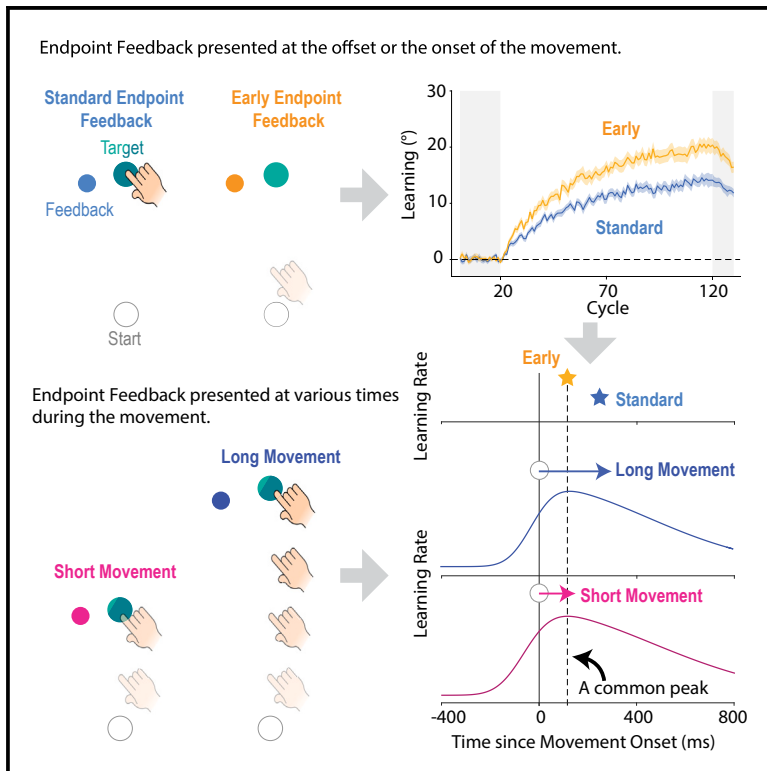


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Advanced feedback enhances sensorimotor adaptation

Graphical abstract



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In brief

Delayed visual feedback is known to disrupt sensorimotor adaptation. Wang et al. show that temporally advancing feedback relative to movement position enhances adaptation. Thus, learning is maximized not when the feedback and movement are synchronized but when the feedback is temporally aligned with an efference prediction from the motor command.

Highlights

- The strength of sensorimotor adaptation is dependent on the timing of the feedback
- Advancing visual endpoint feedback enhances adaptation
- Optimal feedback timing depends on signals linked to motor planning, not execution

Article

Advanced feedback enhances sensorimotor adaptation

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SUMMARY

It is widely recognized that sensorimotor adaptation is facilitated when feedback is provided throughout the movement compared with when it is provided at the end of the movement. However, the source of this advantage is unclear: continuous feedback is more ecological, dynamic, and available earlier than endpoint feedback. Here, we assess the relative merits of these factors using a method that allows us to manipulate feedback timing independent of actual hand position. By manipulating the onset time of “endpoint” feedback, we found that adaptation was modulated in a non-monotonic manner, with the peak of the function occurring in advance of the hand reaching the target. Moreover, at this optimal time, learning was of similar magnitude as that observed with continuous feedback. By varying movement duration, we demonstrate that this optimal time occurs at a relatively fixed time after movement onset, an interval we hypothesize corresponds to when the comparison of the sensory prediction and feedback generates the strongest error signal.

INTRODUCTION

Implicit adaptation ensures that the sensorimotor system remains exquisitely calibrated in the face of a variable environment and fluctuations in the internal state of the agent. This process occurs automatically in response to sensory prediction error, the mismatch between the expected sensory consequences of a movement and the actual feedback.^{1–3} A common way to examine constraints on sensorimotor adaptation is to manipulate the visual error. For example, by occluding the arm and providing cursor feedback, a polar transformation (e.g., visuomotor rotation) can be used to introduce a discrepancy between the actual and perceived position of the hand. This discrepancy serves as an error signal that is used to recalibrate the sensorimotor system to minimize future errors when a similar action is produced.

In studies of visuomotor adaptation, two types of visual feedback are typically used: continuous feedback, where the cursor is visible throughout the movement and thus provides feedback of the movement trajectory, and endpoint feedback, where the cursor is only presented when the hand reached its terminal position or at the radial distance of the target (Figure 1C). It is well established that adaptation in response to endpoint feedback is attenuated compared with adaptation in response to continuous feedback.^{4–6} This effect is especially pronounced in measures of implicit adaptation, with little difference between continuous and endpoint feedback on measures reflective of strategic changes in performance.⁷ Moreover, the efficacy of endpoint feedback is constrained by timing. Specifically, when the

presentation of the feedback cursor is delayed relative to the hand movement, adaptation is markedly attenuated.^{8–12} Indeed, delaying endpoint feedback by just 100 ms can produce a dramatic reduction in the magnitude of implicit adaptation.^{13,14}

At present, it remains unclear why continuous feedback is advantageous relative to endpoint feedback. There are many notable differences between these two modes. First, by definition, continuous feedback is dynamic, and endpoint feedback is static. Given the dynamic nature of most human sensorimotor skills, the nervous system may be more responsive to the ecological nature of continuous feedback. Second, continuous feedback provides a continuous stream of spatiotemporal information. Not only does this provide an opportunity to sample the feedback at multiple points of time and space, but the movement of the cursor might be attentionally engaging.¹⁵ Third, continuous feedback is provided as soon as the movement is initiated, whereas endpoint feedback is only available when the hand reaches the target. Theories of sensorimotor adaptation propose that the feedback is compared with a sensory prediction derived from an efference copy of the motor command. Endpoint feedback might be delayed with respect to the time when the representation of the sensory prediction is strongest, similar to hypotheses concerning the attenuating effect of delayed feedback.

The goal of this study was to systematically investigate the difference in adaptation to continuous and endpoint feedback, assessing the relative contributions of dynamics, continuity, and onset timing. To isolate implicit adaptation, we employed task-irrelevant clamped feedback.¹⁶ In this task, the angular divergence between the feedback and target is fixed, independent

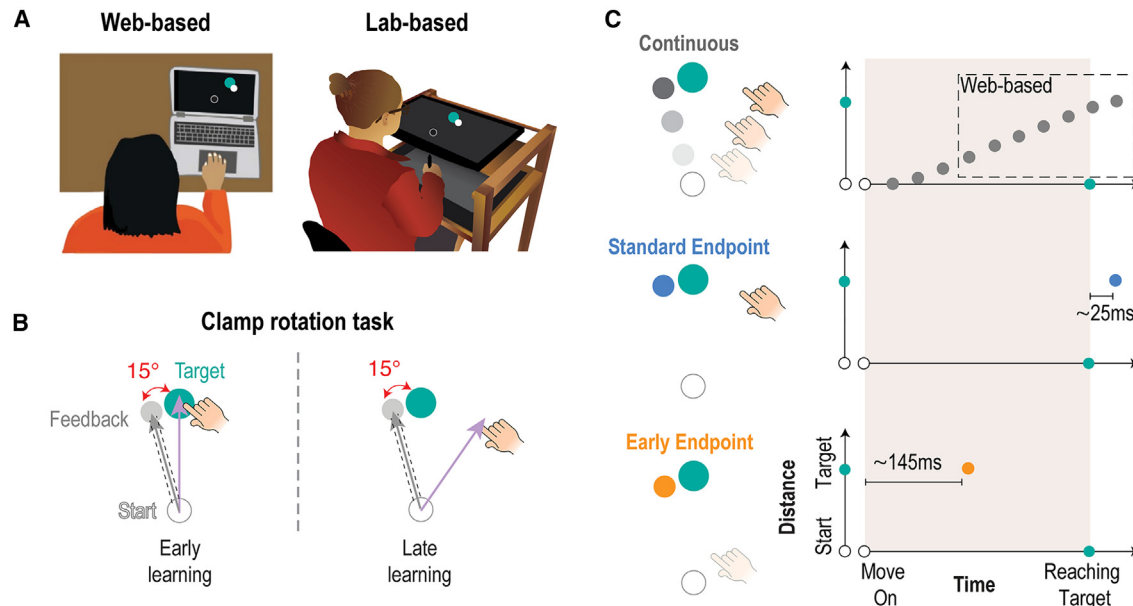


Figure 1. Experimental setup, task, and feedback conditions

(A) Schematics of the web-based experimental setup (left) for experiments 1a, 2, and 3 and the lab-based setup (right) for experiments 1b and 4, depicting the start location (white circle), the cursor (white dot), and a target (cyan circle).

(B) For task-irrelevant clamped feedback, the angular position of the feedback cursor is rotated by 15° with respect to the target, regardless of the heading direction of the hand.

(C) Three types of clamped feedback are illustrated in task space (left) and as a function showing the position and timing of the feedback (right). As detailed in the [STAR Methods](#), the illustration depicts the delays associated with detecting movement onset (web-based) and presenting the visual feedback (web- and lab-based). Each dot represents one refresh cycle on the computer display monitor. Continuous feedback is presented throughout the movement, following the radial distance of the hand from the start location to the target. In the web-based system, the cursor becomes visible ~145 ms after movement initiation. At that point in time, the hand has moved ~1/3 of the distance to the target (region indicated by the dashed square). Standard endpoint feedback is presented for one refresh cycle (~25 ms) after the hand reaches the target distance (corresponding to the last frame of the continuous feedback condition). Early endpoint feedback is presented for one refresh cycle at the radial distance of the target at ~145 ms after movement initiation. The gray area indicates the interval between movement onset and when the radial distance of the movement reaches the target amplitude. For lab-based experiment 1b, we created early endpoint and standard endpoint conditions that were temporally matched to web-based experiment 1a.

See also [Figure S1](#).

of the position (and thus movement) of the participant's hand ([Figure 1B](#)). Participants are fully informed of the feedback manipulation and instructed to ignore the feedback and always reach straight to the target. Despite these instructions, the participant's behavior has all of the hallmarks of implicit adaptation: across trials, the reaching angle of the hand gradually shifts away from the target in the opposite direction of the clamped feedback, and a pronounced aftereffect is observed when the feedback is removed.^{16,17} Participants are not aware of this change in behavior, believing their terminal hand position to be near the target throughout the experiment.¹⁸

Clamped feedback provides a unique opportunity to manipulate the timing of both continuous and endpoint feedback. Because the feedback is movement-invariant and predetermined, we can manipulate the onset, duration, and offset of the feedback. For example, endpoint feedback can be presented at movement onset or even prior to movement onset. Moreover, to examine the influence of temporal continuity, we can manipulate the duration of the feedback to match the endpoint and continuous feedback on this dimension. Through a series of experiments, we manipulate these variables to gain insights into how sensorimotor adaptation is influenced by the spatial-temporal relationship between a movement and its associated feedback.

RESULTS

Implicit adaptation is influenced by the feedback onset time

In the initial experiments, we used a web-based platform to manipulate the temporal and spatial properties of the feedback in a visuomotor rotation task ([Figure 1A](#)).¹⁹ Using their trackpad, participants were instructed to make center-out "reaching" movements. To elicit implicit sensorimotor adaptation, we used clamped feedback in which the cursor was always rotated from the target location by a fixed angle of 15° ([Figure 1B](#)) and thus not contingent on the participant's actual movement direction.

We compared three feedback conditions in experiment 1a ([Figure 1C](#)). Two of these corresponded to the standard modes of feedback, continuous ($n = 60$) and endpoint ($n = 67$), with the feedback cursor presented throughout the movement for the former and only at the endpoint for the latter (see [Table 1](#) for participants' information). We expected to observe greater adaptation to continuous feedback compared with standard endpoint feedback, demonstrating that this well-established effect is manifested on our web-based platform. For the third condition, which we refer to as "early endpoint feedback," we sought to advance the onset time of the endpoint feedback

Table 1. Summary of participants' information on web-based experiments

	Experiment 1a			Experiment 2		Experiment 3a		Experiment 3b	Experiment 3c		
Feedback	Continuous	Standard endpoint	Early endpoint	Endpoint	Early endpoint	Extend endpoint	Extend early endpoint	Advance continuous	Continuous	Early endpoint	Advance continuous
Participants meeting inclusion criteria	60	67	53	30	27	32	30	30	27	25	24
Female	31	31	13	13	11	14	13	17	18	14	14
Age (mean [SD])	25.1(5.4)	24.6(5.5)	24.2(4.7)	25.9(4.7)	23.8(4.4)	23.0(3.5)	25.1(4.8)	24.2(4.5)	24.1(4.0)	26.3(5.3)	29.3(8.3)
CCW	27	33	27	17	14	15	17	15	13	13	14

($n = 53$), presenting it before the hand reached the target distance. To that end, the code was written to present the feedback immediately after movement onset. Due to delays in the web-based interface, the feedback was actually presented ~ 145 ms after the movement onset. Given that the mean movement time was 206.4 ms (SD = 23.1 ms), the early endpoint feedback appeared ~ 61 ms before the hand reached the target (see [Figure S1](#) for details).

Following a baseline period with veridical feedback, clamped feedback was presented for 400 trials, with the three modes of feedback tested in different groups of participants. Participants showed robust adaptation in all three conditions ([Figure 2B](#)), with the shift in reaching angle persisting across a no-feedback washout block. Consistent with prior studies,^{4–7} participants adapted less in response to standard endpoint feedback compared with continuous feedback. Surprisingly, early endpoint feedback resulted in a level of adaptation that was comparable to continuous feedback. Using a non-parametric cluster-based permutation analysis (see [STAR Methods](#)), significant differences between conditions were observed across almost the entire extent of the perturbation and washout blocks. Focusing on a pre-specified epoch near the end of the perturbation block, we performed a series of post hoc pairwise comparisons ([Figure 2C](#)). The reaching angle in the standard endpoint condition was lower than that in the continuous ($t(125) = 3.9$, $p_{\text{FDR}} < 0.001$, $\text{BF}_{10} = 177$, $d = 0.7$) and early endpoint conditions ($t(118) = 3.4$, $p_{\text{FDR}} < 0.001$, $\text{BF}_{10} = 30$, $d = 0.6$). No difference was found between the continuous and early endpoint conditions ($t(111) = 0.42$, $p_{\text{FDR}} = 0.68$, $\text{BF}_{10} = 0.22$, $d = 0.08$). These results provide a striking demonstration of the relevance of feedback onset timing: providing endpoint feedback in advance, even for just a single refresh cycle, was sufficient to offset the attenuating effects of standard endpoint feedback.

We found no evidence of online corrections in all three feedback conditions and no difference in reaction time, movement time, and movement speed ([Figure S2](#)). We also confirmed that the advantage of continuous and early endpoint feedback holds even when we regressed out individual differences in movement duration, reaction time, perturbation direction, age, and gender ([Table S1](#)).

As mentioned above, the web-based system is somewhat limited in that there is a significant delay in detecting the onset of the movement. Moreover, there is the general loss of experimental control associated with remote testing. To verify the advantage of advanced endpoint feedback, we conducted a

replication experiment in the lab (experiment 1b). In terms of timing, the only significant delay is that associated with refreshing the display to present the feedback, a value that is ~ 25 ms, similar to that found in optimized computer-based systems. Participants were assigned to one of three groups ($N = 25$ /group): continuous feedback, standard endpoint feedback, and early endpoint feedback. For the latter, we opted to present the feedback ~ 145 ms after the movement onset, matching the timing used in the experiment 1a. Given the movement time in experiment 1b was ~ 295.8 ms (SD = 98.9 ms), the feedback appeared ~ 150 ms before the hand reached the target distance.

Experiment 1b largely replicated the key results in experiment 1a. First, continuous feedback resulted in higher adaptation compared with the standard endpoint feedback throughout training (early: $t(48) = 6.3$, $p_{\text{FDR}} < 0.001$, $\text{BF}_{10} = 90,603$, $d = 1.8$, late: $t(48) = 2.2$, $p_{\text{FDR}} = 0.037$, $\text{BF}_{10} = 2.4$, $d = 0.66$). Second, early endpoint feedback resulted in a prominent advantage compared with the standard endpoint feedback (early: $t(48) = 4.8$, $p_{\text{FDR}} < 0.001$, $\text{BF}_{10} = 1,315$, $d = 1.4$; late: $t(48) = 2.7$, $p_{\text{FDR}} = 0.024$, $\text{BF}_{10} = 4.5$, $d = 0.78$). Third, early endpoint feedback reached a similar asymptote as continuous feedback (late: $t(48) = 0.26$, $p_{\text{FDR}} = 0.80$, $\text{BF}_{10} = 0.29$, $d = 0.07$).

The results of experiment 1 highlight that the benefit from early endpoint feedback is observed even when this results in reduced synchronization of the position of the feedback and hand. On average, early endpoint feedback appears at a position that is farther from the actual hand position compared with the standard endpoint feedback, yet it results in a stronger adaptation. Importantly, due to the individual difference in movement time, there was considerable variability in terms of the position of the hand at the time of the early endpoint feedback. However, there was no correlation between the degree of late adaptation and movement time ([Figure S2](#)). Thus, the advantage of early endpoint was not driven by those who moved fastest and had reached a position close to the target when the feedback appeared. In sum, these results indicate that the efficacy of endpoint feedback is primarily dependent on the timing of the feedback and not the position of the hand with respect to the position of the feedback.

Although early endpoint feedback reached a similar asymptote as continuous feedback, the latter produced larger adaptation during the initial exposure to the clamp, an effect that reached significance in experiment 1b (experiment 1a: $t(111) = 1.9$, $p_{\text{FDR}} = 0.055$, $\text{BF}_{10} = 1.1$, $d = 0.36$; experiment 1b: $t(48) = 2.9$, $p_{\text{FDR}} = 0.005$, $\text{BF}_{10} = 7.8$, $d = 0.82$). The difference in early adaptation might be because early endpoint feedback is not presented

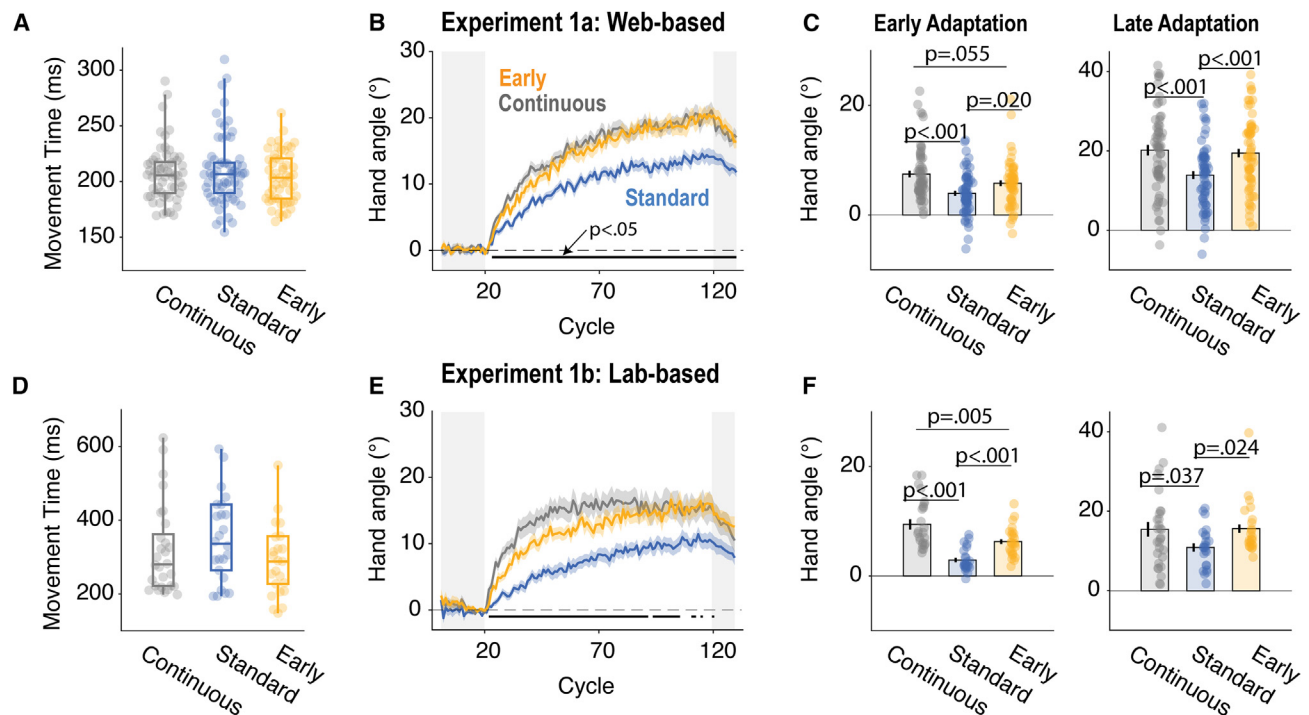


Figure 2. Implicit adaptation is enhanced by advancing endpoint feedback

Top row: web-based results of experiment 1a.

(A) Movement time.

(B) Reaching angle time course for the continuous (gray), standard endpoint (blue), and early endpoint (yellow) conditions. The light gray regions indicate baseline and washout (no feedback) blocks. Black horizontal lines at the bottom indicate clusters showing the significant main effect of feedback.

(C) Implicit adaptation magnitude, as calculated during early adaptation (cycles 21–40) and late adaptation (cycles 111–120).

Bottom row: lab-based results of experiment 1b.

(D–F) Similar to (A)–(C) for the lab-based replication.

The box plots in (A) and (D) indicate the first quartile, median, and third quartile. The shaded areas in (B) and (E) and error bars in (C) and (F) indicate standard error. See also [Table S1](#) and [Figures S2](#) and [S3](#).

at an optimal time and/or because the timing of the feedback is quite variable across trials with respect to hand position or movement offset. Alternatively, other features of the continuous feedback such as feedback duration and its dynamic nature may also influence adaptation.

Before addressing these alternative hypotheses, we first wanted to verify that the benefit observed with early endpoint feedback was not idiosyncratic to the clamp method. In experiment 2, we replaced the visual clamp with position-contingent feedback using the web-based system. We used a 45° rotation and compared the early endpoint ($n = 27$) and standard endpoint conditions ($n = 30$). It is, of course, not possible in the early endpoint condition to precisely position the feedback cursor at movement onset based on the (future) endpoint position of the hand. However, given that the movement trajectories are relatively straight, we could predict the endpoint position of the hand based on the heading angle sampled just after movement onset ([Figure 3A](#)). To keep the spatial information similar across conditions, we applied the same method in the standard endpoint condition (determined angular position of feedback based on the initial heading angle).

Adaptation was larger than in experiments 1 for both conditions ([Figure 3C](#)), as participants followed the instructions to “make the cursor hit the target.” This behavior likely reflects the composite

contributions of both explicit and implicit processes. To estimate implicit adaptation, we focused on the aftereffect, calculated as the mean reaching angle in the first cycle of the washout block. We again observed greater adaptation in the early endpoint condition compared with the standard endpoint condition ($t(56) = 3.9$, $p_{\text{bf}} < 0.001$, $\text{BF}_{10} = 101.1$, $d = 1.0$, [Figure 3D](#)).

In sum, the results of this first set of experiments demonstrate that advancing the timing of endpoint feedback produces a significant increase in implicit adaptation; indeed, the overall extent of adaptation for early endpoint feedback is comparable to that observed in response to continuous feedback. This pattern was observed with feedback signals that varied considerably in terms of error size and movement contingency (clamped or contingent). The absence of evidence of corrective movements ([Figure S3](#)) suggests that, mechanistically, advancing the onset time of endpoint feedback enhances processes involved in the adaptation of a feedforward motor plan rather than processes invoked for online corrections.

Temporal and spatial continuity does not influence implicit adaptation

To this point, we have examined one core difference between continuous and endpoint feedback, namely the timing of feedback

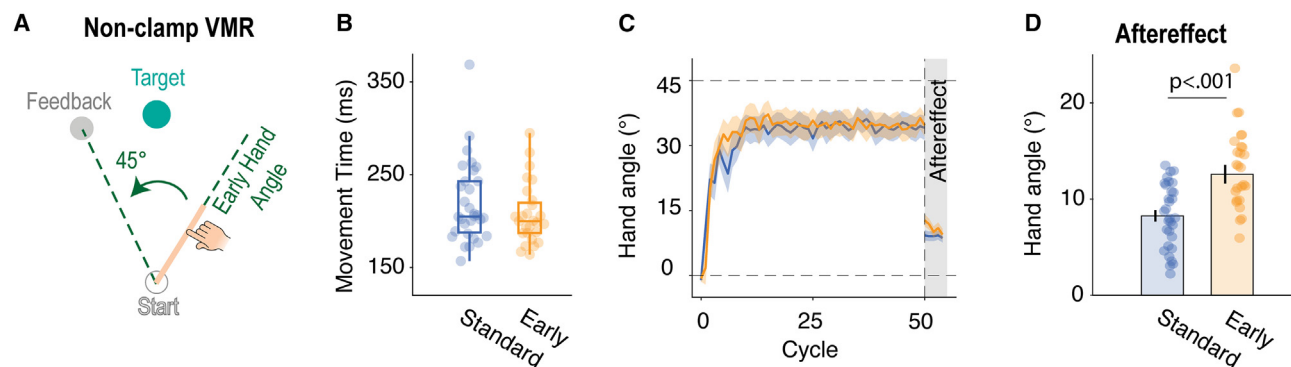


Figure 3. Experiment 2: The advantage in early endpoint feedback persists when the feedback position is contingent on the heading direction of the hand

(A) Illustration of trial in visuomotor rotation task with contingent endpoint feedback; the cursor is rotated by 45° with respect to the projected position of the hand based on actual hand position early in the movement.

(B) Similar to experiment 1a, the average movement time was 209.8 ms; and therefore, the early endpoint feedback appears ~65 ms before the hand reached the target distance.

(C) Time courses of reaching angle.

(D) Magnitude of implicit adaptation calculated over the first cycle in the washout block of experiment 2.

Shaded area in (C) and error bars in (D) represent standard error. Dots in (B) and (D) represent individual participants.

onset. However, these two types of feedback also differ in terms of temporal and spatial extent, with continuous feedback available for a longer duration and traversing a larger spatial distance. We next asked if these variables influence implicit adaptation. We examined the influence of temporal continuity in experiment 3a by testing two new conditions (Figures 4A and 4B). In one condition, we extended the presentation time of the early endpoint feedback to match it to the duration of the entire movement ($n = 30$). In another condition, we extended the duration of the standard endpoint to match the movement time for that trial (on average 84 ms, $n = 32$). Thus, in both conditions, the static feedback is visible for the same mean duration as continuous feedback. Compared with the original conditions in experiment 1 (1 refresh cycle), temporally extending the presentation of endpoint feedback did not influence the time course of adaptation for either the standard endpoint or early endpoint conditions (Figures 4C and 4D). A regression model showed a significant effect of feedback onset time (coefficient 95% CI = [0.83–9.2], $t(178) = 2.4$, $p = 0.019$, $\eta_p^2 = 0.082$) with no effect of the presentation time duration (coefficient 95% CI = [–4.7 to 2.4], $t(178) = -0.63$, $p = 0.53$, $\eta_p^2 = 0.004$).

To look at the effect of spatial continuity, we created an advanced continuous condition ($n = 30$) in experiment 3b. Here, the cursor was presented at the endpoint position upon movement initiation and then moved beyond the target as the participants reached toward the target (Figure 4E). Thus, the initial position of the feedback is matched to that of the standard endpoint conditions. This condition resulted in a similar extent of adaptation as standard-continuous (Figure 4F; $t(88) = 0.8$, $p = 0.43$, $BF_{10} = 0.30$, $d = -0.18$) and early endpoint feedback (Figure 4F; $t(86) = 1.1$, $p = 0.29$, $BF_{10} = 0.29$, $d = -0.24$) visual clamp, surpassing that observed with standard endpoint feedback ($t(95) = 3.8$, $p < 0.001$, $BF_{10} = 85$, $d = -0.83$).

We tested whether the null effect in experiment 3b is due to a ceiling effect given that implicit adaptation is known to saturate in response to a large range of errors (~10°–90°).^{16,17,20,21} Thus,

spatial continuity may benefit adaptation with respect to advanced feedback, but the saturated response to a 15° error may obscure this advantage. In experiment 3c, we used a clamp size of 2°. As expected, the asymptote in response to this error was lower than observed in experiment 1 where the clamp size had been 15°. Importantly, we again did not observe any difference between the three feedback conditions (Figure S4).

Taken together, the results in experiment 3 are consistent with the hypothesis that the sensorimotor adaptation system is sensitive to the onset time of the feedback but not the temporal or spatial extent of the feedback, two fundamental features of continuous feedback.

The optimal feedback onset time is locked to movement onset

We next consider two hypotheses that might account for the advantage of early endpoint feedback over standard endpoint feedback. One hypothesis centers on the idea that optimal adaptation occurs when the error signal is synchronized with the sensory prediction. Considering that the motor command is generated prior to movement onset and the sensory prediction is derived from an efference copy of the motor command,¹ we assume that there is an activation function of the representation of the prediction: it will become strongest at some time after movement onset and then decay. If learning is maximized when the feedback is synchronized with the strongest representation of the prediction, advancing the feedback would be beneficial if the strongest representation of the prediction occurs prior to movement offset. The second hypothesis posits that implicit motor adaptation is maximized when the radial position of the visual feedback is synchronized with the actual hand position. Considering that visual signal processing is typically slower than proprioceptive signal processing,^{22,23} presenting visual feedback in advance may compensate for this latency difference; that is, by advancing the onset of the visual feedback, the visual feedback and hand position might be subjectively synchronized.

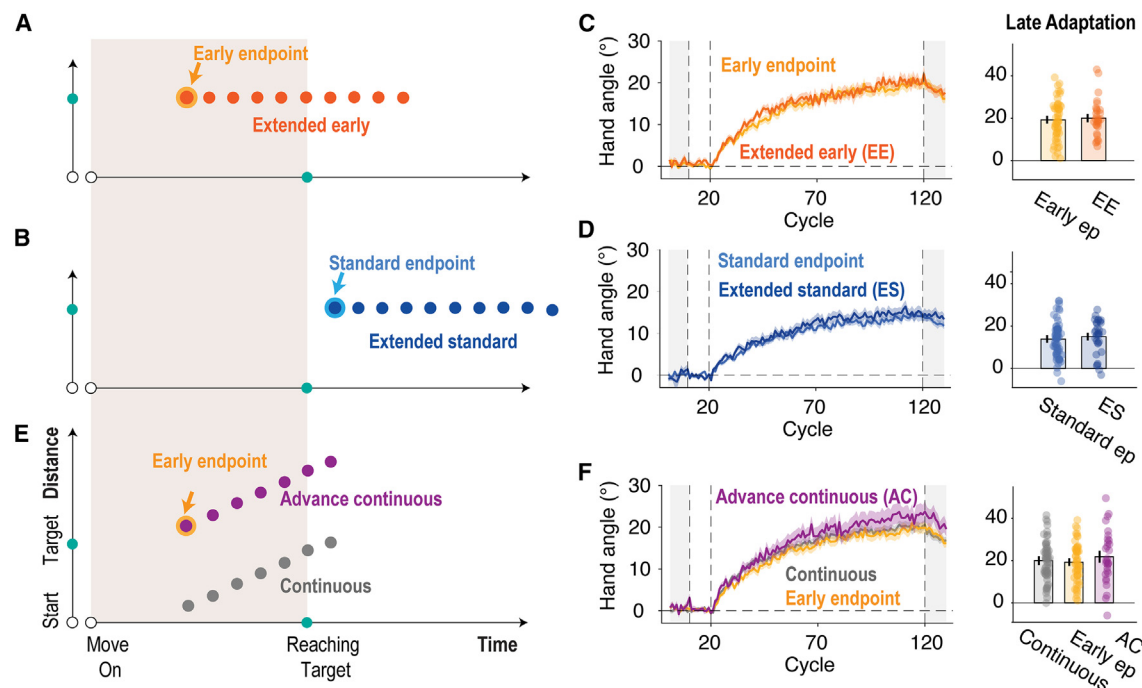


Figure 4. Experiment 3: Temporal and spatial extent do not influence implicit adaptation

(A and B) Illustrations of extended versions of early and standard endpoint feedback conditions. x axis indicates time, and y axis indicates radial distance of the cursor relative to the start position. Each dot represents a refresh cycle. The gray area indicates the movement period. Feedback was presented, on average, for 5 cycles in the extended endpoint conditions. Note that the lighter colors show the timing for the single-cycle variants of early endpoint and standard endpoint used in experiment 1.

(C and D) Left: time course of reaching angle in experiment 3. The shaded area represents standard error. Light gray areas indicate baseline and washout blocks. No significant clusters were found in the comparison of the brief (1 cycle, data from experiment 1a) and extended versions. Right: comparison of reaching angle measured in late adaptation.

(E) In the advanced continuous condition, the feedback cursor appeared at the endpoint location at movement onset and then moved in the direction of the hand movement.

(F) As in (C) and (D), no significant differences were observed in the cluster-based analysis of the learning functions or during late adaptation.

In (C)–(F), the shaded area of the learning curve and error bars of the bar graphs represent standard error.

See also [Figure S4](#).

To evaluate these hypotheses, we set out to empirically derive the optimal feedback time in experiment 4, asking if it was time-locked to movement onset or hand position. To ensure precise timing with minimal delay, the experiment was conducted in the lab. To derive the timing function, we employed a trial-by-trial design in which the direction of a 15° visual clamp was pseudo-randomized to be either clockwise or counterclockwise across trials (and thus prevent accumulated learning). With this method, the index of adaptation is the trial-by-trial change in reaching angle.²⁴ Feedback duration was limited to a single refresh cycle of the monitor, and we varied the onset time of the feedback using intervals designed to range from 200 ms prior to movement onset to 300 ms after movement onset. We set this window based on a running average of each participant's mean movement initiation time ([Figure 5A](#)). To test whether the optimal feedback time is locked with the movement onset or the actual hand position, we manipulated movement duration by varying movement distance (7 or 15 cm) across participants ([Figure 5B](#)). The median movement durations for the two conditions were 172.4 and 247.4 ms, respectively ([Figure 5C](#)).

Feedback onset time had a non-monotonic effect on the trial-by-trial motor correction ([Figures 5D and 5E](#), top). Minimal

adaptation was observed when the feedback led the movement onset. The function rapidly rose, reaching a peak around mid-movement before falling off for longer feedback onset times. The bottom row of [Figures 5D and 5E](#) plots the same data but now aligned to the sample at which the hand reached the target amplitude. For the short movement, the adaptation function peaks close to this time. However, for the long movement, the peak occurs prior to when the hand reached the target distance. Strikingly, adaptation peaked at roughly the same time after movement onset for both the short and long movements. Taken together, these results indicate that the optimal feedback time is time-locked to movement onset and not hand position.

To quantify the peak of the feedback function, we used a model-based approach. Assuming a skewed Gaussian function, we calculated the time of peak adaptation with respect to movement onset and when hand reached the target distance, comparing the functions for the short and long movement durations. With respect to movement onset, the functions for the short and long duration movements were very similar ([Figures 5D and 5E](#), top), with peaks that were indistinguishable (long: 150.6 ± 24.2 ms; short: 162.7 ± 22.4 ms; $z = 0.53$; $p = 0.60$, [Figure 5F](#), top). By contrast, when we compared the functions for

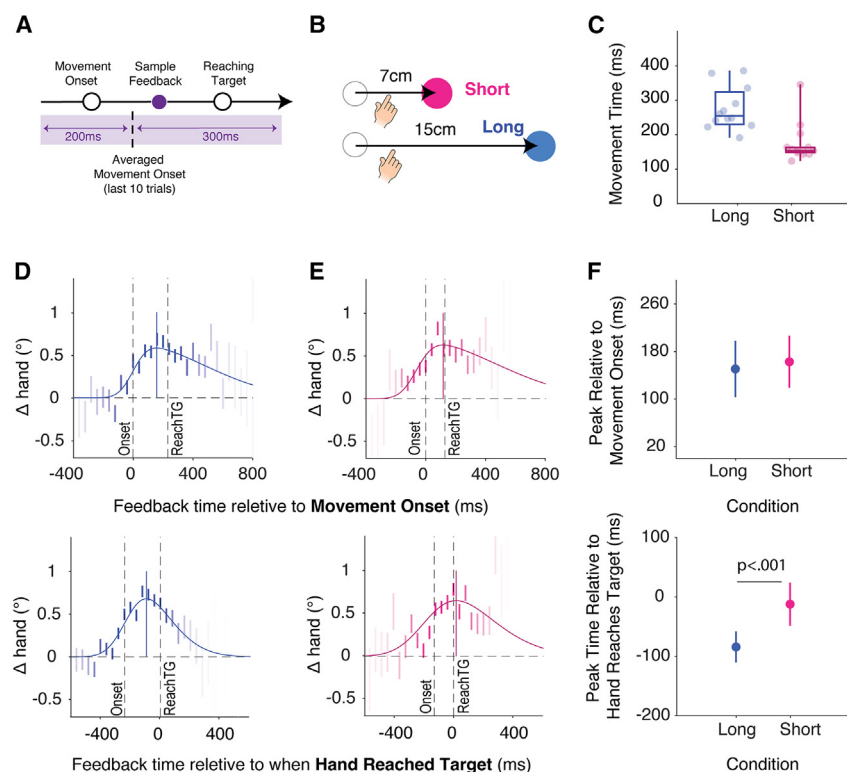


Figure 5. Experiment 4: The optimal timing of endpoint feedback is associated with movement onset

(A) Feedback onset for each trial was pre-determined, selected from a window ranging from -200 ms to +300 ms relative to the running average of movement onset time over the last 20 trials.

(B and C) To vary movement duration, the distance to the target was 7 cm for one group and 15 cm for a second group. As expected, movement time increased for the long movements.

(D and E) Change in reaching angle (i.e., trial-by-trial motor correction) as a function of feedback onset time with respect to movement onset (top row) or when the hand reached the target distance (bottom row) for the long (D) and short movements (E). Negative values mean the feedback is presented before movement onset. The vertical dash lines indicate movement onset and when the hand reached the target distance (ReachTG). Each data point is a bin of 40 ms. The error bars indicate standard errors and the darkness of the bars indicates the relative number of samples in that bin. The colored curves are the best-fitted skewed Gaussian functions, with the colored vertical line marking the peak of each function.

(F) Optimal feedback time relative to movement onset (top) or when the hand reached the target distance (bottom), estimated by bootstrapping (see STAR Methods). The optimal times for the short and long conditions are statistically

indistinguishable when the functions are defined with respect to movement onset, but not when defined with respect to when the hand reached the target distance. Error bars represents 95% confidence intervals. See also Figures S5 and S6.

the short and long duration movements aligned with respect to when the hand reached the target distance, the peaks were markedly different (long: -84.3 ± 13.3 ms; short: -12.2 ± 18.6 ms; $z = 4.8$; $p < 0.001$, Figures 5D–5F, bottom).

In secondary analyses, we examined the relationship between adaptation and other movement-related events to confirm that the optimal feedback time is best predicted by movement onset time rather than other features or stage of the movement (Figure S5). First, we quantified the peak of the motor correction function as a percentage of movement duration and found that the peaks were significantly different across long and short movements. We note that the function for the long condition peaks before the hand reaches the target amplitude, occurring at $\sim 74\%$ (95% CI = 54%–93%) of the movement duration, further confirming that the optimal feedback time occurs before the hand reached the target distance. Second, we aligned the feedback onset to the time that when hand reached 50% of movement distance, and again, the peaks of the motor correction function were different across conditions. Third, we plotted the motor correction as a function of movement speed at the time when the feedback was presented and did not observe any clear peak in the function. Our analyses of the optimal feedback time were further confirmed with a model-free approach in which we identified the peak of the function from the raw data without fitting a skewed Gaussian function (Figure S6). These results provide further support that the optimal feedback is associated with the movement onset rather than with other features.

In summary, these results indicate that the optimal time to present feedback does not correspond to the time at which the hand position and feedback position are aligned. Rather, the optimal time for feedback appears to be at a fixed delay relative to movement onset, consistent with the hypothesis that learning is strongest when the feedback is temporally aligned with the sensory prediction.

DISCUSSION

Within the domain of sensorimotor adaptation, many studies have shown that continuous feedback induces faster learning relative to endpoint feedback.^{4–6} However, the reason for this benefit has not been clear. Not only does continuous feedback provide extended spatiotemporal information, but its onset is also earlier in the movement. In this study, we used non-contingent, clamped feedback to examine various factors that might underlie the disadvantage of endpoint feedback. The results show that, whereas the duration and spatial extent of the feedback had no impact on the strength of adaptation, the onset time of the feedback was critical. Advanced endpoint feedback, even when limited to a single frame, resulting in adaptation comparable to that observed with continuous feedback.

These observations are especially surprising given that continuous feedback provides richer information than endpoint feedback. However, various lines of studies indicate that implicit adaptation is relatively insensitive to the quality of the feedback.

For example, adaptation is insensitive to the uncertainty of the visual feedback, at least for relatively large errors,²¹ suggesting that the implicit learning system may not be sensitive to the quality or ecological validity of the feedback. This point is further underscored by the very fact that robust adaptation is observed in response to clamped feedback despite participants' awareness of the manipulation. These observations point to a system that is highly modular, automatically using an error signal to make feed-forward adjustments to keep the sensorimotor system precisely calibrated. The benefit of continuous feedback may be pronounced in feedback control, enabling online adjustments to ensure that the movement goal is achieved.^{25,26}

The importance of feedback timing has been highlighted in prior studies of sensorimotor adaptation.²⁷ That body of work has emphasized how delaying endpoint feedback can dramatically attenuate adaptation.^{8,9,11,13,28} Implicit in this work is the assumption that the optimal time for endpoint feedback is when the hand reaches the target, that is, when the feedback is temporally and spatially synchronized with the hand.^{13,29} Because these studies used position-contingent feedback, it was only possible to delay the feedback. Taking advantage of the fact that position-independent, clamped feedback is effective in eliciting adaptation, we were able to temporally advance endpoint feedback. The enhancement of learning observed with this method indicates that the advantage of continuous feedback does not rest on its spatiotemporal continuity and that it is not essential that the position of the feedback be synchronized with the position of the hand.

Having demonstrated the advantage of early endpoint feedback, we set out to determine the optimal time for the feedback. The clamp method allowed us to parametrically manipulate the onset time of endpoint feedback. Here, we transitioned from a web-based platform to the lab to minimize measurement delays and test a wider range of values ranging from well before the movement onset to beyond movement ends. Moreover, by using two distinct movement durations (by manipulating movement amplitude), we could examine if optimal timing was linked to movement onset or when the hand reached the target. We observed non-monotonic functions for both amplitudes. The attenuation for the longest feedback onset latencies provides another demonstration of the cost of delayed feedback. Moreover, the attenuation for the shortest latencies indicates that there is a cost for presenting the feedback too early, including the time of movement initiation.

The peak of the function (i.e., the optimal timing for feedback) was observed at a midway point, one in which the position of the feedback was advanced with respect to the position of the hand. One hypothesis to account for this effect is based on models of multisensory integration. In this framework, the perceived hand position, the signal essential for computing the error, is an integrated representation based on a variety of inputs, including vision and proprioception.³⁰ Temporally, one would expect that the contribution of the visual signal will be strongest when it is synchronized with the proprioceptive signal. In terms of neural responses in the brain, visual inputs are delayed by approximately 50 ms relative to proprioceptive inputs.^{22,31,32} Advancing endpoint visual feedback by this interval could enhance visual-proprioceptive synchronization and thus boost learning. Importantly, this hypothesis predicts that the optimal timing of feedback should be constant with respect to when the hand

reached the target. However, this prediction was not supported by the results. More generally, the brain has likely evolved mechanisms to compensate for inherent differences in transmission delays across sensory modalities, negating the need for temporal synchronization in deriving a multisensory signal.³³

Whereas the multisensory integration hypothesis focuses on the observed feedback, an alternative hypothesis focuses on how this information is compared with the predicted sensory outcome. The latter is assumed to be generated from an efference copy of the motor command. We hypothesize that the feedback timing function reflects the strength of the representation of the sensory prediction. When considered as a discrete event, the 170-ms delay may reflect the interval between the efference copy and time in which the prediction is available; when considered as a continuous neural process, the representation of the prediction may reach its maximal strength ~170 ms after movement initiation. By either view, we assume this representation will decay after its peak. When feedback is temporally advanced, adaptation is therefore strengthened since the feedback arrives prior to the decay of the sensory prediction. This hypothesis is consistent with the observation that the optimal time was time-locked to movement onset, independent of movement duration.

Recently, Kim et al. used the clamp method to ask if sensorimotor adaptation can occur when an error is experienced in the absence of a movement.³⁴ Using a Go-NoGo task, they presented a clamp not only on trials in which the movement was executed but also on trials in which a planned movement was aborted in response to a stop signal. Surprisingly, adaptation was observed in both conditions. Presumably, a motor command was generated on the no-go trials, resulting in a sensory prediction that could be compared with the clamped feedback. Interestingly, the magnitude of the effect was smaller following no-go trials compared with go trials. This attenuation could be due to the fact that, on some percentage of the no-go trials, participants were able to abort the movement plan in advance of a motor command. Or it could be that the feedback timing was less optimal on no-go trials since it was more temporally variable with respect to motor command.

Temporal constraints are a prominent feature of cerebellar-dependent learning, including sensorimotor adaptation and eyeblink conditioning.³³ In the latter, the animal learns to make a blink in response to an arbitrary stimulus (conditioned stimulus, CS) that is predictive of an aversive event (unconditioned stimulus, US). This form of learning is highly sensitive to the interval between the CS and the US,³⁵ showing a non-monotonic function similar to that observed in this study. Learning is negligible when the US occurs before or together with the onset of the CS, peaks when the CS leads the US by between 200–400 ms, and decreases for longer intervals.^{36–39} The rise of this function has been assumed to reflect the time required to generate an expectancy of the US and adaptive motor response that will attenuate the aversive effects of the US. The reduced efficacy of learning for longer CS-US intervals is assumed to reflect temporal limitations within the cerebellum for maintaining the sensory prediction. This account of the optimal timing for eyeblink conditioning is similar to our account of optimal timing for visuomotor adaptation. In the latter, the motor commands and visual feedback serve as equivalents for the CS and US, respectively. Consistent with this notion, we have recently shown that when

temporal constraints are imposed, two signature phenomena of classical conditioning, differential conditioning and compound conditioning, are observed in visuomotor adaptation.⁴⁰

It remains to be seen how the current results concerning the timing of the feedback apply to other contexts in which feedback is used to improve motor performance. We have shown how advanced feedback can enhance feedforward control, where the outcome of a movement is used to keep the sensorimotor system precisely calibrated. Whether similar effects would be observed when using the feedback to correct an ongoing movement (e.g., feedback control) remains to be seen. We note that feedback control and feedforward learning can interact with each other.⁴¹ For example, online corrections based on continuous feedback can reduce the target error. This feedback control can attenuate feedforward learning since the error is reduced.¹⁵ Thus, it can be advantageous to design experiments that focus on one or the other process.

By using clamped feedback in this study, we were able to home in on the effect of feedback timing on implicit feedforward adaptation. Future work should examine how feedback timing influences feedback control. A priori, it would seem advantageous to anticipate a forthcoming error in order to adjust the ongoing movement; indeed, models of reaching have postulated such anticipatory mechanisms to account for the presence of corrective sub-movements.⁴² On the other hand, anticipatory corrections might introduce instabilities to an ongoing movement.¹

In a related vein, it is important to consider how these findings may generalize beyond sensorimotor adaptation to motor skill learning. Our experimental manipulations were limited to simple reaching movements, performed at relatively fast speeds. Future studies should examine the effect of feedback timing on more complex movements that span a wider range of durations and contexts. One challenge for such work is that, with more complex tasks, performance is likely to encompass a variety of additional processes (e.g., complex planning that unfolds over time, online correction) that can be difficult to differentiate from each other.

A core principle featured in discussions of sensorimotor adaptation is that endpoint feedback elicits less adaptation than continuous feedback.^{43,44} The present results indicate that a major reason for the disadvantage of endpoint feedback is that it becomes available later than continuous feedback; when endpoint feedback is temporally advanced, implicit adaptation was enhanced, reaching a level comparable to that observed with continuous feedback. By systematically varying the onset time of endpoint feedback, we found that the optimal feedback time was time-locked to movement onset rather than the actual hand position. We hypothesize that adaptation is maximized when the sensory prediction is at maximal strength for comparison with the sensory feedback in generating an error signal. These results underscore novel temporal constraints underlying cerebellar-dependent sensorimotor adaptation.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY

- Lead contact
- Materials availability
- Data and code availability
- EXPERIMENT MODEL AND SUBJECT DETAILS
 - Participants
- METHOD DETAILS
 - Apparatus
 - Procedure
 - Measuring delays associated with the web-based and lab-based experimental setups
- QUANTIFICATION AND STATISTICAL ANALYSIS

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2024.01.073>.

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AUTHOR CONTRIBUTIONS

T.W., G.A., J.S.T., and R.B.I. contributed to the conceptual development of this project. T.W. and T.T. collected the data. T.W. analyzed the data, prepared the figures, and wrote the initial draft of the paper, with all the authors involved in the editing process.

DECLARATION OF INTERESTS

R.B.I. is a co-founder with equity in Magnetic Tides, Inc.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and Algorithms		
MATLAB 2020b	MathWorks	https://www.mathworks.com/
Psychophysics Toolbox	Kleiner et al. ⁴⁵	http://psychtoolbox.org/
Deposited data		
Raw data and code for analysis	This paper	https://osf.io/ej4ba/

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Tianhe Wang (tianhewang@berkeley.edu)

Materials availability

This study did not generate any unique reagents.

Data and code availability

- All data have been deposited at <https://osf.io/ej4ba/> and are publicly available as of the date of publication. DOIs are listed in the key resources table.
- All original code has been deposited at <https://osf.io/ej4ba/> and is publicly available as of the date of publication. DOIs are listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

EXPERIMENT MODEL AND SUBJECT DETAILS

Participants

Testing was conducted on-line for Experiments 1a, 2, 3 and in the lab for Experiment 1b, 4. For on-line studies, a total of 476 participants (203 female, mean age = 24.5, SD = 4.7, see [Table 1](#) for details) were recruited through the website [prolific.co](https://www.prolific.co). They were paid \$8/h. For the lab-based experiment, we recruited 101 undergraduate students (60 female, mean age = 21.1, SD = 3.5) from the University of California, Berkeley community. All of the participants were right-handed based on their scores on the Edinburgh handedness test⁴⁶ and had normal or corrected-to-normal vision. These participants were paid \$15/h. All experimental protocols were approved by the Institutional Review Board at the University of California Berkeley. Informed consent was obtained from all participants.

Power analysis

We are interested in identifying the factors that result in the advantage of continuous feedback over endpoint feedback. For the block design experiments (Experiment 1-3), we computed minimum sample sizes based on the no-feedback washout block from Taylor et al.⁷ in a study that used continuous and endpoint feedback. We estimated the power for an independent samples t-test using a two-tailed test with significance set at 0.05 and a power of 0.9. The effect size was $d=0.91$ (continuous feedback group: mean = 25.9°, SD = 4.9°; endpoint feedback group: mean = 21.6°, SD = 4.1°), indicating a minimum sample size of 24 participants for each condition. For the lab-based experiment (1b), we recruited 25 participants for each feedback condition. For web-based experiments, we decided to recruit 10 additional participants given that we expected some participants would perform poorly based on our previous experience (e.g., fail to pay attention, see details below), resulting in a target of 34 participants for each condition in Experiments 2 and 3. This resulted in a final sample size larger than 24 for all conditions ([Table 1](#)). For Experiment 1a, the sample size was 68. (We had initially run a replication, but combined the two when we added Experiment 1b as an in-lab replication.) In Experiment 4 where we examined trial-by-trial change of hand angle, we used a sample size (13 for each condition) that is typical in sensorimotor adaptation experiments.

METHOD DETAILS

Apparatus

Web-based experiments

On-line experiments were performed using our web-based experimental platform, OnPoint.¹⁹ The code was written in JavaScript and presented via Google Chrome, designed to run on any laptop computer. Visual stimuli were presented on the laptop monitor and

movements were produced on the trackpad. Data were collected and stored using Google Firebase. The experimental session lasted ~40 min.

Lab-based experiment

Participants performed a center-out reaching task on a digitizing tablet (Wacom Co., Kazo, Japan) which recorded the motion of a digitizing pen held in the hand. Stimuli were displayed on a 120 Hz, 17-inches monitor (Planar Systems, Hillsboro, OR) that was mounted horizontally above the tablet, obscuring vision of the arm. The experiment was controlled by a Dell OptiPlex 7040 computer (Dell, Round Rock, TX) running on a Windows 7 operating system (Microsoft Co., Redmond, WA) with custom software coded in MATLAB (The MathWorks, Natick, MA) using Psychtoolbox extensions.⁴⁵

Procedure

Experiment 1a

Clamp rotation task. To start each trial, the participant moved the cursor to a white start circle (radius: 1% of the screen height) positioned in the center of the screen. After 500 ms, a blue target circle (radius: 1% of the screen height) appeared with the radial distance set to 40% of the screen size. There were four possible target locations ($\pm 45^\circ$, $\pm 135^\circ$). The participant was instructed to produce a rapid, out-and-back movement, attempting to intersect the target. The target disappeared when the amplitude of the cursor movement reached the target distance. To help guide the participant back to the start location, a white cursor (radius: 0.6% of screen height) appeared when the hand was within 40% of the target distance. If the movement time was >500 ms, the message 'Too Slow' was presented on the screen for 500ms.

We used a visual clamp to elicit implicit sensorimotor adaptation, manipulating feedback onset time, presentation duration, and spatial continuity. Three types of clamp feedback were employed in Experiment 1 (between-subjects, also see [Figure 1C](#)). The timing of each feedback will be summarized here. Please see the section below for how those presentation delays were measured in the web-based system. (1) Continuous feedback: The radial location of the cursor was based on the radial extent of the participant's hand and was visible during the whole movement (up to reaching the target distance) but was independent of the angular position of the hand. In the web-based system, the cursor becomes visible ~145 ms after movement initiation. At that point in time, the hand has moved ~1/3 of the distance to the target. (2) Standard endpoint feedback: The cursor was presented as soon as the amplitude of the hand movement reached the target distance, subject to a presentation delay of ~25 ms. The duration of the feedback was limited to one refresh cycle (16.7ms for standard 60 Hz monitor; range of 10–20 ms depending on the refresh rate of the participants' monitor). In this manner, the timing and position of the cursor was the same in this condition as the last frame for the Continuous Feedback condition. (3) Early endpoint feedback: The experimental code was written so that the cursor would appear at the target distance as soon as the hand was detected to exit the start circle. Given the delays associated with detecting movement onset in the on-line system, as well as the delay associated with presenting the feedback, the cursor appeared ~145 ms after movement onset.

There was a total of 520 trials in Experiment 1, arranged in four blocks. 1) A no-feedback baseline block (40 trials). 2) A feedback baseline block with veridical continuous feedback (40 trials). 3) A learning block with clamped feedback (400 trials), where the cursor followed a trajectory that was displaced at a fixed angle from the target. Right before the learning block, a set of instructions was presented to describe the clamped feedback. The angle was set to 15° and the direction of the clamp was either clockwise (CW) or counterclockwise (CCW) with respect to the target, counterbalanced across participants. The participant was informed that the cursor would no longer be linked to their movement, but rather would follow a fixed path on all trials. The participant was instructed to always reach directly to the target, ignoring the cursor. To make sure the participant understood the nature of the error clamp, the instructions were repeated. Moreover, after the first 40 trials with clamped feedback, an instruction screen appeared asking the participant to indicate if they were aiming for the target or another location. If the participant indicated they were reaching to another location, the experiment was terminated. 4) A no-feedback washout block (40 trials). Within each block, trials were grouped into cycles of four trials, with each target (45° , 135° , 225° , 315°) appearing once per cycle (order randomized across cycles).

Experiment 1b

Experiment 1b was designed to provide a lab-based replication of Experiment 1a, under conditions in which the timing of the stimulus events was precisely controlled and the same for all participants. The procedure was the same as Experiment 1a with the following exceptions. The start position (radius: 4 mm) was at the center of the screen and the blue target (radius: 8 mm) appeared at a radial distance of 12 cm. As such, the participants used an arm movement to move a pen across a digitizing tablet. The cursor feedback was provided as a white dot (radius: 3 mm).

We again tested three groups of participants ($n=25$ /group). Continuous feedback was provided as soon as movement onset was detected and remained visible, locked to the radial position of the hand, until the hand reached the target distance. For standard endpoint feedback, the cursor appeared at the target distance for ~17 ms (two refresh cycles on the 120 Hz monitor used in the lab) when the hand reached the target distance. For early endpoint feedback ($n=25$), we matched the onset time to the average observed in Experiment 1a; thus, the program was written to present the cursor 120 ms after movement onset and, with the presentation delay, effectively appeared ~145 ms after movement onset.

Experiment 2

Visuomotor rotation task (VMR). To confirm that the results obtained in Experiments 1 were not idiosyncratic to clamped feedback, we used a standard visuomotor rotation task in Experiment 2. Here the position of the feedback cursor during the adaptation block was contingent on the participant's hand position. To encourage strategy use, we opted to use a large 45° rotation (CW and CCW

counterbalanced across participants), limited the target position to two locations ($135^{\circ}/315^{\circ}$), and instructed participants to ‘make the cursor hit the target’⁴⁷

For both endpoint and early endpoint feedback, the position of the feedback was rotated 45° from the reach angle obtained at the second data point collected after movement initiation. Early endpoint feedback was presented right after this data point was sampled, while endpoint feedback was presented when the radial position of the hand reached the target distance.

There were four blocks: No-feedback baseline (20 trials), feedback baseline (40 trials), adaptation with contingent rotated feedback (200 trials), and no-feedback washout (20 trials). Within each block, the trials were grouped into cycles of four trials, with each of the two target positions presented twice per cycle. Prior to the start of the adaptation block, the instructions described the size and direction of the rotation and emphasized that the participant should adjust their aim to compensate for the perturbation and make the cursor hit the target. Prior to the washout block, the participant was instructed to cease using any aiming strategy and to again reach directly to the target.

Experiment 3

Experiment 3 was designed to examine the effect of dynamics and feedback duration. In Experiment 3a, we created two conditions such that the duration of the static feedback approximated that observed with continuous feedback. In the Extended Endpoint condition, the cursor appeared after the hand reached the target distance and remained visible for an interval equal to the movement duration for that trial. In the extended early endpoint condition, the cursor appeared ~ 145 ms after movement onset and remained visible until the hand reached the target distance. This resulted in a presentation time of ~ 90 ms. In Experiment 3b we examined the effect of advancing continuous feedback. The cursor appeared at the endpoint position as soon as movement initiation was detected and then continued along that direction until the hand reached the target distance. Thus, the position of the cursor was advanced relative to the position of the hand.

The procedure of the Experiment 3 was the same as in Experiment 1 and we compared the Extended Endpoint, Extended early endpoint, and advancing continuous conditions with the standard endpoint, early endpoint, and continuous conditions in Experiment 1a, respectively. Experiment 3c was essentially the same as the Experiment 3b but here the clamp size was reduced to 2° .

Experiment 4

Experiment 4 was designed to derive a function describing how feedback timing modulates the strength of adaptation. To ensure the precise timing of the trial events, we conducted this experiment in person. The start position (radius: 4 mm) was located in the lower quarter of the screen at the midline. Since adaptation was now measured on a trial-by-trial basis (see below), we used a single target location (radius: 7 mm, fixed at 45°). The radius from the start position to the target location was set to 7 cm for half of the participants ($n=13$) and 15 cm for the other half of the participants ($n=13$). This manipulation was included to produce different movement times for the two groups of participants. During the inbound portion of the movement, a white circle was visible at the start position with the radius of the circle indicating the participants’ distance from the start position. In this way, participants were guided to the start position without directional feedback of their movement.

The experiment began with a block of 16 trials in which a cursor (radius: 3 mm) provided continuous feedback. This was followed by an extended block of 1200 trials with clamped endpoint feedback. The clamp was offset from the target by 15° , with CW and CCW deviations intermixed within a cycle of 4 trials. By mixing CW and CCW clamps, there is no cumulative effect of adaptation; rather, the dependent variable of adaptation was the trial-by-trial change in reaching angle.²⁴ Prior to the onset of the clamped feedback block, participants were fully informed of the clamp manipulation and instructed to always move directly towards the target. The onset time of the clamped feedback was randomly sampled from a uniform distribution ranging from -200 to 300 ms relative to a running average of the individual’s movement onset time, calculated over the last 20 trials. We did not impose any constraint on movement onset time but allowed that to vary naturally (averaged across all trials: mean = 206 ms, SD= 156 ms). The clamp was presented as endpoint feedback for ~ 17 ms.

Measuring delays associated with the web-based and lab-based experimental setups

Web-based system

To determine delays in our web-based system, we performed a video analysis to measure the delays associated with movement onset, movement offset, and feedback presentation. We recorded the hand movement and the monitor simultaneously using the slow-motion mode (240 fps) of an iPhone 11 Pro, having one lab member perform the web-based experiment in the lab. A ruler with 1 mm markings was placed on the trackpad as a visual reference. To determine the relationship between movement distance on the trackpad and the target distance on the monitor, an experimenter moved their hand very slowly until the endpoint feedback appears.

For estimating the delays, trial videos were analyzed with the Adobe Aftereffect software package. The videos were reviewed on a frame-by-frame basis and the time of key events (i.e., frame number) on each trial was manually marked. Movement onset was defined as the first frame in which the hand was displaced by 1 mm on the trackpad. Movement offset was defined as the first frame in which the hand reached the target distance. Feedback onset was defined as the first frame in which the cursor was visible. This analysis was performed on 100 trials for each condition. The analysis was performed by two individuals, with one individually marking the data from one device and the other marking the data from that same device as well as three other devices. The results for the two judges converged on the common device (e.g., means of 144 and 145 ms respectively for onset of early feedback relative to movement onset).

The summary of the delay analysis is presented in [Figure S1](#). We present the results for measurements from one device since the data are quite similar for the other devices. Early endpoint feedback showed a more prominent delay compared to the endpoint feedback ([Figure S1C](#)). The hardware and software for trackpads are designed to differentiate between intentional movement and incidental contact (e.g., the palm resting on the trackpad). As such, these systems are designed to only detect sustained movement (even if brief) and not respond to slight and/or very brief movements. This requirement introduces an inherent delay for detecting movement onset. However, this detection delay is not relevant once the system has recognized an ongoing movement: There is no similar built-in delay for defining movement offset (or with shooting movements, when the hand reached the target distance). For these reasons, dealing with the delay associated with movement onset in the on-line experiments (i.e., early endpoint feedback) is different from that required to determine the delay associated with presenting cursor feedback or estimating movement offset (i.e., standard endpoint feedback).

We note that the measured movement time does not include the period before movement onset is registered by the system. Therefore, we measured this trackpad detection delay by subtracting the delay associated to the early endpoint feedback to the delay of the standard endpoint feedback. We corrected the movement duration by adding this estimated trackpad detection delay (120 ms) to the raw movement durations measured by the web-based system. This trackpad detection delay is only relevant to the web-based system and does not apply to the lab-based system.

Lab-based system

To determine delays in our lab-based system, we focused on two key temporal events: (1) The timestamp recorded by the tablet with each sample of positional data. This timestamp is not affected by the data transfer time from the tablet to the computer or by the sampling rate of the main control loop. (2) The timestamp from Psychtoolbox⁴⁵ that logs the time when the visual stimuli are presented. This timestamp corresponds to the actual appearance of the stimuli on the screen, not the moment they are queued in the buffer. Hence, this timestamp accounts for any transfer delays and the refresh rate. We calculated the duration between these events by subtracting the first timestamp from the second. This method does not account for delay that would be introduced by the sampling rate of the tablet (100 Hz). We opted to account for this by adding 5 ms (the mean of the 10 ms interval between samples) to all delay estimates.

For the Early Endpoint feedback condition in Exp 1b, we wrote the code to present the feedback 120 ms after the participant's hand left the start circle. However, we used two criteria to define movement onset for the analysis. 1) Position based—when the hand left the start circle or 2) movement based—when the hand had moved 1.5 mm from the hold position. The latter comes into play if the hand has moved 1.5 mm but still is within the start circle; otherwise, movement onset is defined by the position criterion. We opted to use only the position criterion to determine the feedback time because it reduces the risk of interpreting slight movements/tremor as intentional movement. We applied the dual criterion in the analysis to provide a more accurate estimate of movement onset. As a result of the different criteria, the timing of the Early Endpoint feedback can be delayed in relation to the recorded movement onset (i.e., the distance criterion) due to the fact that feedback presentation was based on the position criterion. This is the source of the long tail in [Figure S1D](#), left panel. The average onset of feedback was 145.6 ms, or 25 ms longer than as intended.

For the early endpoint feedback condition in Exp 1b, we wrote the code to present the feedback 120 ms after the participant's hand left the start circle. However, movement onset was not defined by this position criterion in the analysis. Instead, we defined movement onset by identifying when the hand had moved 1.5 mm from the hold position. We opted to use a position criterion for movement onset to determine the feedback time because it reduces the risk of interpreting slight movements/tremor as intentional movement; We applied the movement distance criterion in the analysis to provide a more accurate estimate of movement onset. As a result of the different criteria, the timing of the early endpoint feedback can be delayed in relation to the recorded movement onset (i.e., the distance criterion) due to the fact that feedback presentation was based on the position criterion. This is the source of the long tail in [Figure S1D](#), left panel. The average onset of feedback was 145.6 ms, or 25 ms longer than as intended.

For standard Endpoint feedback, we employed a 120 Hz monitor (n=16) and a 60 Hz monitor (n=9), resulting in average delays of 18.7 ms and 31.2 ms, respectively. These values are comparable to the delays reported in other studies (A. Hadjiosif et al., 2023, *Advances in Motor Learning & Motor Control*, abstract).

QUANTIFICATION AND STATISTICAL ANALYSIS

The initial data analyses were conducted in MATLAB 2020b. Reach angle was calculated as the angular difference between the target and the hand position at the target radius. Positive values indicate reach angles in the opposite direction of the perturbation experienced by that participant, the direction one would expect due to adaptation. Movement initiation is defined as the first sample where the hand surpassed the radius of the start position. The time when the hand reached the target distance was defined as the first data point recorded with a movement distance larger than the target distance.

To minimize online corrections, we instructed the participant to move quickly. We excluded trials with a movement time longer than 600 ms for web-based experiments and 1000 ms for lab-based experiments. We also excluded trials in which the reaching angle at the end of the movement was more than 70° from the target under the assumption that the participant moved to the wrong target on these trials.

A limitation with web-based experiments is that a percentage of the participants appear to pay little attention to the instructions. We adopted a criterion to eliminate the entire data set for any participant who had more than 30% total excluded trials. Of the 476 on-line participants, 71 (15%) were eliminated based on this criterion, a percentage that is similar to that reported in reviews of on-line

experiments.¹⁹ These subjects either failed to meet the movement speed criterion on a large percentage of trials or repeatedly moved to the same location, independent of the target location. No participant was removed in lab-based experiments.

For Experiments 1 and 3, the data were averaged over cycles (4 trials/cycle). We examined learning at two time points, during the late phase of the adaptation block and during the aftereffect block. Late adaptation was defined as the mean reach angle over the last 10 cycles of the perturbation block, minus the mean of the no-feedback baseline block (to adjust for individual biases in reach direction). Aftereffect was defined as the mean reach angle over the washout block, minus the mean of the no-feedback baseline block. As a continuous measure of adaptation, we used a cluster-based permutation test,^{48,49} a method traditionally used to analyze the data with temporal dependencies such as EEG,⁵⁰ and has recently been applied to learning functions.⁵¹ In Experiment 2, late learning is contaminated by the contribution of aiming strategies. As such, we focused solely on the aftereffect data, comparing the average reach angle in the first cycle of this block with the average reach angle during the no-feedback baseline block.

In Experiment 4, adaptation was defined as the difference in reach angle between trial $n+1$ and trial n . To construct functions describing how adaptation changed as a function of feedback timing we computed, for each trial, the actual interval between feedback onset time and either movement onset or the time at which the hand reached the target distance. For example, for the movement onset function, negative and positive values indicate that the feedback preceded or followed movement onset, respectively.

To quantify the peak in the four adaptation functions (two distances, with one function for movement onset and one based on when the hand reached the target distance), we combined the data across trials and participants and fit the data with a skewed-Gaussian function:

$$y = 2 * \frac{e^{-\frac{x^2}{2}}}{\sqrt{2 * \pi}} * CDF_{Gaussian}(\alpha x) * b - c, \quad (\text{Equation 1})$$

$$x = \frac{t - d}{e}, \quad (\text{Equation 2})$$

where y is mean Δ reach angle, t is the feedback onset time subtracted by either movement onset or when the hand reached the target, and $cdf_{Gaussian}$ is the cumulative distribution of the standard Gaussian distribution. There are five free parameters: a , b , c , d , and e , corresponding to the width, height, lower boundary, shift of the mean from zero, and skewedness of the function. To estimate the variability of each parameter, we used a bootstrap procedure, pooling the data of 13 random samples taken from the 13 participants (with replacement) and repeating this procedure 200 times.

To determine the movement trajectory, the radial axis was evenly divided into 150 segments from the initial hand position to the target. We used interpolation to obtain the reach angle for each cut-point. To analyze the curvature of the movements, we calculated initial and final reach angle. The former was calculated by averaging the angular value of the first 30 cut-points; the latter was set to the angular value at the 150th cut-point (target distance).

Between-condition comparisons were performed with t-tests or ANOVAs, with false discovery rate (FDR) corrections for multiple comparisons applied when appropriate. For the t tests, we report the Bayes factor, reflective of the ratio of the likelihood of the alternative hypothesis (H1) over the null hypothesis (H0), and Cohen's d , a measure of effect size. For ANOVAs, the effect size is reported using partial η_p^2 . In all tests, we confirmed that the data met the assumptions of a Gaussian distribution and homoscedasticity.