

Skill learning involves optimizing the linking of action phases

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Säfström D, Flanagan JR, Johansson RS. Skill learning involves optimizing the linking of action phases. *J Neurophysiol* 110: 1291–1300, 2013. First published June 5, 2013; doi:10.1152/jn.00019.2013.—Many manual tasks involve object manipulation and are achieved by an evolving series of actions, or action phases, recruited to achieve task subgoals. The ability to effectively link action phases is an important component of manual dexterity. However, our understanding of how the effective linking of sequential action phases develops with skill learning is limited. Here, we addressed this issue using a task in which participants applied forces to a handle to move a cursor on a computer screen to successively acquire visual targets. Target acquisition required actively holding the cursor within the target zone (hold phase) for a required duration before moving to the next target (transport phase). If the transport phase was initiated prematurely, before the end of the required hold duration, participants had to return to the target to acquire it. The goal was to acquire targets as quickly as possible. Distinct visual and auditory sensory events marked goal completion of each action phase. During initial task performance, the transport phase was reactively triggered by sensory events signaling hold phase completion. However, with practice, participants learned to initiate the transport phase based on a prediction of the time of hold phase completion. Simulations revealed that participants learned to near-optimally compensate for temporal uncertainty, presumably related to estimation of time intervals and execution of motor commands, so as to reduce the average latency between the end of the required hold phase duration and the start of the transport phase, while avoiding an excess of premature exits.

object manipulation; sensorimotor control; motor learning; multisensory; optimality

ALTHOUGH MOST MANUAL TASKS comprise sequentially linked action phases, many studies of manual control concern single actions, such as moving the hand between two positions (Shadmehr et al. 2010; Wolpert et al. 2011). Thus, our understanding of how action phases are linked, and how learning affects such linking, is limited. The role of each action phase in object manipulation is to achieve a task subgoal, and subgoal achievement is generally associated with discrete multimodal sensory events (Johansson and Flanagan 2009). For example, when lifting and replacing an object, the breaking and subsequent making of contact between the object and the support surface, which mark the completion of the loading and replace action phases, can give rise to discrete sensory signals in tactile, visual, and auditory modalities. Although spatial control of movements is obviously an important component of most motor tasks, the linking of action phases essentially involves temporal control where two distinct control strategies can be considered. On the one hand, action phases may be

linked reactively whereby motor commands for the next phase are launched after receiving sensory confirmation of goal completion of the current phase. Alternatively, action phases may be linked predictively whereby motor commands for the next phase are launched in anticipation of the predicted time of sensory events associated with goal completion of the current action phase (Johansson and Flanagan 2009). Given the time delays inherent in sensorimotor feedback loops, reactive linking may result in slow and stuttering phase transitions. In contrast, predictive linking would enable smooth phase transitions and substantially decrease the time required to complete the overall task (Flanagan et al. 2006).

Here, we investigated the linking of action phases using a task involving both spatial and temporal control and that captures several key features of natural object manipulation tasks: discrete sensory events mark goal completion of action phases, each action phase needs to be completed before the task can progress, and premature launching of action phases can incur substantial time costs when they result in errors requiring corrective actions (Flanagan et al. 2006). Participants controlled the position of a cursor on a screen by applying isometric forces to a handle. The task was to, as quickly as possible, successively acquire visual targets by moving the cursor to a target (transport phase) and actively holding the cursor within the target zone (hold phase) for a required duration, before moving to the next target. Discrete visual and auditory feedback marked the goal completion of the transport and hold phases. If the participants moved the cursor to the next target before completing the hold phase, they had to return to the current target and repeat the hold phase to acquire the target, which was detrimental to task performance because of the time cost.

We hypothesized that participants would improve performance (i.e., increase the rate of target acquisition) with practice by shifting from reactive to predictive linking of action phases. We also hypothesized that they would learn to optimize predictive linking in the face of temporal uncertainty related to both estimation of time intervals and execution of motor commands (Harris and Wolpert 1998; Hudson et al. 2008; Rakitin et al. 1998; van Beers et al. 2004; Wing 1977). Specifically, we predicted that participants would reduce the time required to acquire targets by learning to optimally balance exiting the target zone as soon as possible, on average, while avoiding an excess of premature cursor exits.

METHODS

Participants and General Procedure

Nine healthy right-handed participants (5 men and 4 women, aged 21–41 yr) with normal vision participated in the study. They received

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100 Swedish krona (~15 USD) per hour of participation with the chance to double the payment if they were the top performing participant. All participants gave written informed consent prior to the experiment in accordance with the declaration of Helsinki. The local Ethics Committee of Umeå University approved the experiment.

The participants controlled the position of the cursor on a computer screen by applying forces on a spherical knob held in the right hand (Fig. 1A). The task involved moving the cursor to attain sequentially presented targets as quickly as possible. At any given time, the current target was displayed on the screen along with the next target. To attain the current target, participants had to move the cursor into the target zone and to actively apply appropriate forces to keep it there for a required time (0.6 s in standard trials; see below). After the current target had been attained, the forthcoming target became the current target and a new next target was displayed (Fig. 1, B and C). Critically, if the cursor exited the current target zone before the required time, the participant had to return the cursor to the current

target zone and again attempt to keep it there for the required time (0.6 s in standard trials).

We defined a trial as composed of two phases: a hold phase and the following transport phase. The hold phase started when the cursor entered the target zone, and it ended when the cursor exited the target zone after the target was attained. However, if the cursor stayed within the current target zone for <0.2 s, we did not consider that the hold phase had started. The transport phase began when the cursor exited a target zone after the target was attained and ended when the hold phase of the next target started. The time when the cursor entered and exited a target zone was defined as the time the center of the cursor moved across the center of the border that outlined the target on the screen. The participants received both visual and auditory feedback about goal completion of the involved action phases as detailed further below.

Targets were pursued for 72-s periods with 18-s rests in between until at least 1,800 targets were completed in total. Participants were explicitly told that the goal of the task was to attain as many targets as possible within each 72-s period. During rest periods, the screen displayed the number of targets attained during the previous action period and the participant's high score from all previous action periods. This feedback helped in motivating participants to acquire as many targets as possible during each 72-s period.

Apparatus

A vertically oriented computer screen (24.5 × 18.5 cm, 60 frames/s) was located about 37 cm in front of the eyes of the seated participant (Fig. 1A). The right forearm rested on a tabletop. The hand-held knob (4-cm diameter) had its center located 3 cm above the tabletop and was mounted on a six-axis force/torque transducer (FT-Nano 17; Assurance Technologies, Garner, NC) that measured the forces in the horizontal plane at 200 samples/s.

The position of the cursor relative to the center of the screen scaled linearly with force; 1 N force applied to the knob in the horizontal plane moved the cursor 2.88 cm in the plane of the screen. With zero force, the cursor was located in the middle of the screen. To position the cursor at the center top or bottom of the screen, a force of magnitude 3.21 N would have been required, and to position the cursor at the center left or right of the screen, a force of magnitude 4.25 N would have been required. Because skill acquisition in many manipulation tasks involves both spatial and temporal learning, we wanted our task to involve significant spatial learning, in addition to temporal learning. Therefore, the mapping between hand forces and cursor movements was rotated 90° (counterclockwise) compared with the mapping for an ordinary computer mouse. Thus, application of leftward and rightward force on the knob moved the cursor upwards and downwards on the screen, respectively, and forces directed away from and towards the body moved it rightwards and leftwards, respectively. The force signals that controlled the cursor were low-pass filtered at 3.3 Hz to prevent cursor wobble driven by the participants' physiological tremor. An infrared video-based eye tracker recorded the gaze position of the right eye. Data from the gaze recordings are not included in this paper.

Experimental Design and Sensory Feedback

In addition to the cursor (filled circle, 3-mm diameter), the otherwise black screen always displayed the current target and the forthcoming target (Fig. 1B). Both targets were open circles (24.3-mm diameter). The current target was highlighted with a border of 0.9 mm and light intensity of 75% of total white color while the forthcoming target had a thinner border (0.3 mm) shown at a lower intensity (66% of total white color). When the cursor exited the current target after it was attained, the target extinguished, the forthcoming target became the current target, and the new next target appeared (Fig. 1B). Forty-four target locations were distributed equally across the four quadrants of the screen under the constraint that the distance between

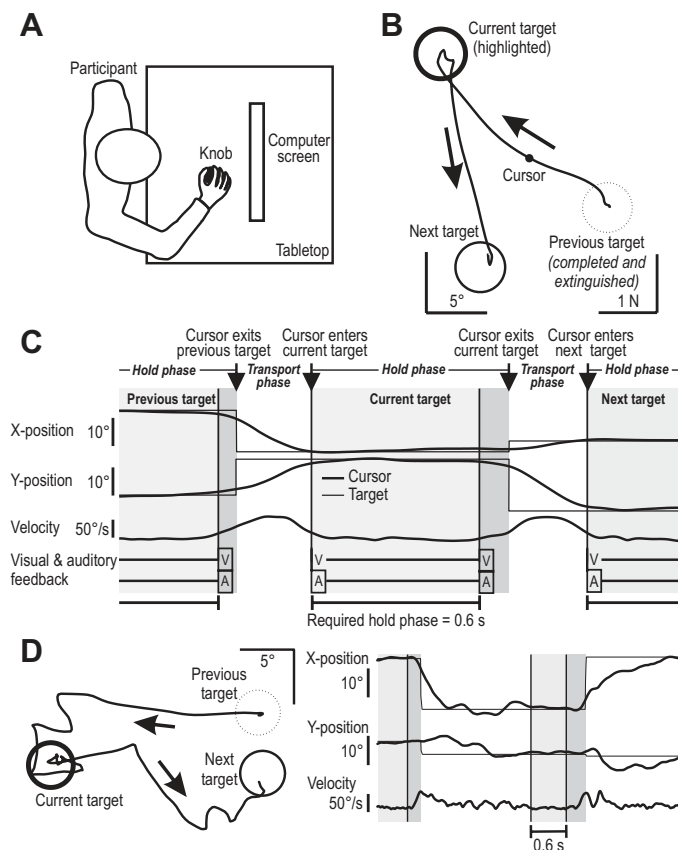


Fig. 1. Experimental setup and exemplary trials. *A*: participants controlled a cursor on a screen by applying forces to a knob instrumented with a force sensor. The cursor position relative to the screen center scaled with force (2.88 cm/N). Application of leftward and rightward force on the knob moved the cursor upwards and downwards on the screen, respectively, and forces directed away from and towards the body moved it rightwards and leftwards, respectively. *B*: examples of target transitions late in the experiment. There were always 2 targets visible on the screen, the current (highlighted) and next targets. The previous target disappeared when the cursor had exited the target zone after goal attainment, which required the participants to keep the cursor in the target zone for 0.6 s before aiming for the next target. *C*: cursor positions and velocity, as a function of time, corresponding to the target transitions shown in *B*. At the time of goal completion of the transport and hold phases (vertical black lines), participants received discrete visual and auditory feedback. Light-shaded areas show the required hold phase duration, and dark-shaded areas show the additional time from goal attainment of the required hold phase duration to cursor exit from the target zone. *D*: examples of target transitions early in the experiment. Same format as in *B–C*. Note the different time scale in *D* compared with *C*.

two successive targets was 10.8 cm and the direction from the previous target was uniformly distributed between 0 and 360° (Sailer et al. 2005). The same set of 44 target locations was used for each participant.

Standard trials. Participants received visual and auditory feedback about completion of both the transport phase and the time required for the hold phase (Fig. 1C). For the visual feedback, once the cursor entered the current target (representing the completion of the transport phase), the thickness of the current target outline increased from 0.9 mm to 1.52 mm and was maintained so until the time the target was attained. At this point, occurring 0.6 s after the start of the hold phase, the target doubled in diameter for 50 ms in a flash-like manner before disappearing. Auditory feedback was given through earphones. The completion of the transport phase was indicated by a click, and target attainment was indicated by a beep (50 ms). If the cursor exited the target zone earlier than the prescribed time (0.6 s), the participant did not obtain feedback about target attainment and the current target remained on the screen. Intermingled with these standard trials were catch trials (~5%) in which the feedback at completion of the transport phase and at completion of the required hold phase was shifted in time in a manner unpredictable to the participants. These trials were included to study multimodal integration at sensorimotor control points during the task. Data related to these trials are not included in the present paper.

Reactive trials. After completing the standard trials, the participants had a break (~10 min) before performing the same target completion task for three additional 72-s periods. In these periods, the required hold phase duration varied randomly between 0.2, 0.4, 0.6, 0.8, and 1.0 s following a uniform distribution. The aim was to obtain trials with a 0.6-s hold phase duration in which the transport phase was launched reactively based on feedback about target attainment. As expected, we found that in these trials, participants reactively launched the transport phase based on sensory events signaling successful completion of the hold phase. (Indeed, reactive launching was seen for all 5 hold phase durations.) Specifically, the cursor exited the target zone, en route to the next target, well after the end of the hold phase (and much later than in predictive trials), and the spread of cursor exit times was substantially smaller than in predictive trials (see RESULTS and Fig. 3). In total, participants performed between 149 and 163 trials during the three 72-s periods, out of which the required hold phase duration was 0.6 s in 29–31 trials depending on the participant.

During both standard and reactive trials, the start of each 72-s period was initiated by an auditory cue (1 kHz beep for 200 ms) followed by the presentation of the first current and next targets.

Statistics

Regression and paired *t*-tests based on median values obtained from each participant were used to analyze the data. We used Bonferroni correction to counteract the problem of multiple comparisons. In all tests, $P < 0.05$ was considered statistically significant.

RESULTS

We first describe changes in performance while participants learned the task and then focus on their steady-state performance. Finally, by means of simulation, we assess our hypothesis that participants learn to perform nearly optimally with respect to the linking of action phases.

Learning

All participants improved task performance, measured as trial rate (i.e., targets completed per second), with practice over the ~1,800 standard trials executed. The improvement was fastest in the beginning and gradually slowed with the number

of trials executed. Figure 2A shows the trial rate as a function of trial number for a single participant. An exponential equation of the form $y = a - b \times e^{-cx}$ fit to the data yielded a half-life of 245 trials for this participant. Averaged across participants, the half-life was 206 ± 15 trials (means \pm SE; Fig. 2B). Nonlinear regression revealed that all three parameters of the exponential were significant ($P < 0.05$) for all participants. Two factors contributed to the improvement in performance with practice. First, improved spatial control of the cursor occurred with practice when the participants learned the novel sensorimotor transformation between hand forces and cursor movements. Second, the time the cursor was held in the target zone before being moved to the next target decreased with practice.

Figure 2C illustrates, for the same participant as shown in Fig. 2A, the improvement of the spatial control of the cursor with practice by showing the duration of the cursor transport phase for each consecutive trial (see METHODS). Fitting an exponential to the data yielded a half-life of 100 trials for this participant. Averaged across the participants, the half-life was 90 ± 14 trials (means \pm SE; Fig. 2D). Nonlinear regression revealed that all three parameters of the exponential were significant ($P < 0.05$) for all participants. Concomitant with the decrease in the duration of the transport phase, the cursor path index, calculated as the distance the cursor traveled during the transport phase divided by the shortest intertarget distance, also decreased with a half-life averaged across participants of 65 ± 20 trials (not illustrated).

Figure 2E shows, for the same participant as shown in Fig. 2, A and C, the time the cursor exited the target zone, relative to the start of the hold phase, as a function of trial. All cursor exits are shown, including those relatively few that occurred prematurely, i.e., before 0.6 s after cursor entry into the target zone. Learning was gradual, and fitting an exponential to the data yielded a half-life of 245 trials for this participant. Averaged across participants, the half-life was 315 ± 33 trials (means \pm SE; Fig. 2F). All three parameters of the exponential were significant ($P < 0.05$) for all participants. The half-life for the time of cursor exits was significantly longer than the half-life for the time of transport phase duration ($t_8 = 4.91$; $P < 0.002$). Notably, the decrease in transport phase duration was almost completed within ~400 trials, whereas the decrease in cursor exit times plateaued after ~1,200 trials.

To facilitate data analysis, we partitioned the series of standard trials into seven consecutive stages representing about equal intervals on a logarithmic scale: trials 1–20, 21–60, 61–140, 141–300, 301–620, 621–1,260, and a final stage with the remaining trials (trial # >1,260). Figure 2G shows, for each stage, the distribution of cursor exit times with reference to the onset of the hold phase for data pooled across all participants. With practice, the launching of the transport phase to the forthcoming target gradually occurred earlier. We considered the final stage (stage 7, trial # >1,260) as representing steady-state behavior because most of the changes in performance occurred prior to this stage (Fig. 2, A–F). During stage 7, the cursor left the target zone 0.73 ± 0.07 s (means \pm SD) after it had entered, which was 0.13 ± 0.07 s after goal attainment (i.e., after completion of the 0.6-s required hold phase duration). We estimated the timing of cursor exits when reactively triggered, based on sensory feedback about goal completion of the hold phase in a separate condition where we

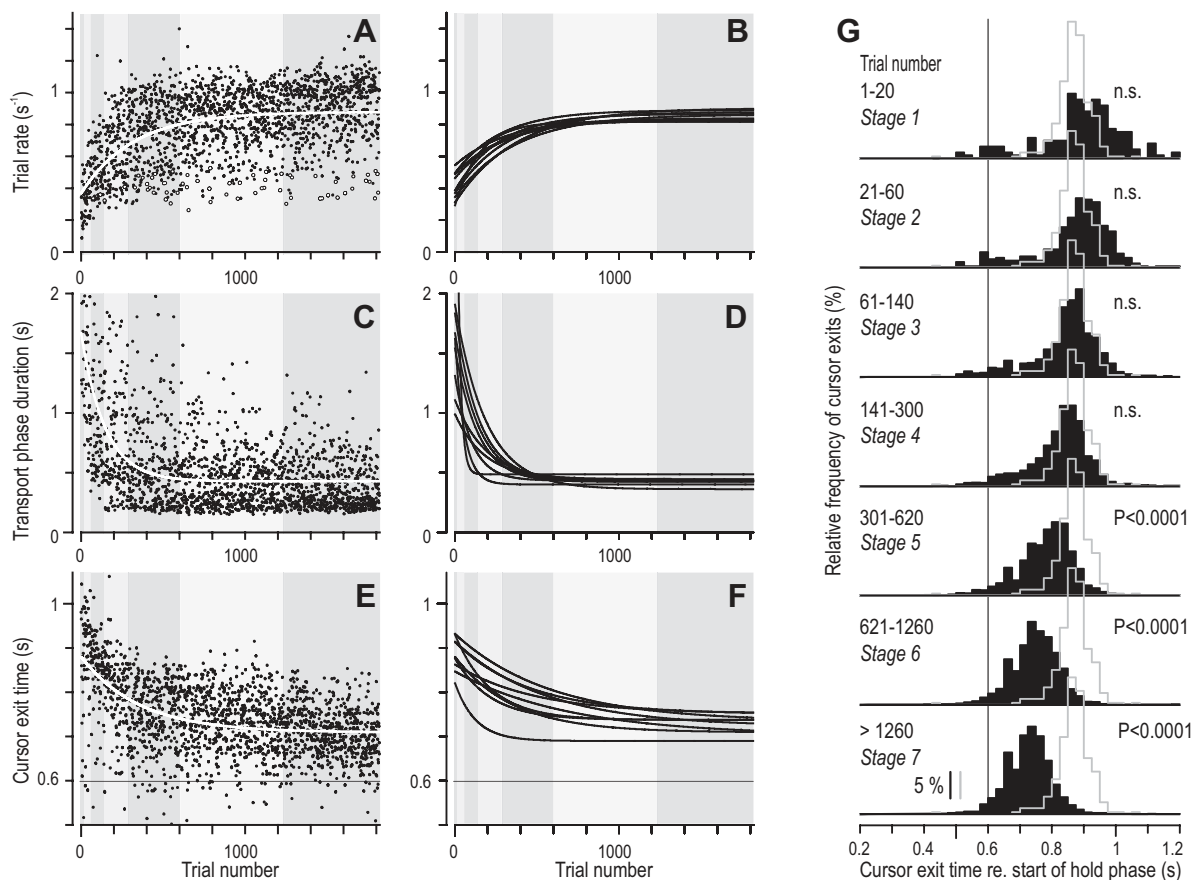


Fig. 2. Evolution of task performance with practice. *A, C, E*: trial rate (number of completed targets per second), transport phase duration (time between targets), and cursor exit time (relative to the start of the hold phase) for a single participant, as a function of trial. The curves show exponential fits to the data. *B, D, F*: corresponding plots showing exponential fits for all 9 participants. *A–F*: to facilitate data analysis, we partitioned the trials into 7 stages representing about equal distances on a logarithmic scale. Light and dark gray zones delineate the 7 stages. *G*: filled bars represent the distribution of cursor exit times, with reference to the start of the hold phase, as a function of stage. Gray lines represent the distribution of cursor exit times from the reactive condition. Data pooled across all 9 participants.

varied the required hold phase duration unpredictably across trials between 0.2, 0.4, 0.6, 0.8, and 1.0 s (see METHODS). The gray line histogram in Fig. 2*G* shows the distribution of reactive cursor exit times performed with the required hold phase duration of 0.6 s. On average, the cursor exited the target zone 0.87 ± 0.04 s after it was entered, which was 0.27 ± 0.04 s (means \pm SD) after goal attainment. Importantly, the cursor exits occurred significantly later during the reactive trials than during the standard trials for the last three stages ($P < 0.001$, corrected for multiple comparisons based on 7 paired *t*-tests). This strongly suggests that the participants with practice learned to launch the transport phase based on a prediction of the time of goal completion after initially launching the transport phase reactively.

Figure 1 illustrates the improved spatial control of the cursor that occurred with practice, as well as the shift from reactive to predictive launching of the transport phase, by showing traces of cursor movements for exemplary trials performed early (*stage 1*; Fig. 1*D*) and later during the practicing period (*stage 7*; Fig. 1, *B* and *C*). In the beginning of the experiment (Fig. 1*D*), the participants were unable to move the cursor straight between targets. Also, there was usually a lengthy time span between target attainment and cursor exit from the target zone, suggesting a reactive launching of the transport phase (in the exemplary trials 0.27 s and 0.33 s, respectively; Fig. 1*D*). In

contrast, at the end of the practicing period (Fig. 1, *B* and *C*), the cursor moved approximately straight towards the next target. Also, the participants started to move the cursor before completion of the required hold phase, and there was generally a small time clearance between target attainment and cursor exit (in the exemplary trials 0.065 s and 0.11 s, respectively; note the different time scales in Fig. 1, *C* and *D*).

In summary, the participants' overall performance improved with practice because they 1) quite quickly learned the sensorimotor transformation between manual forces and cursor movements and 2) more gradually learned to launch the transport phase based on prediction of the time of goal completion of the hold phase rather than on feedback about goal completion.

Steady-State Performance

Figure 3*A* shows, for each participant, the cursor exit times as a function of trial number during the final stage (*stage 7*, *trial #* >1,260). A linear regression between trial number and cursor exit time failed to reveal a significant slope for data pooled across all participants ($r = -0.02$; $P = 0.20$). Linear regression performed on each participant, however, revealed a significant drift in the cursor exit times for three of the participants (P3, P6, and P8; $P < 0.001$ in each case, corrected for multiple comparisons). For two of these participants (P3

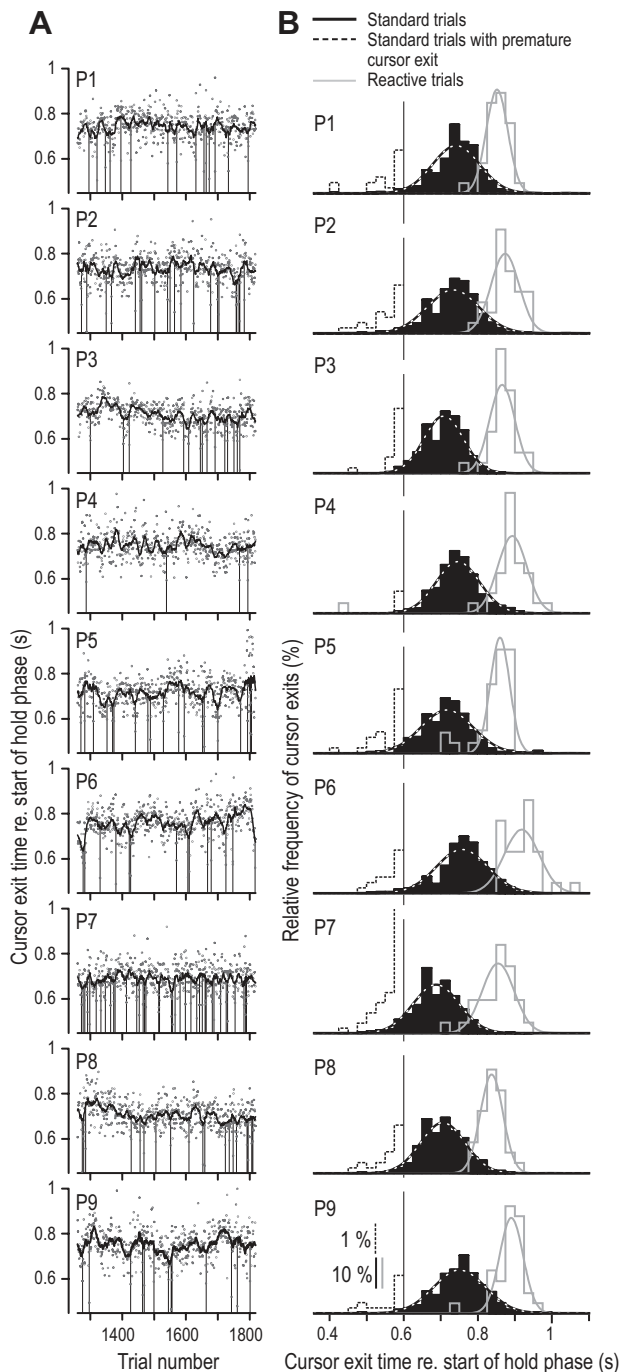


Fig. 3. Steady-state performance. *A*: the cursor exit times as a function of trial number during the final stage (*stage 7, trial # > 1,260*) for each participant. The curves represent a moving average of the cursor exit times (± 10 exits). The vertical lines mark the occurrence of premature cursor exits. *B*: distribution of cursor exit times, for each participant, during the final stage of the standard trials (filled black bars) and during the reactive trials (gray lines). Cursor exit times were normally distributed for both the standard and reactive trials. Note that for all 9 participants, the cursor exited early in a small percentage of trials (dotted lines).

and P8), the cursor exit time tended to decrease, whereas it tended to increase for one (P6).

For each participant, the cursor exit time was essentially normally distributed for both the standard trials and for the reactive trials (Fig. 3*B*). As measures of the accuracy of the

prediction of goal completion, we computed the SD and the coefficient of variation ($CV = SD/\text{mean}$) of the cursor exit times with reference to the start of the hold phase. For the standard trials, the average SD was 0.069 s (range across participants: 0.057–0.075 s), and the average CV was 0.095 (range across participants: 0.082–0.105). The SD in the reactive trials performed with 0.6-s required hold phase duration was 0.035 s (range: 0.026–0.47 s), and the CV was 0.041 (range: 0.030–0.052). The smaller variance of cursor exit times for the reactive trials than for standard trials ($t_8 = 10.7$, $P < 0.0001$ when considering the SD; and $t_8 = 14.8$, $P < 0.0001$ when considering the CV) seems reasonable assuming that the cursor exits in the reactive trials were triggered by discrete sensory events signaling the completion of the hold phase.

As a consequence of the variability in the cursor exit times during the standard trials combined with the small average time clearance (0.13 ± 0.07 s) with reference to goal completion of the hold phase, the cursor occasionally exited the target zone prior to the time prescribed for goal completion (0.6 s after cursor entry). Averaged across participants, such premature exits occurred in $3.34 \pm 1.93\%$ of trials (means \pm SD; range: 0.71–7.87%). Following premature exits, participants did not receive auditory and visual feedback verifying goal completion of the hold phase, and the current and next targets remained unchanged. This absence of sensory feedback about goal completion triggered a corrective action implying abortion of the motor command that moved the cursor towards the next target, as well as the launching of a command that brought the cursor back to the target zone where they were required to keep it for 0.6 s (Fig. 4*A*).

Because of the occurrences of premature cursor exits, the hold phase duration, defined as the period from the first stable cursor entry into the current target zone to last cursor exit from the target zone after goal completion, had a clear bimodal distribution during the standard trials (Fig. 4*B*; data pooled across participants). The dominating mode corresponded to trials in which the cursor exited without premature exits, whereas the hold phase was dramatically prolonged in trials with premature cursor exits requiring reentries. Averaged across participants, the geometric mean of the reentry times was 1.03 ± 0.21 s (means \pm SD), and the geometric SD was 1.50 ± 0.13 s (Fig. 4*B*). There was no reliable correlation between reentry time and time of the preceding cursor exit ($R = 0.12$, $P = 0.12$ for data pooled across all participants).

Figure 4*C* shows the distribution of transport phase durations for data pooled across all participants. This distribution was lognormal (see Fig. 4*C inset*) with a geometric mean of 0.36 ± 0.03 s and a geometric SD of 1.53 ± 0.09 s. During the steady-state period, all participants moved the cursor approximately straight between targets; across the participants, the cursor path index ranged between 1.01 and 1.03. The distributions of transport phase duration were similar in the standard trials with and without premature cursor exits, and in the reactive trials.

In summary, during the final stage of the experiment (*trial # > 1,260*), the participants' cursor exit times did not, on average, significantly improve. The cursor exit times were normally distributed with a narrow time clearance (0.13 ± 0.07 s) with reference to goal completion. Occasionally, the cursor exits occurred prematurely, in which case the participants had to return to the target zone and keep the cursor in the target zone

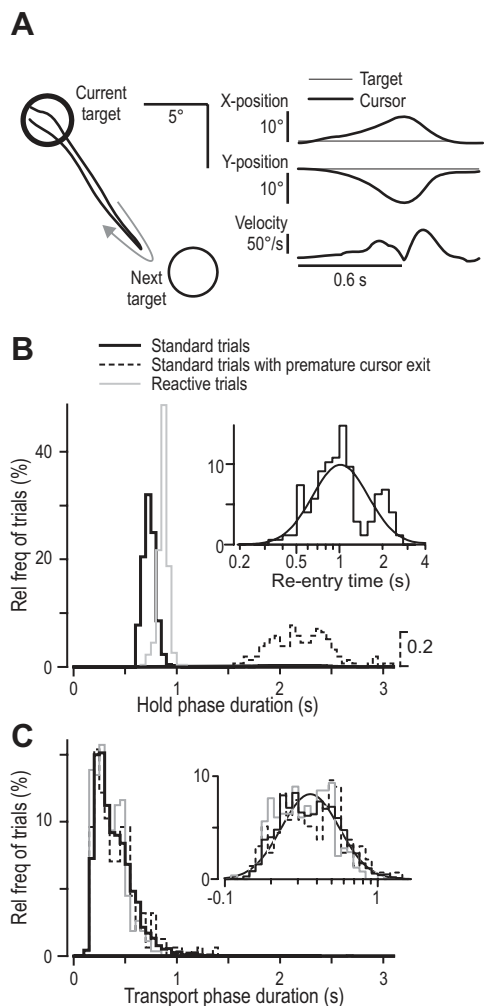


Fig. 4. Corrective actions and duration of phases. *A*: trial where the participant made a premature exit and had to return to the target. *Left*: the line indicates the position of the cursor on the screen, and the circles indicate target zones. *Right*: cursor and target positions along with cursor tangential velocity as a function of time for the same trial as shown at *left*. *B* and *C*: distributions of hold phase duration (time from cursor entry into the target to successful exit) and transport phase duration (time between targets) during the final stage. Separate distributions are shown for standard trials, standard trials with premature exits, and reactive trials. Data pooled across all 9 participants. When the cursor exited prematurely, hold phase duration markedly increased. Note that similar transport phase durations were seen in all trial types. *Inset* shows in *B* the distribution of log transformed reentry times for standard trials with premature cursor exits, and *inset* in *C* shows the distribution of log transformed transport phase durations for all 3 trial types.

for 0.6 s. Therefore, the hold phase duration had a clear bimodal distribution during the standard trials.

Near Optimal Performance

To optimally link the hold and transport phases, participants had to balance two different costs. On the one hand, if the participant targeted a cursor exit time that narrowly exceeded the required time for goal completion of the hold phase, this would result in a relatively high number of premature exits because of the timing variability in estimating the required hold phase duration and in the execution of motor commands. Premature exits are detrimental to performance because they greatly prolong the hold phase (see Fig. 4, *A* and *B*). On the other hand, if the participant used a cautious approach and

targeted a cursor exit time that substantially exceeded the required time (effectively eliminating any chance of a premature exit due to timing variability), performance would decrease because the hold phase duration would on average be prolonged. Thus, in practice, an optimal linking of the action phases required participants to balance large time costs associated with occasional premature exits against minor costs in the majority of trials associated with being too cautious.

By means of simulation, we asked how close to optimal the participants performed with respect to linking the hold and transport phases. To that end, we estimated the duration of the hold phase for cursor exit times randomly drawn from normal distributions with mean values that were varied between 0.6 s and 1 s and with variances that were set by the coefficient of variation estimated from the experimental data. That is, we assumed that the variability in participants' ability to predict the required hold phase duration is proportional to the mean value of the time interval; previous evidence indicates that the standard deviation during prediction of time intervals is approximately proportional to the length of the interval (Rakitin et al. 1998). Likewise, the cursor reentry time was derived from the data recorded by randomly sampling data from a lognormal distribution, with the mean and variance estimated from the experimental data. Importantly, as indicated above, there was no correlation between the cursor reentry time and the cursor exit time for premature exits. These model parameters correspond to the sources of information that participants may have used to achieve optimal performance. In our simulations, we examined, for each participant, the optimal mean cursor exit time given that participant's timing variability and time cost associated with premature cursor exits (return time).

Figure 5*A* illustrates the procedure by showing simulated hold phase durations based on 1,000 cursor exits for 9 mean cursor exit times in 50-ms steps. In this example, the model parameters (CV and return time) were from one of the participants (P1). Note the increasingly manifest bimodal distribution of hold phase durations as the mean cursor exit time decreases and more premature cursor exits occur. Optimal performance corresponds to the minimum mean value of the simulated hold phase durations.

Figure 5, *B–E*, illustrates the results of our simulation based on model parameters taken from the same participant (P1) and in which hold phase durations were estimated for mean cursor exit times in 5-ms steps with 10,000 simulated cursor exits per step. Figure 5*B* shows cumulative frequency plots of the simulated distribution of the hold phase durations for the same nine mean values of cursor exit times as in Fig. 5*A*. Note that at a mean cursor exit time of 0.6 s, one-half of the cursor exits are premature and require reentry, and since this likelihood persists for the next attempt to complete the target, there is also a 50% chance that this attempt results in a premature exit and so on, yielding very long durations of the hold phases. In contrast, at an average cursor exit time of 1 s, premature exits rarely occur and no second mode of the hold phase distribution is observed.

Figure 5*C* illustrates the mean hold phase duration as a function of the mean cursor exit time. The curve has a minimum at a simulated mean cursor exit time of 0.74 s, which indicates the simulated optimal mean cursor exit time for this participant. This time closely matches the mean cursor exit time used by the participant. At shorter cursor exit times, the

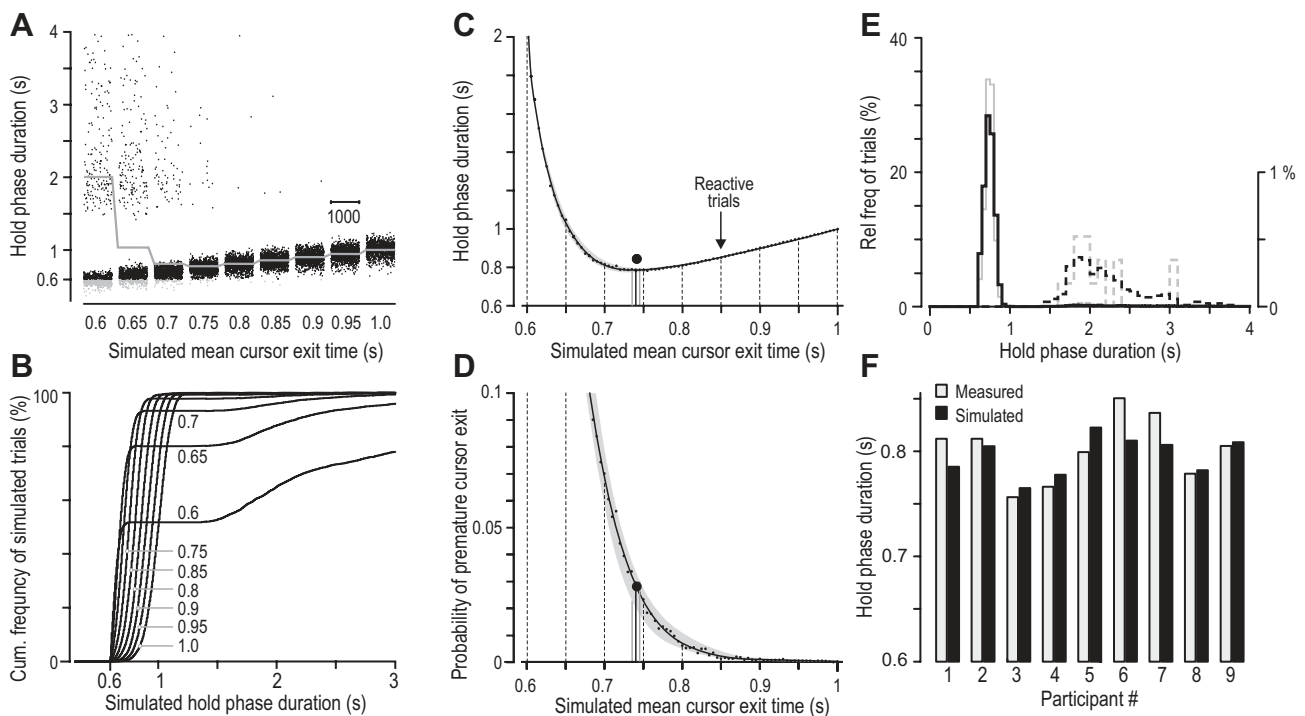


Fig. 5. Simulated and actual steady-state performance. *A*: simulated hold phase durations using cursor exit times randomly drawn from a normal distribution of cursor exit times with mean values between 0.6 s and 1 s, and variances set by the coefficient of variation estimated from the experimental data. The mean and variance of reentry times for premature exits were also estimated from experimental data. Note that the number of premature exits, and hence long hold phase durations, decreases as the mean exit time increases. The gray line represents the mean hold phase duration. Simulation input parameters estimated using data from *participant 1*. *B*: cumulative frequency plot of the simulated distributions of the hold phase durations for the same 9 mean values of cursor exit times as in *A*. *C*: simulated mean hold phase duration as a function of the mean cursor exit time (now with small steps in mean cursor exit time). Input parameters based on data from *participant 1*. The minimum occurred at a simulated mean cursor exit time of 0.74 s (vertical black line), which closely matches the actual mean cursor exit time used by this participant (x-position of black dot). The arrow indicates the mean cursor exit time during the reactive trials by the same participant. *D*: simulated probability of premature cursor exits as a function of the mean cursor exit time. The participant illustrated in Fig. 5, *A–E*, showed an actual probability of such exits corresponding to 2.8% of the exits (y-position of black dot) and the simulated optimal behavior predicted 2.7% (estimated from the mean cursor exit time yielding the minimum hold phase duration; see vertical black line). *E*: Distributions of simulated (black trace) and measured (gray trace) hold phase durations for *participant 1*. The dashed curves correspond to premature cursor exits. *F*: simulated optimal and measured mean hold phase durations for each of the 9 participants.

curve indicates that the hold phase duration would increase in an accelerating manner. On the other hand, with longer cursor exit times the hold phase duration would more gradually increase, soon approaching a linear function. Despite the shallow increase in the hold phase duration with increasing cursor exit time, apparently the participant was able to find a more optimal cursor exit time than that offered by the reactive control mechanism.

A corresponding simulation performed based on input parameters obtained from each participant indicated that they were close to optimal, using exit times that on average were 0.02 ± 0.01 s earlier than optimal (means \pm SD, $n = 9$). The simulation also provided an estimate of the frequency of premature cursor exits as a function of the mean value of the cursor exits (Fig. 5*D*). The participant illustrated in Fig. 5, *A–E*, produced premature exits in 2.8% of all exits and the simulated optimal behavior predicted 2.7%. On average across participants, the frequency of premature cursor exits deviated by $0.8 \pm 1.8\%$ from those predicted by the simulation of optimal performance. The participant illustrated in Fig. 5, *A–E*, showed a simulated optimal hold phase duration of 0.78 s and the measured one was 0.81 s. Figure 5*E* compares the distribution of simulated and measured hold phase durations and indicates a good match. Averaged across participants, the

difference between the measured mean hold phase duration and the estimated optimal mean duration was 6 ± 22 ms (Fig. 5*F*).

In summary, our simulations indicate that the participants performed nearly optimally with regard to the temporal linking of the hold phase and the subsequent transport phase during steady-state performance. That is, they balanced nearly optimally the trade-off between exiting the target zone as soon as possible, on average, while avoiding an excess of premature cursor exits.

Impact of Premature Cursor Exits

Given the quite dramatic cost of premature cursor exits on performance, we asked whether these events affected the cursor exit time during succeeding trials. To address this question, we analyzed the mean cursor exit times for cursor exits occurring before and after premature exits. Following a premature exit, the cursor exit time increased compared with the exit times occurring before the premature exit. However, this increase was small (~ 25 ms) and was only present for three exits (Fig. 6). For cursor exit times slightly longer than required for goal completion (0.6–0.65 s), there was no increase in the cursor exit time in subsequent trials, even though these exits were close to being premature. Similarly, cursor exits in the center of the distribution (0.7–0.75 s) or that were

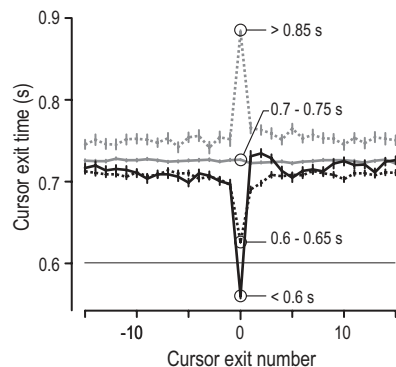


Fig. 6. Impact of premature cursor exits. Each curve shows the average cursor exit times (\pm SE) for 15 cursor exits before and after premature exits (<0.6 s), early but approved exits ($0.6\text{--}0.65$ s), exits close to the average exit time ($0.7\text{--}0.75$ s), and late exits (>0.85 s). Data pooled across participants. Premature exits were followed by a small increase in exit time for ~ 3 cursor exits. Note that early and late cursor exits tended to be preceded and followed by early and late exits, respectively, suggesting a slow fluctuation in the average cursor exit times across trials.

late (>0.85 s) did not lead to a change in cursor exit times in subsequent trials.

Figure 6 also reflects the presence of a slow fluctuation in the average cursor exit time across trials during steady-state performance. That is, early and late cursor exits tend to be preceded and followed by early and late exits, respectively. This slow fluctuation, which had a cycle time in the order of ~ 50 exits, is clearly visible in the curves shown in Fig. 3A, each of which represents a moving average of the cursor exit times (± 10 exits). Interestingly, the peak-to-peak magnitude of these fluctuations (~ 100 ms) is considerably larger than the average increase in cursor exit time due to a premature exit.

In summary, we found that during steady-state performance, the cursor exit time increased slightly following a premature exit and only for a few target exits. We also found slow fluctuations in the average cursor exit times that were substantially larger in peak-to-peak magnitude than the increase following a premature exit.

DISCUSSION

We have demonstrated that when learning a novel task involving a sequence of action phases, there was a gradual transition from reactive to predictive control, whereby the participants learned to launch the motor commands of the next phase in anticipation of sensory events associated with completion of the current phase. This facilitated smooth and fast phase transitions. In addition, we found that with sufficient practice, participants learned to compensate near optimally for temporal uncertainty when performing the task.

Previous studies have suggested that continuous hand movements, such as those observed in writing and drawing, may be composed of a series of smoothly linked simpler movement elements (Bizzi and Abend 1983; Denier van der gon et al. 1962; Morasso and Mussa Ivaldi 1982; Soechting and Terzuolo 1987; Viviani and Cenzato 1985). Several studies have examined the learning of linking movement elements in the context of via point reaching tasks in which participants make hand movements through a series of targets (Flash and Hochner 2005). Initially, participants achieve this task through a sequence of roughly straight-line movements between successive

targets. However, with practice, these straight movements are replaced with smoothly linked curved movements, and movements between targets come to be influenced by the preceding and following ones, a process known as “coarticulation” (Jerde et al. 2003; Sosnik et al. 2004; Todorov 1998). Manual coarticulation has also been documented in typing (Soechting and Flanders 1992) and piano playing (Engel et al. 1997).

In object manipulation tasks, such coarticulation or blending of action phases is not always functional because of task constraints. For example, when lifting an object it must be contacted before a stable grasp can be established. Likewise, to smoothly place a grasped object on a surface, the object must contact the surface before the grasp is released. Despite the fact that most of the manual tasks we perform on a daily basis involve object manipulation, to our knowledge the question of how people learn to link discrete action phases in manipulation tasks has not previously been investigated. To address this issue, we designed a laboratory task that requires both spatial and temporal control and that captures several key features of natural manipulation tasks: discrete multimodal sensory events mark the completion of each action phase, each phase needs to be completed before the next phase can be executed, and launching the next action phase before the current phase is completed can result in performance errors and substantial delays in overall task completion time (Flanagan et al. 2006). Of course, we acknowledge that our task differs in some respects from many natural tasks. For example, haptic feedback (in addition to visual and auditory feedback) about goal completion plays an important role in manipulation tasks (Johansson and Flanagan 2009), and many action tasks do not include action phases with externally specified durations.

In our task, we found that improvements in the temporal linking of action phases, which involved learning to predict the time of goal completion of the hold phase, began immediately with practice of the task and continued for $\sim 1,200$ trials. Likewise, improvements in cursor control, which presumably involved learning the relation between cursor speed and variability as well as adaptation to the spatial transformation between motor commands and their consequences (Kawato 1999; Wolpert and Miall 1996), also began immediately, but was completed within ~ 400 trials. The fact that improvements in temporal linking started immediately indicates that participants did not have to master cursor control before starting to learn about the timing of the task. Moreover, the fact that temporal learning continued well after cursor control was mastered suggests that these two learning processes involved distinct mechanisms. However, some interaction may have occurred, and it is possible that temporal learning may have been quicker if we had used a simpler mapping between forces and cursor motion.

The improvements in the temporal linking of action phases involved a transition from reactive to predictive control, indicating that participants learned to estimate the time required for goal completion of the hold phase. There is evidence that predictive linking of action phases based on time estimates also supports the linking between the reaching phase and the execution of motor commands aimed to apply forces on the object during grasping movements (Säfström and Edin 2008). When using reactive control in our task, the key sensory event that participants respond to is feedback about goal completion of the hold phase. In contrast, when using predictive control,

sensory events related to the end of the transport phase (and start of the hold phase) become critical because participants can use this information when estimating the expected completion of the hold phase. However, although sensory events associated with hold phase completion are not used within a trial to trigger the transport phase during predictive control, these events are presumably important for upholding the representation of the required hold phase duration (Johansson and Flanagan 2009).

The results of our simulations indicate that, during steady-state performance, participants compensated for temporal uncertainty in a near-optimal fashion when predictively linking the hold and transport phases. This uncertainty is presumably related to variability in estimating the duration of the hold phase (Hudson et al. 2008; Rakitin et al. 1998) and variability in the execution of the motor commands (Harris and Wolpert 1998; van Beers et al. 2004). Our finding that people represent temporal uncertainty in the process of predictively linking action phases is in line with a previous study where it was demonstrated that people can represent temporal uncertainty related to estimations of time intervals to calibrate their performance (Coull and Nobre 2008; Grondin 2010; Ivry and Spencer 2004; Jazayeri and Shadlen 2010; for reviews on timing and time perception and estimation, see Wing 1993). Specifically, when participants were required to reproduce a time interval between two visual cues by pressing a key, the timing estimates were influenced by the temporal uncertainty related to the underlying distribution from which the time intervals were drawn. Our participants' near-optimal performance indicates that they, in addition to knowledge about their temporal uncertainty in launching the transport phase, also had knowledge about the time cost associated with premature cursor exits. Our results extend previous work examining how people compensate for temporal uncertainty and externally imposed and explicit costs in action. Specifically, people take into account uncertainty in movement duration when making pointing movements to targets given costs associated with arriving at the target too early or too late (Hudson et al. 2008). Near-optimal compensation for spatial uncertainty has also been demonstrated for pointing movements. For instance, when pointing to target configurations that have different reward and penalty regions, participants choose their average pointing location so as to minimize the loss that accrues through the variability of pointing (Trommershäuser et al. 2008).

Premature cursor exits, which were highly detrimental to task performance because participants had to return to the target and acquire it, led to an increase in the cursor exit time in the following few trials. Note that had participants performed optimally, they should not have changed their behavior since occasional premature exits are expected due to random variability in cursor exit times because of temporal uncertainty. However, the small size of this increase (~25 ms) and its presence for only three subsequent trials is consistent with our simulations showing that participants were near-optimal in the control of cursor exits. The small increase in cursor exit time following premature exits resembles the phenomenon of post-error slowing, where reaction times following incorrect responses in a variety of decision-making tasks tend to increase (Rabbitt 1966; Rabbitt and Rogers 1977). Posterror slowing is often accompanied by small decreases in reaction time follow-

ing correct responses, providing a mechanism through which "the system self-regulates to a state of homeostasis characterized by fast responses and few errors" (Dutilh et al. 2012).

We observed low frequency fluctuations in the cursor exit time captured by a moving average based on ± 10 trials. We speculate that these fluctuations reflect a mechanism for upholding near-optimal performance. Suppose that the cursor exit time on a particular trial represents a planned cursor exit time plus error. A possible way to uphold near-optimal performance in the presence of substantial trial-to-trial variability is to 1) accumulate data about performance from several previous trials to obtain a reasonable estimate of the performance associated with the current planned cursor exit time, and 2) use this information to slowly adjust the planned cursor exit time so as to uphold near-optimal performance. Specifically, we suggest that the low frequency fluctuations in the cursor exit time represent slow changes in the planned cursor exit time, which the participants adjusted continuously in an ongoing effort to come close to optimal performance. The frequency of these fluctuations may reflect the number of trials needed to obtain a reasonable moving estimate of the performance associated with a particular planned cursor exit time given temporal uncertainty.

In summary, we have shown that learning to link sequential action phases involves developing predictive control strategies that near-optimally compensate for temporal uncertainty. Given that humans spend some 60% of their waking hours manipulating objects (Kilbreath and Heard 2005), the number of action phase transitions made every day is presumably very large. Thus, the ability to learn to efficiently link action phases in manipulation tasks is highly important.

DISCLOSURES

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

AUTHOR CONTRIBUTIONS

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

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