

# The dissociable effects of punishment and reward on motor learning

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*Motivation in Motor Learning:  
Dissociable effect of Punishment and Reward*

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## Abstract

A common assumption regarding human error-based motor learning (motor adaptation) is that its underlying mechanism is automatic and insensitive to reward or punishment. Contrary to this hypothesis, we show in a double-dissociation that the two have independent effects on the learning and retention components of motor adaptation. Negative feedback, whether graded or binary, accelerated learning. While it was not necessary for the negative feedback to be coupled to monetary loss, it had to be clearly related to the actual performance on the preceding movement. Positive feedback did not speed up learning, but increased retention of the motor memory when performance feedback was withdrawn. These findings reinforce the view that independent mechanisms underpin learning and retention in motor adaptation, reject the assumption that motor adaptation is independent of motivational feedback, and open new research questions regarding the neural basis of negative and positive motivational feedback in motor learning.

## Introduction

Seeking reward and avoiding punishment are powerful motivational factors that shape human behaviour<sup>1, 2</sup>. Although previous research has focused on the response to reward and punishment during cognitive (decision making) tasks<sup>3-5</sup>, recent work has suggested positive and negative feedback to have dissociable effects on procedural<sup>6</sup> or skill<sup>7</sup> motor learning. Despite this, surprisingly little is currently known regarding the influence of reward- and punishment-based feedback on error-based motor learning (motor adaptation)<sup>8</sup>. Traditionally, motor adaptation has been thought as an implicit process which is unaffected by motivational feedback<sup>9-11</sup>. This view has had significant implications for how adaptation has been utilised during rehabilitation as a tool to improve motor deficits following an illness or injury<sup>12, 13</sup>.

Contrary to the assumption that motor adaptation is insensitive to motivational feedback, we hypothesized that punishment and reward would have dissociable effects on the learning and retention components of motor adaptation. Error-based motor learning depends on the cerebellum<sup>14, 15</sup>, which encodes aversive stimuli<sup>16</sup> and negative behavioural outcomes<sup>17</sup>, and is essential for aversive conditioning<sup>18</sup>. Therefore, we predicted that error-based motor learning would be enhanced by the punishment of movement errors<sup>19</sup>. In contrast, the retention of a motor memory depends on the primary motor cortex (M1)<sup>14, 20, 21</sup>. Interestingly the neuromodulator dopamine, which is considered essential for reward-based learning<sup>22, 23</sup>, is known to project to the M1<sup>24</sup> and is vital for long-term M1-dependent motor skill retention<sup>25, 26</sup>. Consequently, we predicted that memory retention would be enhanced following reward<sup>27</sup> possibly through reward-related dopaminergic signalling to M1<sup>28</sup>.

To test for this double-dissociation, we used a well-established motor adaptation task that required participants to update their reaching direction to compensate for a novel visuomotor rotation<sup>29</sup>. By providing participants with reward- or punishment-based monetary feedback that was based on their ability to maintain movement accuracy, we were able to examine the influence of positive and negative feedback on the learning and retention components of motor adaptation. In support of our hypothesis, we found a striking double-dissociation whereby punishment led to faster learning but reward caused greater memory retention. These results have significant implications for the understanding and optimisation of motor adaptation.

## Results

### *Punishment enhanced learning during randomly alternating visuomotor rotations*

We first sought to investigate whether reward- or punishment-based monetary feedback influenced a motor adaptation paradigm that is thought to be entirely automatic and non-strategic<sup>30</sup>. In experiment 1, we therefore exposed participants to randomly alternating visuomotor rotations during a reaching task in which the main aim was to strike through a visual target as accurately as possible (Fig. 1a,b). Although the perturbation on one trial was non-predictive of the next, participants systematically adapted their next movement to the experienced error. To quantify trial-by-trial adaptation, we used a single-rate state-space model (SSM) that estimated how much behaviour was adjusted based on each performance error (learning rate) and the degree of memory decay on each trial (decay rate)<sup>30, 31</sup> (*online methods*). Within each block, trial-by-trial endpoint angular error was associated with graded monetary reward, punishment or null feedback (Fig. 1c). Participants' earned money during reward blocks based on the accumulated positive points, and lost money during punishment blocks based on the accumulated negative points. In contrast during the null blocks, these points were replaced by two uninformative horizontal lines<sup>7</sup> (*online methods*). We observed a significant greater learning rate during punishment blocks ( $F_{(2,22)}=4.30, p=0.027$ ) relative to reward ( $t_{(11)}=2.27, p=0.045$ ) or null ( $t_{(11)}=3.67, p=0.004$ ; Fig. 1d). In contrast, reward showed an equivalent learning rate to null ( $t_{(11)}=0.34, p=0.74$ ). There were no significant differences in reaction time (RT) ( $F_{(2,22)}=0.26, p=0.77$ ; punishment=521±105ms, reward=479±91, null=485±84), movement time (MT) ( $F_{(2,22)}=0.84, p=0.44$ ; punishment=223±12ms, reward=216±11, null=221±9), decay parameter ( $F_{(2,22)}=0.21, p=0.81$ ; punishment=0.833±0.034, reward=0.793±0.072, null=0.825±0.035), or goodness of fit ( $R^2$ , supplementary table 1). A partial correlation (controlling for block type) indicated that reaction times were not correlated with the rate of learning ( $z=0.19, p=0.31$ ; 2-tailed). This suggests that the increased learning rate was unlikely to be a result of participants using a conscious strategy to avoid punishment<sup>10, 32</sup>. As the motivational feedback provided no additional directional information, it could not serve as an additional signal for error-based learning (*online methods*). Rather it must have modulated learning by changing the participant's sensitivity to the perceived directional reaching error.

## [Figure 1]

### *Punishment caused faster learning to a fixed visuomotor rotation*

These initial findings indicated that learning rate could be increased through punishment-based feedback. However, adaptation to random perturbations does not lead to a build-up of memory. To test how punishment or reward influences memory retention, experiment 2 used a block design that allowed learning to accumulate (Fig. 1e; *online methods*)<sup>14</sup>. During adaptation to a fixed visuomotor rotation, participants were provided with graded monetary reward (positive points based on endpoint error), graded monetary punishment (negative points based on endpoint error) or random positive feedback (random positive points that had no monetary value and were not associated with performance). For adaptation, we observed a significant difference for learning rate (estimated via a SSM;  $F_{(2,41)}=3.77, p=0.032$ ; Fig. 2a,b and supplementary Fig. s1a,b). Specifically, punishment was associated with faster learning compared to reward ( $p=0.017$ ) or random positive feedback ( $p=0.030$ ). The reward and random positive groups showed equivalent learning ( $p=0.81$ ). There were no significant differences for the decay parameter ( $F_{(2,41)}=0.08, p=0.93$ ; punishment= $0.957\pm 0.008$ , reward= $0.956\pm 0.007$ , random positive= $0.951\pm 0.013$ ). As similar differences in learning rate were observed when a generalisation function was added to the SSM (Fig. s2), we believe that the effects of punishment on adaptation do not depend on specific assumptions about generalisation. However, to ensure differences between the groups were not dependent on the choice of model, we performed an additional model-free analysis in which reach direction was averaged across the adaptation phase<sup>14</sup>, excluding the first 8 trials (*online methods*). As participants attempted to adapt to a 30° visuomotor rotation, an increased reach angle represented greater learning<sup>14</sup>. The analysis confirmed our results. Specifically, punishment led to greater learning during adaptation ( $F_{(2,41)}=5.73, p=0.007$ ) relative to either reward ( $p=0.045$ ) or random positive feedback ( $p=0.002$ ; Fig. 2c). There were no significant differences between groups for either RT or MT during the main experimental blocks (Table 1). RTs during adaptation were uncorrelated with the rate of learning ( $z=0.07, p=0.61$ ; 2-tailed), again suggesting that the increased learning speed of the punishment group was not caused by a more cautious, strategic approach. In addition, the average points received or lost on each trial during adaptation was comparable for reward ( $+2.00\pm 0.12$ ) and punishment ( $-2.05\pm 0.09$ ) ( $t_{(26)}=0.33, p=0.74$ ; 2-tailed; absolute value used for statistical comparison). Finally, the SPSRQ questionnaire<sup>33</sup> was used to score each participant's sensitivity to reward and punishment. Across participants, there was no overall bias towards either reward or punishment (punishment sensitive=20; reward sensitive=19; neutral=3). In addition, no significant correlations were observed between this score and participant's SSM learning or decay rate ( $z<0.17, p>0.27$ ; 2-tailed).

## [Table 1]

### *Reward caused greater memory retention*

Next, we characterised memory retention by measuring the gradual drift back to baseline performance when visual feedback of performance was removed<sup>14</sup>. For the no vision blocks, the SSM provided a poor fit to the data (supplementary Table s1) because the reach direction did not relax back to baseline, especially in the reward group (Fig. 2a). We therefore quantified retention by averaging reach direction across the 2<sup>nd</sup> half of the no vision trials (model-free analysis). Retention was greater for the reward group (greater reach angle;  $F_{(2,41)}=5.02, p=0.012$ ) relative to either the punishment ( $p=0.021$ ) or random positive ( $p=0.005$ ) groups (Fig. 2d). In contrast, there was no significant difference between groups ( $F_{(2,41)}=2.94, p=0.065$ ) for the first set of 8 trials within the no vision block (epoch 61, Fig. 2a). For completeness, we applied the SSM to the no vision blocks with the learning rate fixed to 0. The reward group's decay parameter was significantly larger (indicating increased retention;  $F_{(2,41)}=3.77, p=0.032$ ) than either the punishment ( $p=0.015$ ) or random positive ( $p=0.037$ ) group (Fig. 2e). These results confirm our prediction that reward would improve motor memory retention.

#### *Punishment was associated with faster readaptation*

When participants readapt after complete washout to a recently experienced visuomotor rotation, they usually exhibit faster learning rates, a phenomenon called savings<sup>29</sup>. Here, we used the dissociation between reward and punishment to determine whether faster relearning is associated with faster initial learning, as induced by negative feedback, or by greater retention, as induced by positive feedback. During washout the error returned quickly to baseline levels (Fig. 2a). In the last 8 trials of washout, the error was statistically indistinguishable from the last 8 trials of baseline, and there was no significant effect of group ( $F_{(2,39)}=0.75, p=0.48$ ), phase ( $F_{(1,39)}=1.64, p=0.21$ ) or interaction ( $F_{(2,39)}=0.46, p=0.63$ ). Importantly, additional positive or negative feedback was not provided during readaptation. Despite this, the SSM estimates showed that the punishment group adapted significantly faster ( $F_{(2,41)}=4.05, p=0.025$ ) than the reward ( $p=0.010$ ) or random positive ( $p=0.042$ ) group (Fig. 2b). In the presence of an directional error signal, the decay parameter was similar across groups ( $F_{(2,41)}=1.25, p=0.30$ ; punishment= $0.794 \pm 0.042$ , reward= $0.881 \pm 0.023$ , random positive= $0.848 \pm 0.049$ ). We then compared the learning rate parameter for the adaptation and readaptation blocks. Although there was a significant block ( $F_{(1,39)}=55.91, p=0.0005$ ) and group ( $F_{(2,39)}=5.89, p=0.006$ ) effect, the interaction was not significant ( $F_{(2,39)}=1.45, p=0.25$ ). Thus the increased learning rate observed after punishment was maintained during savings (Fig. 2b). We confirmed these results using a model-free analysis in which we averaged hand direction for the readaptation phase, except the first 8 trials. Punishment was associated with significantly greater learning ( $F_{(2,41)}=3.42, p=0.043$ ) relative to random positive ( $p=0.019$ ), with the comparison with reward nearing significance ( $p=0.052$ ; Fig. 2c).

### **[Figure 2]**

#### *Replication of the double dissociation using a 1-target design*

In experiment 2, we used 8-targets to make the use of strategic components of adaptation less likely. However, we wanted to ensure that our results generalised to a single target paradigm as used in experiment 1. Therefore, we decided to replicate experiment 2 using a 1-target design, also making the study more comparable to existing literature on motor memory retention<sup>27, 34</sup> (*online methods*). Once again, punishment led to a faster learning rate during adaptation (independent t-test:  $t_{(20)}=2.16, p=0.044$ ; 2-tailed; Fig. 3a,b). However, no significant difference was observed during readaptation ( $t_{(20)}=0.59, p=0.57$ ). Because adaptation rates were much higher than in the 8-target version, the lack of difference may have resulted from a ceiling effect in the learning rate of the punishment group. The decay parameter was similar for reward and punishment during both adaptation ( $t_{(20)}=0.31, p=0.76$ ; reward:  $0.969 \pm 0.008$ , punishment:  $0.966 \pm 0.006$ ) and readaptation ( $t_{(20)}=0.33, p=0.74$ ; reward:  $0.937 \pm 0.014$ , punishment:  $0.944 \pm 0.014$ ). These results were confirmed using a model-free analysis: The average reach angle was larger in the punishment than the reward group ( $t_{(20)}=2.22, p=0.038$ ; 2-tailed), without a significant difference during readaptation ( $t_{(20)}=0.90, p=0.38$ ; Fig. 3c). We also replicated the increased retention observed in the no vision blocks (Fig. 3a): For the reward group, the behaviour did not decay back to baseline. The model-free analysis showed that the average reach angle during the second half of the no vision group was larger for the reward than for the punishment group ( $t_{(20)}=2.35, p=0.029$ ; Fig. 3c). Although the SSM failed to capture the changed asymptotic behaviour, the decay parameter was significantly larger (indicating increased retention) than the punishment group ( $t_{(20)}=2.58, p=0.018$ ; Fig. 3b). Finally, there were no significant differences between groups for either RT or MT during the main experimental blocks (Table 2). These results clearly replicate the double dissociation whereby punishment led to faster learning and reward caused greater retention.

**[Figure 3]**

**[Table 2]**

*The effect of punishment is consistent across binary and graded feedback*

There are several possibilities that could explain how punishment-based monetary feedback led to faster learning during adaptation. In order to understand this result in more detail, we performed 3 additional control groups using the 8-target design.

First, it is possible that the graded feedback provided during punishment acted as an additional error signal which enhanced the rate of learning. Although this cannot explain the difference between punishment and reward, we decided to run a control group who were exposed to binary punishment-based feedback during adaptation (*online methods*). This group showed a significantly faster learning rate when compared to the random positive group (independent t-test:  $t_{(20)}=2.63, p=0.016$ ; 2-tailed; Fig. 4a,b) with model-free analysis revealing a similar difference between groups ( $t_{(20)}=3.22, p=0.004$ ; Fig. 4c). The decay parameter was comparable across groups (punish binary:  $0.9600 \pm 0.008$ ;  $t_{(20)}=0.53, p=0.61$ ). Therefore, the beneficial influence of negative feedback is consistent across binary and graded feedback.

### *Negative feedback does not have to be coupled with monetary loss*

We then asked whether the effect of punishment was a result of participants being sensitive to the loss of money or to negative performance feedback per se. A control group were exposed to punishment feedback while being explicitly informed that this had no bearing on the payment which was fixed (*online methods*). Once again, this group showed significantly faster learning during adaptation relative to the random positive group (independent t-test:  $t_{(20)}=2.67, p=0.014$ ; 2-tailed; Fig. 4a,b) with model-free analysis revealing a similar difference ( $t_{(20)}=2.64, p=0.016$ ; Fig. 4c). The decay parameter was similar across groups ( $t_{(20)}=0.11, p=0.92$ ; punish performance only:  $0.953 \pm 0.011$ ). This suggests that for young healthy participants, negative feedback associated with their performance is sufficient to induce a substantial increase in the rate of error-based learning.

### *Negative feedback does have to be directly related to actual performance*

A final possibility is that act of losing points could enhance learning, even if they are not related to the actual performance. Therefore, a final control group was exposed to random but negative points (random negative) during adaptation (*online methods*). If the sign (+ or -) of the points was important, then the random negative group should show significantly faster learning than the random positive group. Crucially, there was no significant difference between the random negative and random positive groups for learning rate (independent t-test:  $t_{(20)}=0.47, p=0.64$ ; 2-tailed; Fig. 4a,b) or when using model-free analysis ( $t_{(20)}=0.60, p=0.56$ ; Fig. 4c). The decay parameter was also similar across groups ( $t_{(20)}=0.90, p=0.38$ ; random negative:  $0.913 \pm 0.05$ ). This demonstrates that negative points unassociated with performance or monetary incentive failed to enhance the rate of learning.

Finally, we compared the 3 punishment group's (punishment/punish performance only/punish binary) learning rate. We found no significant differences ( $F_{(1,29)}=1.04, p=0.37$ ), suggesting that direct negative feedback related to poor performance is the critical factor that increases learning rate.

## **Discussion**

### *Punishment led to faster learning*

Punishment-based feedback (binary or graded) directly related to performance was associated with faster error-based motor learning. There are several possibilities as to how punishment could accelerate motor adaptation. First, negative feedback signals may have increased cerebellar sensitivity to sensory prediction errors (SPE), i.e. the directional mismatch between the expected and the perceived location of the cursor<sup>11, 35</sup>. Alternatively a punishment prediction error (PPE), which signals the unexpected loss of points or money<sup>1, 19</sup>, could have led to greater behavioural exploration<sup>36, 37</sup> and thereby increased the speed with which the correct



solution was found<sup>38, 39</sup>. Experiment 1 allowed us to distinguish between these two mechanisms: Unlike the SPE, the PPE is by definition unsigned and does not provide any information regarding the direction of error<sup>8</sup>. Increased variability in the output therefore cannot lead to increases in the learning rate during random visual perturbations. Hence the differences in experiment 1 must have arisen from participants becoming more sensitive to the directional information provided by a SPE. This conclusion is supported by the control experiments of experiment 2 in which it was found that binary punishment lead to a similar, if not greater, effect on the rate of learning. Finally, we did not observe any sign of increased output variability (i.e. decreased goodness of fit) or increased reaction time for any of the punishment groups. As cerebellar function is sensitive to negative behavioural outcomes<sup>17</sup> and aversive stimuli<sup>16</sup>, we believe that the punishment-induced improvements in error-based learning were a direct outcome of the cerebellum being more sensitive to a SPE associated with negative stimuli. In other words, a negative motivational signal may directly enhance cerebellar-dependent SPE learning<sup>19</sup>, possibly through increased levels of serotonin within the cerebellum<sup>40</sup>.

### *Loss aversion*

Loss aversion describes the behavioural avoidance of choices that can lead to losses, even when accompanied by equal or larger gains<sup>41, 42</sup>. Across many studies, losses typically loom about 1.5-2 times as large as gains, with loss aversion being well documented in the laboratory<sup>42</sup> and in many field settings<sup>43, 44</sup>. Therefore, loss aversion may have contributed to the punishment results. Importantly, a merely quantitative difference between reward and punishment conditions cannot explain the dissociable influence on learning and retention components of motor adaptation – which clearly shows that the two modes of feedback act on different systems. We decided to fix the amount of reward and punishment for this study rather than attempting to provide participants with calibrated amounts of financial rewards. Indeed, the result of our punish performance only control group indicates that such a calibration would not have been straightforward, as the points themselves appear to carry motivational value. It would be insightful, however, to further examine the modulation of learning with the amount of reward and punishment provided<sup>45</sup>.

### *Reward caused greater memory retention*

Reward-based feedback during adaptation led subsequently to greater retention when the directional feedback was fully withdrawn. Previous work has shown that positive reinforcement can influence both online (retention across trials) and offline (retention across time) motor retention<sup>7, 27, 47</sup>. Although there was an observable difference between groups at the beginning of the no vision block, this did not reach statistical significance. Nonetheless, it is possible that reward had a beneficial effect on both the retention of the memory trace during the preceding rest period (offline)<sup>7</sup> and on the rate of memory decay across errorless performance (online)<sup>27</sup>. We believe the positive influence of reward on retention was most likely a consequence of a stronger memory trace for the new visuomotor transformation in the cerebral cortex. There

is now substantial evidence that the M1 is essential for the retention of motor adaptation<sup>20, 46</sup>. The neuromodulator dopamine, critical for reward-based learning<sup>22, 23</sup>, is known to project to the M1<sup>24</sup> and is also vital for long-term M1-dependent motor skill retention<sup>25, 26</sup>. Therefore, the improvement in motor memory retention could be a result of reward-related signals to M1 during adaptation<sup>28</sup>.

#### *Previous work on reward and punishment in motor learning*

Two previous studies have investigated the influence of reward and punishment on motor learning. Wachter et al., (2009) found that during implicit sequence learning, punishment led to significantly better online motor performance, whereas reward was associated with greater learning and retention<sup>6</sup>. Abe et al. (2011) studied motor skill learning and found that while reward enhanced memory retention, punishment was not associated with any significant changes in behaviour<sup>7</sup>. Therefore, it seems reward enhances memory retention across multiple motor learning paradigms. In contrast, the influence of punishment appears more specific to error-based learning.

#### *Conclusions*

These findings reinforce the view that multiple independent mechanisms underpin motor learning<sup>27, 34, 48</sup>. Here we show that the learning and retention components of motor adaptation are differentially affected by reward and punishment. Previous work has concentrated on the potential translational impact of reward-based feedback<sup>27, 48</sup>. For instance, the use of reward has been suggested to have significant implications for stroke rehabilitation where motor learning interventions suffer from an inability to cause long-term changes in behaviour<sup>49</sup>. However, the present results indicate that focal and well-measured negative feedback may have utility during rehabilitation where an acceleration of learning is desired. Once the desired behaviour has been reached, reward signals could be introduced to facilitate the retention of the newly acquired behaviour.

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### **Author contributions**

J.M.G designed experiment 1. J.M.G and J.D designed experiment 2. J.M.G and E.M performed research. J.M.G, E.M and J.D analysed data. J.M.G, E.M, J.R and J.D wrote the paper.

### **Competing financial interests**

The authors declare no competing financial interests.

## Figure captions

**Figure 1:** Experimental design. **(a)** Experimental apparatus. Participants made reaching movements towards visual targets presented on a screen **(b)** Experimental task. Shooting reaching movements were performed with online (green) and endpoint (yellow) feedback. Reward and punishment feedback were represented by positive and negative points and based on endpoint error. **(c)** Experiment 1: 1-target adaptation to randomly alternating visuomotor rotations; positive=12° clockwise (CW), negative=12° counter clockwise (CCW). Within each block (vertical black line: 100 trials) participants received reward (red), punishment (green) or null (black) motivational feedback. **(d)** Experiment 1 (n=12): punishment was associated with greater trial-by-trial learning relative to either reward or null (SSM learning rate parameter). \* =  $p < 0.05$ . Error bars = SEM. **(e)** Experiment 2: 8-target adaptation to a fixed 30° CCW (negative) visuomotor rotation. Participants experienced 13 blocks (horizontal lines: 96 trials) which were separated by short rest periods (< 1minute). Shaded grey = participants received reward, punishment or random positive feedback during adaptation (adapt): reward (R)/punishment (P)/random positive (RP). Blocks 2,6-8: online and end-point visual feedback were removed (no vision; purple). Readaptation (readapt) involved a 30° CCW visuomotor rotation however reward/punishment was no longer provided.

**Figure 2:** Punishment led to faster learning, while reward caused greater retention during motor adaptation. **(a)** Experiment 2 (n=42). Epoch (average across 8 trials) angular reach direction data (°) for the random positive (blue), reward (red) and punishment (black) groups. Dashed/solid vertical lines = short rest periods (<1minute). For each section (vertical solid lines), a separate SSM was estimated. **(b)** Punishment led to faster learning compared to the random positive and reward groups during both adaptation and readaptation. **(c)** Model-free behavioural analysis revealed similar differences between groups. Specifically, punishment led to greater learning (increased reach angle) during adaptation and readaptation. **(d)** With no vision, reward was associated with enhanced retention (model-free analysis: increased reach angle) and **(e)** a larger decay rate (signifying increased retention) compared to punishment and random positive. \* =  $p < 0.05$ . \*\* =  $p < 0.06$ . Solid lines = mean, error bars/shaded areas = SEM.

**Figure 3:** Replication of the double dissociation between reward and punishment using a 1-target design. **(a)** Experiment 2 using a 1-target design (n=22). Trial-by-trial angular reach direction data (°) for reward (red) and punishment (black). Dashed/solid vertical lines = short rest periods (<1minute). For each section (vertical solid lines), a separate SSM was estimated. **(b)** Punishment led to faster learning compared to the reward group during adaptation but not readaptation. During no vision, reward was associated with a larger decay rate (signifying increased retention) compared to punishment. **(c)** Model-free behavioural analysis revealed similar differences between groups. Specifically, punishment led to greater learning (increased

reach angle) during adaptation, whereas reward caused enhanced retention during no vision. \* =  $p < 0.05$ . Solid lines = mean, error bars/shaded areas = SEM.

**Figure 4:** Direct negative feedback related to poor performance is the critical factor that increases learning rate. **(a)** Experiment 2: control conditions (n=24). Epoch (average across 8 trials) angular reach direction data (°) for the control conditions: random negative (orange), punishment performance only (black), punishment binary (red) and the original random positive group (blue). Dashed vertical lines indicate short rest periods (<1minute). **(b)** Punish performance only and punish binary were associated with an increase in the rate of learning when compared to random positive. There was no significant difference between random negative and random positive. **(c)** Model-free behavioural analysis revealed similar differences between groups. Specifically, punishment performance only and punish binary led to greater learning (increased reach angle) during adaptation. Solid lines = mean, error bars/shaded areas = SEM. \* =  $p < 0.05$ .

## Tables

**Table 1:** Reaction time and movement time across groups for experiment 2. Mean  $\pm$  SEM

	<i>Punishment</i>	<i>Reward</i>	<i>Null</i>	<i>ANOVA</i>
<i>Adaptation</i>				
RT (ms)	561 $\pm$ 60	589 $\pm$ 105	487 $\pm$ 46	$F_{(2,41)}=0.49, p=0.62$
MT (ms)	266 $\pm$ 17	259 $\pm$ 16	294 $\pm$ 22	$F_{(2,41)}=1.06, p=0.36$
<i>No vision</i>				
RT	555 $\pm$ 61	589 $\pm$ 11	487 $\pm$ 46	$F_{(2,41)}=0.47, p=0.63$
MT	280 $\pm$ 21	269 $\pm$ 16	294 $\pm$ 22	$F_{(2,41)}=0.83, p=0.46$
<i>Readaptation</i>				
RT	472 $\pm$ 34	532 $\pm$ 120	430 $\pm$ 39	$F_{(2,41)}=0.46, p=0.63$
MT	213 $\pm$ 12	202 $\pm$ 13	230 $\pm$ 14	$F_{(2,41)}=1.13, p=0.33$

**Table 2:** Reaction time and movement time across groups for 1-target control experiment. Mean  $\pm$  SEM.

	<i>Punishment</i>	<i>Reward</i>	<i>t-test (2-tailed)</i>
<i>Adaptation</i>			
RT (ms)	356 $\pm$ 42	376 $\pm$ 47	$t_{(20)}=0.30, p=0.77$
MT (ms)	280 $\pm$ 28	286 $\pm$ 46	$t_{(20)}=0.10, p=0.92$
<i>No vision</i>			
RT	357 $\pm$ 20	360 $\pm$ 27	$t_{(20)}=0.10, p=0.93$
MT	269 $\pm$ 22	282 $\pm$ 41	$t_{(20)}=0.26, p=0.80$
<i>Readaptation</i>			
RT	312 $\pm$ 31	348 $\pm$ 30	$t_{(20)}=0.83, p=0.42$
MT	267 $\pm$ 31	236 $\pm$ 28	$t_{(20)}=0.73, p=0.48$

## Methods

### *Experimental procedures*

#### *Participants*

All of the 100 young individuals ( $22\pm 6$  years, 58 females) were right-handed (self-reported) and gave informed consent to participate. None of the participants had a history of neurological or psychiatric diseases, or took chronic medication. The study was approved by the local research ethics committee of the Institute of Neurology, UCL, UK and University of Birmingham, UK.

#### *Experimental Task*

In all experiments, participants controlled a cursor through either a robotic manipulandum or a motion tracking system with their right hand and made 8cm, fast shooting movements towards visual targets (Fig. 1a). Their main aim was to strike through the target as accurately as possible (Fig. 1b). Following a baseline block, participants were exposed to a novel visuomotor transformation, in which the cursor movement was rotated around the starting position from the hand movement. This visuomotor transformation introduced a performance error. To compensate for this novel environment and return to accurate performance, participants were required to alter the trajectory of their reaching movements (hand direction). Experiment 1 was performed at the Institute of Neurology, UCL, and experiment 2 was performed at the School of Psychology, University of Birmingham. Despite this, a similar setup was used. Participants were seated with their forehead supported on a headrest. Their semipronated right hand either gripped a manipulandum (UCL) or was attached to a Polhemus motion tracking system (Birmingham) underneath a horizontally suspended mirror. The mirror prevented direct vision of the hand and arm, but showed a reflection of a computer monitor mounted above that appeared to be in the same plane as the hand. The visual display was comprised of a 1cm diameter starting box, a green cursor (0.3cm diameter) representing the position of the manipulandum, and a circular white target (0.5cm diameter). During experiment 1, the target was located 8cm vertically in front (on the screen) of the starting box. During experiment 2, a target was displayed in 1 of 8 positions arrayed radially at 8cm from the central starting box. At the start of each trial, the participant moved the cursor into the start box, a target then appeared. Participants were required to make a fast shooting movement through the target, such that online corrections were effectively prevented. At the moment the cursor passed through the invisible boundary circle (invisible circle centred on the starting position with an 8 cm radius), the cursor was hidden, and the intersection point was marked with a yellow square to denote the endpoint error. In addition, the start box changed colour based on movement speed. If the movement was completed within 100-400ms then it remained white. If the movement was slower than 400ms then the box turned red (too slow). Importantly, the participants were clearly instructed that the main goal of the task was to strike through the target as accurately as possible. After each trial, subjects moved back to the start. The cursor indicating their hand position only reappeared when they were within 2 cm. For experiment 2, the targets were presented pseudo-randomly so that every set of 8 consecutive trials included 1 of each of the target positions. Visual feedback could differ between blocks. First, a rotation of the cursor relative to the

hand around the starting location could be imposed. Second, online visual feedback and endpoint error feedback could be removed so that participants made reaching movements without vision; they simply saw a target but received no feedback as to their movement accuracy. Finally, a points system based on endpoint error could be visible:

*Reward:*

4 point: hit the target

3 point:  $< 10^\circ$  error

2 point:  $< 20^\circ$  error

1 point:  $< 30^\circ$  error

0 point:  $\geq 30^\circ$  error

*Punishment:*

0 point: hit the target

-1 point:  $< 10^\circ$  error

-2 point:  $< 20^\circ$  error

-3 point:  $< 30^\circ$  error

-4 point:  $\geq 30^\circ$  error

*Null*

Points are replaced by two uninformative horizontal lines.

*Random positive:*

A random number between 0 and 4 is presented which has no monetary value and is not associated with performance.

Participants began each block with 0 points. These points accumulated across the block. However, the reward and random positive group accumulated positive points whereas the punishment group accumulated negative points. Participants could see the points they received on a trial-by-trial basis and the total points accumulated for the block. The reward group/block earned money based on the accumulated points (win 1 pence per positive point), whereas the punishment group/block lost money based on the accumulated negative points (lose 1 pence per negative point). During null blocks for experiment 1, the points were replaced with horizontal lines. For experiment 2, the random positive group were explicitly informed that the points had no monetary value and were not associated with performance. This feedback was used to control for the presence of numbers on the screen within the reward and punishment conditions (Figure 1B). Thus differences between random positive and either reward or punishment feedback would suggest that the points had to be directly associated with performance/monetary incentive. Finally to ensure similar attention, participants were required to report the points total at the end of each block.



## *Experimental Protocol*

### *Experiment 1*

For experiment 1 (Fig. 1c), participants (within-subject design; n=12) were exposed to 1 block (1 block=100 trials) of veridical visual feedback (baseline). In the next 6 blocks the visuomotor rotations alternated randomly (12° CW/12° CCW/0°) on a trial-by-trial basis<sup>50</sup>. For each block, the feedback was either reward (R), punishment (P) or null (N) (2 blocks of each). Each participant was given £10 prior to the start of the study. They were instructed that they could lose money during punishment blocks, gain money in reward blocks or that money did not change during null blocks. Due to the random nature of the perturbations, participants received approximately £10.

### *Experiment 2*

For experiment 2 (Fig. 1e), participants were allocated to the reward, punishment or null group (between-subject design; n=42). The following blocks were then performed:

*Baseline:* 2 blocks (1 block = 96 trials): one with veridical visual feedback and the other without visual feedback. Null feedback.

*Adaptation:* 3 blocks with 30° CCW visuomotor rotation. Dependent on the group, the points system was reward, punishment or random positive. Importantly, motivational feedback was only provided during adaptation.

*No-vision:* 3 blocks without visual feedback. This restricted adaptation and therefore allowed errorless retention to be examined. The observed gradual drift back to baseline performance characterizes the degree of memory retention. Null feedback.

*Washout:* 3 blocks with veridical visual feedback. Null feedback.

*Readaptation:* 2 blocks with 30° CCW visuomotor transformation. Null feedback.

Each block was separated by a short rest period (< 1minute) in which participants were instructed to maintain their arm underneath the mirror. Unlike previous work<sup>7</sup>, improvements in readaptation could only be attributed to faster relearning, as we ensured washout was complete. Initially, we estimated the state-space model independently for the baseline/adaptation, no-vision and washout (last block)/readaptation phase.

The reward group began with £0 and won approximately £5-7. The punishment group were given £12 before the start of the task however ended with approximately £5-7. The random positive group randomly received either £12 before the task or £6 after. This was irrespective of performance but designed to control for the initial payments and time points of payment between the reward (begin with £0, end with £6) and punishment groups (begin with £12, end with £6). Each group were explicitly instructed of both the points-error relationship and the maximum points/money they could win or lose (£11.52) across the 3 blocks of adaptation.

### *1-Target*

In experiment 2, we used 8 targets to make the use of strategic components of adaptation less likely<sup>10</sup>. However, we wanted to ensure that our results generalised to a single target paradigm as used in experiment

1. Therefore, we decided to replicate experiment 2 using a single-target design making the study more comparable to existing literature on motor memory retention<sup>34</sup>. A reward and punishment group (n=22) were tested on a task that was identical to experiment 2 except only a single target position was used. In order for the groups to end the experiment with approximately the same monetary reward, and to account for the faster adaptation, the reward and punishment group started the experiment with different values as compared to experiment 2. Reward began with £2 and earned approximately £4-6, whereas punishment began with £10 and lost approximately £2-4. The target was located 8cm in front of the starting box, similar to experiment 1. Although a similar protocol to experiment 2 was employed, the number of trials was slightly reduced:

*Baseline with vision: 50 trials*

*Baseline without vision: 50 trials*

*Adaptation: 200 trials*

*No vision: 200 trials*

*Washout: 100 trials*

*Readaptation: 100 trials*

*Punish Binary*

It is possible that the graded feedback provided during punishment acted as an additional error signal, which enhanced the rate of motor-based learning. Although this cannot explain the difference between punishment and reward, we decided to run a control group (n=8) in which participants received binary punishment feedback during adaptation. Participants were told that they would receive 0 points for hitting the target ( $\pm 5^0$ ) and -1 for any error above this value. Each negative point was related to losing 1pence with participants beginning with £8. Note for all remaining control groups, only the 2 baseline blocks and adaptation were tested.

*Punish Performance Only*

We asked whether the effect of punishment was a result of participants being sensitive to negative feedback on their performance or whether they were sensitive to the loss of money. Therefore, a control group (n=8) was exposed to the punishment feedback, while being explicitly informed that this had no bearing on the payment which was fixed at £6.

*Random Negative*

The random positive group in experiment 2 involved random but positive points. It is possible that even though these positive points were unrelated to performance, they could still be implicitly rewarding to the participant. Therefore, a control group (n=8) were exposed to random but negative points (random negative) during adaptation. If the sign (+ or -) of the points was important, rather than them being related to performance or money, then random negative should show significantly faster learning during adaptation.

*Code and data availability*

Custom computer code was used to control the experimental task, collect behavioural data and perform all data and statistical analysis. All computer code and raw behavioural data is available on request to the corresponding author.

### *Data Analysis*

Reach position data (x,y) was collected at 100Hz. Data and statistical analysis was performed using Matlab (The Mathworks, Natwick, USA). For each trial, angular reach direction ( $^{\circ}$ ) was calculated as the difference between the angular hand position and angular target position at the point when the cursor intersected the 8-cm invisible circle centred on the starting position. During veridical feedback, the goal is for reach direction to be  $0^{\circ}$ . However, with a visuomotor transformation, reach direction had to compensate; i.e. for a  $-30^{\circ}$  (CCW) visuomotor rotation, a reach direction of  $+30^{\circ}$  (CW) was required. In addition, reaction time (RT: ms difference between target appearing and movement reaching 10% of maximum velocity) and movement time (MT: ms difference between reaction time and movement end) were calculated for each trial. For both experiments, we removed any trial in which reach direction exceeded  $60^{\circ}$ <sup>51</sup> or that MT exceeded 600ms. This accounted for less than 4% of trials.

### *Model-based*

We analysed the trial-by-trial angular reach direction in response to the visuomotor transformations using a single-rate state-space model<sup>30, 31, 48, 52</sup>. The application of such a model was necessary to allow for the quantification of the adaptation rate in experiment 1, which otherwise would not be accessible. For experiment 2, it would also be possible to simply analyse the behavioural data by averaging the reaching angle across certain phases of the task<sup>53</sup>. Although this analysis is provided to substantiate our model-based results, the advantage of the state-space model is that it estimates learning rates from all available data and does not require the experimenter to arbitrarily select time points/trials of interest.

Adaptation may be captured better using a double-exponential learning curve; therefore it would have also been possible to model our results using a 2-rate state-space model<sup>34</sup>. However, as we wished to apply the model only to obtain a quantification of the overall learning rate, this would have provided little additional information regarding our main result. The single-state state-space model equations took the following form:

$$\hat{y}_n = -z_n^t$$

$$z_{n+1}^t = Az_n^t + B(r_n - z_n^t)$$

$\hat{y}_n$  represents the angular hand direction (relative to the target) on trial  $n$ ;  $z_n^t$  is the state of the learner that represents the current estimated visuomotor rotation associated with the target  $t$ ;  $r_n$  represents the visuomotor rotation that was imposed on trial  $n$ ;  $r_n - z_n^t$  is the direction of the cursor relative to the target and thus the cursor error<sup>48</sup>. Therefore, the learning rate ( $B$ ) determines how much of the cursor error ( $r_n - z_n^t$ ) is adapted for. The decay parameter ( $A$ ) determines the rate of forgetting of the state/estimated visuomotor mapping ( $z_n^t$ ) and is only applied to the executed movement<sup>54</sup>.

During blocks without visual feedback, we assumed that  $B = 0$ . Therefore, under these conditions, the system forgets with constant  $A$ . Previous studies have included a generalisation function which determines how much error in one target direction affects mapping estimates in neighbouring directions<sup>30, 48</sup>. Initially, we assumed no generalisation between target positions that are  $45^\circ$  apart however return to this issue in the supplementary results. Using the matlab function `fmincon`, we estimated  $A$  and  $B$  to minimize the squared error between trial-by-trial predicted hand direction ( $\hat{y}_{t(n)}$ ) and actual trial-by-trial hand direction, subject to the constraints ( $0 < A < 1$ ) and ( $-1 < B < 1$ ).

### *Model-free*

To ensure differences between the groups were not solely dependent on the model, we performed behavioural (model-free) analysis in which the angular reach direction ( $^\circ$ ) was averaged across trials. The specific trials were chosen in an attempt to reflect either the learning component during re/adaptation<sup>53</sup> or the retention component during no vision<sup>27</sup>. For the adaptation and readaptation blocks in the 8-target task, the average reach direction was calculated across all trials, excluding trials 1-8. For no vision, the average reach direction was calculated across the 2<sup>nd</sup> half of the no vision trials. Within the 1-target task, the average reach direction was calculated across the first 15 trials of adaptation and readaptation, excluding trial 1. Finally for no vision, we calculated the average reach direction across the second half of the no vision trials.

### *Statistical analysis*

For experiment 1, independent state-space models were estimated for each participant and block. We assumed that at the beginning of each block:  $z_0^t = 0$ . The parameter estimates for  $A$  and  $B$  were then averaged for each block type, providing 3  $A$  and  $B$  parameter values for each participant (reward, punishment, null). To test for differences in these parameter values between block types, we conducted within-subject repeated measures ANOVAs followed by post-hoc paired t-tests.

For experiment 2, independent state-space models were estimated for baseline/adaptation (5 blocks), no vision (3 blocks) and washout (last block)/readaptation (3 blocks). We assumed that for each section,  $z_0^t$  was set by the participant's initial hand movement direction at the beginning of that section .i.e. an average across trials 1-8. Unless stated otherwise, differences between groups for the  $A$  and  $B$  parameter values and model-free analysis were examined using a one-way between-subject ANOVAs followed by Tukey post-hoc tests.

No statistical methods were used to pre-determine sample sizes but our sample sizes are similar to those reported in previous publications<sup>38,48,53</sup>. Epoch data shown in figures depicts the average angular reach direction across 8 movements (1 movement towards each target). Significance level was set at  $p < 0.05$ . All data are reported as mean  $\pm$  standard error of the mean (across subjects) (SEM). A supplementary methods checklist is available.

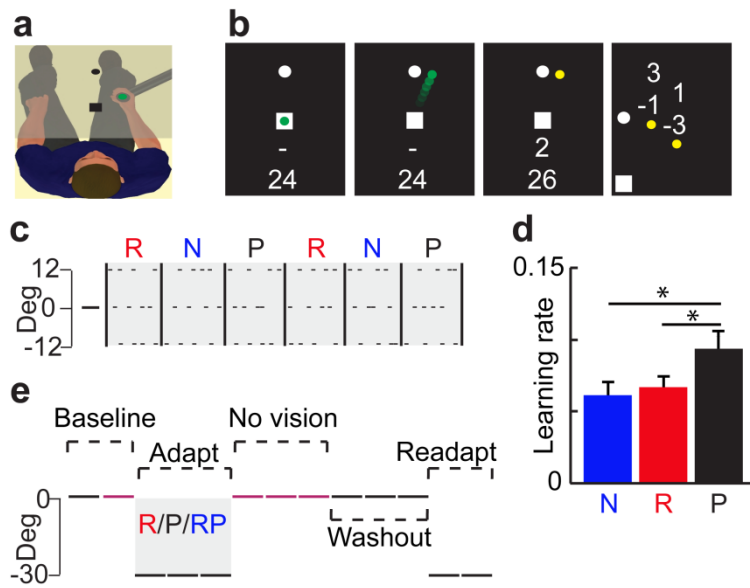
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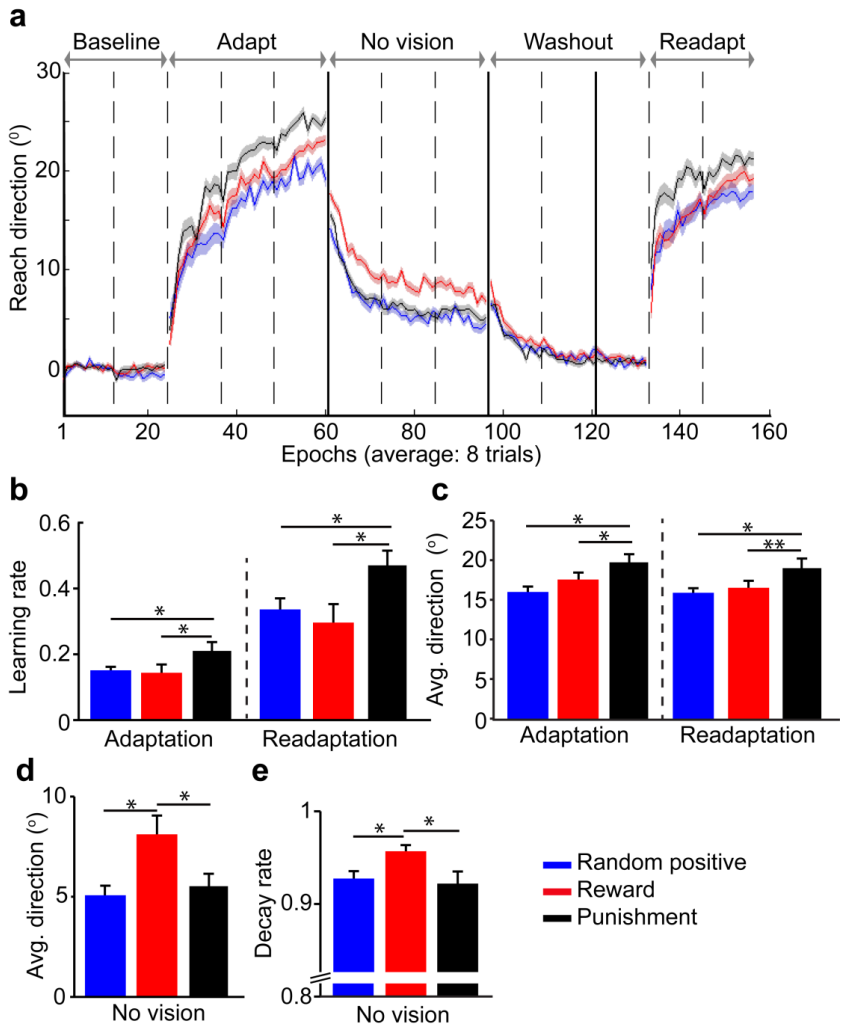
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**Fig.1**

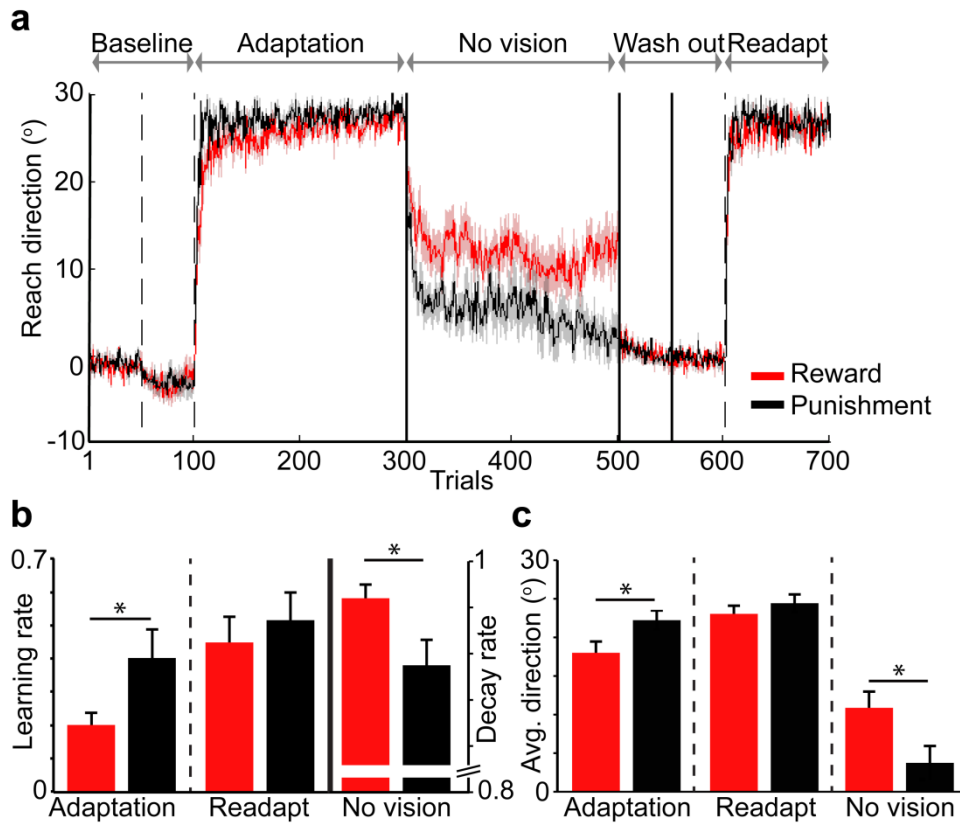


**Fig.2**

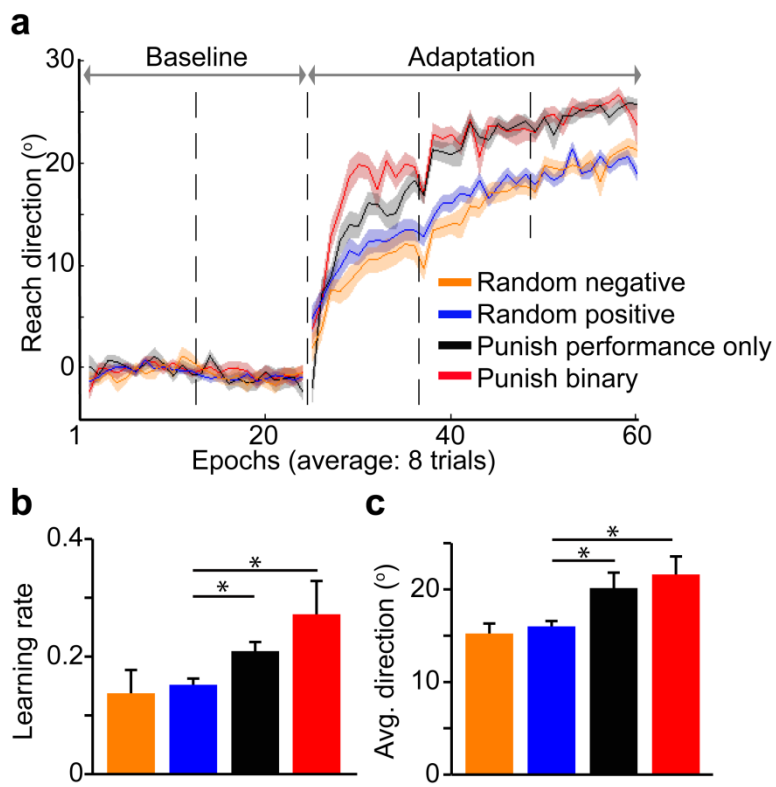




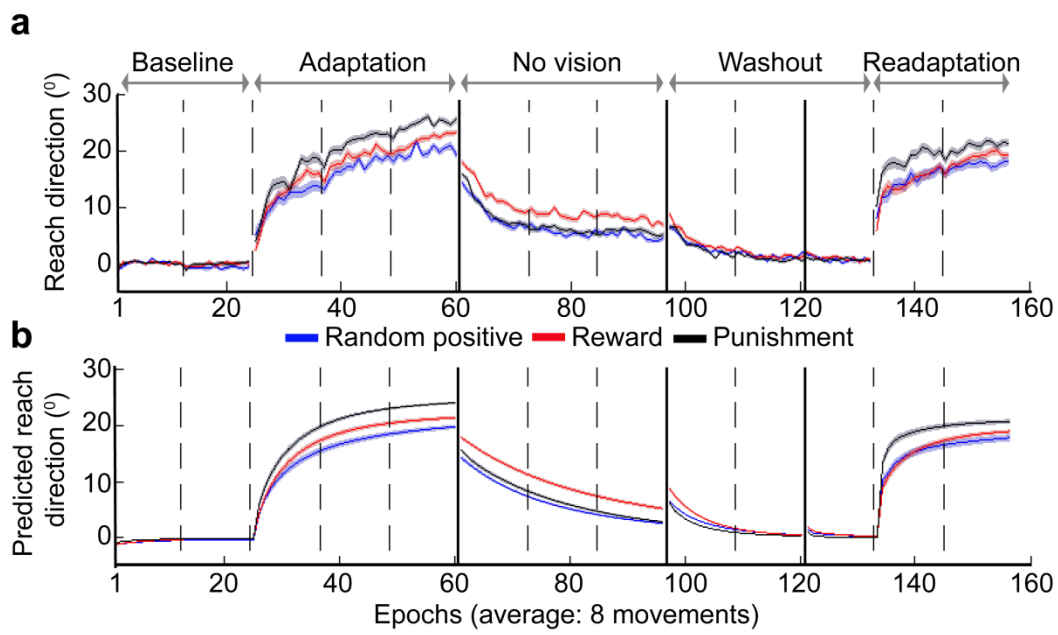
**Fig.3**



**Fig.4**



Supp.1



Supp.2

