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The dissociable effects of punishment and reward on motor learning

Joseph M Galea[1], Elizabeth Mallia[2], John Rothwell[2] & Jörn Diedrichsen[3]

A common assumption regarding error-based motor learning (motor adaptation) in humans is that its underlying mechanism is automatic and insensitive to reward- or punishment-based feedback. 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feedback did not speed up learning, but it increased retention of the motor memory when performance feedback was withdrawn.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 raise new questions regarding the neural basis of negative and positive motivational feedback in motor learning.

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

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[14,15], which encodes aversive stimuli[16] and negative behavioral outcomes[17] and which is essential for aversive conditioning[18]. Therefore, we predicted that error-based motor learning would be enhanced by the punishment of movement errors[19]. In contrast, the retention of a motor memory depends on the primary motor cortex (M1)[14,20,21]. Neurons releasing the neuromodulator dopamine, vital for reward-based learning[22,23], have projections to M1 (ref. 24) that are crucial for long-term M1-dependent motor skill retention[25,26]. Consequently, we predicted that memory retention would be enhanced following reward[27], possibly through reward-related dopaminergic signaling to M1 (ref. 28).

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[29]. 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 implications for the understanding and optimization 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 task that is thought to be entirely automatic and nonstrategic[30]. In experiment 1, we therefore exposed participants to randomly alternating visuomotor rotations during a reaching task in which the aim was to strike through a visual target as accurately as possible (**Fig. 1a**,**b**). Although the perturbation on one trial did not predict 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 behavior was adjusted on the basis of each performance error (learning rate; SSM parameter B) and the degree of memory decay on each trial (decay rate; SSM parameter A)[30,31] (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 on the basis of the accumulated positive points and lost money during punishment blocks on the basis of the accumulated negative points. In contrast, during the null blocks, the graphical representations of these points were replaced by two uninformative horizontal lines[7] (Online Methods). We observed a significantly greater learning

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[1]School of Psychology, University of Birmingham, Birmingham, UK. [2]Sobell Department for Motor Neuroscience and Movement Disorders, Institute of Neurology, University College London, London, UK. [3]Insititute of Cognitive Neuroscience, University College London, London, UK. Correspondence should be addressed to J.M.G. (j.galea@bham.ac.uk).

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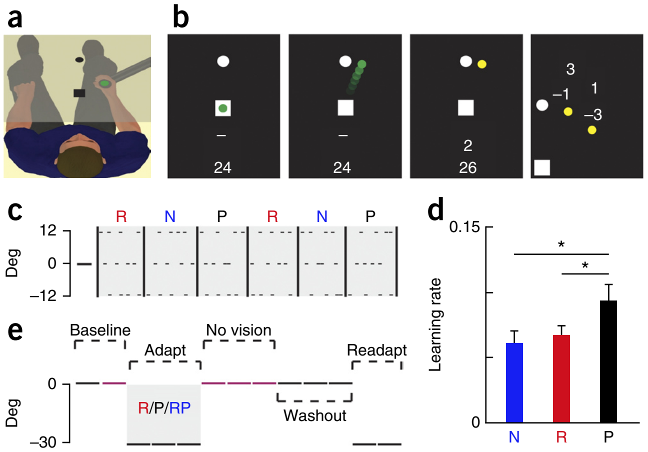

Figure 1 Experimental design. (**a**) Experimental apparatus. Participants made reaching movements toward visual targets presented on a screen. (**b**) Experimental task. Shooting reaching movements were performed with online (green) and endpoint (yellow) feedback. Reward and punishment feedback were represented by positive and negative points and based on endpoint error. (**c**) Experiment 1: one-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 (R), punishment (P) or null (N) motivational feedback. (**d**) Experiment 1 ($n = 12$). Punishment was associated with greater trial-by-trial learning relative to either reward or null (SSM parameter B). $^*P < 0.05$. Error bars, s.e.m. (**e**) Experiment 2: eight-target adaptation to a fixed 30° CCW (negative) visuomotor rotation. Participants experienced 13 blocks (horizontal lines: 96 trials) that were separated by short rest periods (<1 min). Shaded gray: participants received reward (R), punishment (P) or random positive (RP) feedback during adaptation (adapt). Blocks 2 and 6–8: online and end-point visual feedback were removed (no vision; purple). Readaptation (readapt) involved a 30° CCW visuomotor rotation, with reward or punishment no longer provided.

rate during punishment blocks (SSM parameter B: $F_{2,22} = 4.30$, $P = 0.027$) relative to reward ($t_{11} = 2.27$, $P = 0.045$) or null ($t_{11} = 3.67$, $P = 0.004$) blocks (**Fig. 1d**). In contrast, reward blocks showed an equivalent learning rate to null blocks ($t_{11} = 0.34$, $P = 0.74$). There were no significant differences in reaction time (RT) ($F_{2,22} = 0.26$, $P = 0.77$; punishment, 521 ± 105 ms; reward, 479 ± 91 ms; null, 485 ± 84 ms), movement time (MT) ($F_{2,22} = 0.84$, $P = 0.44$; punishment, 223 ± 12 ms; reward, 216 ± 11 ms; null, 221 ± 9 ms), decay parameter (SSM parameter A: $F_{2,22} = 0.21$, $P = 0.81$; 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 ($z = 0.19$, $P = 0.31$; two-tailed). This suggests that the increased learning rate was unlikely to be a result of participants using a conscious strategy to avoid punishment[10,32]. As the motivational feedback provided no extra 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.

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 an accumulation of memory. To test how punishment or reward influences memory retention, experiment 2 used a block design that allowed learning to accrue (**Fig. 1e** and Online Methods)[14]. 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 (SSM parameter B: $F_{2,41} = 3.77$, $P = 0.032$; **Fig. 2a**,**b** and **Supplementary Fig. 1a**,**b**). Specifically, punishment was associated with faster learning than 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 (SSM parameter A: $F_{2,41} = 0.08$, $P = 0.93$; punishment, 0.957 ± 0.008; reward, 0.956 ± 0.007; random positive, 0.951 ± 0.013). As similar differences in learning rate were observed when a generalization function was added to the

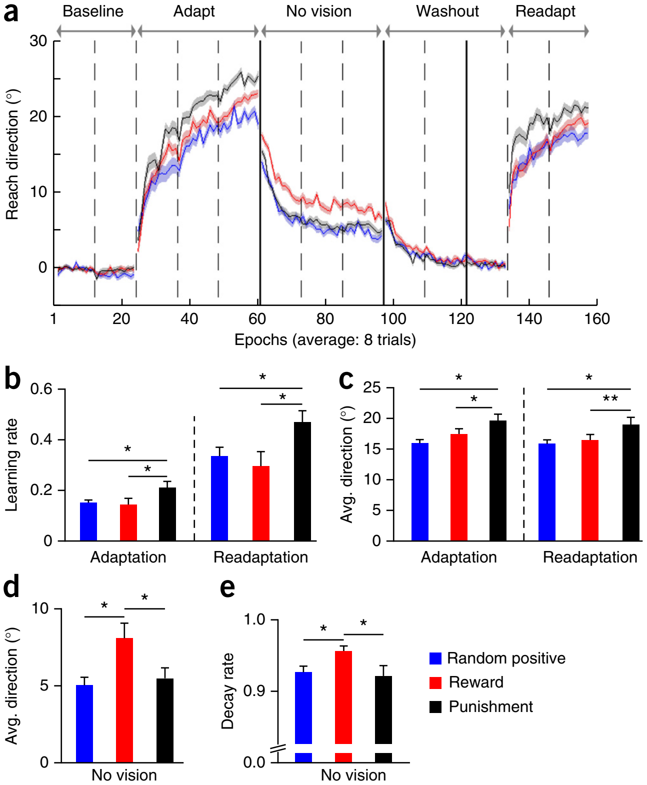

Figure 2 Punishment led to faster learning, while reward caused greater retention during motor adaptation. (**a**) Experiment 2 ($n = 42$). Epoch (average across eight trials) angular reach direction data for the random positive (blue), reward (red) and punishment (black) groups. Dashed and solid vertical lines, short rest periods (<1 min). For each section (vertical solid lines), a separate SSM was estimated. (**b**) The punishment group showed faster learning than the random positive and reward groups during both adaptation and readaptation (SSM parameter B). (**c**) Model-free behavioral 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 (SSM parameter A). $^*P < 0.05$. $^{**}P < 0.06$. Solid lines, mean; error bars or shaded areas, s.e.m.

Table 1 Reaction time and movement time across groups for experiment 2

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

Means ± s.e.m.

SSM (**Supplementary Fig. 2**), we believe that the effects of punishment on adaptation do not depend on specific assumptions about generalization. However, to ensure that differences between the groups did not depend on the choice of model, we performed a model-free analysis in which reach direction was averaged across the adaptation phase[14], excluding the first eight trials (Online Methods). As participants attempted to adapt to a 30° visuomotor rotation, an increased reach angle represented greater learning[14]. 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 ($z = 0.07$, $P = 0.61$; two-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 number of points received or lost on each trial during adaptation was comparable for reward (2.00 ± 0.12) and punishment (−2.05 ± 0.09) ($t_{26} = 0.33$, $P = 0.74$; two-tailed; absolute value used for statistical comparison). Finally, the SPSRQ questionnaire[33] was used to score each participant's sensitivity to reward and punishment. Across participants, there was no overall bias toward either reward or punishment (punishment sensitive, 20; reward sensitive, 19; neutral, 3). In addition, no significant correlations were observed between this score and the participant's SSM learning or decay rate ($z < 0.17$, $P > 0.27$; two-tailed).

Reward caused greater memory retention

Next, we characterized memory retention by measuring the gradual drift back to baseline performance when visual feedback of performance was removed (no vision; **Fig. 1e** and Online Methods)[14]. For the no-vision blocks, the SSM provided a poor fit to the data (**Supplementary Table 1**) 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 second 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 eight trials within the no-vision block (**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 (SSM parameter A: $F_{2,41} = 3.77$, $P = 0.032$) than either the punishment ($P = 0.015$) or random positive ($P = 0.037$) group (indicating increased retention; **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[29]. 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 eight trials of washout, the error was statistically indistinguishable from the last eight 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 ($F_{2,39} = 0.46$, $P = 0.63$). Additional positive or negative feedback was not provided during readaptation. Despite this, the SSM estimates showed that the punishment group adapted significantly faster (SSM parameter B: $F_{2,41} = 4.05$, $P = 0.025$) than the reward ($P = 0.010$) or random positive ($P = 0.042$) group (**Fig. 2b**). In the presence of a directional error signal, the decay parameter was similar across groups (SSM parameter A: $F_{2,41} = 1.25$, $P = 0.30$; punishment, 0.794 ± 0.042; reward, 0.881 ± 0.023; random positive. 0.848 ± 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

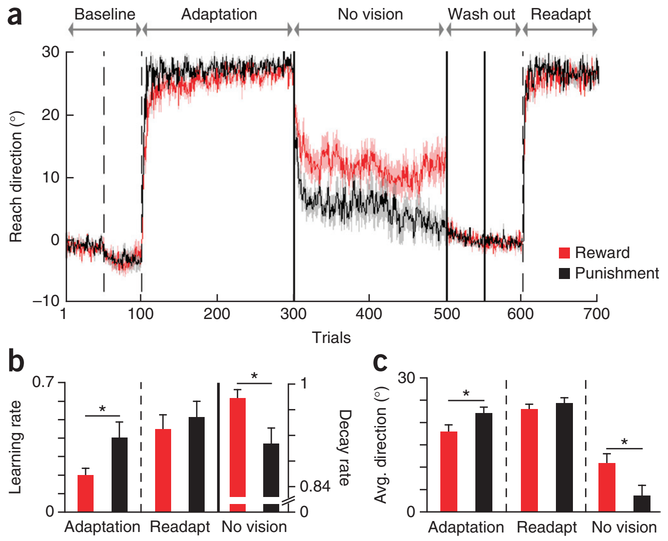

Figure 3 Replication of the double dissociation between reward and punishment using a one-target design. (**a**) Experiment 2 using a one-target design ($n = 22$). Trial-by-trial angular reach direction data for reward (red) and punishment (black). Dashed and solid vertical lines, short rest periods (<1 min). For each section (vertical solid lines), a separate SSM was estimated. (**b**) The punishment group showed faster learning than the reward group during adaptation but not readaptation (SSM parameter B). During no vision, reward was associated with a larger decay rate (signifying increased retention) than punishment (SSM parameter A). (**c**) Model-free behavioral 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 or shaded areas, s.e.m.

Table 2 Reaction time and movement time across groups for one-target control experiment

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

Means ± s.e.m.

phase, except the first eight 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**).

Replication of the double dissociation using a one-target design

In experiment 2, we used eight targets to make the use of strategic components of adaptation less likely. However, we wanted to ensure that our results generalized to a single-target task as was used in experiment 1. Therefore, we decided to replicate experiment 2 using a one-target design, also making the study more comparable to existing literature on motor memory retention[27,34] (Online Methods). Once again, punishment led to a faster learning rate during adaptation (SSM parameter *B*: independent *t*-test: $t_{20} = 2.16$, $P = 0.044$; two-tailed; **Fig. 3a**,**b**). However, we observed no significant difference during readaptation ($t_{20} = 0.59$, $P = 0.57$). Because adaptation rates were much higher than in the eight-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 (SSM parameter *A*: $t_{20} = 0.31$, $P = 0.76$; reward, 0.969 ± 0.008; punishment, 0.966 ± 0.006) and readaptation ($t_{20} = 0.33$, $P = 0.74$; reward, 0.937 ± 0.014; punishment, 0.944 ± 0.014). These results were confirmed using a model-free analysis: the average reach angle was larger in the punishment than the reward group ($t_{20} = 2.22$, $P = 0.038$; two-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 behavior did not decay back to baseline. The model-free analysis showed that the average reach angle during the second half in 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 behavior, the decay parameter was significantly larger (indicating increased retention) than in the punishment group (SSM parameter *A*: $t_{20} = 2.58$, $P = 0.018$; **Fig. 3b**). Finally, there were no significant differences between groups for either RT or MT during the main experimental blocks (**Table 2**). These results replicate the double dissociation whereby punishment led to faster learning and reward caused greater retention.

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. To understand this result in more detail, we performed experiments with three more control groups using the eight-target design.

First, it is possible that the graded feedback provided during punishment acted as an additional error signal that 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 (binary punishment; Online Methods). This group showed a significantly faster learning rate when compared to the random positive group (SSM parameter *B*: independent *t*-test: $t_{20} = 2.63$, $P = 0.016$; two-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 (SSM parameter *A*: $t_{20} = 0.53$, $P = 0.61$; binary punishment: 0.9600 ± 0.008;). Therefore, the beneficial influence of negative feedback is consistent across binary and graded feedback.

Negative feedback need not 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 (punish performance only; Online Methods). Once again, this group showed significantly faster learning during adaptation relative to the random positive group (SSM parameter *B*: independent *t*-test: $t_{20} = 2.67$, $P = 0.014$; two-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 (SSM parameter *A*: $t_{20} = 0.11$, $P = 0.92$; punish performance only, 0.953 ± 0.011). This suggests that for young, healthy participants, negative feedback

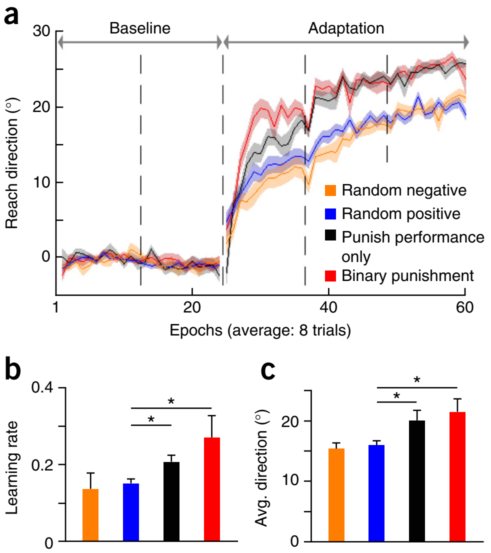

Figure 4 Direct negative feedback related to poor performance is the critical factor that increases learning rate. (**a**) Experiment 2: control conditions (*n* = 24). Epoch (average across eight trials) angular reach direction data for the control conditions: random negative, the original random positive group, punishment performance only and binary punishment. Dashed vertical lines indicate short rest periods (<1 min). (**b**) Punish performance only and binary punishment were associated with a higher rate of learning than random positive (SSM parameter *B*). There was no significant difference between random negative and random positive ($P = 0.64$). (**c**) Model-free behavioral analysis revealed similar differences between groups. Specifically, punishment performance only and binary punishment led to greater learning (increased reach angle) during adaptation. Solid lines, mean; error bars or shaded areas, s.e.m. $^{*}P < 0.05$.

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 during adaptation (random negative; Online Methods). If the sign (positive or negative) 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 (SSM parameter *B*: independent *t*-test: $t_{20} = 0.47$, $P = 0.64$; two-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 (SSM parameter *A*: $t_{20} = 0.90$, $P = 0.38$; random negative, 0.913 ± 0.05). This demonstrates that negative points unassociated with performance or monetary incentive failed to enhance the rate of learning.

Finally, we compared the three punishment groups' (punishment, punish performance only, binary punishment) learning rates. We found no significant differences (learning rate parameter *B*: $F_{1,29} = 1.04$, $P = 0.37$), suggesting that direct negative feedback related to poor performance was the critical factor that increased the rate of motor learning.

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 for how punishment could accelerate motor adaptation. First, negative feedback signals may have increased cerebellar sensitivity to sensory prediction errors (SPE)—that is, the directional mismatch between the expected and the perceived location of the cursor[11,35]. Alternatively, a punishment prediction error (PPE), which signals the unexpected loss of points or money[1,19], could have led to greater behavioral exploration[36,37] and thereby increased the speed with which the correct solution was found[38,39]. 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[8]. 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 binary punishment led to a similar, if not greater, effect on the rate of learning. Finally, we did not observe any sign of increased output variability (that is, decreased goodness of fit) or increased reaction time for any of the punishment groups. As cerebellar function is sensitive to negative behavioral outcomes[17] and aversive stimuli[16], we believe that the punishment-induced improvements in error-based learning were a direct outcome of the cerebellum being more sensitive to an SPE associated with negative stimuli. In other words, a negative motivational signal may directly enhance cerebellum-dependent SPE learning[19], possibly through increased levels of serotonin in the cerebellum[40].

Loss aversion

Loss aversion describes the behavioral avoidance of choices that can lead to losses, even when accompanied by equal or larger gains[41,42]. Across many studies, losses typically loom about 1.5–2 times as large as gains, with loss aversion being well documented in the laboratory[42] and in many field settings[43,44]. Therefore, loss aversion may have contributed to the punishment results. However, 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 that 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 informative, however, to further examine the relationship between learning and the magnitude of reward and punishment provided[45].

Reward caused greater memory retention

Reward-based feedback during adaptation led subsequently to greater retention when the directional feedback was fully withdrawn (no vision). Previous work has shown that positive reinforcement can influence both online (retention across trials) and offline (retention across time) motor retention[7,27,46]. 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)[7] and on the rate of memory decay across errorless performance (online)[27]. 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 M1 is essential for the retention of motor adaptation[20,47]. Neurons releasing the neuromodulator dopamine, vital for reward-based learning[22,23], are known to have projections to M1 (ref. 24) that are crucial for long-term M1-dependent motor skill retention[25,26]. Therefore, the improvement in motor memory retention could be a result of reward-related signals to M1 during adaptation[28].

Previous work on reward and punishment in motor learning

Two previous studies have investigated the influence of reward and punishment on motor learning. Wächter *et al.* found that during implicit sequence learning, punishment led to significantly better online motor performance, whereas reward was associated with greater learning and retention[6]. Abe *et al.* studied motor skill learning and found that while reward enhanced memory retention, punishment was not associated with any significant changes in behavior[7]. Therefore, it seems reward enhances memory retention across multiple motor learning models. 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[27,34,48]. 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[27,48]. For instance, the use of reward has been suggested to have significant implications for stroke rehabilitation, where motor learning interventions struggle to produce long-term changes in behavior[49]. 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 behavior has been reached, reward signals could be introduced to facilitate the retention of the newly acquired behavior.

METHODS

Methods and any associated references are available in the online version of the paper.

Note: Any Supplementary Information and Source Data files are available in the online version of the paper.

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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. analyzed data. J.M.G., E.M., J.R. and J.D. wrote the paper.

COMPETING FINANCIAL INTERESTS

The authors declare no competing financial interests.

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ONLINE METHODS

Participants. All of the 100 young individuals (22 ± 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, University College London and University of Birmingham.

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 fast, 8-cm shooting movements toward 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 semi-pronated 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 consisted of a 1-cm-diameter starting box, a green cursor (0.3 cm diameter) representing the position of the manipulandum, and a circular white target (0.5 cm diameter). During experiment 1, the target was located 8 cm vertically in front (on the screen) of the starting box. During experiment 2, a target was displayed in one of eight positions arrayed radially at 8 cm from the central starting box. At the start of each trial, the participant moved the cursor into the start box and 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 (an invisible circle centered 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 color based on movement speed. If the movement was completed within 100–400 ms, then it remained white. If the movement was slower than 400 ms, then the box turned red (too slow). The participants were 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 eight consecutive trials included one 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 points: hit the target; 3 points: <10° error; 2 points: <20° error; 1 point: <30° error; 0 points: ≥30° error.

Punishment. 0 points: hit the target; −1 point: <10° error; −2 points: <20° error; −3 points: <30° error; −4 points: ≥30° error.

Null. Points were replaced by two uninformative horizontal lines.

Random positive. A random number between 0 and 4 was presented that had no monetary value and was not associated with performance.

Participants began each block with 0 points. These points accumulated across the block. However, the reward and random positive groups 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 or block earned money based on the accumulated points (winning 1 pence per positive point), whereas the punishment group or block lost money based on the accumulated negative points (losing 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 (**Fig. 1b**). Thus, differences between random positive and either reward or punishment feedback would suggest that the points had to be directly associated with performance or monetary incentive. Finally to ensure similar attention, participants were required to report the points total at the end of each block.

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

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

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

Adaptation. Three blocks with 30° CCW visuomotor rotation. Depending on the group, the points system was reward, punishment or random positive. Motivational feedback was provided only during adaptation.

No vision. Three 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. Three blocks with veridical visual feedback. Null feedback.

Readaptation. Two blocks with 30° CCW visuomotor transformation. Null feedback.

Each block was separated by a short rest period (<1 min) in which participants were instructed to maintain their arm underneath the mirror. Unlike in previous work[7], improvements in readaptation could only be attributed to faster relearning, as we ensured complete washout. 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 was given £12 before the start of the task and 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 was explicitly instructed of both the points-error relationship and the maximum points and money they could win or lose (£11.52) across the three blocks of adaptation.

One-target. In experiment 2, we used eight targets to make the use of strategic components of adaptation less likely[10]. However, we wanted to ensure that our results generalized to a single target paradigm as was 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[34]. A reward and punishment group ($n = 22$) were tested on a task that was identical to that in experiment 2 except that 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 than in 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 8 cm in front of the starting box, as in 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.

Binary punishment. 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 (±5°) and −1 for any error above this value. Each negative point was related to losing 1 pence, with participants beginning with £8. Note that for all remaining control groups, only the two 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 ($n = 8$) was exposed to random but negative points (random negative) during adaptation. If the sign (positive or negative) of the points was important, rather than them being related to performance or money, then this random negative group should show significantly faster learning during adaptation.

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

Data analysis. Reach position data (x,y) was collected at 100 Hz. Data and statistical analysis was performed using Matlab (The MathWorks, Natick, USA). For each trial, angular reach direction (°) 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 centered on the starting position. During veridical feedback, the goal was for reach direction to be 0°. However, with a visuomotor transformation, reach direction had to compensate; that is, for a −30° (CCW) visuomotor rotation, a reach direction of +30° (CW) was required. In addition, reaction time (RT: difference between target appearing and movement reaching 10% of maximum velocity) and movement time (MT: 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° (ref. 51) or MT exceeded 600 ms. This accounted for less than 4% of trials.

Model-based analysis. We analyzed the trial-by-trial angular reach direction in response to the visuomotor transformations using a single-rate state-space model[30,31,48,52]. The application of such a model was necessary to allow 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 analyze the behavioral data by averaging the reaching angle across certain phases of the task[53]. 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 or 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 two-rate state-space model[34]. 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:

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

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

$\hat{y}_n$ 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[48]. 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[54].

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 generalization function that determines how much error in one target direction affects mapping estimates in neighboring directions[30,48]. Initially, we assumed no generalization between target positions that were 45° apart; however, we return to this issue in **Supplementary Figure 2**. 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 analysis. To ensure that differences between the groups were not solely dependent on the model, we performed behavioral (model-free) analysis in which the angular reach direction (°) was averaged across trials. The specific trials were chosen in an attempt to reflect either the learning component during re/adaptation[53] or the retention component during no vision[27]. For the adaptation and readaptation blocks in the eight-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 second half of the no-vision trials. In the one-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 three 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 (five blocks), no vision (three blocks) and washout (last block)/readaptation (three 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; that is, 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-subjects ANOVAs followed by Tukey *post hoc* tests.

No statistical methods were used to predetermine sample sizes, but our sample sizes are similar to those reported in previous publications[38,48,53]. Epoch data shown in figures depicts the average angular reach direction across eight movements (one movement toward each target). Significance level was set at $P < 0.05$. All data are reported as mean ± s.e.m. across subjects.

A **Supplementary Methods Checklist** is available.

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