

Reduced feedback barely slows down proprioceptive recalibration

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Abstract

Introducing altered visual feedback of the hand produces quick adaptation of reaching movements. Our lab has shown that the associated shifts in estimates of the felt position of the hand saturate within a few training trials. The current study investigates whether the rapid changes in felt hand position that occur during classic visuomotor adaptation are diminished or slowed when training feedback is reduced. We reduced feedback by either providing visual feedback only at the end of the reach (terminal feedback) or constraining hand movements to reduce motor adaptation related error signals such as sensory prediction errors and task errors (exposure). We measured changes as participants completed reaches with a 30° rotation, a -30° rotation and clamped visual feedback, with these two “impoverished” training conditions, along with classic visuomotor adaptation training, while continuously estimating their felt hand position. Training with terminal feedback slightly reduced the initial rate of change in overall adaptation. However, the rate of change in hand localization, as well as the asymptote of hand localization shifts in both the terminal feedback group and the exposure training group were not noticeably different from those in the classic training group. Taken together, shifts in felt hand position are rapid and robust responses to sensory mismatches and are at best slightly modulated when feedback is reduced. This suggests that given the speed and invariance to the quality of feedback of proprioceptive recalibration, it could immediately contribute to all kinds of reach adaptation.

Introduction

Visuomotor adaptation leads not only to changes in motor behaviour but also changes in felt hand position (1–4). Our lab has recently demonstrated that shifts in estimates of felt hand position during visuomotor adaptation develop surprisingly quickly (4). However, it is unknown whether this quick and robust rate of change can be slowed down, like in the case where the feedback during adaptation is impoverished. To test this, we use two training paradigms with reduced feedback that still lead to visuomotor adaptation: terminal feedback and cross-sensory exposure. We characterize both the rate of adaptation and shift in hand localization in these two paradigms and compare it with that produced during classical visuomotor adaptation.

In terminal feedback training the cursor representing the unseen hand is provided only at the end of the reach movement. Reducing visual feedback to the end of the reach during visuomotor rotation training has been shown in some studies to reduce the extent of learning and the magnitude of reach aftereffects (3, 5–7) although this is not always the case (8–10). Whether terminal feedback also affects the rate of adaptation is usually not quantified. Compared to classic continuous cursor feedback, training with terminal feedback has been shown to also reduce or slow down the changes in estimates of hand location (3, 11) but the rate of change has not been determined yet. Here we model learning on a trial-by-trial basis to be able to directly compare learning rates between terminal and continuous visual feedback.

Cross-sensory exposure training involves either passively moving the unseen hand or using a force-channel that deviates its direction, while the cursor moves directly to a target. Despite minimizing the motor or efferent signals involved, this passive exposure to a discrepancy between seen and felt hand location leads to similar or smaller reach aftereffects (2, 12–14) and can facilitate subsequent adaptation to the same perturbation in a classic visuomotor paradigm (15–17). Not surprisingly, such training also leads to changes in hand localization, which are similar in size to those elicited when the reaches are self-generated during classical visuomotor adaptation. This suggests that this proprioceptive recalibration is primarily driven by the visual-proprioceptive mismatch between the hand and the cursor. We have previously measured hand localization shifts on a trial-by-trial basis, allowing us to assess the rate of change for these shifts. Given that these shifts in hand localization saturate within a single trial during classical visuomotor adaptation, our aim was to determine if a similar saturation rate occurs when the motor system is less engaged.

It is reasonable to assume that reducing and removing availability of certain types of feedback, like in terminal feedback or exposure training, should affect the time-course and/or asymptotic level of adaptation. Central to this paper, it is unknown whether reducing this feedback can also slow down the rapid saturation of shifts in hand localization. It is possible that shifts in felt hand position develop so rapidly that they are unaffected by error information that generally takes time to fully saturate such as task

error. Our goal is to quantify and model the rate by which these changes in felt hand position saturate on a trial-by-trial basis and how they compare across exposure, continuous or terminal feedback training. By measuring shifts in felt hand position after every training trial with these three feedback types, we can identify the role feedback has during ongoing proprioceptive recalibration.

Methods

Participants

96 (mean age=22.17, range=18-46, males=22) right-handed, healthy adults participated in this study, and gave prior, written, informed consent. All procedures were in accordance with institutional and international guidelines and were approved by the York Human Participants Review Subcommittee.

Apparatus

The experimental set-up is illustrated in Fig 1. While seated, participants held a vertical handle on a two-joint robot manipulandum (Interactive Motion Technologies Inc., Cambridge, MA, USA) with their right hand such that their thumb rested on top of the handle. A reflective screen was mounted horizontally, 14 cm above the robotic arm. A monitor (Samsung 510 N, 60 Hz) 28 cm above the robotic arm presented visual stimuli via the reflective screen to appear in the same horizontal plane as the robotic arm. A Keytec touchscreen 2 cm above the robotic arm recorded localizations of the unseen thumb of the trained right hand, made the left hand's index finger (see (18) for more details). Subject's view of their training (right) arm was blocked by the reflective surface and a black cloth, draped between the touch screen and their right shoulder. The untrained, left hand was illuminated, so that any errors in reaching to the unseen, right target hand could not be attributed to errors in localizing the left, reaching hand.

Stimuli

Illustrated in Fig 1B-D, at the beginning of each trial, we displayed one of four potential targets, (white 1 cm diameter circles), 12 cm from the start position at 60°, 80°, 100° and 120°. The home position (green 1 cm circle) and the participants' hand cursor (blue 1 cm circle) were also visible at the beginning of the trial (for 2 of the 3 paradigms). During proprioceptive localization trials Fig 1E a white arc, 12 cm from the home position, was visible on the screen spanning from 0° to 180°. Participants were required to hold their hand still at the home position for 250 ms before any trial would begin.

Trial Types

Classic continuous training trials

Participants (N=32) reached as accurately as possible with their right hand to one of four possible target locations, while their hand cursor was continuously visible (Fig

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1B). In all reaching trials, i.e., with cursor and with clamped cursor (explained below), participants had to reach out 12 cm from the home position to a force cushion within 800 ms. Participants received auditory feedback throughout training indicating if they met the distance-time criteria or not. The target would then disappear, and the robot manipulandum returned the right hand to the home position where they waited 250 ms for the next trial. The hand cursor was aligned with the hand for the first 64 training trials, then rotated 30° CW for 160 training trials and then rotated 30° CCW for 16 training trials. This was followed by 48 visual error-clamped trials, dashed lines in Fig 2, which were identical to the reach training trials except that the cursor always moved on a straight line to the target. The distance of the visual error-clamped cursor from the home position was identical to the distance of the hand from the home position.

Terminal training trials

Terminal training trials were identical to classic training trials, except that the participants' (N=32) hand cursor was not visible during the entire reach movement, from the home position to the target (Fig 1C). Once the participant moved their hand 12 cm from the home position, the robot locked their hand in place and the hand cursor became visible for 500 ms for the participant to be able to see any potential movement errors. The auditory cues were present to encourage consistent speed throughout the experiment. These participants also experienced a phase of visual error clamped trials

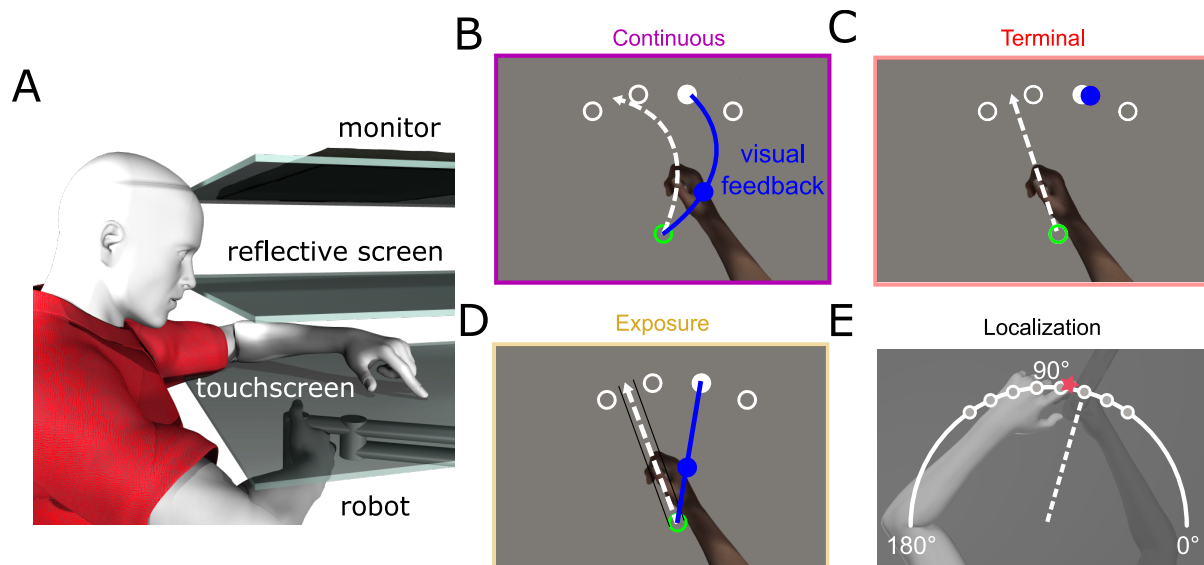


Figure 1. Experimental setup and design. **A:** Side view of the experimental set-up. The top layer is the monitor, middle layer is the reflective screen, and the bottom opaque layer is the touchscreen. The robot is depicted beneath with the participants' right hand grasping it. **B-D:** Top views of task specific set-ups. **B:** Continuous training trial. The home position is represented by a green circle with a 1 cm diameter; located approximately 20 cm in front of the subject. Targets are represented by white circles with a 1 cm diameter located 12 cm radially from the home position at 60°, 80°, 100° and 120°. Participants hand cursor was also a 1 cm diameter blue circle. **C:** Terminal training trial. The same hand cursor was only visible at the end of the movement for 500 ms to allow for comparison to the visible target. **D:** Exposure training trial. The robot constrained the participants movements (denoted by solid black lines either side of white dashed line), so they perfectly countered the rotation and only decided the speed of movement. **E:** Localization test trial. Participants were passively moved to one of the eight target locations, 55°, 65°, 75°, 85°, 95°, 105°, 115° and 125°. Subsequently, participants used a touch screen to indicate on a white arc spanning 180° where their unseen right hand was.

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which were identical to the classical clamp trials, with the cursor being visible the entire trial, not just at the end.

Exposure training trials

Exposure training trials differ from those in the previous two paradigms (Fig 1D). Participants ($N=32$) were not in control of the direction they moved during reach training trials. The handle at the end of the robot arm they were grasping was constrained to a force channel, so participants only chose the speed of movement, not direction, removing any performance error. If they attempted to move outside of the pathway, a resistant force, proportional to the depth of penetration with a stiffness of 2 N/mm and a viscous damping of 5 N/(mm/s), was created perpendicular to the pathway (19). During the visual error clamp phase of the experiment, participants were instructed to actively move their hands, so these trials were identical to the previous two paradigms. Participants still heard the auditory feedback to encourage consistent speed across training paradigms.

Localization test trials

All three groups completed a passive localization of their hand position after every training trial. These proprioceptive localization trials (Fig 1E) were executed to one of two targets, 5° on either side of the previous training target. The localization targets were close to the preceding training targets to maximize generalization, but not on the same location to be able to detect if participants simply touched the remembered visual target from the previous trial. All eight hand-targets (55° , 65° , 75° , 85° , 95° , 105° , 115° and 125° ; one on each side of each of the training targets) were cycled through before being repeated. After the white arc appeared on the screen, participants' right unseen, adapted hand was dragged to one of the target locations. Then once their

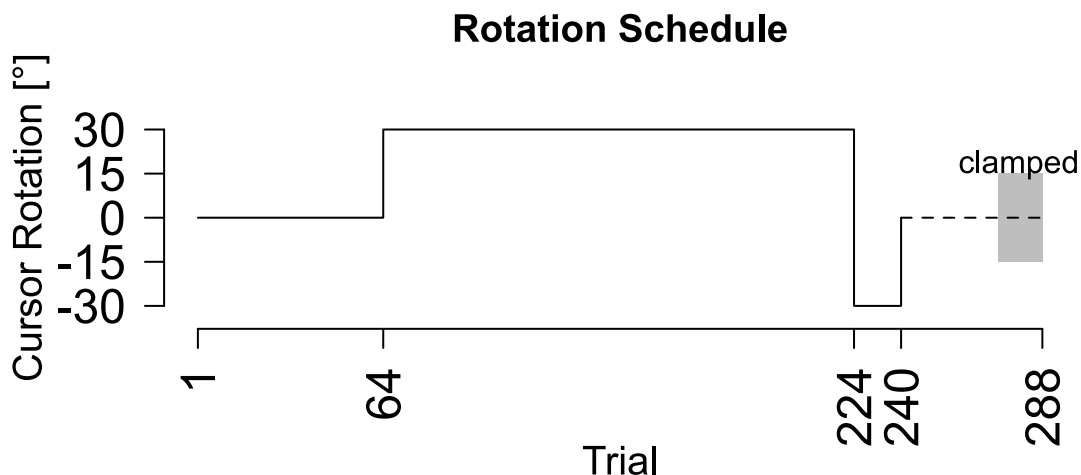


Figure 2. Experimental Schedule. Participants reached to visual targets with a perturbation denoted by the black line. The dotted line at the end of the paradigm signifies visually clamped trials where there was no visual error as the cursor always moved to the target regardless of the participants movement direction. The final 16 clamped trials were used in the rebound analysis trials: 273–288.

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target hand was locked in place, participants used their visible, left index finger, to indicate on the touchscreen, along a 180° arc, where they believed their right, stationary, unseen hand was. The arc was continuously visible until the touchscreen registered the participants estimate. We tested if localization responses were biased towards the preceding visual target in both the end of the aligned and the end of the rotated phase in all three conditions, but there was no bias in 5 of 6 tests. There is a 2.4° bias in the aligned phase of the terminal condition, which is much smaller than the 10° distance between the localization target pairs.

Data Analysis

We analyzed hand localization and reach training trials separately from each other, but their rates of change (see Table 1) can be compared.

Hand Localization

Estimates of hand location were based on the angular endpoint error between the movement endpoint of the right unseen hand and the left hands responses on the touchscreen, relative to the home position.

Reaching with a cursor and visual error-clamp trials

To quantify reach performance during training, the angular difference between a straight line from the home position to the target and a straight line from the home position and the point of maximum velocity is computed. This was calculated for all training trials both classic and terminal training but only for the error clamp trials for exposure training.

Analyses

All data was visually screened for incorrect trials by lab volunteers naïve to the purpose of the study. Subsequently, outliers of more than three standard deviations across participants within each trial were also deleted, in total, we removed 2.4% of the trials. All measures were normalized, by subtracting out each subjects' average performance during the second half of the aligned session (trials 33-64). The same preprocessing steps were applied to both localization and reach trials.

To quantify the time courses of changes in reaching and localization trials, we fit an exponential decay model to the first rotation (trial 65-224) separately for hand localizations and reach data. In this model, the value of each process on the next trial (P_{t1}) is the current process' value (P_{t0}) minus the product of the rate of change (L) multiplied by the error on the current trial, which is the difference between the asymptote (A) and the process' value on the current trial (P_{t0}).

$$P_{t1} = P_{t0} - L * (A - P_{t0})$$

The parameter L was constrained to the range $[0,1]$, and the parameter A to $[0, 2 \cdot \max(\text{data})]$. We allowed for negative asymptotes indicating individuals had proprioceptive recalibration in the unexpected direction to ensure that all participants had a meaningful learning rate (4 of 96 participants showed this pattern of recalibration). For all paradigms using only the first rotations data (trials 65-224), the model was fit to

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1) the localization data and 2) the reach data. For the localization data fit, a zero was prepended to account for the fact that responses in these trials already changed because of the previous training trial. The parameters were also bootstrapped (1k resamples per fit) across participants to get a 95% confidence interval for both parameters.

The decay model was used to fit a rate of change and asymptote for training and hand localization data for each of the feedback types. We then used the rate of change and bootstrapped 95% confidence interval of the mean for the asymptote to calculate the saturation trial for illustration purposes. The first trial where the mean response moved inside the confidence interval of the asymptote was considered the saturation trial (20). We used the bootstrapped 95%CI to compare across the three types of feedback on three parameters (rate of change, asymptote and saturation trial) describing the time courses. Parameter values which don't overlap with the CIs of those for the other groups indicate significant differences (20). This allows us to not only characterize the rate of change but detect even small differences, across feedback conditions that would normally be obscured when comparing the average of a block of trials. We used Bayesian statistics to compare learning rates and asymptotes across feedback types and to zero. In cases where we did not have a decay model parameter such as the rebound phase of training, we averaged the last 16 trials and did simple Bayes Factors to identify equivalence or significant differences. Bayes Factors are the ratio of how likely the alternative hypothesis (there is a difference) is over how likely the null hypothesis (there is equivalence) is, given a non-informative prior and the data. With $BF_{10} = 1$ both are equally likely. Within the interval $\frac{1}{3}$ to 3 (either hypothesis is up to 3 times more likely than the other) there is only anecdotal evidence (21, 22). However, a $BF_{10} > 3$ or $BF_{10} < \frac{1}{3}$ (or 0.333) is considered moderate evidence in favor of the alternative hypothesis or the null hypothesis, respectively, whereas values of $BF_{10} > 10$ or $BF_{10} < 0.1$ are considered strong evidence.

Similar to our previous study (4) we applied a simple proportional model that stipulates the size of shift in hand estimates will be a proportion of the size of the visual distortion. We also fit a one-rate model to the localization data and computed AIC's for both simple models, where the smaller AIC by at least two was considered the superior model.

The data sets for the current study are available on Open Science Framework, <https://osf.io/6q2zd/> while the code and analysis scripts are available on Github <https://github.com/JennR1990/VisualFeedback>.

Results

We used multiple approaches to investigate if reducing sensory prediction and performance errors during training slows the rapid changes in estimates of hand location or reduces rate of adaptation in motor learning. Specifically, we used an exponential decay model to compute rates of change and asymptotes (and their bootstrapped 95% confidence intervals), as reported in Table 1, for localization and reaches. Figure 3 shows all estimates of hand location across the three feedback groups (Fig 3A&B) as well as reach training trials for both the continuous and terminal

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groups and the visual error clamp trials for the exposure paradigm (Fig 3C&D). The saturation-timepoint occurs for the first trial where the signal as modelled by its rate of change is equal to or greater than the lower bound of the 95% CI for its asymptote. These saturation timepoints are also reported in Table 1 and depicted in figure 3E&F.

Bootstrapped Decay Model Parameters				
		Continuous	Terminal	Exposure
Localization	rate of change	100% [29.0% - 100%]	43.5% [7% - 100%]	69% [47% - 100%]
	asymptote	6.9° [5.9° - 8.0°]	6.3° [5.3° - 7.8°]	5.1° [3.8° - 6.4°]
	saturation trial	1 [1 - 7]	4 [1 - 23]	2 [1 - 3]
Reach training	rate of change	27.0% [20.1% - 32.8%]	14.2% [10.0% - 20.0%]	-
	asymptote	28.6° [27.8° - 29.5°]	27.1° [26.1° - 29.7°]	-
	saturation trial	12 [10 - 16]	19 [13 - 27]	-

Table 1. Adaptation estimates for localization trials and reach training trials. Rate of change estimates, asymptote and average trial participants reached asymptote are provided for each training condition and estimates of hand location, this was computed on the averaged participant data. Bootstrapped 95% confidence intervals are included for each estimate. Parameters were estimated using an exponential decay model.

Speed of Estimates of hand location

The main focus of this study is to compare the speed of proprioceptive recalibration across feedback types. Following every training trial (analysis below), we measured changes in hand estimates by having participants indicate the felt location of their unseen right hand after it was passively displaced. All three feedback groups produced robust shifts in felt hand position of $\sim 6^\circ$, (asymptotes in Table 1) that were significantly different from baseline ($BF_{10} > 1000$ for all three asymptotes), but fairly similar across all training conditions ($BF_{10}=0.26$). More importantly, the rates of change were very high resulting in the shift saturating within 1-4 rotated training trials regardless of training as shown in Table 1 (rate of change, saturation trials) and depicted by the colored arrows in Fig 3A. While the very rapid shift in hand localization in the continuous group appears to saturate even faster than those of the exposure and terminal feedback groups, their bootstrapped confidence intervals for the rate of change and saturation overlap suggesting no significant effect of feedback on the speed by which proprioception recalibrates. However, when we calculate saturation trial (Table 1) we can see these hand localization shifts take on average 4 trials for terminal, compared to only 1 for continuous and 2 for exposure. Bayesian statistics on learning rates show anecdotal support for a difference between continuous and terminal ($BF_{10}=1.9$) and support similarity between continuous and exposure ($BF_{10}=0.26$). Thus, the type of feedback had no or at best minimal effect on rate of change of proprioceptive

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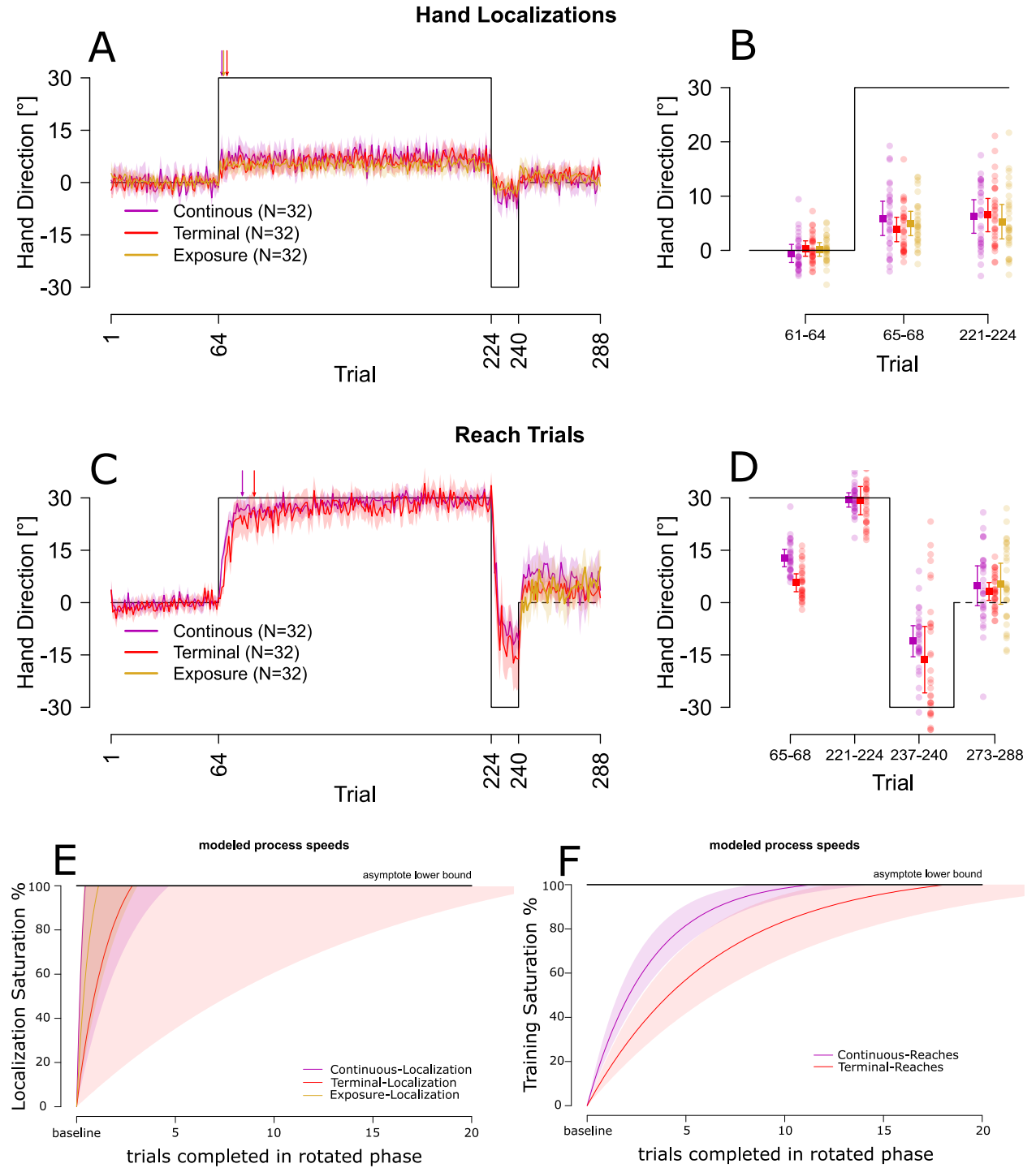


Figure 3. Localization and reach trials for all feedback types. **A.** Estimates of hand location throughout the course of training. The solid-colored lines are the deviations between actual and indicated hand position averaged across all participants within a paradigm, the corresponding shaded regions are 95% confidence intervals. Colored arrows indicate the trial participants reached asymptote on average, saturation trial. **B.** Close-up of estimates of hand location for different time points in the training schedule. Individual participant data are coded by color along side paradigm averages with error bars representing ± 2 SE. **C.** Endpoint error for all three paradigms across the entire training paradigm. Solid lines are the averages across participants within each paradigm, and the corresponding shaded regions are the 95% confidence intervals. Colored arrows indicate the average trial at which participants reached asymptote, saturation trial. **D.** Average reach direction during different time points of the training schedule. Individual data is shown around the mean for each paradigm. **E&F.** Saturation trial depicted as a curve. **E.** Localization. **F.** Reach saturation trials. The shades regions in both E & F represent the 95% confidence intervals.

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recalibration. In summary, proprioceptive recalibration emerged and saturated surprisingly quickly even in the reduced feedback-training groups.

Speed of visuomotor adaptation

As is customary, we wanted to ensure overall adaptation had occurred and whether adaptation differed across the different feedback groups. Participants in the exposure training group were not in control of movement direction during the first three phases of the experiment and thus were not included in this analysis. As reported in Table 1, rates of change in the initial learning phase are faster for continuous training [27%, 95%CI: 20.1% - 32.8%] than for the terminal training paradigm [14.2%, 95%CI 10.0% - 20.0%], which is evidenced by mean learning rate for continuous training being outside the confidence interval of the terminal training. Moreover, adaptation saturated at trial 12 for continuous (at 28.6°) and at trial 19 for terminal training (27.1°) as reported in Table 1 and indicated by arrows in Fig 3C and plotted in Fig 3F. This is reflected in the average degree of compensation in the early phase of training (Fig 3D&F) which shows that compensation for terminal feedback (5°) was lower than that for continuous feedback (12°). However, a closer inspection of these trial-by-trial reaches in Fig 3C shows that while continuous feedback reaches maximum compensation by the 12th trial (purple arrow), by that same trial for the terminal feedback shows that compensation is

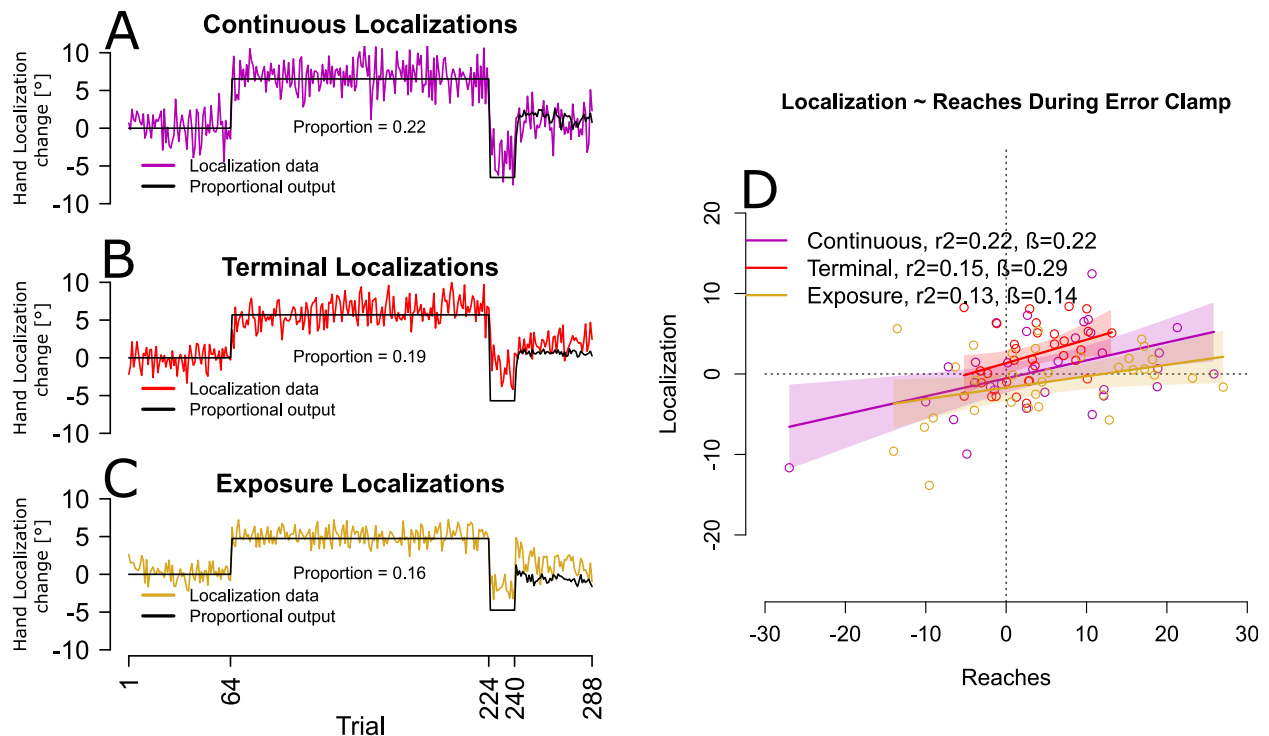


Figure 4. Visuo-proprioceptive discrepancy. **A-C.** A simple proportional model, that says the size of the shifts in hand estimates should be directly related to the size of the visual distortion, is applied to each set of localization data visible in figure 3. **D.** Comparison of reach deviations and shifts in hand location during error clamp. Each training paradigm has its own color, and each dot represents one participant. The regression line and the 95% confidence interval around the regression line is included in the corresponding color.

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merely a few degrees or 10% behind. This last 10% compensation is what requires the additional 7 training trials to reach a similar asymptotic level.

Despite the slower rate of adaptation in the terminal feedback group the asymptote was equivalent for terminal and continuous feedback ($BF_{10}=0.25$, shows moderate evidence for the null hypothesis) which can be seen in Fig 3C and in the overlapping CI for asymptote for reach training in Table 1. Together, these results indicate terminal feedback reduces learning rate, but extent of learning is comparable after ~20 trials.

To test if the participants with exposure feedback produced motor changes, we used the reach deviations in the visual error-clamp phase since this was the only time the exposure training group controlled the direction of their hand movements. Bayes Factors₁₀ of > 3 indicate moderate evidence for a rebound in these error-clamped trials relative to baseline for all three groups ($C= 4.8^\circ$, $T=3.2^\circ$, $E=5.4^\circ$, far right of Fig 3C&D). There was also moderate evidence that they are the same across feedback groups ($BF_{10}=0.14$). This result shows that there was adaptation in the exposure training group, and that at least during the error-clamp phase this was comparable to that in the other groups.

Our earlier work suggests that proprioceptive recalibration is driven by the visual-proprioceptive discrepancy (2, 12, 14), which for the visually-clamped trials, is equal to the size of the rebound which varies across individual participants. Hence, here we investigate the relationship between the size of the hand localization shift and the size of this rebound (Fig 4D). A simple linear regression showed a moderate positive relationship between reach deviation during error clamp trials and estimates of hand location for all three training paradigms. Regression values are: Continuous $R^2=.22$, $F(1,30)=8.51, p=.006$ Terminal $R^2=.15$, $F(1,30)=5.19, p=.03$ Exposure $R^2=.13$, $F(1,30)=4.59, p=.04$. The fitted slopes (β s in Fig 4D) all indicate that proprioceptive recalibration is around 20% of the rotation, as we found earlier (4). We also fit a simple model that suggests shifts in estimates of hand location are directly proportional to the visual distortion during regular cursor training (Fig 4A-C). We find the proportions suggested by the model are visually similar to the beta values given by the regression between reach deviations during the clamp phase and shifts in estimates of hand location. The proportional model also provides a better fit than just a simple one-rate model fit to the localization data based on all AIC's being smaller for the proportional model (Continuous= $17.68 < 25.52$; Terminal= $16.26 < 22.63$; Exposure= $12.15 < 22.73$).

Discussion

We have previously shown that changes in estimates of unseen hand location saturate after a single trial of classic visuomotor adaptation with a continuously visible cursor. Here we measure the extent that this surprisingly rapid saturation may be slowed down with reduced feedback during training. We reduced feedback with terminal feedback or with robot constrained movements in an exposure paradigm. By measuring

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estimates of unseen hand position after every training trial, we captured the time course of proprioceptive recalibration in finer detail. Training with terminal feedback or with passive exposure of a 30° rotation only slightly slowed the saturation of these shifts in proprioceptive estimate of hand position by a few trials, although not significantly. On average, the terminal group took 4 trials (1-23), the exposure group took 2 trials (1-3) compared to 1 trial (1-7) for continuous feedback, but an equally large shift in felt hand position. We found that even with reduced feedback, changes in felt hand position saturate very quickly during training, perhaps earlier than motor adaptation saturates.

A secondary finding is that motor adaptation was slowed down when feedback was reduced to only the endpoint position, requiring 19 (13-27) trials for participants to reach saturation for terminal adaptation compared to only 12 (10-16) trials for classical visuomotor adaptation. Nonetheless, final adaptation was equal for the terminal feedback and continuous feedback groups, and all visual feedback types, including exposure training, produced the same rebounds. In short, motor adaptation also saturated fairly quickly with only a small reduction in the speed of these changes.

Learning-induced Changes in Hand Localizations

Following the completion of every training trial participants indicated the felt position of their then passively displaced hand. Shifts in felt hand position have been shown to be implicit (23) and driven by the visual-proprioceptive mismatch between visible cursor location and felt position of the hand (1, 12, 14). Previous work in our lab and others has shown that the shift in felt hand position is a robust feature of learning under various conditions (1, 4, 11, 13, 24, 25). Here we were able to go a step further by measuring shifts in felt hand position after every training trial so that we can accurately compare the rate of change of hand localization between various kinds of training feedback.

As in the classic continuous-cursor training, the changes in unseen hand location estimates were rapid; with most participants for all groups saturating within a few trials. Nonetheless, terminal feedback required a few additional trials for changes in hand localization to reach a similar asymptote compared to continuous training. In our previous study comparing terminal and continuous feedback training, we found that proprioceptive recalibration (change in estimates of hand location) required a third block of 99 trials before achieving the same magnitude of proprioceptive recalibration (3). This is most likely because the method for measuring perceived hand location used in the previous study was a two-alternative force choice (2-AFC) method involving 50 trials to get a single estimate. While the 2-AFC method does an equivalent job of measuring the magnitude of proprioceptive recalibration as the method used in this and other studies, it requires far more training to overcome decay during measurement (26–28). The method used in the current study is able to measure hand localization shifts much faster with the same consistency (28).

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Exposure training led to a similar rate of change in hand localization as classical visuomotor training, requiring only one more training trial to reach asymptote. This is consistent with our previous study (13), where we found a similar rate and size of changes in estimates of hand location, and reach aftereffects, only after every 6-12 cursor-rotation training trials. In this previous paper, the average proprioceptive recalibration for exposure training was 10° , which is larger than the 5° - 7° shift usually seen in both our exposure (2, 12, 14) and classical training paradigms (3, 23, 27), including those measured in the current study. However, all these shifts in perceived hand location are within a reasonable range and really emphasize the robustness and rapidness of changes in felt hand position that co-occur when experiencing altered visual feedback of the hand.

The position of our hand is crucial in reach adaptation: both the starting position and the goal of the movement are defined by it. It may very well be possible that reach adaptation is, to some degree, driven by our sense of limb position: proprioception, even when it is recalibrated (29). We have previously shown that proprioception can recalibrate so quickly, that it fully precedes reach adaptation (4). In such cases it is a signal capable of driving reach adaptation. Since the speed of hand localization shifts in exposure training is indistinguishable from that in continuous training, this could suggest that in any situation with a visuo-proprioceptive discrepancy and proprioceptive recalibration, the shifted hand position could be driving some part of reach adaptation. That is: before sensory prediction error or task errors have had a chance to influence reach directions. Since we see recalibrated proprioception in a wide variety of tasks, such as when people are told about the perturbation (23) or can clearly see where perturbation comes from (25) and told to ignore it (30) the current results may indicate that proprioceptive recalibration happens in time for it to drive reach adaptation under many varying conditions. Of course, it has not yet been shown that recalibrated proprioception causally drives reach adaptation, so this remains speculation.

Adaptation to Varying Types of Feedback

While not the main focus of this study, the data allows a glance at the processes underlying motor adaptation as well, by testing how they respond to various kinds of feedback. Humans are very visually dominant beings and favour vision over many other senses for guiding reaching movements. Thus, it is not surprising that reducing visual feedback of the reach to the end of the reaching movement, when adapting to a visual perturbation can result in poorer learning performance compared to when the cursor is continuously visible. Nonetheless, many studies, including ours, find that given enough training trials similar levels of asymptote are achieved for both training paradigms (8–10, 31–33), although in some cases, learning extent is smaller (3). The exact difference in the rate of the learning is not usually measured or reported in previous studies; few studies compare whether the average first block of trials differ between the different paradigms (7). In the current study, when we fit a single exponential to the two training paradigms, we find that compensation for a terminal feedback visuomotor rotation is

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only half as fast as that for a continuous distortion (14.2% vs 27%) and takes 58% more training trials (19 vs 12) to saturate. By the 12th trial, however, compensation produced with terminal feedback is only 10% lower than those for continuous. The rate of learning could explain conflicting results regarding whether performance in terminal and continuous feedback training paradigms differ. Taken together, this indicates the same mechanisms may facilitate learning in these conditions, but the reduced feedback merely diminishes the overall speed by which motor and sensory changes hit asymptote levels.

During reaching trials in the clamp phase, participants showed small but significant rebounds that were similar in all three training groups, including in the exposure group where the preceding training did not involve active hand movements. This confirms that as in our previous studies using exposure training (2, 12–14), that visual-proprioceptive discrepancies are sufficient to lead to changes in hand movements.

Conclusion

Extending our previous work, here we show that regardless of available feedback type, changes in felt hand position appear incredibly quickly. Reducing feedback did not slow down proprioceptive recalibration. The impact was greater for reach adaptation, with rate of adaptation for terminal being slower than continuous. With similar asymptotes, the extent of learning was significant regardless of training paradigm. In conclusion, changes in felt hand position, are a rapid and resilient feature of adaptation which saturates before reach training trials, regardless of feedback during visuomotor training.

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