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State space analysis of timing: exploiting task redundancy to reduce sensitivity to timing

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Cohen RG, Sternad D. State space analysis of timing: exploiting task redundancy to reduce sensitivity to timing. *J Neurophysiol* 107: 618–627, 2012. First published October 26, 2011; doi:10.1152/jn.00568.2011.—Timing is central to many coordinated actions, and the temporal accuracy of central nervous system commands presents an important limit to skilled performance. Using target-oriented throwing in a virtual environment as an example task, this study presents a novel analysis that quantifies contributions of timing accuracy and shaping of hand trajectories to performance. Task analysis reveals that the result of a throw is fully determined by the projectile position and velocity at release; zero error can be achieved by a manifold of position and velocity combinations (solution manifold). Four predictions were tested. 1) Performers learn to release the projectile closer to the optimal moment for a given arm trajectory, achieving timing accuracy levels similar to those reported in other timing tasks (~10 ms). 2) Performers develop a hand trajectory that follows the solution manifold such that zero error can be achieved without perfect timing. 3) Skilled performers exploit both routes to improvement more than unskilled performers. 4) Long-term improvement in skilled performance relies on continued optimization of the arm trajectory as timing limits are reached. Average and skilled subjects practiced for 6 and 15 days, respectively. In 6 days, both timing and trajectory alignment improved for all subjects, and skilled subjects showed an advantage in timing. With extended practice, performance continued to improve due to continued shaping of the trajectory, whereas timing accuracy reached an asymptote at 9 ms. We conclude that skilled subjects first maximize timing accuracy and then optimize trajectory shaping to compensate for intrinsic limitations of timing accuracy.

skill acquisition; coordination; trajectory planning; throwing; learning

TIMING IS OF CRITICAL IMPORTANCE in a wide range of human behaviors, from high-performance skills such as pole vaulting or playing the violin to everyday actions like stepping off a curb when the “walk” light comes on. Although timing is often discussed as if it were a unitary concept, a closer look at these examples reveals that there are at least two different kinds of timing: extrinsic and intrinsic. Extrinsic timing involves the coupling of one’s actions to something in the external world, such as the changing of a traffic signal or the rhythm of one’s fellow musicians. It is often studied in the laboratory with tasks such as tapping to a prespecified beat. Intrinsic timing, also referred to as relative timing, involves the coupling (or coordination) of two or more internally generated elements to produce a complex action. For instance, initiating a step requires coupling the stepping leg with the weight shift onto the stance leg, whereas

pole vaulting requires coordinating an intricate series of movements of the legs, torso, arms, and fingers.

One task for which timing has been credited with special importance is throwing. For any kind of throwing, the intrinsic timing of the release of the projectile with respect to the hand trajectory is crucial, as the position and velocity at the moment of release fully determine the projectile trajectory (neglecting air resistance and rotations). An important consideration is that accurate throwing, like many other real-world tasks, is a redundant task with more than one solution for a given outcome. As highlighted in previous studies on throwing, the number of position and velocity combinations of the hand at release that lead to success is theoretically infinite (Cohen and Sternad 2009; Dupuy et al. 2000; Müller and Sternad 2003, 2009; Sternad and Abe 2010). This set of state variable combinations defines the manifold of successful solutions or “solution manifold.” Previous work has highlighted how the solution manifold structures improvement over many practice trials by analyzing the distribution of sets of data at release (Cohen and Sternad 2009; Müller and Sternad 2004; Sternad et al. 2011). The present work expands this research by considering the effect of the trajectory of the arm before projectile release. It is important to consider that arm trajectories always vary slightly across trials, and therefore each trajectory requires a different timing of the release that affects the sensitivity to timing error. Hence, for accurate throwing, two possible routes exist to improve accuracy. First, throwers could improve their timing such that they release the projectile closer to the best position/velocity state available for a given arm trajectory. Second, throwers could adapt their arm trajectories such that a larger set of successful angle/velocity combinations become available, i.e., the trajectory follows the solution manifold.

Two major problems plague most of the prior work on timing in throwing. The first is the reliance on some landmark from which to measure the timing of the release of the thrown object. Landmarks that have been used include activation of wrist flexors (Chowdhary and Challis 1999), arm position (McNaughton et al. 2004), forward movement of hand (Hore et al. 1999), and zenith of the arced hand path (Smeets et al. 2002). However, all of these landmarks are themselves subject to interdependent variation and hence may introduce confounding variability. On the other hand, the redundant nature of throwing means that covariation between elements can compensate for variability and lead to success (Kudo et al. 2000; Müller and Loosch 1999). Hence, no one variable can serve as a consistent reference point to measure variability and accuracy in timing.

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A second, related limitation of most previous studies is the reliance on an invariant hand path (Calvin 1983; Chowdhary and Challis 1999; Hore et al. 1995). Modeling and data analyses based on these assumptions have suggested that to achieve the performance levels seen, throwers must control timing with standard deviations as low as 1 ms. If true, this is impressive, given that in fast rhythmic tapping to a metronome with periods of ~ 200 ms, standard deviations are ~ 10 ms (Spencer et al. 2003; Sternad et al. 2000). One might even expect better timing performance in a rhythmic tapping task, an extrinsic timing task in which the synchronizing event can be anticipated and “practiced” repeatedly, than in a single discrete action such as throwing (Hogan and Sternad 2007). However, even if this reasoning is wrong, it is still questionable whether the central nervous system (CNS) can control any event with 1-ms variability, given the noise present at all levels in the nervous system (Faisal et al. 2008). It is likely that previous studies of throwing have overestimated the temporal precision of the release due to model assumptions, most notably the invariance of the speed profile of the arm trajectory.

Two studies have investigated changes in arm trajectories across practice, using dart throwing as their task. Müller and Loosch (1999) studied performance both in realistic three-dimensional performance and in a controlled single-joint version of the task. These authors found that subjects displayed covariation between position and velocity at release such that release states clustered around the solution manifold, with experts showing more covariation than average performers. This finding was confirmed by subsequent studies that included two additional descriptors of improvement, tolerance and noise reduction (Cohen and Sternad 2009; Müller and Sternad 2004; Sternad and Abe 2010; Sternad et al. 2011). Müller and Loosch (1999) argued that subjects achieve this covariation by modifying their movements to approximate a trajectory that maximizes the sequence of states that could lead to a successful hit, and they evaluated this hypothesis by comparing temporally shifted and averaged trajectories with the optimal trajectory. Results supported the hypothesis that sensitivity to temporal error decreases as covariation increases, leading to the conclusion that subjects exploit this fact as they learn a throwing task.

Smeets and colleagues (2002) challenged these results and presented experimental data and simulations that appear to contradict this claim. The arm model in their sensitivity analysis traversed a semicircular hand path around a center of rotation at the elbow joint with a set velocity profile (either constant or smoothly accelerating) so that release time fully determined the position and velocity of the dart at the moment of release. With practice, subjects decreased their hand path radius and released later with respect to the zenith of the hand path. According to the model and sensitivity calculations, this change increased sensitivity to errors in the moment of release, counter to the findings of Müller and Loosch (1999). Smeets and colleagues (2002) interpret this result as evidence that improvement in throwing does not rely on modification of the trajectory to reduce sensitivity to timing errors. We will present a new approach and data that shed more light on these seemingly contradictory results.

The objectives of the present study were to describe quantitatively the intrinsic timing of a discrete throwing action across practice and across skill levels. The study presents a

new approach to timing analysis, based on full knowledge of the task solution space and the solution manifold. Our approach allows a quantitative testing of four predictions. 1) Timing improves with respect to optimal release time consistent with timing reported for other skills but does not reach the 1-ms accuracy level previously reported. 2) With practice, subjects shape their trajectories to create maximum opportunities for successful release. This strategy exploits the redundancy of the task and thereby relaxes the constraints on timing. Importantly, these two routes to improvement are independent and complementary. Given that our previous study (Cohen and Sternad 2009) reported a continued increase in covariation among skilled throwers together with a decrease in noise (dispersion) that reaches a plateau, we further hypothesized that 3) compared with unskilled throwers, skilled throwers exhibit greater changes both in timing (releasing closer to the optimal time for a given trajectory) and in hand trajectory (approaching alignment with the solution manifold). Lastly, we predicted that 4) during extended practice, performers achieve continued improvement by shaping the trajectory so that limitations on timing accuracy do not limit performance.

To assess the timing and trajectory-shaping strategies as a function of practice and skill, this study examined performance over a relatively long course of practice. All subjects practiced a minimum of 6 days for a total of 1,080 throws each, and 3 skilled throwers continued to practice for a total of 15 days that amounted to 2,700 throws each.

METHODS

Subjects

Fourteen right-handed subjects (2 female and 12 male) participated in the experiment after providing written informed consent. All were members of the Pennsylvania State University community; they ranged in age from 23 to 48 yr and included students, faculty, and staff. The experiments were approved by the Pennsylvania State University Institutional Review Board, and all procedures were in accord with the Declaration of Helsinki. Eleven of the subjects were healthy individuals without any special experience in throwing skills (the average group). They practiced for 6 days. Three individuals reported considerable prior experience in throwing skills: one was an intramural Frisbee player, one was a semiprofessional cricket player, and one was an all-around athlete. Hence, these three were labeled as experts. These expert performers were asked to practice for a total of 15 days.¹

The predefined division by self-report into expert and average groups was validated post hoc by examining performance on *day 6*. Consistent with their self-report, the three expert throwers performed better than all of the average throwers; each of these individuals was beyond a 95% confidence interval of the remaining average group based on number of target hits and better than 100% of the average group based on the error measure. The data from one self-reported average thrower (a volleyball player) whose performance approximated that of the expert group but who did not practice for 15 days were removed from the analysis.

Apparatus and Task

To investigate strategies by which people achieve accuracy in throwing, subjects practiced throwing a projectile to a target in a virtual environment. The design of the experimental task was inspired

¹ The same data were the basis of an earlier study presenting the Tolerance, Noise, and Covariation (TNC) analysis method, published in Cohen and Sternad (2009).

by a British pub game called “skittles” in which a ball hangs from a pole and a target (the skittle) is placed on the far side of the pole from the player. The player attempts to throw the ball so that it goes around the pole and hits the target. In the virtual version of the game developed for this experiment, the subject stood ~60 cm from a back projection screen (width of 250 cm and height of 180 cm), as seen in Fig. 1A. The subjects were free to position themselves to meet the specific task demands. A computer-generated image of a top-down view of the workspace (shown in Fig. 1B with 3 sample ball trajectories) was projected onto the vertical screen so that it filled most of the participant’s field of view. Near the center of this workspace, at a height of 173 cm (close to most subjects’ eye height), was the center post, represented as a circle of 16-cm diameter. A circular target of 3-cm diameter was displayed 20 cm to the right and 50 cm above the center post. The virtual arm was 12 cm long, and its rotation point was fixed 50 cm below the center of the post. A virtual ball with 3-cm diameter was attached to the free end of the virtual arm.

The movement was constrained to a single-joint elbow rotation in the horizontal plane, with an extension of the index finger triggering the projectile release. The subject rested his or her forearm on a horizontal metal arm that pivoted around an axle centered at the elbow joint. The metal arm was padded with foam, and its height was adjusted to a comfortable level for each subject. A tennis ball was attached to the free end of the metal arm, with a pressure-sensitive switch on its distal end. The subject grasped the tennis ball so that his or her index finger closed the switch and then swung the arm in an outward motion, like throwing a Frisbee backhand. For the specific

target used in this experiment, subjects had to position themselves sideways with their right shoulder close to the screen to throw the ball with release angles in the range between -110 and -70° .

When the subject released the switch by extending the index finger, the virtual ball traversed a path initialized by the angle and velocity of the subject’s arm at the moment of release. Movements of the virtual arm and the ball were displayed on screen to the subject in real-time (refresh rate of the screen was 75 Hz). A potentiometer at the axle recorded angular rotation of the arm. Custom-written software written in C++ sampled the potentiometer data at ~700 Hz, calculated the trajectory of the ball (based on the measured angle and derived velocity at the time of release), and displayed the trajectory in real-time to the subject. The visuomotor delay was measured in separate tests to be 22 ± 0.5 ms. To reduce the effect of measurement noise on the displayed data efficiently, the program continuously fitted a straight line to a window of 10 samples of angular position to obtain a continuous estimate of angular velocity. At the moment of release, this velocity estimate was used as initial condition for the ball trajectory. This calculation added minimal delay to the display (in the order of $1 \mu\text{s}$).

The ball trajectory, as determined by the simulated physics of the task, described an elliptic path around the pole. This trajectory was not immediately intuitive to subjects, and they had to learn the mapping of their arm movements, the finger lifts, and the ball trajectories in the projected workspace. Hence, the task was novel even for the subjects with extensive throwing experience. If the ball made a direct hit to the target (<1.2 cm), the color turned from yellow to red to signal a hit. Subjects were encouraged to maximize the number of hits they achieved in each block of practice.

Model of the Task

The ball trajectory described an elliptic path around the pole as determined by the simulated physics of the task. The ball trajectories were generated by a two-dimensional model in which the ball was attached by two orthogonal massless springs to the origin of a coordinate system at the center post. Because of restoring forces proportional to the distance between the ball and the center post, the ball was accelerated toward the center post. The motions were lightly damped by multiplication with the exponential term to approximate realistic behavior. The equations for the position of the ball in x - and y -dimensions (at time t) are:

$$x(t) = A_x \sin(\omega t + \phi_x) e^{-\frac{t}{\tau}}$$

$$y(t) = A_y \sin(\omega t + \phi_y) e^{-\frac{t}{\tau}}$$

where A_x and A_y describe the amplitudes in x - and y -dimensions, ω denotes the natural frequency of the system, and τ indicates relaxation time. The phases ϕ_x and ϕ_y are determined by the ball release angle as described in the APPENDIX.

Execution Space, Solution Manifold, and Hit Zone

The execution space and associated solution manifold were calculated numerically in a forward manner using the equations described above. For each point in execution space, defined by angle and velocity at release, the ball trajectory was computed for one traversal. The minimum distance to the target on that traversal defined the error. If that value was below 1.2 cm, the throw was considered a hit, and the target color turned from yellow to red to signal the hit to the subject.

Perfect hits to the target (zero error) defined the one-dimensional solution manifold. Figure 2A shows the execution space for a subset of release angles and velocities with the U-shaped solution manifold denoted by a black line; the shading denotes the magnitudes of the error. Darker shades show increasing error. The white region surrounding the black line defines the region in which a release would

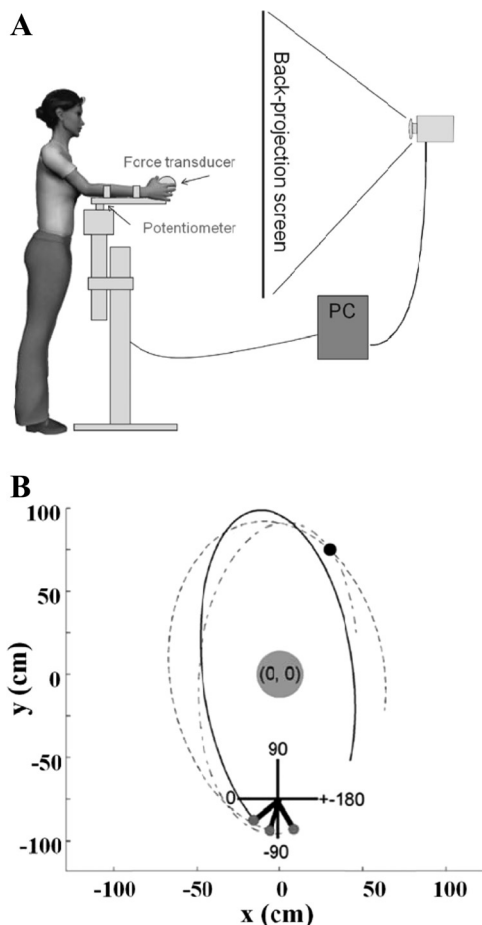


Fig. 1. Experimental setup. A: schematic of subject and virtual environment. B: 3 exemplary throws in workspace. The view of the ball, center post, and target is top-down, as it is presented to subjects on the large screen in front of them. (Subjects only see their current throw, but 3 throws are shown here for illustrative purposes.) PC, personal computer.

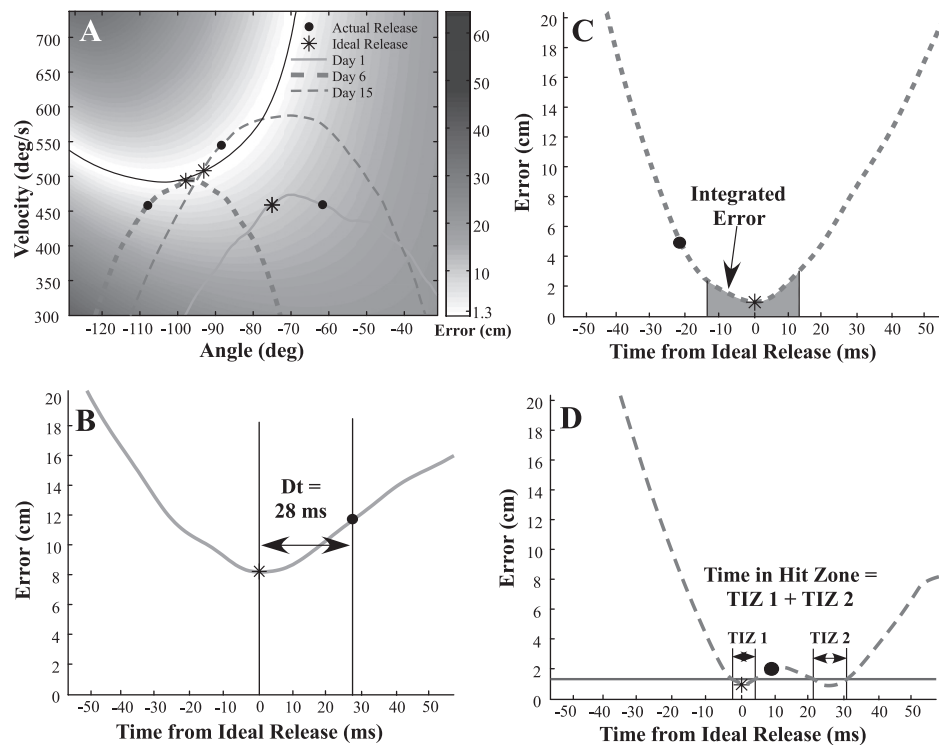


Fig. 2. Three example trajectories and calculation of dependent measures. For all subplots, the optimal release moment is represented with an asterisk, and the actual release is indicated with a filled dot. *A*: execution space spanned by angle and velocity at release. Background shading denotes the error (distance to target) calculated for each pair of release variables. The broad white band denotes the set of release angles and velocities that lead to a target hit (error < 1.2 cm), and the thin black strip denotes the solution manifold, the set of combinations of angles and velocities that lead to zero error. The 3 trajectories shown were executed by 1 subject on different days. *B*: calculation of Timing Error. The example trajectory from *day 1* was transformed into error over time so that the y-axis shows the error that each throw would have yielded had the subject released the ball at that moment in the trajectory. The difference between the actual release and the ideal release quantifies the Timing Error. Dt , Δt (Δ actual release time – ideal release time = timing error). *C*: calculation of Integrated Error. The example trajectory from *day 6* was transformed into error over time. The gray shaded zone indicates the integrated error over the time window of 25 ms centered on the ideal release moment. *D*: calculation of Time in Hit Zone. The example trajectory from *day 15* was transformed into error over time. The horizontal line indicates the threshold below which a target hit occurred (the target hit zone). The total amount of time that the trajectory spends below the horizontal line is the Time in Hit Zone (TIZ).

lead to an error < 1.2 cm, which was reported to the subject as a successful hit. Note that the solution manifold is nonlinear; it includes solutions with release angles near -100° and release velocities near $500^\circ/\text{s}$ as well as solutions around -70° and $750^\circ/\text{s}$ (example throw not shown).

Figure 2 also illustrates three sample arm trajectories from one subject in state space and as time series of error over time. Figure 2*A* shows three arm trajectories in state space (as sequence of position/velocity pairings) with the optimal release moment marked by an asterisk and the actual release moment indicated with a filled dot. Theoretically, the arm preparing to release the ball could pass through a sequence of combinations of angle and velocity, such that a release at any one of them would be equally good, i.e., would lead to a perfect throw with zero error. To achieve this, the arm would have to follow the solution manifold. The advantage of following the solution manifold would be reduced sensitivity to imprecision in release timing.

Dependent Measures

We calculated two dependent measures of outcome, one measure of timing, and two measures of arm trajectory shaping. Error and Target Hits were measures of outcome or result, used to quantify overall improvement. These measures were visible to the subject on the screen. The measures of timing and arm trajectory shaping were more indirect, determined after having converted the arm trajectory in state space to one of error over time. They were not explicitly available to the subject. Timing Accuracy described release time relative to ideal release moment for a given trajectory. This was the primary measure to test *prediction 1*. Time in Hit Zone and Integrated Error quantified

how the actual arm trajectory was shaped with respect to the solution manifold. These two measures were used to evaluate *prediction 2*.

Error and Target Hits. Error was defined as the minimum distance between the ball trajectory and the center of the target for a given throw (see Fig. 1*B*). Target Hits was defined as the number of throws per day with Error < 1.2 cm. These target hits were signaled to the subject by a color change of the target.

Timing Error. To quantify timing accuracy, the arm trajectories were converted to error over time: every point on the trajectory was evaluated as a potential release moment, and its associated error was computed. Figure 2*B* illustrates how an arm trajectory from *day 1* (also shown in Fig. 2*A*) was converted into a time series of error values over time. The optimal release moment was defined as $t(0)$, represented by the vertical line at $t(0)$ and an asterisk. The actual release moment is indicated with a vertical line and a filled dot. In cases where the trajectory crossed the manifold twice, $t(0)$ was defined as the intersection that was closer in time to the actual release. The absolute difference between the actual release time and $t(0)$ was defined as Timing Error. We predicted that this measure would decrease in both subject groups as performance improved (*prediction 1*), that it would decrease faster for the expert group than for the average group (*prediction 3*), and that it would reach a plateau in extended practice (*prediction 4*).

Integrated Error. A seemingly obvious way to quantify the difference between the solution manifold and the actual arm trajectory would be to calculate the integrated distances between time points on the two curves. However, this value is not calculable because angle and velocity have different units and the space has no defined metric

(Sternad et al. 2010). Therefore, we computed this distance in the space of error, based on the previously calculated trajectories expressed as a time series of error. Figure 2C shows an example from *day 6* (also shown in Fig. 2A): for every time point in a 25-ms time window centered on $t(0)$, the corresponding error measure was computed. The window of 25 ms was chosen based on previous estimates of timing accuracy of ± 11 –15 ms (Repp 2010b; Spencer et al. 2003; Sternad et al. 2000) and on the window size chosen by Smeets et al. (2002). The computed errors were averaged to produce Integrated Error.

Time in Hit Zone. This measure quantified the amount of time the arm trajectory spent in a region of the state space at which ball release would result in a throw with an error <1.2 cm (Hit Zone). To calculate this measure, we computed error for every 1-ms time point in the trajectory and calculated the number of samples with error <1.2 cm. Figure 2D illustrates this computation for a throw from *day 15* (also shown in Fig. 2A). The Hit Zone is indicated by a horizontal line at error = 1.2 cm. The asterisk for optimal release and dot for actual release are shown for consistency, although they are not used in this calculation. Note that for arm trajectories that cross the solution manifold twice, this method includes points around both intersections. In this display, the trajectory that follows the solution manifold perfectly would be a horizontal line with error = 0.

We predicted that the two trajectory measures would change with practice in both subject groups, with Integrated Error decreasing and Time in Hit Zone increasing (*prediction 2*). We further predicted that expert subjects would show larger changes than the average group and that they would continue to improve during extended practice (*predictions 3 and 4*).

Data Processing and Statistical Analyses

Signal processing was conducted with custom software written in MATLAB (MathWorks, Natick, MA), and inferential statistics were computed with MATLAB and R (R Foundation for Statistical Computing, Vienna, Austria). The raw data were sampled at a variable rate due to limitations of the Windows operating system. Therefore, subsequent offline analysis applied a Savitzky-Golay filter with a window size of 50 ms on both sides to create data with equal sampling. This filter first spline-fitted and then resampled the data at equal 1-ms intervals and finally differentiated the interpolated data.² Means and standard deviations of the dependent measures were computed across subjects in each group. To characterize the data, exponential fits were applied using the EzyFit toolbox in MATLAB (Levenberg-Marquardt optimization).

To statistically evaluate the predictions that practice has an effect on timing and arm trajectory shaping and that the two groups show different changes, we conducted a model selection procedure. To begin, three models were fitted to the pooled data of all subjects using the EzyFit toolbox for MATLAB. To make a fair comparison, we used only 6 days of data from the three expert subjects to match the 6 days of data available from the average subjects. The residuals of the least-square fits of the models were compared in a pairwise manner using the F statistic to evaluate statistical difference. The three models were nested such that pairwise comparisons tested the effect of the additional model component:

model A: $y = a$,

where a is a constant;

model B: $y = a + b \times \exp(c \times \text{day})$,

where $[a, b, c]$ parameterizes an exponential function of day;

and *model C:* $y = a1 + b1 \times \exp(c1 \times \text{day}) + a2 + b2 \times \exp(c2 \times \text{day})$, where $[a1, b1, c1]$ parameterizes the expert group fits and $[a2,$

$b2, c2]$ parameterizes the average group fits as a function of day.

Model A represented the null hypothesis, fitting a constant to all subjects' data. This model assumed that there was no change with practice and no group difference. *Model B* captured the exponential change over days in the dependent measures when all subjects' data were pooled assuming that both groups improved with practice in the same manner. *Model C* applied separate fits for the two groups including their exponential change with practice. This model assumed that each group showed change with practice in a significantly different fashion. To test whether adding parameters to the model significantly improved the goodness of fit, the difference in the residual sums of squares (RSS) was evaluated with the F -test statistic:

$$F = \frac{\frac{RSS_B - RSS_A}{df_B - df_A}}{\frac{RSS_A}{df_A}}$$

For comparing *models A* and *B*, the degrees of freedom for the F statistic were $(df_B - df_A, df_A)$. The degrees of freedom for each model were the number of parameters, e.g., 3 for *model B* and 1 for *model A*. Pairwise comparisons were conducted for *B-A* to test for an effect of practice and for *C-B* to test for group difference.

To evaluate changes in performance associated with long-term practice, we fitted two models to the last 10 days of practice:

model D: $y = a$,

where a is a constant;

and *model E:* $y = a + b \times \text{day}$,

where $[a, b]$ parameterizes a linear function of day. The models were compared in the same manner as described above.

RESULTS

Figure 3 shows example arm trajectories from 3 expert subjects from early (*day 1; A*), intermediate (*day 6; B*), and late (*day 15; C*) in practice. Each panel shows the middle 20 throws out of 180 performed that day. The figure clearly shows changes both in arm trajectory and in release timing across practice. On the 1st day, release timing was highly variable, and subjects only rarely entered the hit zone (represented in the figure by the white band indicating the solution manifold with release states that would lead to subthreshold errors). By *day 6*, subjects were reliably entering into the hit zone but only for a short time. The release was consistently at the peak velocity of the throw, which was a good default strategy but did not assure optimal release timing for all arm trajectories. By *day 15*, the trajectories had evolved so that subjects spent more time aligned with the solution manifold, and release timing was no longer concentrated at the peak velocity of the arm trajectory.

Outcome Variables

To attest that the subjects showed the necessary prerequisites of performance improvement consistent with many other motor learning studies, the first two analyses evaluated traditional error measures. Figure 4 displays the mean error (*A*) and number of target hits per block (*B*) for each group. The error bars denote the standard error of the mean across the individual subjects. Exponential functions have been fitted to three subsets of the data: 1) the 6 days of the average subjects; 2) the 1st 6 days of the expert subjects (for statistical comparison with the average subjects); and 3) all 15 days of practice of the expert subjects. On *day 1*, one expert subject had extremely deviant values from the rest of the group for Error, Integrated

² To confirm that the data processing did not distort the data, we compared the separation into hits and misses produced by the post hoc filtered data with that produced by the online regression method that provided subjects with performance feedback. The separation into hits and nonhits was identical.

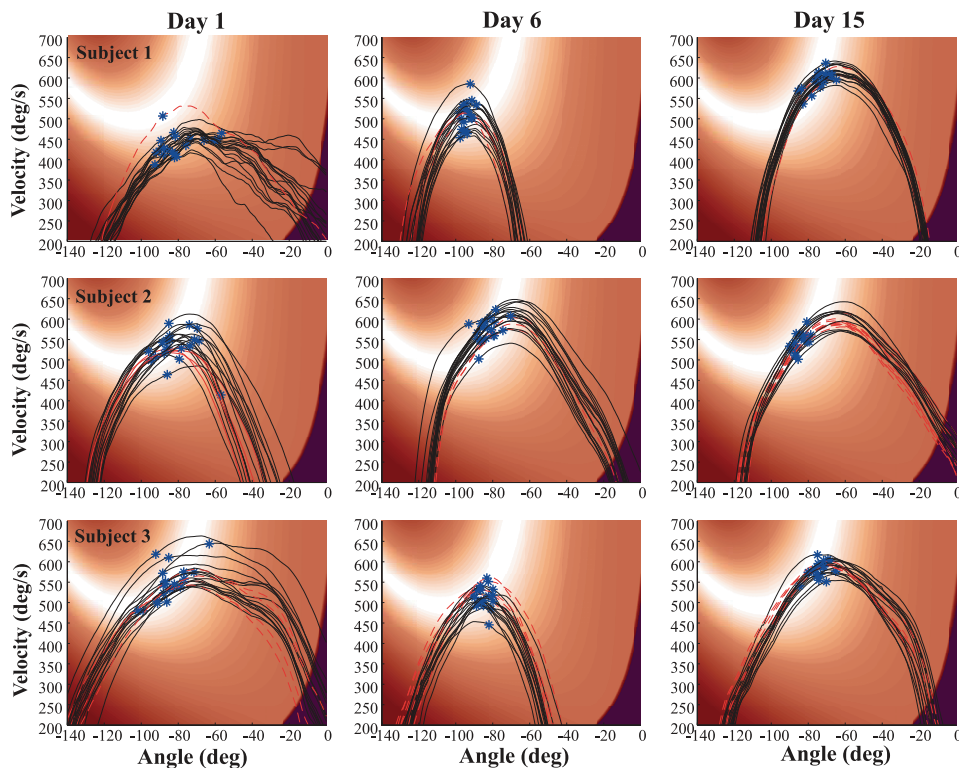


Fig. 3. Exemplary trajectories in execution space of 3 subjects. For 3 subjects in the Expert group, 20 trajectories from 3 selected days (*days 1, 6, and 15*) are shown. The 20 trajectories are from the middle block. The blue asterisks denote the release moments. Trajectories for throws that resulted in a target hit are shown in red; those that did not are shown in black.

Error, and Time in Zone. These three data points were excluded from the plots and from the statistical comparisons.

As expected, Error decreased across practice, with the greatest changes occurring at the beginning. In the 1st 6 days of practice, Error decreased from 8.5 to 3.6 cm in the average group and from 4.0 to 2.5 cm in the expert group, decreasing further to 1.8 cm in experts after 15 days. The statistical tests comparing *models A* and *B* for the 1st 6 days of practice showed a significant improvement in fit for *model B*, indicating that there was an effect of practice, $F(2,75) = 29.5$, $P < 0.0001$. The comparison of *models B* and *C* showed that across the 1st 6 days, the expert group performed significantly better than the other group, $F(3,72) = 8.7$, $P < 0.0001$. During extended practice, errors decreased further as indicated by a significant slope of *model E*, $F(1,28) = 15.2$, $P = 0.0005$.

The number of Target Hits also increased across practice, from 15.4 to 25.6 hits per day for the average group and from 16.8 to 34.7 hits per day for the expert group in the 1st 6 days, increasing further to 56.7 hits per day after 15 days. The *A-B* model comparison found a significant effect of practice, $F(2,75) = 11.5$, $P < 0.0001$. The *B-C* model comparison found no significant effect of group, $F(3, 72) = 3.3$, $P = 0.08$. Analysis of performance changes from *day 6* to *15* in the experts revealed that there was significant further improvement with extended practice, $F(1,28) = 5.7$, $P = 0.03$.

Timing Accuracy

With practice, subjects learned to release the ball nearer to the point on their trajectory that was closest to (or intersected with) the solution manifold. Figure 5 shows the absolute difference between actual and ideal release times across days of practice. Subjects in the average group released 23 ms away from the best moment on *day 1* and 14 ms away from the best moment on *day 6*. Subjects in the expert group released 18 ms

away from the best moment on *day 1* and on *day 6* reached an asymptote of 9 ms that remained the limit through *day 15*. Model comparisons confirmed a significant effect of practice, $F(2,75) = 28.4$, $P < 0.0001$, and a significant difference between the two groups, $F(3, 72) = 6.6$, $P = 0.0005$, in the 1st 6 days of practice. During the extended practice period, this measure did not show any significant additional change, $F(1,28) = 2.2$, $P = 0.15$.

Arm Trajectory Shaping

Integrated Error. Figure 6A shows the difference in error between actual and optimal trajectories measured as the error averaged over a 25-ms window centered on the release moment. In 6 days of practice, Integrated Error decreased from 3.0 to 1.8 cm for subjects in the average group and from 2.1 to 1.6 cm for subjects in the expert group, decreasing further to 1.1 cm after 15 days. Model comparisons confirmed a significant effect of practice, $F(2,75) = 23.2$, $P < 0.0001$, but no effect of group, $F(3, 72) = 0.5$, $P = 0.71$. Analysis of the change with extended practice in the experts showed that improvement was still significant, $F(1,28) = 18.3$, $P = 0.00002$.

Time in Hit Zone. Figure 6B shows the average amount of time per trial subjects spent in the hit zone across the days of practice. Considering all throws, subjects in the average group increased their Time in Hit Zone from 9 ms on *day 1* to 12 ms on *day 6*, and subjects in the expert group maintained their time at 12 ms between *days 1* and *6*, increasing to 18 ms on *day 15*. Model comparisons confirmed a significant effect of practice, $F(2,75) = 4.5$, $P = 0.01$, but not of group, $F(3, 72) < 0.1$, $P = 0.98$. In addition, the late-practice change by the experts was significant, $F(1,28) = 13.4$, $P = 0.001$.

In summary, in the 1st 6 days of practice, trajectory shaping improved significantly overall and did not differ between the two groups. This contrasted with timing accuracy, which was

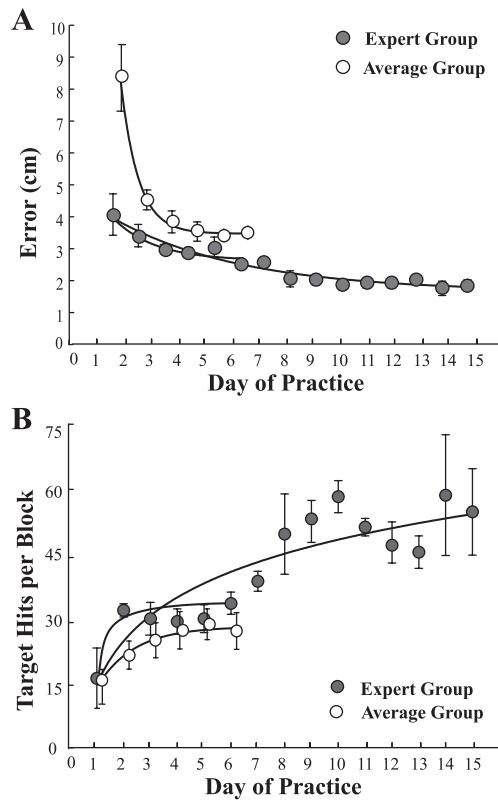


Fig. 4. Result measures. *A*: average Error over practice days. Each point is an average across 180 throws per day. *B*: Target Hits (error < 1.2 cm) per block, averaged across 3 blocks per day. Error bars indicate standard error across subjects. Note that for the expert group, the number of hits per block continues to climb after the average error per day has leveled off.

better in experts. Furthermore, the extended practice of experts led to continued improvement in both trajectory measures, whereas timing plateaued at 9 ms.

DISCUSSION

When performing actions that require the coordination of multiple components, be they different limb movements or synergetic activation of muscles, the timing among those components plays an important role in determining the outcome. Throwing a ball is one such action. Releasing the ball at the right moment in the arm trajectory may distinguish experts

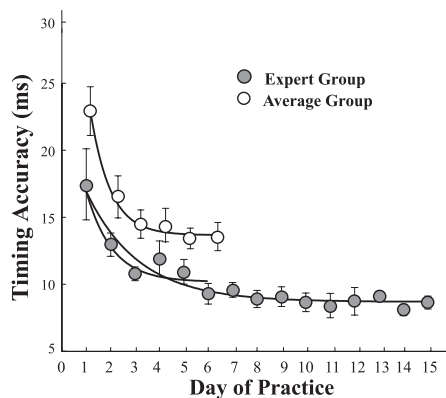


Fig. 5. Timing accuracy. Absolute difference between the actual and optimal release times for each trial averaged across 180 trials per day. Error bars indicate standard error across subjects.

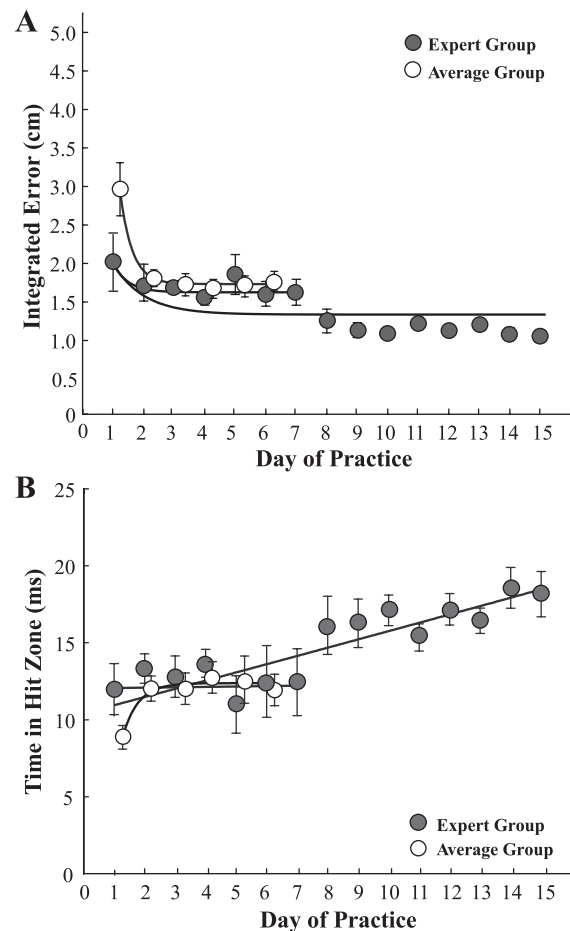


Fig. 6. Trajectory shaping. *A*: Integrated Error: average difference in error between actual trajectory and solution manifold during a 25-ms window centered on the release moment. *B*: Time in Hit Zone: average time per trial that subjects spent in regions of the execution space where releasing the ball would have led to a successful hit (Error < 1.2 cm). Error bars indicate standard error across subjects.

from average performers who all too often miss their target. In this study, we tried to elucidate fundamental mechanisms underlying improvement of accuracy in performance where timing is critical, using a virtual throwing task as an illustrative action. How is the single release moment timed given the continuous evolution of the arm trajectory?

A critical foundation of this analysis was the explicit model of the task that afforded the representation of its execution and solution space. Thus each trajectory could be evaluated in the space of all solutions, which made it possible to estimate both timing accuracy and changes in the shape of the trajectory with respect to an objective reference. Importantly, these two paths to improvement are independent: it is possible to learn to release at the best moment for a given trajectory without learning to shape the trajectory, and it is possible to shape the trajectory without improving timing accuracy.

Prediction 1 stated the seemingly obvious expectation that performance would become better by improving accuracy in timing. However, given the novel analysis of timing in state space, this expectation was not completely evident at the outset. Furthermore, the aim was to revisit claims of previous work on dart throwing that release timing can be as good as 1 ms (Smeets et al. 2002). Given the bandwidth of neural signals

and muscular contraction speed, this would seem a remarkable feat. This claim also conflicts with at least one study of throwing that reported standard deviations of release times close to 10 ms (Hore et al. 1995). Thus one goal of this experiment was to quantify the timing accuracy that could be achieved in skilled performance with extensive practice.

Results clearly supported predictions: timing accuracy improved. However, release timing in the present study was far less accurate than previous simulations have suggested: after 6 days of practice, unskilled throwers converged to an average timing error of 12 ms, and skilled throwers converged to 9 ms. After 15 days of practicing 180 throws per day (2,700 throws in a relatively controlled experimental setting), the 3 subjects with advanced throwing expertise still had a mean timing error of 9 ms. Note that the limit in timing accuracy in our study is close to what has been reported in the literature on rhythmic timing. For rhythmic finger-tapping movements, standard deviations of tapping periods in a 500-ms condition are 11 ms for professional musicians and 15 ms for nonmusicians (Repp 2010b). In a perception study, Repp (2010a) found that for melodies with a 200-ms baseline interval, musicians could detect changes with 65% accuracy when intervals were lengthened by 8 ms or shortened by 9 ms. Thus the results presented here suggest that timing accuracy in throwing may reveal the same limit as in rhythmic tapping and time discrimination tasks.

Prediction 2 stated that subjects change their trajectory in a way that exploits the redundancy of the task. Thus a successful result would no longer be dependent on accurate timing only. Previous results that are consistent with this strategy are the reported increase in covariation with practice, i.e., the finding that ball releases tend to cluster along the solution manifold (Cohen and Sternad 2009; Müller and Sternad 2004). However, previous work did not examine how subjects achieved this covariation, as the analyses focused on the release moments only, not the trajectory leading up to (or following) the release. Do subjects merely learn release moments, or do they generate trajectories with the goal to follow the solution manifold as long as possible? A key advantage of a trajectory-shaping strategy is that the trajectory can be planned in advance, taking advantage of feedback from previous throws and not relying on feedback from the current throw, which would be too slow to allow useful compensation. Thus we hypothesized that the hand trajectory changes across practice in service of performance improvement.

This prediction was supported by results showing that hand trajectories changed significantly across practice. Subjects of both skill-level groups learned to spend more time in the vicinity of the solution manifold (increasing Time in Hit Zone) and followed the solution manifold more closely (reducing Integrated Error). The two measures of trajectory shaping developed here capture subtly different aspects of trajectory shaping. Integrated Error reflects the alignment of the arm movement with the solution manifold. Improvement in this measure is consistent with a strategy of general improvement of the trajectory. In contrast, Time in Hit Zone reflects the amount of time the hand spent in a state where release of the projectile would lead to a target hit, as reported to the subject with immediate feedback after the throw. Improvement in this measure is consistent with a strategy of maximizing the number of target hits and the amount of success feedback.

Prediction 3 stated that skilled subjects improve timing and exploit trajectory shaping more than unskilled subjects. Examination of the results revealed that during the 1st 6 days of practice, skilled throwers had lower error and better timing than the less skilled throwers but did not differ significantly in either of the trajectory measures. The trajectory measures were developed as a way to explain how subjects might achieve the covariation between release angle and velocity seen in our previous work (Cohen and Sternad 2009). Reexamination of those results (Fig. 6C) reveals that expert and average performers did not differ on covariation until the 5th day of practice. The present finding that trajectory measures do not differ early in practice is consistent with these results.

Prediction 4 stated that long-term improvement in skilled performers relied on the continued optimization of the arm trajectory to compensate for the limited accuracy of the CNS in timing. This prediction was derived from previous evidence that skilled subjects continue to increase covariation even in late stages of practice, whereas noise reduction seems to be less available as a path to improvement (Cohen and Sternad 2009). The results reported here from the expert subjects showed that although timing plateaued at 9 ms, performance continued to improve, and the trajectory of the arm continued to be refined. Note that the fine tuning of the trajectory exemplified in Fig. 3 was not apparent until after 6 days (1,080 throws). These results suggest that some of what has previously been attributed to extremely accurate timing in expert throwers may actually reflect the use of refined arm trajectories.

There are important methodological differences between the present study and the study of Smeets et al. (2002), which claimed to demonstrate much better timing than we showed here. First, the amount of practice we used was much more extensive; subjects in the present study completed a total of 2,700 throws, compared with only 120 in the previous study. In addition, previous results were evaluated in variability or precision, whereas the present study evaluated accuracy.

Although our goal was to investigate principles of timing control that underlie all actions, we of necessity examined one particular task in this experiment. The virtual throwing task was more constrained than most real-world throwing tasks in that the hand path was prespecified. The physics of the virtual task was intentionally kept as simple as possible and excluded “spin” or air resistance on the projectile. As the projectile only existed virtually, it was released when the pressure sensor detected a finger lift below a threshold. This release is clearly a simplified rendering of real throwing, where for example a baseball rolls off the fingers and thereby provides rich haptic information and additional modulation of the throw. However, the purpose of this controlled experiment was to examine the control of timing and not the timing of a specific ball-handling technique. The virtual task reduces the naturalness of the throwing action, but it also permits more precision in what it measures.

Our analysis may also provide a potentially interesting insight to racquet sports: coaches frequently instruct athletes to “follow through” with their racquet trajectory, i.e., to continue their swing even after the critical moment of ball contact, which, from a mechanical analysis standpoint, seems futile. However, it could be that following through with the racquet aids the development of a racquet trajectory with a longer

window of successful possible contact moments so that the stroke is less susceptible to timing errors.

Although there were differences in ability within and between the groups tested here, all subjects were relatively young and neurologically healthy. We propose that the method developed here could be useful for examining coordination in impaired populations. Coordinative or state-dependent timing is thought to depend on the cerebellum (Diedrichsen et al. 2007) and basal ganglia (Wu et al. 2010), and deficits have been observed in subjects with a wide range of neurological disorders, including adults with Parkinson's disease (Gross et al. 2008; Tagliabue et al. 2009), Huntington's disease (Klein et al. 2010), and cerebellar lesions (McNaughton et al. 2004) and children with reading delay autism (D'Cruz et al. 2009) and attention-deficit/hyperactivity disorder (Frings et al. 2010). Intrinsic timing deficits have even been proposed to be central to the etiology of schizophrenia (Andreasen et al. 1998; Andreasen and Pierson 2008). What is not known is whether individuals with coordinative deficits due to any of the above conditions can take advantage of the trajectory-shaping strategy demonstrated here by healthy subjects.

APPENDIX

Equations of motion:

$$x(t) = A_x \sin(\omega t + \varphi_x) e^{-\frac{t}{\tau}}$$

$$y(t) = A_y \sin(\omega t + \varphi_y) e^{-\frac{t}{\tau}}$$

where A_x and A_y describe the amplitudes in x - and y -dimension over time t , ω denotes the natural frequency of the system, and τ indicates relaxation time.

The phases φ_x and φ_y are determined by the ball release angle as described below.

States at release are determined by release angle θ :

$$x_0 = l * \cos \theta$$

$$y_0 = l * \sin \theta$$

$$\dot{x}_0 = -l * \sin \theta$$

$$\dot{y}_0 = l * \cos \theta$$

where l represents the length of the manipulandum, x_0 , y_0 , \dot{x}_0 , and \dot{y}_0 represent the initial position and velocity of the projectile, and θ describes the release angle as defined in Fig. 1.

$$A_x = \sqrt{x_0^2 + \left(\frac{\dot{x}_0}{\omega} + \frac{\tau}{\omega} \right)^2}$$

$$A_y = \sqrt{y_0^2 + \left(\frac{\dot{y}_0}{\omega} + \frac{\tau}{\omega} \right)^2}$$

If $A_x = 0$, then $\varphi_x = 0$; otherwise:

$$\varphi_x = \arccos \left[\frac{1}{A_x} * \left(\frac{\dot{x}_0}{\omega} + \frac{x_0}{\tau} \right) \right]$$

If $A_y = 0$, then $\varphi_y = 0$; otherwise:

$$\varphi_y = \arccos \left[\frac{1}{A_y} * \left(\frac{\dot{y}_0}{\omega} + \frac{y_0}{\tau} \right) \right]$$

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

AUTHOR CONTRIBUTIONS

R.C. and D.S. conception and design of research; R.C. and D.S. performed experiments; R.C. analyzed data; R.C. and D.S. interpreted results of experiments; R.C. and D.S. prepared figures; R.C. drafted manuscript; R.C. and D.S. edited and revised manuscript; R.C. and D.S. approved final version of manuscript.

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