

# The cost of correcting for error during sensorimotor adaptation

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## Article

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2 **The cost of correcting for error during sensorimotor adaptation**

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6

## 1 Abstract

2 Learning from error is often a slow process. To accelerate learning, previous motor adaptation studies have focused on  
3 explicit factors such as reward or punishment, but the results have been inconsistent. Here, we considered the idea that a  
4 movement error carries an implicit cost for the organism because the act of correcting for error consumes time and energy.  
5 If this implicit cost could be modulated, it may robustly alter how the brain learns from error. To vary the cost of error, we  
6 considered a simple saccade adaptation task but combined it with motion discrimination: movement errors resulted in  
7 corrective saccades, but those corrections took time away from acquiring information in the discrimination task. We then  
8 modulated error cost using coherence of the discrimination task and found that when error cost was large, pupil diameter  
9 increased, and the brain learned more from error. However, when error cost was small, the pupil constricted, and the brain  
10 learned less from the same error. Thus, during sensorimotor adaptation, the act of correcting for error carried an implicit  
11 cost for the brain. Modulating this cost affects how the brain learns from error.

12

## 13 Introduction

14 In machine learning, the error in the output of a network  
15 is evaluated by a loss function that depends on the  
16 difference between the output of the network, and the  
17 desired one. This loss function is a mathematical  
18 description of the cost of error, which in turn is the  
19 principal driver of how much the network should learn  
20 from error. In analogy to machine learning, during  
21 sensorimotor tasks learning in humans also depends on a  
22 loss function (Kording and Wolpert, 2004) that tends to  
23 grow with error magnitude (Marko et al., 2012). This  
24 implies that in principle, altering the landscape of the  
25 sensorimotor loss function should affect the rate of  
26 learning. However, it has been difficult to find ways to  
27 modulate the sensorimotor loss function.

28 Previous approaches have considered  
29 inducements such as monetary reward or punishment,  
30 thus associating an explicit cost to the movement error.  
31 Initial results suggested that associating error magnitude  
32 with monetary loss was effective in accelerating  
33 adaptation (Galea et al., 2015; Song and Smiley-Oyen,  
34 2017). However, later work questioned this observation  
35 (Quattrocchi et al., 2018). Other work noted that  
36 associating error magnitude with reward enhanced the  
37 rate of adaptation (Nikooyan and Ahmed, 2015), but that  
38 result was also difficult to replicate (Galea et al., 2015;  
39 Spampinato et al., 2019). More recent results suggest  
40 that even when there is an effect of reward on rate of  
41 learning, it acts primarily through recruitment of the  
42 explicit, cognitive component of adaptation, not the  
43 implicit, unconscious component (Codol et al., 2018).

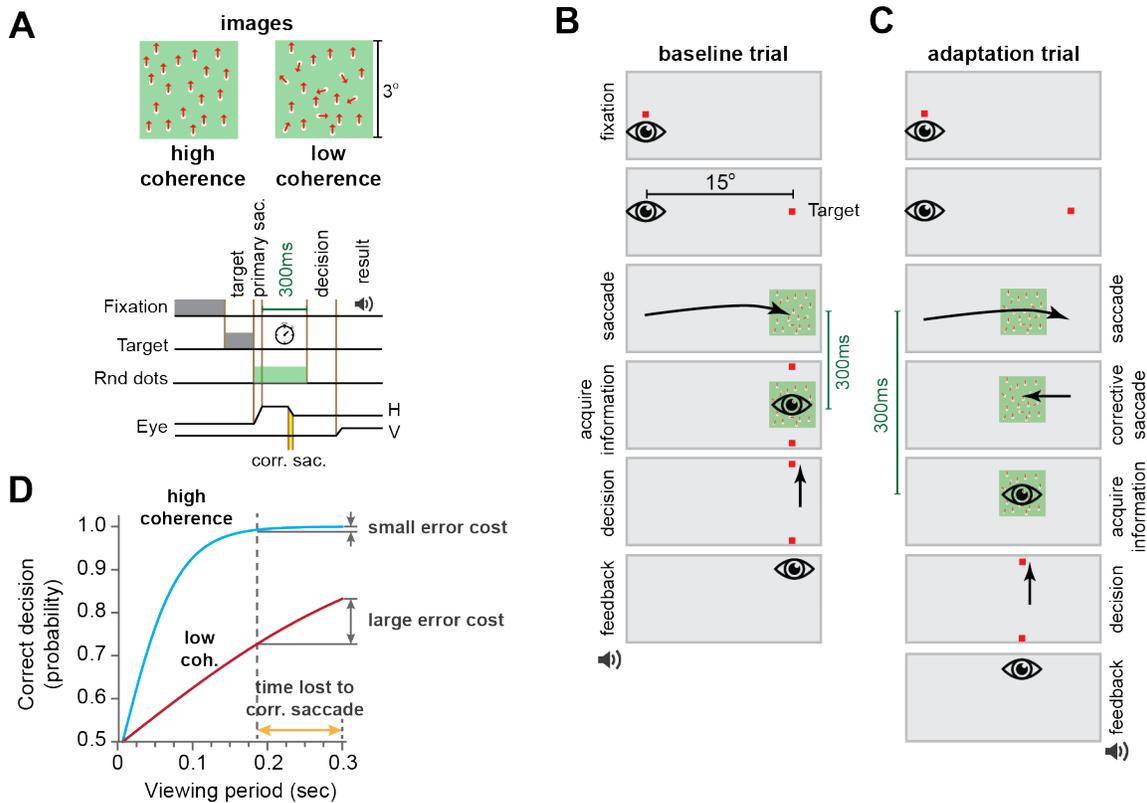
44 Here, we began with the observation that  
45 movement errors are often followed by corrective  
46 actions. For example, if a saccadic eye movement misses

47 the target, the resulting error encourages the brain to  
48 generate a corrective saccade. However, corrective  
49 movements carry an implicit cost in that they consume  
50 time, which in turn delays acquisition of reward  
51 (Shadmehr et al., 2010). Thus, a natural loss function for  
52 movement error is the time that is expended in the act of  
53 producing the correction. If this time could be linked with  
54 a utility, then the landscape of the loss function may be  
55 altered, resulting in modulation of learning rates.

56 To test this idea, we designed a paradigm that  
57 combined saccade adaptation with decision-making in a  
58 random dot motion discrimination task. Like traditional  
59 saccade adaptation tasks, subjects made a saccade  
60 toward a visual target and experienced an error that  
61 required a corrective movement. However, unlike  
62 traditional tasks, the corrective saccade carried a cost: it  
63 consumed time needed to acquire information for the  
64 decision-making task. We varied this cost via motion  
65 coherence of the random dots in the discrimination task  
66 and found that modulating the cost of correcting for  
67 error was a robust factor in how much the brain learned  
68 from error.

## 70 Results

71 Subjects made center-out horizontal saccades to a visual  
72 target (a green dot,  $0.5 \times 0.5^\circ$ ) at  $\pm 15^\circ$ . At the conclusion  
73 of their primary saccade, they were presented with an  
74 image that contained random dot motion (Fig. 1A). The  
75 objective was to detect the direction of motion of the  
76 random dots, which was either upward or downward,  
77 and was reported by making a vertical saccade. After this  
78 vertical saccade, feedback was provided regarding  
79 decision accuracy.

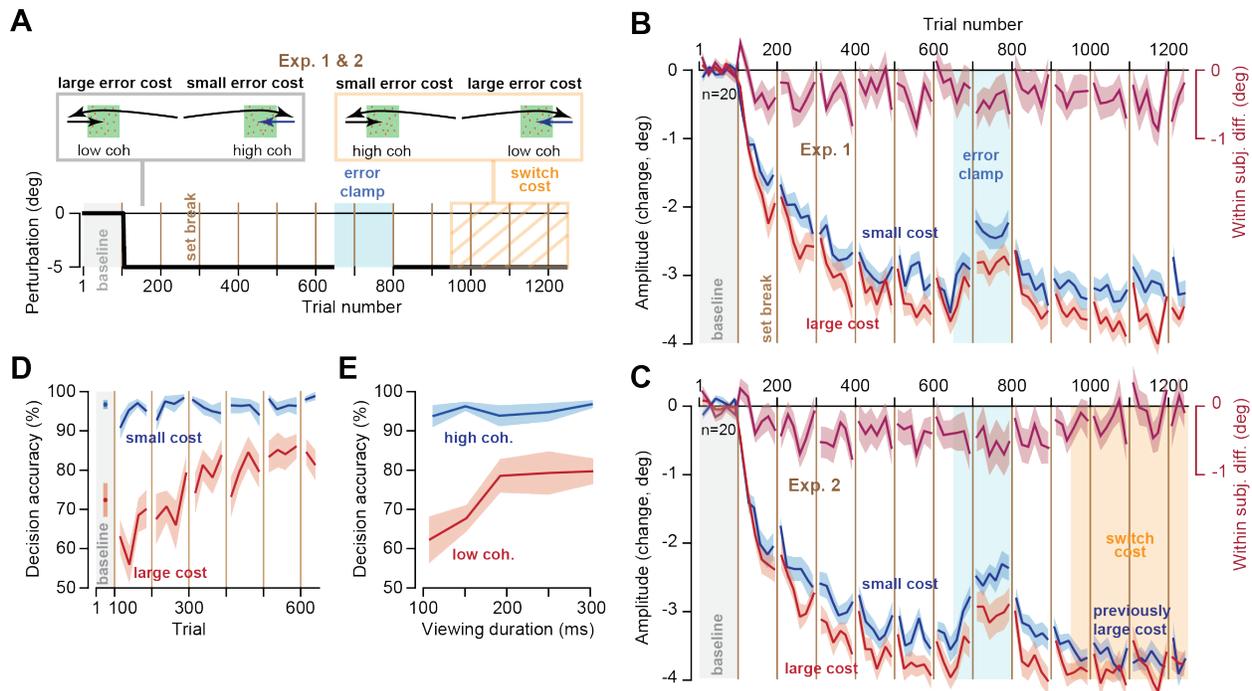


1  
 2 **Fig. 1.** Experiment design. **(A)** Each trial began with a random fixation interval (250-750ms) after which a primary target was placed at 15°  
 3 randomly to the right or left along the horizontal axis. After conclusion of primary saccade, subjects were presented with a random dot  
 4 motion image with high or low coherence. The task objective was to detect the direction of motion of the random dots, which was either  
 5 upward or downward, and was reported by making a vertical saccade. After this vertical saccade, feedback was provided regarding  
 6 decision accuracy. Subjects had only 300 ms from the end of their primary saccade to view the image. Thus, the time consumed by the  
 7 corrective saccade reduced the time available to place the image on the fovea. **(B)** During the first 100 trials of each session (baseline  
 8 block) the random dot motion was presented at the primary target location. **(C)** During adaptation trials the image was consistently  
 9 placed at a location 5° away from the primary target which acted as a movement error and induced a corrective saccade. **(D)** Hypothetical  
 10 error cost landscape. The period spent correcting for error carried a cost that depended on stimulus coherence. Low coherence images  
 11 induced large cost and high coherence stimuli induced a small cost in terms of decision accuracy.

12  
 13 In the baseline block, the image was centered at  
 14 the target (Fig. 1B). However, during the adaptation  
 15 block the image was centered 5° away from the target  
 16 (Fig. 1C). As a result, during adaptation the subjects  
 17 made a saccade to the target, and then followed that  
 18 with a corrective saccade to a location near the center of  
 19 the image (Supplementary Fig. 1). Importantly, the  
 20 movement error and the resulting corrective saccade  
 21 carried a cost because the subject had only 300 ms from  
 22 the end of their primary saccade to view the image. Thus,  
 23 if the subject learned from movement error and adapted  
 24 their primary saccade, the corrective saccade would  
 25 consume less time, allowing them to view the random  
 26 dots for a longer period, and therefore arrive at a more  
 27 accurate decision.

28 To modulate the landscape of the loss function,  
 29 we varied the coherence of the random dots. We

30 assumed that as the subject viewed the random dots, the  
 31 brain accumulated evidence for each possibility (upward  
 32 or downward motion). As shown in Fig. 1D, the evidence  
 33 accumulation is roughly the temporal integral of the  
 34 instantaneous difference between the number of dots  
 35 that moved upward vs. downward, and thus grows faster  
 36 when the motion is more coherent (more of the dots  
 37 move in a single direction). As a result, for the low  
 38 coherence image the time lost in correcting the error has  
 39 a large effect on decision accuracy. In contrast, for the  
 40 high coherence image, expending the same period of  
 41 time has little or no effect on decision accuracy (Pilly and  
 42 Seitz, 2009). Thus, by varying motion coherence, we  
 43 varied the cost of error in terms of decision accuracy,  
 44 which we hypothesized would result in changes in  
 45 learning rates.



**Fig. 2.** Cost of error modulated rate and asymptote of learning. **(A)** Subjects experienced 550 adaptation trials followed by 150 error clamp trials. In Exp. 1, this was followed by another 450 adaptation trials (trials 801-1250) which established the asymptote of performance. In Exp. 2, after an initial 150 adaptation trials (trials 801-950), at trial 951 (switch cost) suddenly and without warning the side that previously displayed large cost stimuli (low coherence) switched to displaying small cost stimuli (high coherence). **(B & C)** Amplitude change of primary saccades with respect to baseline. Large cost of error increased both the rate and the asymptote of adaptation. **(D)** Decision accuracy for small and large cost stimuli over the course of the experiment. Reward rate was consistently higher for the high coherence (small error cost) image. **(E)** Actual error landscape (compare with hypothetical landscape shown in Fig. 1D). A change in viewing period produced large changes in decision accuracy for the low coherence image, but it had little or no consequence for the high coherence stimulus. Bin size in B & C is 8 trials, in D is 12 trials, and in E is 50 ms. Error bars are SEM.

When the target was presented to one side of the screen, motion coherence of the image was always low. As a result, the corrective saccade was costly because it took precious time away from viewing the image. However, when the target was presented to the other side of the screen, motion coherence was high, thus making time expenditure less costly. Critically, probability of success was higher for the stimulus that had high coherence. If reward rate is the principal modulator of adaptation, then adaptation should be faster toward the side that was more rewarding (high coherence). On the other hand, if the error cost is the principal factor, then adaptation should be faster toward the side for which error was more costly (low coherence).

*Cost of error increased both the rate and the asymptote of adaptation*

In Exp. 1 ( $n=20$  subjects), following baseline trials (Fig. 1B), subjects made saccades to a target that was always

associated with large error cost (low image coherence), and to another target that was always associated with small error cost (high image coherence) (trial structure is shown in Fig. 2A). In baseline trials, as well as during adaptation, the probability of a correct decision was much higher for the small cost target (Fig. 2D, RM-ANOVA, trials 101-650, main effect of cost,  $F(1,19)=56.831$ ,  $p<0.0005$ ). Yet, the subjects learned more from errors that carried a large cost (Fig. 2B), as indicated by the fact that adaptation rate was faster for the low coherence image (RM-ANOVA on amplitude change, trials 101-650, main effect of trial  $F(32,608)=76.099$ ,  $p<0.0005$ , and trial by cost interaction  $F(32,608)=2.515$ ,  $p<0.0005$ ). Following a block of adaptation trials, we imposed a block of error-clamp trials that eliminated movement error. As expected, without errors to sustain adaptation saccade amplitude returned toward baseline levels (Fig. 2B, RM-ANOVA, trials 651-800, main effect of trial,  $F(8,152)=14.787$ ,  $p<0.0005$ , no trial by cost interaction,

1  $F(8,152)=0.746$ ,  $p=0.65$ ). Following the error-clamp block,  
2 further training brought performance toward a plateau  
3 (Fig. 2B, trials 951-1250). However, adaptation remained  
4 higher for the side with the larger error cost: RM-ANOVA,  
5 trials 951-1250, main effect of cost  $F(1,19)=5.439$ ,  
6  $p=0.031$ ).

7 Thus, the rate of adaptation was greater toward  
8 the target that carried a large cost of error, not the target  
9 that carried a greater probability of success. More  
10 importantly, the asymptote of adaptation was also  
11 greater when the error cost was larger.

### 12 *Increasing the cost of error rescued low adaptation*

13 If error cost is a causal mechanism that modulates  
14 learning from error, then a change in error cost should  
15 produce a change in adaptation. Because Exp. 1 had  
16 established that the asymptote of adaptation was  
17 greater for the stimulus with large error cost, we checked  
18 whether we could rescue adaptation by increasing the  
19 error cost.

20 In Exp. 2, subjects ( $n=20$ ) began with stimuli that  
21 were identical to Exp. 1: large error cost to one side,  
22 small error cost to the other. However, at trial 951 (Fig.  
23 2A, switch cost), suddenly and without warning the side  
24 that previously displayed large cost images (low  
25 coherence) switched to displaying small cost images  
26 (high coherence). Similarly, the side that previously  
27 displayed small cost images switched to displaying large  
28 cost images.

29 During the initial phase of the experiment (trials  
30 101-650), adaptation rate was faster toward the side that  
31 carried a large error cost (Fig. 2C, RM-ANOVA, trial by  
32 cost interaction,  $F(32,608)=2.461$ ,  $p<0.0005$ ), thus  
33 confirming the findings of Exp. 1. Following an error  
34 clamp period and initial relearning, we switched the  
35 stimuli. This switch from small to large cost coincided  
36 with convergence of saccade amplitudes for the two  
37 sides (Fig. 2C, RM-ANOVA, trials 801-1250, main effect of  
38 trial by cost interaction,  $F(26,494)=2.781$ ,  $p<0.0005$ , no  
39 main effect of cost,  $F(1,19)=1.6$ ,  $p=0.221$ ). We next  
40 compared saccade amplitude during trials 801-1250 in  
41 Exp. 1 when there was no switch in cost, with the  
42 condition in which the cost switched (Exp. 2). As  
43 illustrated in Supplementary Fig. 2, switch in cost  
44 appeared to rescue a zero slope learning curve to one  
45 that exhibited further learning (Multivariate test, main  
46

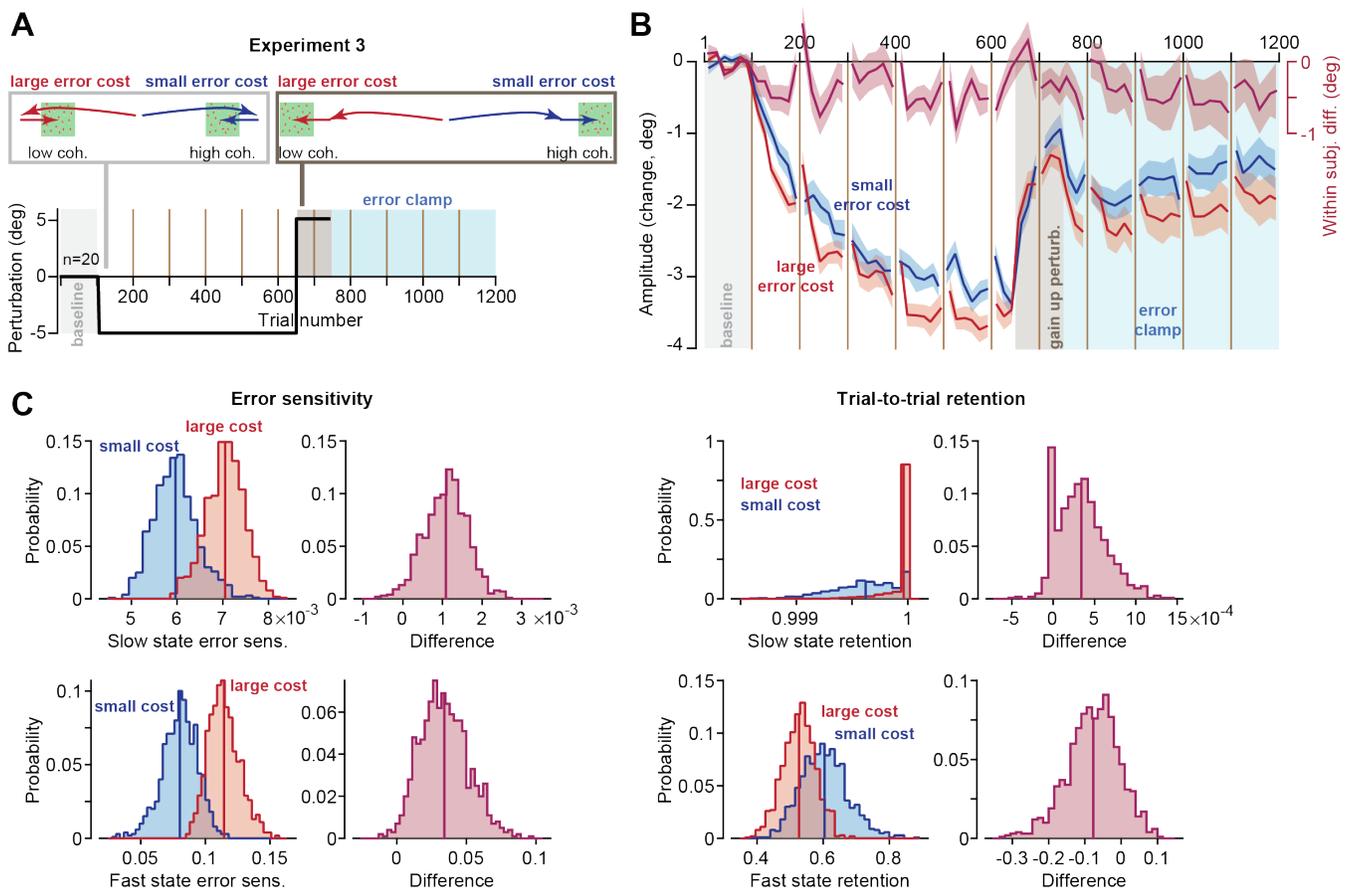
47 effect of trial by switch interaction,  $F(26, 13)=2.522$ ,  
48  $p=0.042$ ).

49 It is noteworthy that adaptation rate was greater for the  
50 large cost stimulus, despite the fact that the stimulus on  
51 the opposite side was more rewarding (Fig. 1D, RM-  
52 ANOVA on probability of success, trials 101-650, main  
53 effect of cost  $F(1,19)=56.831$ ,  $p<0.0005$ , as well as a trial  
54 by cost interaction  $F(21,399)=4.624$ ,  $p<0.0005$ ). The  
55 consequences of greater reward for the small cost  
56 stimulus was readily visible in the reaction time of the  
57 primary saccades: as in many previous experiments  
58 (Manohar et al., 2015; Milstein and Dorris, 2007;  
59 Sedaghat-Nejad et al., 2019b; Shadmehr and Ahmed,  
60 2020; Takikawa et al., 2002; Yoon et al., 2018, 2020),  
61 saccades toward the more rewarding stimulus exhibited  
62 a shorter reaction time (Supplementary Fig. 3, RM-  
63 ANOVA, trials 101-650, Exp. 1, main effect of cost,  
64  $F(1,19)=9.162$ ,  $p=0.007$ , trial by cost interaction,  
65  $F(32,608)=2.288$ ,  $p<0.0005$ ). That is, greater reward rate  
66 was associated with greater vigor (earlier reaction time),  
67 but not greater adaptation. Rather, adaptation rate was  
68 higher for the stimulus that carried a greater cost.

69 Our experiments were based on the assumption  
70 that the time period spent correcting for error carried a  
71 cost that depended on stimulus coherence (Fig. 1D). To  
72 check the validity of this assumption, we quantified the  
73 relationship between decision accuracy and viewing time  
74 for each stimulus. For the high coherence stimulus, a  
75 change in the viewing period produced little or no  
76 change in decision accuracy (Fig. 2E). On the other hand,  
77 for the low coherence stimulus a change in viewing  
78 period produced large changes in decision accuracy (Fig.  
79 2E, interaction of viewing period by decision accuracy,  
80  $F(4,76)=3.513$ ,  $p=0.009$ ). This confirmed that the time  
81 spent correcting for the movement error carried little or  
82 no cost for the high coherence stimulus (small cost),  
83 whereas the same expenditure was quite costly for the  
84 low coherence stimulus (large cost).

85 In summary, adaptation rate was greater toward  
86 the stimulus that carried a greater error cost, not the  
87 stimulus that was more rewarding. When the error cost  
88 increased (switch cost), so did the asymptote of  
89 performance, suggesting a causal relationship between  
90 the cost of error and adaptation.

91



**Fig. 3.** Cost of error affected sensitivity to error but not retention. **(A)** Experiment design of spontaneous recovery paradigm. **(B)** Amplitude change of primary saccades with respect to baseline. **(C)** A two-state model was fitted to the data and error sensitivity and retention were estimated for the fast and slow states using a bootstrap procedure. The plots show the resulting SEM distribution of parameter values and the differences in parameter values due to change in cost. Bin size in B is 8 trials. Error bars are SEM.

6

7 *Cost of error increased learning from error but not*  
 8 *retention*

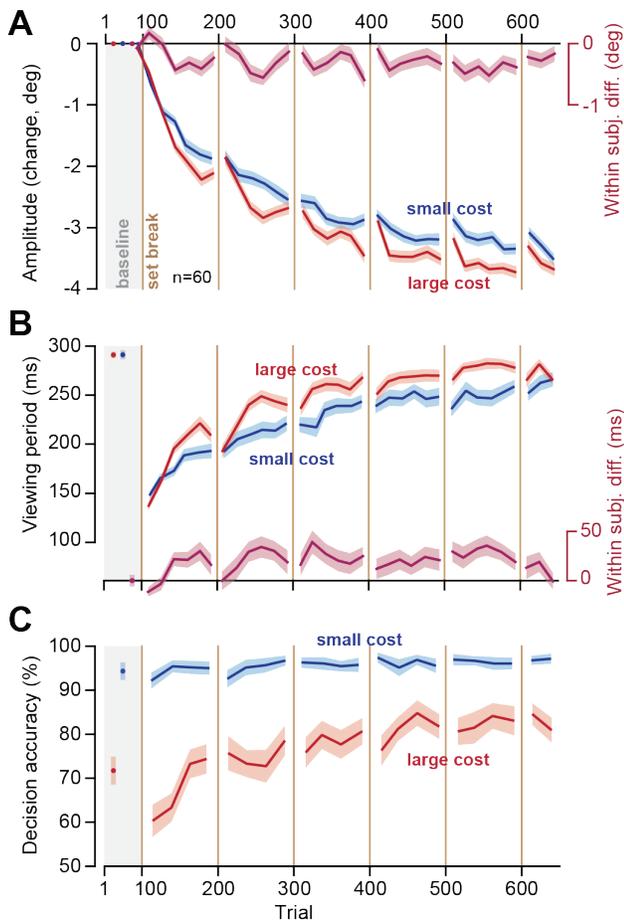
9 The fact that cost of error modulates the rate of  
 10 adaptation as well as the asymptote of performance  
 11 raises the question of whether this cost affects sensitivity  
 12 to error, trial-to-trial retention, or both. To consider  
 13 these possibilities, in Exp. 3 we implemented a  
 14 spontaneous recovery paradigm and then analyzed the  
 15 results using a state-space model of adaptation (Albert  
 16 and Shadmehr, 2018).

17 In Exp. 3 (Fig. 3A), subjects (n=20) began with  
 18 stimuli that were identical to Exps. 1 and 2: large error  
 19 cost to one side, small error cost to the other. We again  
 20 observed that the adaptation rate was faster toward the  
 21 stimulus with large error cost (Fig. 3B, RM-ANOVA, trials  
 22 101-650, trial by cost interaction,  $F(32,608)=2.944$ ,  
 23  $p<0.0005$ ). After the initial adaptation period we  
 24 reversed the direction of movement errors (trials 651 to  
 25 750) to induce “extinction”, resulting in a sharp change in

26 saccade amplitude toward baseline. Following error  
 27 reversal subjects experienced a long period of error  
 28 clamp trials (trials 751-1200). As expected (Ethier et al.,  
 29 2008), during the error clamp period saccade amplitude  
 30 exhibited spontaneous recovery toward the adapted  
 31 state (Fig. 3B, trials 751-800, RM-ANOVA, main effect of  
 32 trial,  $F(3,57)=24.709$ ,  $p<0.0005$ ).

33 We next applied a state space model to  
 34 estimate error sensitivity and trial-to-trial retention.  
 35 When the cost of error was large, error sensitivity was  
 36 elevated for both the slow (Fig. 3C, paired t-test,  
 37  $p=0.019$ ) and the fast state (Fig. 3C, paired t-test,  
 38  $p=0.023$ ). In contrast, cost of error did not appear to  
 39 affect trial-to-trial retention (Fig. 3C, slow state, paired t-  
 40 test,  $p=0.119$ ; fast state, paired t-test,  $p=0.846$ ).

41 To check the robustness of this result, we  
 42 reconsidered the data in Exp. 1, with the caveat being  
 43 that because this experiment did not contain a  
 44 spontaneous recovery period, we did not have sufficient



**Figure 4.** Faster adaptation of the primary saccade provided more viewing time to perform motion discrimination. **(A)** Change in primary saccade amplitude from baseline. **(B)** Image viewing period over the course of adaptation. Faster adaptation provided more viewing time to perform motion discrimination. **(C)** Decision accuracy over the course of the adaptation. The impact of the increased viewing period on decision accuracy was much greater for large cost stimulus as compared to the small cost stimulus. Data are from Exp. 1-3 combined. Bin size in B & C is 8 trials and in C is 12 trials. Error bars are SEM.

1  
13 power to consider a two-state model, and thus fitted a  
14 single-state set of equations. We again found that error  
15 sensitivity was larger for the large cost target, with no  
16 significant effect on the trial-to-trial retention (small cost  
17 and large cost error sensitivity were  $14.0 \times 10^{-3} \pm 1.95 \times 10^{-3}$   
18 and  $17.5 \times 10^{-3} \pm 1.56 \times 10^{-3}$ , within-subject difference was  
19  $3.5 \times 10^{-3} \pm 1.97 \times 10^{-3}$ , in contrast, we found no significant  
20 difference between estimated trial-to-trial retention,  
21 small cost and large cost trial-to-trial retentions were  
22  $0.9954 \pm 7.34 \times 10^{-4}$  and  $0.9961 \pm 6.66 \times 10^{-4}$ , within-subject  
23 difference was  $6.7 \times 10^{-4} \pm 9.1 \times 10^{-4}$ , paired t-test,  $p=0.23$ ).

24 In summary, cost of error affected adaptation by  
25 up-regulating sensitivity to error, not retention.

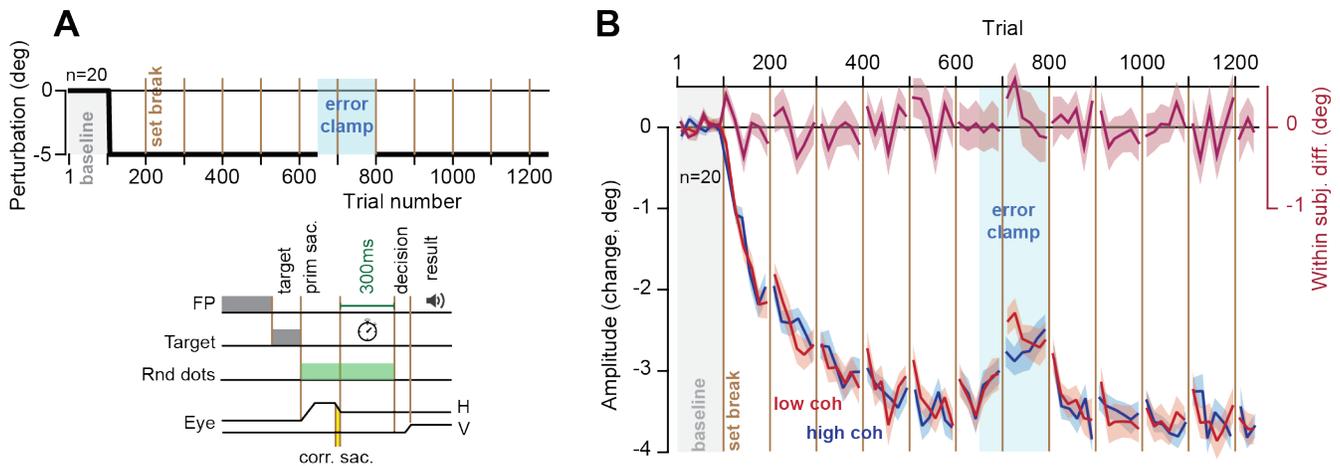
26  
27 *Faster adaptation provided more viewing time to perform*  
28 *motion discrimination*

29 We had assumed that adaptation would afford subjects  
30 more time to view the image, and thus help them make  
31 more accurate decisions. To check for this, we combined  
32 the data for the three experiments ( $n=60$  subjects). As  
33 expected, large error cost coincided with a faster rate  
34 and a greater extent of adaptation (Fig. 4A, RM-ANOVA,  
35 trials 101-650, main effect of trial,  $F(32,1888)=233.864$ ,

36  $p<0.0005$ , main effect of cost,  $F(1,59)=9.245$ ,  $p=0.004$ ,  
37 and trial by cost interaction,  $F(32,1888)=3.735$ ,  
38  $p<0.0005$ ). This increased rate of adaptation for the large  
39 cost stimulus provided more time to view the moving  
40 dots (Fig. 4B, RM-ANOVA, trials 101-650, main effect of  
41 trial,  $F(32,1888)=84.999$ ,  $p<0.0005$ , main effect of cost,  
42  $F(1,59)=6.841$ ,  $p=0.011$ , and trial by cost interaction,  
43  $F(32,1888)=3.072$ ,  $p<0.0005$ ). Finally, as saccades  
44 adapted and the viewing period increased, so did  
45 decision accuracy (Fig. 4C). But as expected, the impact  
46 of the increased viewing period on decision accuracy was  
47 much greater when time was more valuable (i.e., low  
48 coherence stimulus, Fig. 4C, main effect of trial by cost  
49 interaction,  $F(21,1239)=4.994$ ,  $p<0.0005$ ).

50  
51 *Control experiment: eliminating the error cost equalized*  
52 *rates of adaptation*

53 There is a potential confound in our interpretation: the  
54 task was harder for the low coherence stimulus. Thus, it  
55 is possible that learning rate was not driven by cost of  
56 error, but rather the difficulty of the task. To test for this,  
57 we performed a control experiment in which the cost of  
58



**Fig. 5.** Control experiment: eliminating the error cost equalized rates of adaptation. **(A)** Block design (top panel) was identical to Exp. 1. Trial design was also very similar with one crucial difference; the time to view the random dot image did not start until conclusion of the corrective saccade. This change effectively provided subjects with 300 ms to view the random dots regardless of the primary saccade amplitude. **(B)** Amplitude change in primary saccades with respect to baseline. We found no significant within-subject difference in either rate or asymptote of adaptation between the low and high coherence stimuli. Bin size in B is 8 trials. Error bars are SEM.

error was equal for the two stimuli, but task difficulty was greater for one of them (Fig. 5A).

As before, subjects ( $n=20$ ) made a primary saccade to targets at  $\pm 15^\circ$ , and again were presented with an image that was centered  $5^\circ$  away. However, unlike the main experiments, in this control experiment subjects were provided with 300 ms to view the random dot image regardless of the primary saccade amplitude. That is, the time allowed to view the image did not start until conclusion of the corrective saccade (Fig. 5A). With this subtle change we removed the cost associated with the movement error: now the time spent making a corrective saccade did not take away time from viewing the image.

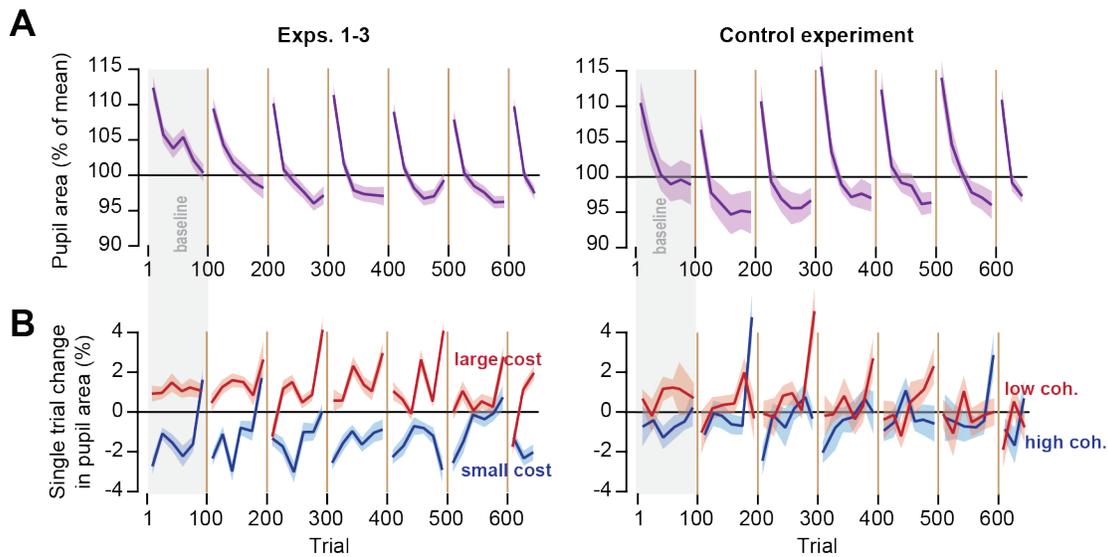
As before, decision accuracy was greater for the side that contained the high coherence image, thus confirming that the task on one side remained more difficult than the other (RM-ANOVA, trials 101-650, main effect of coherence,  $F(1,19)=60.096$ ,  $p<0.0005$ ). However, while saccade amplitude exhibited adaptation (Fig. 5B, RM-ANOVA, trials 101-650, main effect of trial,  $F(32,608)=74.049$ ,  $p<0.0005$ ), there were now no significant within-subject differences between the low and high coherence stimuli (Fig. 5B, RM-ANOVA, trials 101-650, no main effect of coherence,  $F(1,19)=0.018$ ,  $p=0.895$ ). Furthermore, we found no significant within-subject difference in the asymptotic learning between the two types of stimuli (Fig. 5B, RM-ANOVA, trials 951-1250, no main effect of coherence,  $F(1,19)=0.008$ ,  $p=0.931$ ).

In summary, in this control experiment we found that eliminating the cost of error, while maintaining the difference in task difficulty, eliminated modulation of learning rates.

#### *Pupil dilation coincided with increased cost of error*

What might be the neural mechanism that links cost of error with adaptation? To approach this question, we looked at pupil dilation as a proxy for activation of the brainstem neuromodulatory system (Vazey et al., 2018). We measured pupil diameter as subjects fixated the center target and found that at the onset of each block the pupil was dilated, but then progressively constricted as the trials continued (Fig. 6A). Following the set break, the pupil once again became dilated. These patterns were present in both the main experiment and the control experiment (Fig. 6A, RM-ANOVA, trials 101-650, main effect of trial, main experiments:  $F(1,59)=22.642$ ,  $p<0.0005$ , and control experiment:  $F(1,19)=10.975$ ,  $p<0.0005$ ). If we view pupil diameter as a proxy for arousal, then it appears that there was a general decline in arousal within each block of trials, followed by sharp recovery due to set breaks.

Next, we asked how the conditions of each trial affected pupil diameter. For each subject and each trial, we compared pupil size at center fixation (trial onset), to the fixation at the onset of the next trial before the target was displayed. This within trial response served as our proxy for how the neuromodulatory system



**Fig. 6.** The pupil diameter changed in response to trial conditions. **(A)** Pupil area at the end of each trial, normalized to the overall mean. Pupil was most dilated when the block of trials started. It gradually constricted as the trials continued within the block, then recovered following a set break. **(B)** Effect of trial conditions on pupil diameter. The plots show the change in pupil diameter from fixation at start of a trial to onset of fixation at the start of the subsequent trial. Bin size is 8 trials. Error bars are SEM.

responded to the experience of the subject during that trial.

We found that in the baseline block, the trials that were more difficult (low coherence) produced pupil dilation, whereas trials that were easy (high coherence) produced pupil constriction (Fig. 6B). The difference in the pupil response to the stimulus content of each trial was present in the baseline block of both the main group, and the control group (Fig. 6B, RM-ANOVA, trials 1-100, main effect of coherence, main experiments:  $F(1,59)=29.015$ ,  $p<0.0005$ , and control experiment:  $F(1,19)=4.460$ ,  $p=0.048$ ). Thus, as has been noted before (Kahneman and Beatty, 1966), the difficulty of the decision-making process within each trial appeared to drive pupil dilation.

In the main experiment, as the adaptation blocks began the pupil continued to dilate in trials that were difficult and had large cost (Fig. 6B, RM-ANOVA, trials 101-650, main effect of cost,  $F(1,59)=51.226$ ,  $p<0.0005$ ). In the control experiment the trials were still more difficult for the low coherence stimulus, but the error cost was equalized between the two stimuli. Interestingly, in the control experiment the pupil response to trial difficulty appeared to dissipate (Fig. 6B, RM-ANOVA, trials 101-650, no main effect of coherence,  $F(1,19)=0.920$ ,  $p=0.349$ ). We were concerned that this difference in the two groups may have been because of the larger group size in the main experiment. However, the statistical pattern was also present in each of the

main experiments (RM-ANOVA, trials 101-650, main effect of cost, Exp-1:  $F(1,19)=32.439$ ,  $p<0.0005$ , Exp-2:  $F(1,19)=10.752$ ,  $p=0.004$ , Exp-3:  $F(1,19)=7.873$ ,  $p=0.011$ ).

In summary, the pupil progressively constricted during each block of trials, suggesting a waning of attention, but then dilated following the set break, suggesting partial recovery. Within each trial the pupil diameter responded to the trial conditions: low coherence stimuli constituted more difficult trials, and in those trials the pupil dilated. However, in the adaptation block, trials in which the movement error carried a large cost continued to produce pupil dilation, as well as greater learning. In contrast, both effects diminished when we maintained trial difficulty but equalized the cost of error (control experiment).

## Discussion

When movements produce an unexpected outcome, the nervous system often produces a reflexive response that corrects for error. This corrective movement consumes time, potentially providing an implicit loss that can modulate learning from error. Here, we used saccade adaptation as a model of sensorimotor learning and explored whether imposing a cost on the time spent correcting for error could modulate learning from that error. We found that an increased error cost coincided with increased rates of adaptation. In contrast, task difficulty and reward rate altered reaction time,

1 producing movements that responded sooner to the  
2 more rewarding stimulus. However, while reaction time  
3 was faster toward the stimulus that provided higher rate  
4 of reward, learning was greater from the stimulus that  
5 carried a larger error cost.

6 In a control experiment, we maintained the  
7 disparity in the rate of reward of the stimuli but  
8 equalized the error cost. This led to elimination of the  
9 effect on learning rate, suggesting that a principal factor  
10 in modulating learning from error is not the absolute rate  
11 of reward, but rather a cost that links errors with the  
12 change that they impose on probability of success.

13 Earlier studies have considered the effects of  
14 explicit inducements on retention of motor memories  
15 (Abe et al., 2011; Galea et al., 2015; Wachter et al.,  
16 2009). For example, Abe et al. (2011) showed that  
17 monetary reward was effective in improving retention of  
18 motor memories during a force-tracking task. Galea et al.  
19 (2015) also found that during a visuomotor rotation task  
20 presence of reward was associated with greater  
21 retention. In contrast, Steel et al. (2016) reported that  
22 during serial-reaction-time and force-tracking tasks,  
23 neither reward nor punishment benefitted retention. We  
24 implemented a spontaneous recovery paradigm and  
25 assessed how cost of error affected error sensitivity, as  
26 well as trial-to-trial retention. We found that while cost  
27 of error up-regulated sensitivity to error, it did not have a  
28 significant effect on retention.

29 There are other factors that influence how much  
30 the brain learns from error (Herzfeld et al., 2014; Leow et  
31 al., 2020; Marko et al., 2012; Wei and Kording, 2009). For  
32 example, Marko et al. (2012) and Hanajima et al. (2015)  
33 noted that error sensitivity was relatively high for small  
34 errors and low for large errors. Herzfeld et. al. (2014)  
35 showed that in environments where errors were likely to  
36 be consistent, subjects increased their error sensitivity.  
37 Albert et al. (2020) observed that large variability in the  
38 trial-by-trial sequence of errors tended to suppress  
39 learning from error. Conscious of these potential pitfalls,  
40 we kept the perturbation size consistent over the course  
41 of the experiment, and also controlled the statistics of  
42 the error that the subjects experienced as they made  
43 saccades. Despite this, the rate of learning was greater  
44 toward the stimulus that carried a greater error cost.

45 We found that increasing the cost of error  
46 rescued low adaptation, suggesting a potentially causal  
47 relationship between the cost of error and adaptation  
48 rates. Previous studies (Albert et al., 2020; Kim et al.,

49 2019) have also found that modulating error sensitivity  
50 affected the asymptote of performance during motor  
51 learning.

52 In our saccade task, the pupil progressively  
53 constricted as the trials wore on within a block of trials,  
54 suggesting a decline in arousal (Mathot, 2018), but then  
55 dilated following the set break at the start of the next  
56 block, suggesting a partial recovery. The resulting saw-  
57 tooth pattern in pupil diameter was reminiscent of  
58 behavioral changes during adaptation in many other  
59 experiments: rapid adaptation that follows set breaks,  
60 and gradual adaptation that ensues with progression of  
61 trials (Chen-Harris et al., 2008; Ethier et al., 2008; Xu-  
62 Wilson et al., 2009).

63 Within each trial, during the baseline block the  
64 pupil dilated in response to stimuli that required greater  
65 mental effort (low coherence stimuli) and constricted in  
66 response to stimuli that required smaller effort (high  
67 coherence stimuli). During the adaptation block, when  
68 the stimuli carried an error cost the pupil continued to  
69 dilate in response to the high cost, greater mental effort  
70 stimuli. However, when the error cost was equalized in  
71 the control experiment, the dilation in response to  
72 stimuli that required greater mental effort waned. These  
73 results raise the possibility that pupil dilation is not only a  
74 correlate of attention and mental effort invested in the  
75 task, but also a correlate of learning from error.

76 The potential link between pupil diameter and  
77 learning from error is noteworthy because it may  
78 highlight the neural mechanism with which the brain  
79 modulates learning. Changes in pupil size are due to a  
80 band of muscles that surround the pupil, which in turn  
81 are controlled by motoneurons that reside in the  
82 Edinger-Westphal nucleus in the brainstem. Neurons in  
83 the intermediate layers of the superior colliculus project  
84 to this nucleus (May et al., 2016). As a result, weak  
85 micro-stimulation of the intermediate layers of the  
86 superior colliculus can produce a transient increase in  
87 pupil diameter that reaches its peak at around 300-500  
88 ms (Joshi et al., 2016; Wang et al., 2012). Notably,  
89 superior colliculus neurons also project to the  
90 contralateral inferior olive (Harting, 1977), which provide  
91 climbing fibers that carry error information to Purkinje  
92 cells of the cerebellum. The climbing fiber carries  
93 information regarding the visual error following  
94 conclusion of a saccadic eye movement (Herzfeld et al.,  
95 2015; Sedaghat-Nejad et al., 2019a; Soetedjo et al.,  
96 2008), which in turn guides plasticity in Purkinje cells and

1 affects trial-to-trial change in saccade kinematics  
2 (Herzfeld et al., 2018). Notably, the amount that the  
3 cerebellum learns from error may be related to the state  
4 of the superior colliculus: in trials in which collicular  
5 neurons respond more strongly to the visual error, there  
6 is greater trial-to-trial learning (Kojima and Soetedjo,  
7 2018, 2017). Thus, on the one hand the superior  
8 colliculus contains the neural machinery to control pupil  
9 size, and on the other hand, it provides information to  
10 the cerebellum regarding saccade related visual errors.

11 Our results raise the possibility that in trials in  
12 which there is greater error cost, pupil dilation reflects an  
13 elevated state of excitability in the superior colliculus,  
14 which in turn results in a greater response to the visual  
15 error following conclusion of the primary saccade. This in  
16 turn may produce a greater probability of complex spikes  
17 in the cerebellum, and thus a larger trial-to-trial change  
18 in behavior. The coincidence of these two effects in our  
19 experiments raise the possibility that superior colliculus  
20 may play a central role in controlling cost of error during  
21 sensorimotor adaptation.

22

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## 1 **Methods**

### 2 *Subjects*

3 A total of n=80 healthy subjects (18-54 years of age,  
4 mean±SD = 24±6, 42 females) participated in our study.  
5 The procedures were approved by the Johns Hopkins  
6 School of Medicine Institutional Review Board. All  
7 subjects signed a written consent form.

### 8 *Data collection procedure*

9 Subjects sat in front of an LED monitor (27-inch,  
10 2560x1440 pixels, light gray background, refresh rate 144  
11 Hz) placed at a distance of 35 cm while we measured  
12 their eye position at 1000 Hz (Eyelink 1000). Each trial  
13 began with presentation of a fixation point (a green dot,  
14 0.5x0.5 deg) that was randomly drawn near the center of  
15 the screen: the fixation point was placed randomly in a  
16 virtual box at -1 to +1 deg along the horizontal axis, and -  
17 1 to +1 deg along the vertical axis, where (0, 0) refers to  
18 center of the screen. After a random fixation interval of  
19 250-750ms (uniform distribution), the fixation point was  
20 erased and a primary target (a green dot, 0.5x0.5 deg)  
21 was placed at 15 deg to the right or left along the  
22 horizontal axis.

23 Removal of the central fixation and presentation  
24 of the primary target served as the go signal for the  
25 primary saccade. This saccade was detected in real-time  
26 via a speed threshold of 20 deg/s, or an eye position  
27 change of 2 deg from fixation, whichever happened first.  
28 After detecting saccade onset, the primary target was  
29 erased, and a random dot image was displayed. The  
30 image was a 3x3 deg box with invisible borders  
31 containing a 0.5x0.5 deg green dot at the center and 100  
32 0.1x0.1 deg white dots moving at 5 °/s either upwards or  
33 downwards with a predefined coherence. The location of  
34 random dot image was defined based on the trial type:  
35 during baseline trials the image was centered at primary  
36 target location. During perturbation trials the image was  
37 centered at 5 deg from the primary target toward the  
38 center of the screen. During error clamp trials the image  
39 was centered at the location of the primary saccade  
40 offset.

41 During adaptation trials, following the  
42 completion of the primary saccade subjects produced a  
43 corrective saccade to place the random dot image on  
44 their fovea. This corrective movement carried a cost  
45 because it reduced the time available for the subject to  
46 view the image. This is because following detection of  
47 primary saccade onset, the image was displayed on the  
48

49 screen, but the duration that the image was available  
50 was limited and was a key factor in our experiment  
51 design.

52 In the main experiments (1, 2, and 3) the image  
53 was present for only 300 ms after primary saccade offset.  
54 This was the only time available to view the image and  
55 decide on the direction of motion of the random dots.  
56 Following this 300 ms period, the image was erased, and  
57 two targets were displayed at 5 deg above and below the  
58 image. Subjects reported their perceived direction of  
59 motion by making an upward or downward saccade.  
60 Following this decision, they received feedback regarding  
61 their decision accuracy via an auditory tone: a 1000Hz  
62 (*beep*) 30 ms long sound for a correct decision, and a 500  
63 Hz (*boop*) 30 ms long sound for an incorrect decision. At  
64 the end of this period the decision targets were removed  
65 and the center fixation point appeared at a random  
66 location near the center of the screen, in the bounding  
67 box defined above.

### 68 *Modulating cost of error*

69 During the adaptation phase of the main experiments,  
70 although the viewing period was set to be up to 300ms  
71 from primary saccade offset, in practice, at the beginning  
72 of learning, it was around just 150 ms due to reaction  
73 time and duration of corrective saccades. Thus, by  
74 adapting the primary saccade (reducing the size of the  
75 corrective saccade), subjects would have more time to  
76 view the image, increasing the accuracy of perceiving the  
77 direction of motion. To vary the cost of error, trials  
78 consisted of two types of stimuli. For targets on one side  
79 of the screen, coherence of the random dots was low.  
80 For this image the error cost was great: the corrective  
81 saccade took precious time away from viewing the  
82 moving dots. For targets on the other side of the screen,  
83 coherence of the random dots was high. Here the error  
84 cost was small: the time consumed by the corrective  
85 saccade was irrelevant to the ability to perceive motion  
86 of the dots.

87 In a separate control experiment (described  
88 below), subjects received 300 ms to view the random dot  
89 image irrespective of the level of the adaptation. This  
90 served to remove the cost of error for the low and high  
91 coherence stimuli.

### 92 *Experiment design*

93 We performed 4 experiments consisting of 3 main  
94 experiments and one control experiment. N=20 subjects

1 participated in each experiment. The trial sequence for  
2 Exp. 1 and 2 is shown in Fig. 1E, for Exp. 3 in Fig. 2A, and  
3 for the control experiment in Fig. 4A.

4 All experiments started with 50 familiarization  
5 trials (no perturbations). During these trials the images  
6 appeared at the primary target location at various  
7 coherence levels to familiarize the participants with the  
8 saccadic task and motion discrimination paradigm. The  
9 collected data during the familiarization period was  
10 excluded from analysis.

11 After the familiarization block, the baseline  
12 block commenced. The baseline consisted of 100 trials  
13 and ended with a 30 sec set break. In this block, subjects  
14 experienced 50 low coherence trials on one side of the  
15 screen and 50 high coherence trials on the other side.  
16 The coherence side was counter-balanced between  
17 subjects. Since each subject experienced both type of  
18 stimuli (low vs high coherence), we used a within subject  
19 comparison for all statistical analysis.

20 Next, subjects experience 550 gain down  
21 perturbation trials (trials 101-650), during which the  
22 random dots image was displayed 5 deg away from the  
23 primary target toward the center of the screen. The  
24 consistent experience of this perturbation gradually  
25 resulted in adaptation of the primary saccades. We asked  
26 how does cost of error modulated the rate of adaptation.

27 All experiments included an error-clamp period.  
28 In these trials, the perturbation was removed and the  
29 image was centered at the end position of the primary  
30 saccade.

31 In contrast to the main experiment in which the  
32 time to view the image was reduced because of the  
33 corrective saccade, in the control experiment (Fig. 4A)  
34 the timer did not start until the end of the corrective  
35 saccade. This made it so that the time spent correcting  
36 for error did not compete with the time needed to view  
37 the random dot motion, thus equalizing the cost of error  
38 for the low and high coherence images.

#### 39 *Data analysis*

41 Eye position data were acquired using an EyeLink 1000+  
42 system (SR Research) at 1000 Hz. Eye position data were  
43 filtered with a second-order Butterworth low-pass filter  
44 with cutoff frequency of 100 Hz. Eye velocity data in  
45 offline analysis were calculated as the derivative of the  
46 filtered position data. Saccades were identified with a  
47 speed magnitude threshold of 20°/sec, and minimum  
48 hold time of 10 ms at saccade end (i.e. velocity

49 magnitude could not exceed the cutoff for a minimum 10  
50 ms after endpoint). Corrective saccade onset and offset  
51 were detected identically to the primary saccades, using  
52 20°/sec threshold on velocity magnitude. We measured  
53 change in primary saccade amplitude with respect to the  
54 average saccade amplitude in the first block in each  
55 condition. Viewing period of the image was measured  
56 based on the amount of time that the eye was inside of  
57 the random dot stimulus box from the offset of the  
58 primary saccade up to the point that the stimulus was  
59 erased and the decision targets were displayed. Decision  
60 accuracy was measured based on the number of correct  
61 decision responses divided by the total number of trials  
62 for each condition (high vs. low coherence).

63 Pupil area was measured by EyeLink 1000+  
64 system (SR Research) and was reported in the system's  
65 arbitrary pixel coordinate system. We blanked this data  
66 during eyeblink events to account for divergence in eye  
67 tracking. To combine and compare the pupil data across  
68 participants and experiments, we measured the  
69 percentage change for each participant by dividing the  
70 pupil data by the average pupil area over the entire  
71 recording for that subject. To control for differences in  
72 visual stimulus properties, we computed the average  
73 normalized pupil area during 200 ms window of time  
74 when participants were fixating on the start target  
75 (0.5x0.5 deg green dot). Next, we measured the change  
76 in normalized pupil area from one trial to the next to  
77 quantify how the conditions of each trial affect pupil  
78 dilation (Fig. 6B).

79 Statistical analyses were performed using SPSS  
80 and general linear models, with stimulus type (e.g., low  
81 or high coherence) serving as the within-subject factor.  
82 We reported results of Repeated Measure ANOVA (RM-  
83 ANOVA) with main effects of stimulus-type and trial, and  
84 stimulus-type x trial interaction.

#### 85 *State-space model of learning*

87 After the experience of a movement error, humans and  
88 other animals change their behavior on future trials. In  
89 the absence of error, adapted behavior decays over time.  
90 Here we used a state-space model (Albert and  
91 Shadmehr, 2018) to capture this process of error-based  
92 learning. Here, the internal state of an individual  $x$ ,  
93 changes from trials  $n$  to  $n+1$  due to learning and  
94 forgetting.

$$95 \quad x^{(n+1)} = ax^{(n)} + b^{(n)}e^{(n)} + \varepsilon_x^{(n)} \quad (1)$$

1 Forgetting is controlled by the trial-to-trial retention  $a$ .  
2 The rate of learning is controlled by the error sensitivity  
3  $b$ . Learning and forgetting are stochastic processes  
4 affected by internal state noise  $\varepsilon_x$ : a normal random  
5 variable with zero-mean and standard deviation of  $\sigma_x$ .

6 While we cannot directly measure the internal  
7 state of an individual, we can measure their movements.  
8 The internal state  $x$  leads to a movement  $y$  according to:

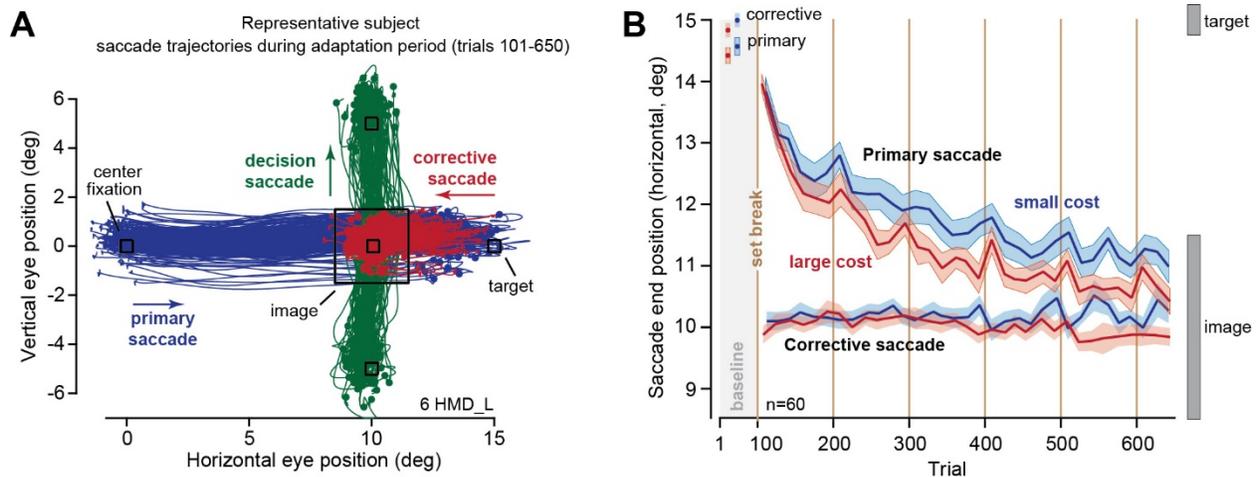
$$9 \quad \mathbf{y}^{(n)} = \mathbf{x}^{(n)} + \varepsilon_y^{(n)} \quad (2)$$

10 The desired movement is affected by execution noise,  
11 represented by  $\varepsilon_y$ : a normal random variable with zero-  
12 mean and standard deviation of  $\sigma_y$ . To complete the  
13 state-space model described by Eqs. 1 and 2, we must  
14 operationalize the value of an error,  $e$ . In sensorimotor  
15 adaptation, movement errors are determined both by  
16 motor output of the participant ( $y$ ) and the size of the  
17 external perturbation ( $r$ ):

$$18 \quad \mathbf{e}^{(n)} = \mathbf{r}^{(n)} - \mathbf{y}^{(n)} \quad (3)$$

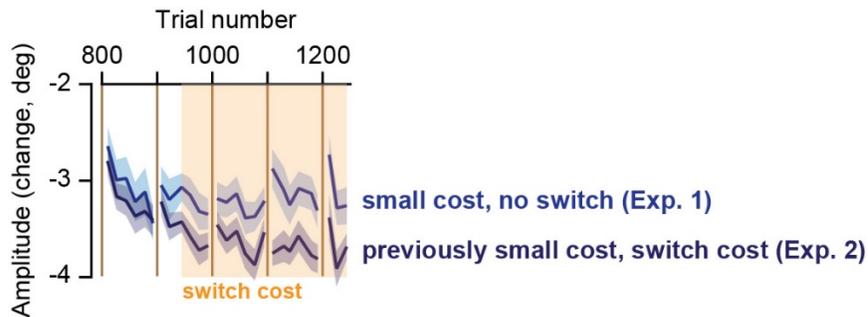
19 We used Eqs. (1-3) to estimate the trial-to-trial retention  
20  $a$  and error sensitivity  $b$  during each experiment design.

21  
22

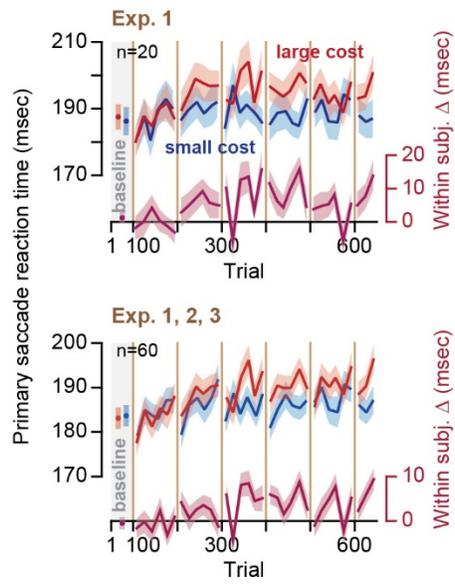


1  
 2 **Supplementary Fig. 1.** Saccade trajectory and end positions for a representative subject and for the main groups. **A.** Data  
 3 for a representative subject (6\_HMD\_L) during the adaptation trials for the target on the right. Primary saccade is followed  
 4 by a corrective saccade, and then a decision saccade. **B.** End position of the primary and corrective saccades for all subjects  
 5 in the main experiments (n=60). In the baseline condition, the image was centered at the target, located at 15° along the  
 6 horizontal axis. Primary saccades were slightly hypometric. They were followed by a corrective saccade that brought gaze to  
 7 center of the image. In the adaptation trials (101-650), the image was centered 5° away from the target. The corrective  
 8 saccade again brought gaze to near center of the image. This movement carried a large cost for some images, and a small  
 9 cost for other images. The rate of adaptation in the primary saccade was greater when the cost of error was large. Bin size  
 10 in B is 8 trials. Error bars are SEM.

11



12  
 13 **Supplementary Fig. 2.** Increasing the error cost from small to large appeared to rescue adaptation levels. Data from  
 14 Experiments 1&2. In Exp. 1, the side that had small cost retained that cost. In Exp. 2, the side that had small cost was  
 15 suddenly switched to a large cost. Bin size is 8 trials. Error bars are SEM.



1

2 **Supplementary Fig. 3.** Reaction times of primary saccades were faster toward the stimuli that promised greater reward  
 3 rate, not the stimuli that carried a greater cost. Note that the reaction times for the two stimuli start at approximately the  
 4 same value but separate as the experiment continues. Bin size is 8 trials. Error bars are SEM.

# Figures

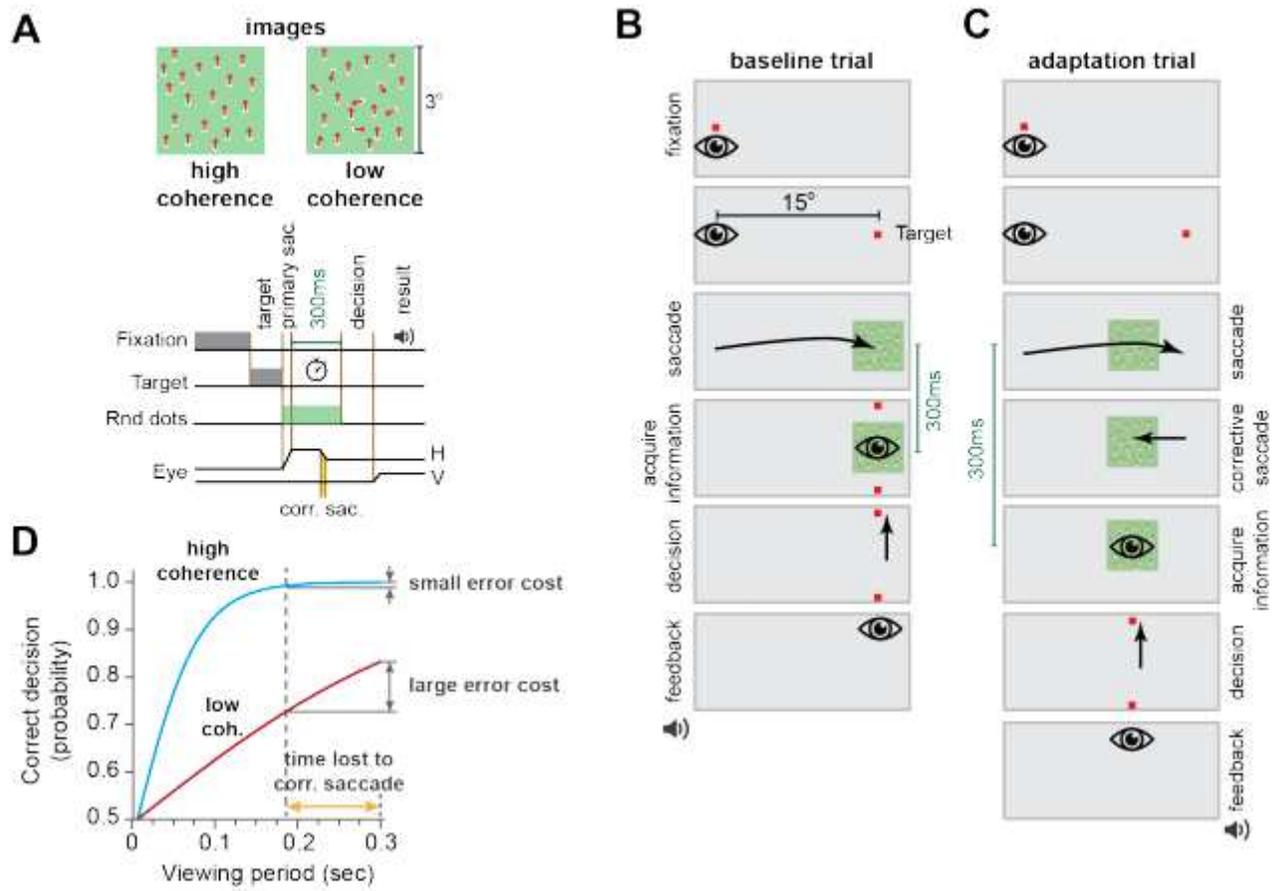
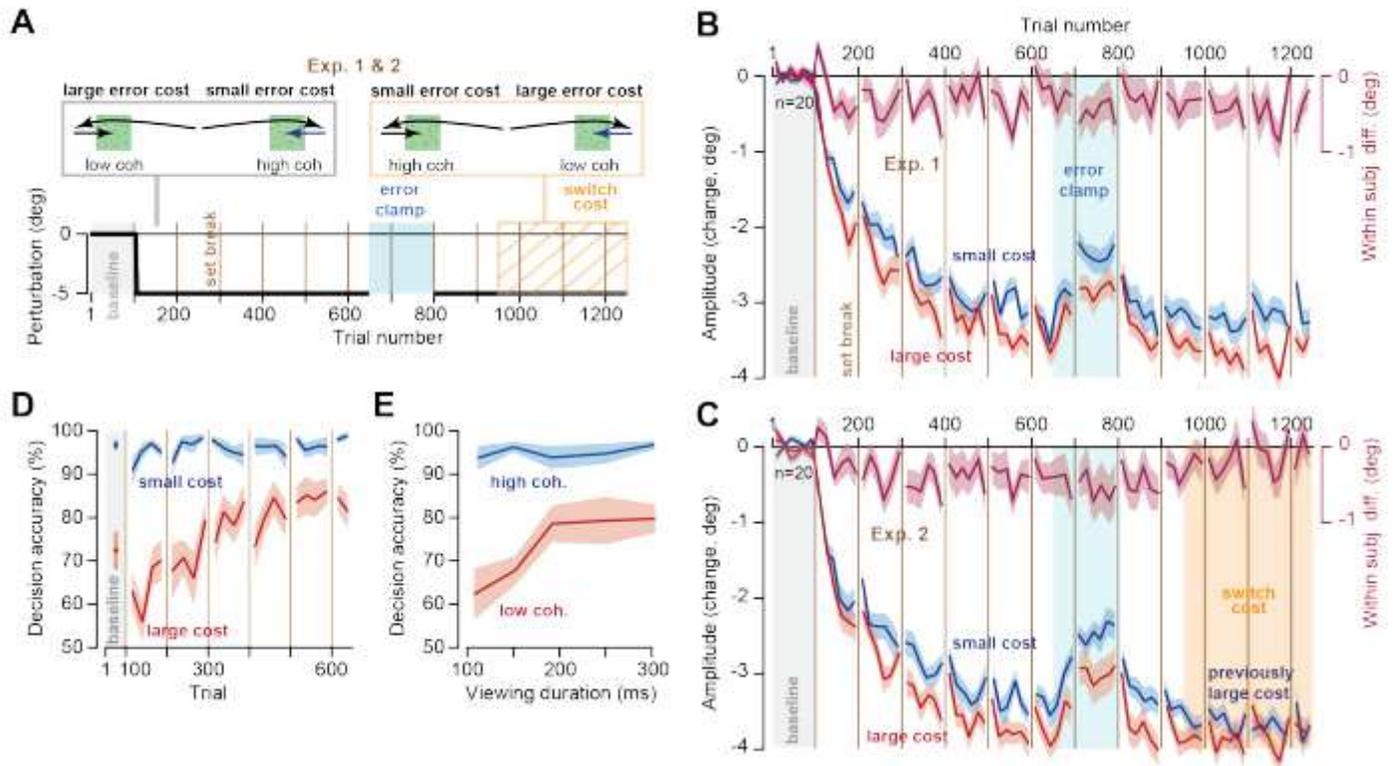


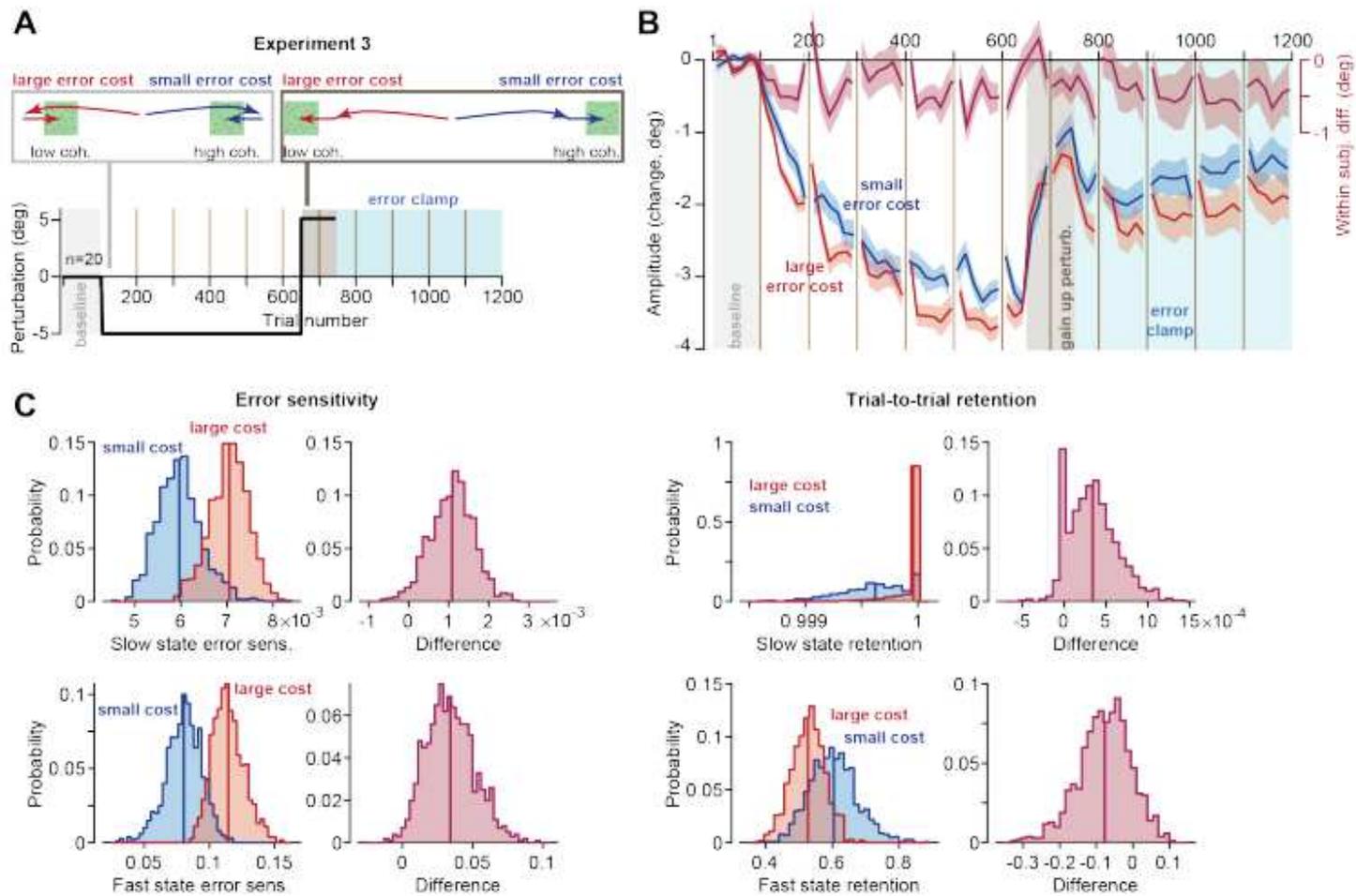
Figure 1

Experiment design.



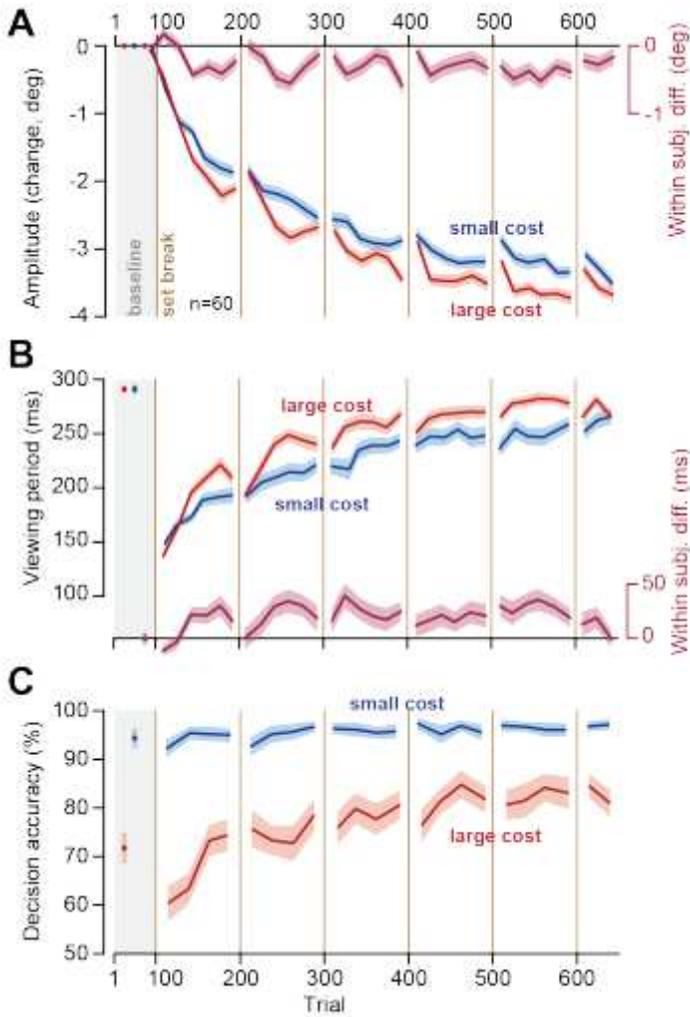
**Figure 2**

Cost of error modulated rate and asymptote of learning.



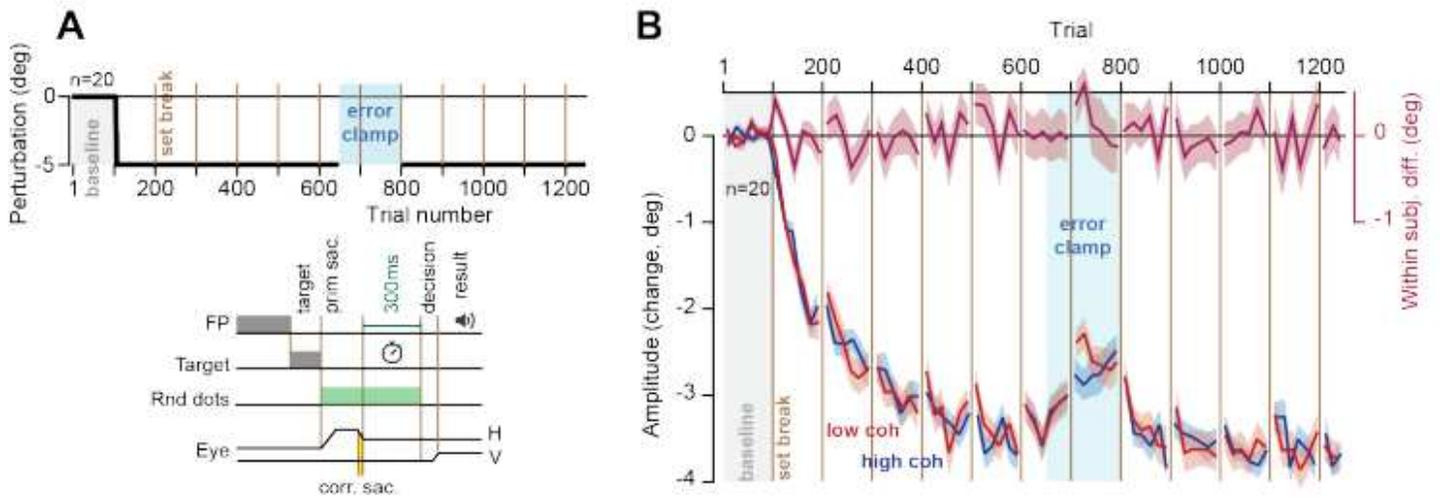
**Figure 3**

Cost of error affected sensitivity to error but not retention.



**Figure 4**

Faster adaptation of the primary saccade provided more viewing time to perform motion discrimination.



**Figure 5**

Control experiment: eliminating the error cost equalized rates of adaptation.

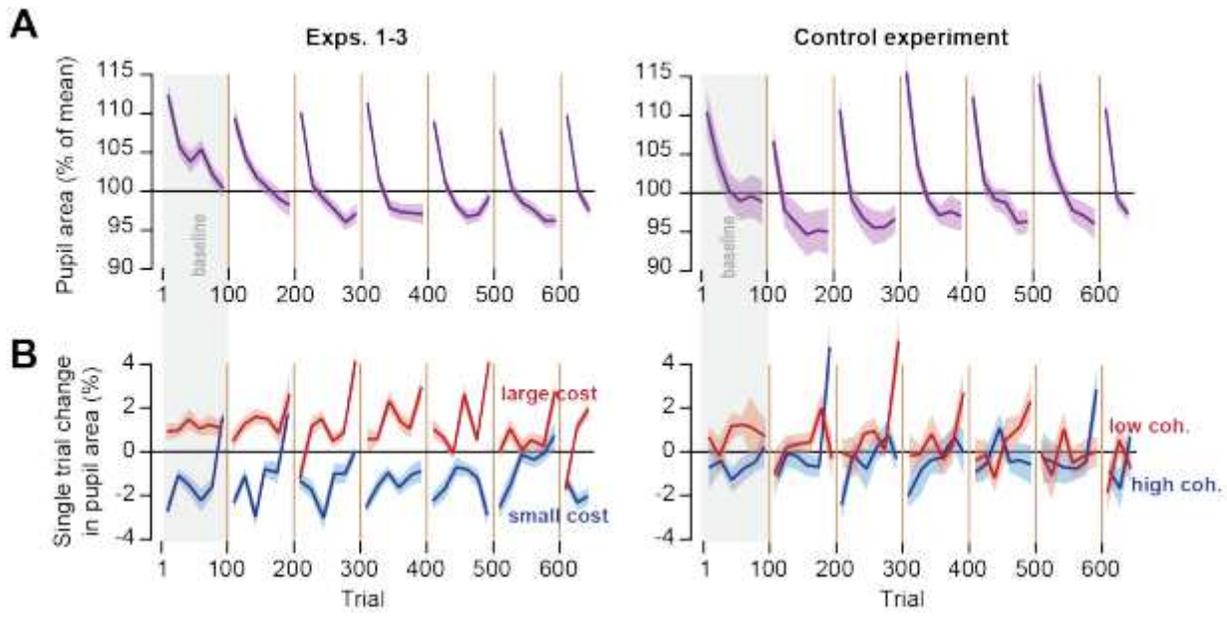


Figure 6

The pupil diameter changed in response to trial conditions.