td>
<td>4.7 ± 1.2</td>
<td>−22.1 ± 2.8</td>
<td>32.0 ± 3.0</td>
<td>−10.8 ± 1.9</td>
<td>0.1 ± 1.5</td>
<td>0.1 ± 4.7</td>
<td>0.32</td>
</tr>
<tr>
<td>JF</td>
<td>−1.0 ± 4.3</td>
<td>−18.1 ± 4.5</td>
<td>46.3 ± 3.8</td>
<td>−20.1 ± 2.7</td>
<td>0.7 ± 3.3</td>
<td>0.7 ± 7.7</td>
<td>0.43</td>
</tr>
<tr>
<td>KK</td>
<td>−7.0 ± 1.2</td>
<td>−6.4 ± 2.9</td>
<td>29.5 ± 3.3</td>
<td>−13.1 ± 2.0</td>
<td>0.0 ± 1.9</td>
<td>0.0 ± 5.0</td>
<td>0.38</td>
</tr>
<tr>
<td>TM</td>
<td>1.8 ± 2.1</td>
<td>−22.4 ± 4.4</td>
<td>34.5 ± 3.3</td>
<td>−10.2 ± 2.6</td>
<td>−0.8 ± 3.9</td>
<td>−0.8 ± 6.5</td>
<td>0.60</td>
</tr>
<tr>
<td>GS</td>
<td>−3.8 ± 1.3</td>
<td>−22.9 ± 2.4</td>
<td>47.5 ± 3.1</td>
<td>−16.0 ± 2.8</td>
<td>−0.1 ± 4.3</td>
<td>−0.1 ± 5.1</td>
<td>0.84</td>
</tr>
<tr>
<td>SH</td>
<td>11.0 ± 3.2</td>
<td>−30.2 ± 8.5</td>
<td>33.4 ± 5.5</td>
<td>−11.4 ± 2.2</td>
<td>−0.2 ± 3.0</td>
<td>−0.1 ± 11.0</td>
<td>0.28</td>
</tr>
<tr>
<td>KZ</td>
<td>−1.0 ± 1.2</td>
<td>−24.0 ± 2.8</td>
<td>36.1 ± 2.6</td>
<td>−8.8 ± 1.7</td>
<td>−0.3 ± 1.8</td>
<td>−0.3 ± 4.4</td>
<td>0.41</td>
</tr>
</tbody>
</table>

The means ± SD of each of the four body angles before donning prisms are listed for each subject. In addition, the means ± SD of the actual ball hit locations (ball angle) are listed. The results of the Monte Carlo analysis are listed as well (simulated ball angle). The coordination index (CI) is a ratio of the last two values (ball angle and simulated ball angle; see text).
the Monte Carlo analysis (5,000 simulations) have been normalized to a block of 50 throws, making the area under each—and in each—equivalent. The means ± SDs from the Monte Carlo analysis are summarized in Table 2.

Subject DL (Fig. 3A) showed the lowest variability in actual ball-hit location. The SD of the ball-hit locations (PC) was 1.5° (Table 2). This subject also showed a relatively tight distribution of ball-hit locations simulated by the Monte Carlo analysis (a relatively narrow shaded distribution, Fig. 3A). The SD of the simulated ball-hit locations was 4.7°, indicating a low degree of overall variability of the body angles. Compare this subject’s results to those of subject GS (Fig. 3B), who had a similar distribution of simulated throw locations based on the Monte Carlo analysis: thus GS had a similar overall variability of the body angles. However, the actual ball-hit locations of subject GS had a distribution almost as wide as the simulated ball-hit locations, indicating that the subject had coordinated actions across joints only slightly better than a random combination of angles. The results of subject SH (Fig. 3C) tell yet another story. This subject varied body part angles much more greatly than did the other subjects (as indicated by a broader distribution of simulated ball-hit locations; Fig. 3C, □). However, the actual ball-hit locations for this subject were relatively tight, indicating interdependency and complementarity in combining the highly varied angles. These results indicated that—especially for subject SH and to a varying degree for all subjects—coupling between body angles was utilized to decrease variability of the resulting throws. The CI values for each subject are also listed in Table 2 (see METHODS) and are discussed in the following text.

**Trial-to-trial variability**

Are subjects’ throws made with body angles that vary randomly from trial to trial, or is there a progression of change in angles due to practice or fatigue? Figure 4A shows trial by trial the before-prisms throwing session of one subject (subject DL). In this figure, the calibration factor has not been added to the four body angles, resulting in a small offset between the sum of
the angles and the actual ball-hit location. This subject had a relatively low degree of variability in each of the four angles. Yet each angle varied from trial to trial with only the eyes-in-head angle varying less than the ball-hit location (see Fig. 2D). Two of the angles showed no trend across trials (eyes-in-head and head-on-trunk). The subject showed a slight trend in trunk-on-arm \( [r = -0.41; p(r = 0) < 0.05] \) and arm-on-ball \( [r = 0.48; p(r = 0) < 0.001] \) angles. A greater degree of trial-to-trial variability was seen in subject SH. Figure 4B showed trial-by-trial the before-prisms throwing session of subject SH. This subject’s eyes-in-head, head-on-trunk, trunk-on-arm, and arm-on-ball angles all varied between trials, but there were also trends in all of these angles across the block of trials.

The correlation coefficients of angle versus trial for each subject indicate that 18 of the 32 body angles (4 angles/subject) showed some degree of gradual change across trials \( (12/18, P < 0.001; 6/18, P < 0.05) \). The remaining 14 angles showed no statistically significant trend from trial to trial. Interestingly, despite seven of the eight subjects having a statistically significant trend in at least one angle, none of the eight subjects had a significant correlation between ball-hit location and the trial number in the 50-throw before-prisms block, indicating that the trial-to-trial trends in the body angles were negated by covariance of the angles.

How do the angles change in response to a prismatic perturbation? Fig. 5A shows the first 25 throws for subject DL while wearing prisms. In this graph, each angle was plotted as a change from the mean value of the angle during the last five baseline throws (before prisms). Thus the summation of the four angles across adaptation trials reflects the change in the gaze-throw angle from a baseline value of 0° to a fully adapted value of 17.2° (30 dipters). However, the subject’s first throw landed at a value of \(-4°\) to the right of the gaze position, which was 17.2° to the left of the target. This initial deviation of the first throw to the right of the gaze position while wearing prisms was seen to varying degrees across all subjects. Subsequent throws landed nearer the center of the target. By throw 25, the full 17.2° compensation was made up by a positive change in the eyes-in-head, head-on-trunk, and trunk-on-arm angles. The arm-on-ball angle, however, continued to subtract from the desired gaze-throw calibration. Changes in the trunk-on-arm and arm-on-ball angles were the main components of this subject’s adaptation. Figure 5B shows graphs of a second subject (KZ), who showed changes across all four angles, resulting in the final 17.2° gaze-throw angle. Six of eight subjects showed this trend of changes in all four body angles. There was no apparent relationship between the values of the angles making up the gaze-throw calibration at the end of the adaptation and the angles making up this calibration during the first aftereffect trials. Finally, the body angles did not always change smoothly from trial to trial but in some subjects, appeared to change unpredictably, sometimes adding to the change in gaze-throw relationship in one trial and subtracting from it in the next. An example is the trunk-on-arm angle for subject DL at trials 2 and 3 (Fig. 5A).

Covariance

Covariance of the body angles is implied in the data in that the SDs of the four body angles are usually larger than the SDs of the sum of the angles. We studied covariance to probe further the relationships between different angles. A principal components analysis (see Methods) was used to look for covariance between angles that would suggest that the angles were controlled together as a unit. Table 3 shows the results of the principal components analysis on the four body angles during the 50-throw block of before prisms throws. Variables loading on a principal component (factor loading: \( >0.700 \)) are shown as well as the amount of variance accounted for by each component. For two of eight subjects, two principal components were sufficient to characterize the variability of throwing postures, accounting for \(-85\%\) of the variance. In other words, for two of eight subjects, the four body angle variables were essentially reduced to two variables that could be controlled by the nervous system: in subject SB, for example, the eyes-in-head (EH), head-on-trunk (HT), and trunk-on-arm (TA) angles were controlled as one unit and the arm-on-ball (AB) angle was controlled as a second unit (Table 3). For five of eight subjects, three principal components were necessary to describe the covariance, and for one of eight subjects, four principal components were required. The principal components accounted for a mean value of 94.4 ± 5.8% of the variance across the eight subjects (range: 83.8--100%).

Most striking among these data are the relationship between which angles load together on a single principal component and the throwing precision of the subject. First, five of eight subjects had a principal component on which loaded both the
head-on-trunk and trunk-on-arm angles. The three subjects who did not control these angles as a single unit (i.e., the angles did not load on the same principal component) showed the greatest amount of variability in throws (PC) and the largest CI ratios (the ratio of the variability in throws to the overall variability of the body angles, see methods). Second, subject GS required four principal components to characterize the variability. This subject had the CI ratio near 1.0 (0.85) and the largest PC (4.0°), indicating that there was almost no covariance among the four body angles, each controlled as if independent of the others. Third, the arm-on-ball angle was controlled independently of all other angles in all eight subjects. Finally, the angular variance of subject SH, who had the smallest CI ratio, was accounted for by only two principal components. While this subject had the greatest amount of variability in two of four body angles among all subjects and a large variability in the other two body angles, the strategy appeared to be to control three of these angles (eyes-in-head, head-on-trunk, and trunk-on-arm) as a single unit, thus decreasing his potential degrees of freedom.

There was no obvious pattern in the principal components when comparing the 25 throws closer to the target to the 25 throws farther from the target or when comparing the 25 more leftward throws to the 25 more rightward throws before wearing prisms for each subject. However, a comparison of the first 25 throws with prisms to the second 25 throws with prisms showed that in three of the five subjects who controlled the head-on-trunk and trunk-on-arm angles as a single unit before wearing prisms, these angles became dissociated (less covariant) during the first 25 prisms throws (adaptation), loading on different principal components, and then re-established their before-prisms pattern (more covariant) during the second 25 prisms throws (adapted).

**Discussion**

In throwing, the nervous system must control actions across multiple joints. As more joints are allowed unrestricted movement, the degrees of freedom and complexities of the task increase. Bernstein (1967) observed that in untrained or unskilled individuals, a common tendency is to restrict the degrees of freedom of the limb by making a number of segments act as a unit, decreasing the complexity of the movement, thereby assuring a greater likelihood of a desirable outcome.

Hore (1994) demonstrated that during a “natural” throw, at ball release, the entire arm was constrained to 2 of its possible 7 df. Further observation has shown that the angles controlled as a unit in skilled behaviors are often not contiguous, sometimes spread across multiple limbs (e.g., Marteniuk et al. 2000). Such a control strategy in which multiple body angles or segments are controlled in emergent patterns to decrease the demands of a task has been documented in many movements including pinching (Cole and Abbs 1986), grasping (Santello and Soechting 1997), speech (Hughes and Abbs 1976), reaching (Abend et al. 1982), typing (Soechting and Flanders 1997), piano playing (Engel et al. 1997), locomotion (Winter 1984), pointing (Marteniuk et al. 2000), and shooting (Arutyunyan et al. 1968, 1969).

Coupling among many moving body parts is not always the norm in skilled behavior. The phenomenon is specific to the requirements of the task (Abbs and Cole 1987; McDonald et al. 1989). In shooting, for example, experienced marksmen tend to couple the wrist and shoulder joints when aiming at a target (Arutyunyan et al. 1968, 1969). In skilled dart throwing, however, where the movement is often voluntarily limited to motion at the elbow and distal joints, subjects learn to uncouple the wrist-elbow and wrist-shoulder angles when practicing 500 dart throws with the dominant hand spread over 10–14 days (McDonald et al. 1989). Subjects practicing with the nondominant hand show higher cross-correlations among all joints, presumably to increase accuracy with the unskilled nondominant hand.

Thus the coupling or uncoupling of specific body angles during a movement, and the manipulation of the covariance of the body angles, appears to be a common and effective strategy in previously studied movements. In the current paper, we have studied the strategies that emerge during overhand throwing and its adaptation.

**What do the variability and covariance of body angles during throwing reveal about the nervous system?**

In this study, subjects used a varying combination of joint angles, often with angles changing in a seemingly random fashion from trial to trial. It was also the case that the angular variation of the hits on the target was in most cases significantly smaller than the angular variation among coupled body parts. To account for the high accuracy of ball on target...
throughout throwing sessions, the distribution of coupled body parts changed unpredictably and independently from throw to throw.

Of the subjects (7/8) that did produce a significant trend in at least one angle from trial to trial, none of them had a significant correlation between ball-hit location and the trial number in the before-prisms block. Most subjects coordinated the head-on-trunk and trunk-on-arm body angles as one unit (5/8 subjects, Table 4). Subjects who did not control these angles as a unit showed the greatest variation of their baseline throwing variability (PC, Table 1) and the largest ratio of variability. The results demonstrate that to a varying degree for all subjects, coupling between body angles (covariance) was used to decrease variability of the resulting throws and that the trial-to-trial variability in body angles were overcome by covariance of the angles.

The fact that the arm-on-ball was independently controlled from other measured principal components could be due to the special problems of timing finger extension, and distal forces during throwing. Hore showed that high-low inaccuracies in throwing were due to inappropriate timing of ball release (Hore et al. 1996) and that finger flexor torques progressively increased to counteract progressively increasing back forces from the ball (Hore et al. 2001). This control could be independent of proximal joint rotations.

Does allowing for greater degrees of freedom during a throw enable a person to adapt that throw more efficiently? Despite the significant variability of individual angles from trial to trial, the relative variability among each of the angles stayed fairly constant across prismatic conditions. However, the body parts that had been tightly coupled became less covariant during visuomotor perturbation by laterally shifting prisms. In a majority of our subjects who coupled head-on-trunk and trunk-on-arm angles during throws before donning prisms, these angles became less covariant when the subject was required to adapt to prisms only to regain covariance on the subject reaching a stable pattern of throws hitting the target. The gaze-throw adjustment during adaptation to prisms was not confined to any one angle but instead was distributed across sets of body parts. This observation is consistent with the hypothesis that subjects search through joint space to find a solution to the visuomotor discordance.

In a previous study, we have shown that subjects challenged by vertically shifting wedge prisms modify more degrees of freedom and more sources of potential error to achieve a gaze-throw recalibration than are employed during no-prism conditions (Martin et al. 2001). One might also have predicted that subjects with a lower degree of angular covariance would have a significantly faster adaptation rate. These subjects might be able to find a suitable solution to the visuomotor discordance more quickly by exploring more diverse body angle combinations than subjects who showed a higher degree of covariance. However, there was no apparent relationship between the number of principal components used by an individual and that individual’s adaptation rate (AC) during adaptation trials (data not shown). Hence, subjects that used more principal components (less covariance) did not adapt faster than other subjects. The number of principal components used in this throwing task do not seem to relate to the ability to adapt faster. This would suggest that the principal components used would not be affected or have an effect on prior practice of adaptation. From these observations, it is apparent that the control strategy is task dependent and that covariance and variability have important roles in motor control.

Although our study does not directly address the issue of the source of the variability or of the covariance, we can offer suggestions for their usefulness. Foremost, variability and covariance may serve as a mechanism by which a subject searches through joint space for optimal solutions to the motor-control problem facing the subject. This searching mechanism may include the volume of such space through which the subject searches as well as the step size the subject utilizes when moving from one point to another in that space. Covariance of body angles may also be a solution of the CNS to compensate for muscle fatigue, injury, and changes in the environment. This covariance may affect both the thrower’s performance (variability) and adaptation.

What is the neural substrate of covariance and adaptation of gaze-directed throwing?

Covariance and complementarity imply that body parts are somehow interconnected, so that each may “know” what the other is doing. This communication must be sufficiently complete so that there is a wide range of complementary angles between one body part versus another. Any proposed neural substrate must account for trial-to-trial variability in body angles, their complementary covariance, and the motor equivalence thereby demonstrated in this and other studies. Furthermore, it is clear that this complementary covariance may exist independent of the adaptation because it is present in individuals with disparate performances but similar adaptation rates (Martin et al. 1996a). In addition, subjects with lesions in different areas of the motor system may have an impairment in performance of overhand throwing without an impairment of adaptation rate and vice versa (Martin et al. 1996a; Wiener et al. 1993).

Based on our observations as well as those of others, we would favor a model of cerebellar participation in prism adaptation that incorporates our findings of body angle complementarity and motor equivalence. As we have outlined elsewhere (Martin et al. 1996a; Thach et al. 1992), on anatomical and theoretical grounds, the olivo-cerebellar system has been suggested as a site for motor adaptation and learning (Albus 1971; Gilbert 1975; Ito 1972; Marr 1969). Further, studies of prism adaptation of visually guided arm movements in experimental subjects have consistently shown that adaptation is impaired or absent when there is an adequate lesion in the olivo-cerebellar system (Baizer and Glickstein 1974; Baizer et al. 1999; Gauthier et al. 1979; Martin et al. 1996a; Weiner et al. 1983). In addition, the anatomy of the cerebellar cortex seems uniquely structured to allow for a wide range of body angle complementarity and motor equivalence (see following text).

A cerebellar circuit model can in theory account for the change in muscle actions controlling constituent body parts in a compound movement during short-term motor adaptation. The essence of the model is the effect that the cerebellar output has on motor repertoires resident in the downstream movement generators (Thach et al. 1992). This effect is not only modulatory, controlling gain of the downstream generators but also combinatorial, mixing motor elements within and across generators to adapt old and develop new synergies of multiple
body parts. The agency of this combining power would be the parallel fiber which, via Purkinje cell beams, spans the width of up to two different body representations within the deep cerebellar nuclei. The parallel fiber-Purkinje cell synapse is adjustable under the influence of the climbing fiber (Ito and Kano 1982; Ito et al. 1982). This could seem a likely mechanism for changing synergic combinations (Thach et al. 1992).

One possible candidate for the complementary control of multiple joints within the cerebellar circuit is the reciprocal inhibitory connections between neighboring Purkinje cells. Thus one Purkinje cell firing at high frequencies (such as to control 1 body angle) would a priori ensure that a neighboring Purkinje cell (controlling another body angle) would fire proportionately less and exert proportionately less control. Another possible candidate in higher vertebrates is the inhibition of Purkinje cells “off” the parallel fiber beam reciprocal to those “on” the beam exerted by the basket cells.

Recent studies have suggested that additional areas of the CNS may play roles in prism adaptation. Lesions of the ventral premotor cortex in monkeys impair prism adaptation of reaches (Kuratora and Hoshi 1999), and a positron emission tomography (PET) study of normal human subjects implicated involvement of the posterior parietal cortex (Clower et al. 1996). Motor equivalence, as well as prism adaptation, is likely to be distributed among several neural structures. We would stress that complementarity and motor equivalence are also important features of movement coordination. It may prove useful in future studies to consider the roles of cerebellar circuit elements as well as other neural substrates in complementary covariance of body parts in motor control.

On a suggestion from R. Held, N. Daw, and T. Wiesel originally developed this task for teaching.

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