Rewarding feedback promotes motor skill consolidation via striatal activity

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Abstract

Knowledge of performance can activate the striatum, a key region of the reward system and highly relevant for motivated behavior. Using functional magnetic resonance imaging, striatal activity linked to knowledge of performance was measured during the training of a repetitive arc-tracking task. Knowledge of performance was given after a random selection of trials or after good performance. The third group received knowledge of performance after good performance plus a monetary reward. Skill learning was measured from pre- to post- (acquisition) and from post- to 24 h posttraining (consolidation). Our results demonstrate an influence of feedback on motor skill learning. Adding a monetary reward after good performance leads to better consolidation and higher ventral striatal activation than knowledge of performance alone. In turn, rewarding strategies that increase ventral striatal response during training of a motor skill may be utilized to improve skill consolidation.

Keywords

Motor skill learning, Monetary reward, Performance feedback, Knowledge of performance, fMRI, Striatum, Pointing task, Consolidation

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[*]Deceased July 26, 2014.

Abbreviations

fMRI	functional magnetic resonance imaging
GLMM	generalized linear mixed model

1 INTRODUCTION

Extrinsically motivated actions, are performed because they lead to an outcome, eg, to a reward (Ryan and Deci, 2000). By increasing the extrinsic subjective value, rewards augment the overall subjective benefit of a task, making people tolerate higher subjective costs, and are thus traditionally defined as stimuli an organism is willing to work for (Knutson and Cooper, 2005; Lutz and Widmer, 2014). Intrinsic motivation, on the other hand, refers to doing something because it is inherently interesting or enjoyable, which is influenced by factors such as the subject's perceived autonomy, competence for or relatedness to a task (Ryan and Deci, 2007). Similar to motivation, reward can be classified as extrinsic or intrinsic (Deci et al., 1999, 2001; Reitman, 1998). While extrinsic reward refers to the receipt of material (eg, food or money) for a specific activity, the term "intrinsic reward" refers to reward derived from task inherent stimulation (eg, information about an achieved performance, watching a self-painted picture, or feeling self-produced movements). Evidence from behavioral studies implies that extrinsic reward might undermine intrinsic motivation and thus may lead to a decrease in performance (Callan and Schweighofer, 2008; Deci et al., 1999; Kohn, 1999; Murayama et al., 2010; Spence, 1970). For instance, the time children spend drawing decreases below baseline after this behavior had been (externally) rewarded and the reward has then been withdrawn (Greene and Lepper, 1974).

In experiments using functional magnetic resonance imaging (fMRI), both intrinsic and extrinsic (performance-dependent) reward have been shown to increase the neural activity in the striatum (Lutz et al., 2012), a key locus of reward processing (Knutson et al., 2008). In these experiments, only the ventral striatum was active during performance feedback, while feedback plus monetary reward activated both ventral and dorsal parts of the striatum. However, other studies found activation elicited by feedback alone also in the dorsal striatum (Poldrack et al., 2001; Tricomi and Fiez, 2008; Tricomi et al., 2004, 2006). Furthermore, dorsal striatal activity was shown to be modulated by the subject's sense of agency for having achieved a goal (Han et al., 2010; Tricomi and Fiez, 2008).

Previous research has investigated the influence of feedback and reward on the acquisition of cognitive tasks, eg, decision-making paradigms (den Ouden et al., 2013; Frank et al., 2004; Robinson et al., 2010). Our animal studies suggest that dopaminergic signals originating in reward-coding brain regions (ventral tegmental area) are required for motor skill acquisition. In rodents, dopaminergic projections from the ventral tegmental area to the primary motor cortex enable motor learning and long-term potentiation in cortico-cortical projections (Hosp et al., 2011;

Molina-Luna et al., 2009). These projections are not necessary for task execution (Molina-Luna et al., 2009). We hypothesize that this system can be used to facilitate motor skill learning by amplification of rewarding stimuli.

Indeed, recent work suggests positive effects of monetary reward on procedural (Wachter et al., 2009) and skill motor learning (Abe et al., 2011) as well as on motor adaption (Galea et al., 2015). Notably, all of these studies reported dissociable effects of positive and negative reward, and the latter two found positive reward to impact task consolidation/retention. Moreover, the reward-related learning effect reported by Wachter et al. (2009) was found to be mediated by the dorsal striatum. However, these studies exclusively used money as an extrinsic reward, albeit, as illustrated earlier, also intrinsic rewards (eg, knowledge of performance) were shown to activate the human reward circuits and thereby possibly influence motor learning.

Dopaminergic neurons in the midbrain signal outcomes that are better than expected (positive prediction error (Schultz, 2000)). Being informed about unexpectedly good performance may thus cause a positive prediction error. Indeed, only being informed about positive task outcome resulted in better performance than being informed about the outcome of poorly solved trials (Chiviacowsky and Wulf, 2007). Whether these findings come along with higher reward activity after good performance feedback remains to be elucidated.

In the present study, a modified version of the arc-pointing task that involves a visually guided precision movement of the wrist (Shmuelof et al., 2012) was used to test the hypothesis that striatum activation is increased if knowledge of performance is given after good performance instead of a random selection of trials. Adding a performance-dependent monetary reward was expected to further increase this activation. In addition, we hypothesized that motor skill learning is improved in conditions with enhanced striatum activity.

2 METHODS
2.1 PARTICIPANTS

Forty-five healthy right-handed volunteers (22 females, 20–34 years of age, 24.5 years on average; Table 1) participated in this study that was approved by the cantonal ethics committee (KEK-LU 13054). Hand preference and dominance were

Table 1 Subject Characteristics

	Overall	KP$_{random}$	KP$_{good}$	KP$_{good}$ + MR
N (Dropouts)	44 (1)	15 (—)	14 (1)	15 (—)
Age (SD)	24.5 (3.2)	25.9 (2.8)	25.1 (3.7)	22.9 (2.5)
Sex, male/female	23/21	7/8	7/7	9/6

N reports the number of subjects per group with dropouts listed in brackets. SD is standard deviation. Note that groups were allocated randomly, not by matching any of the reported characteristics.

assessed using the Edinburgh Handedness Inventory (Oldfield, 1971) and the Hand Dominance Test (Steingruber and Lienert, 1971), respectively, confirming that all participants were classified as right handed. Subjects were recruited from the University community or shared a similar educational status. They were not specifically skilled or trained in comparable motor tasks. All participants gave written informed consent before being randomly assigned to one of three groups. Allocation was according to a computer-generated random number sequence. Subjects were unaware of the other groups and the scientific rationale of the study. All subjects received financial compensation in comparable amounts, but only for one group payments depended on individual performance during the training of the motor task.

2.2 STUDY DESIGN

Subjects participated in the study for 2 consecutive days. Neutral (group-independent) test sessions were performed to assess momentary performance on day 1, before and after the group-specific training. To assess overnight task consolidation, subjects returned 20–28 h after finishing day 1 training.

2.3 MOTOR TASK

Originally, the arc-pointing task (Shmuelof et al., 2012) was developed to investigate the speed-accuracy trade-off function during motor skill learning. To examine the influence of knowledge of performance with or without monetary reward on brain activity and motor skill learning, we modified the task. Here, the task required subjects to perform wrist movements to steer a cursor on a computer screen through a semicircular channel (Fig. 1). To maximize the dynamic range of learning the nondominant left rather than the right wrist was chosen assuming that initial performance would be worse with the left. Ideally, the cursor had to be guided along the middle of an arc-channel with the nominal movement speed dictated by a clock hand pointing at the current nominal position (Fig. 2A). For each frame (at 60 frames per second), the absolute distance from the actual to the nominal position was calculated and the average over the whole movement was used as performance measure to determine a score (with or without monetary consequences, Fig. 2B).

Prior to each new block of movements, subjects viewed a computer-generated demonstration of the clock hand moving along the channel in the required movement time. At the beginning of each trial, subjects placed the cursor in the red starting box. After a variable delay (800–1600 ms), the box turned green as an "ok-to-go" signal (reaction time was not a measure of performance and subjects were told to start any time after the box turned green). As soon as the cursor had left the box in positive y-direction (=upward), the clock hand started to move with uniform angular velocity continuously pointing at the nominal cursor position that subjects tried to adhere to. The cursor was visible throughout the movement (online feedback; Fig. 2A) and the trial automatically ended when the clock hand arrived at the end of the channel. Then the screen froze for a variable period of time (500–4500 ms). During test sessions,
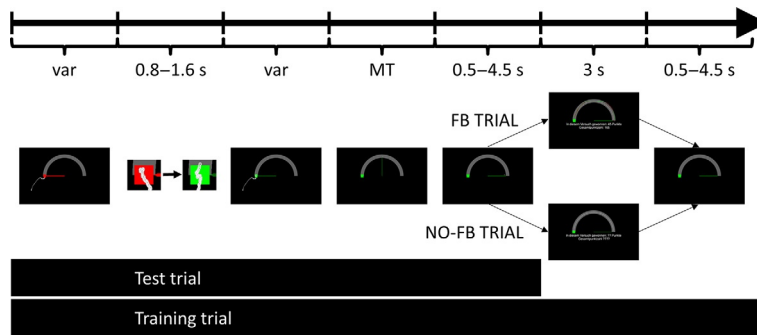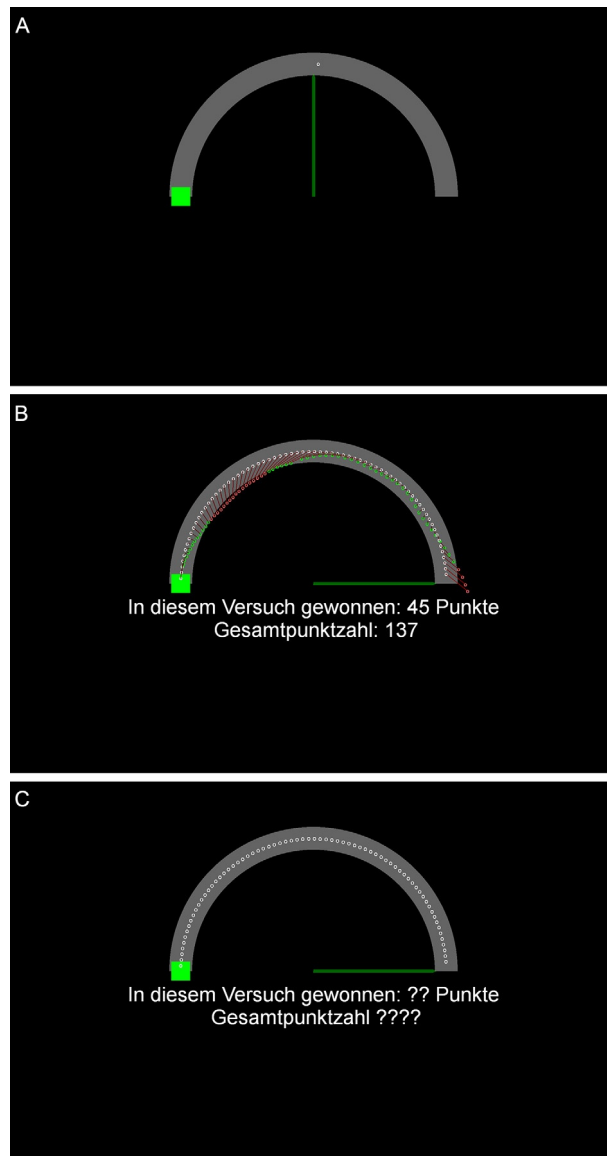
FIG. 1

Trial sequence. After placing the cursor in the start box, the box eventually turned *green* ("ok-to-go" signal) and subjects were free to start the movement whenever ready. The placing of the cursor in the start box, as well as the period from "ok-to-go" to the actual start of the movement were self-paced and hence of variable length (var). A specific movement time (MT) according to the speed requirements of the current block of trials was allowed to steer the cursor through the semicircular channel. As soon as movement time elapsed, the screen froze. During test sessions, the next trial directly followed. In case of a training trial, a group-specific knowledge of performance feedback was presented after feedback trials (FB TRIAL), or subjects were shown a neutral visual control stimulus after no-feedback trials (NO-FB TRIAL). Either way, the next training trial began after another delay period.

the subsequent trial directly followed. For training trials knowledge of performance or knowledge of performance plus monetary reward was presented for 3000 ms at this point, followed by another variable delay period (500–4500 ms) before the subsequent trial began. Fig. 1 shows a schematic summary of the paradigm.

To assess skill level in the absence of knowledge of performance and monetary reward, participants had to perform the arc-pointing task at five different movement speeds defined by the movement time that was allowed to move the cursor through the arc-channel (the clock hand uniformly travelled along the arc in exactly that time). Per test session, seven consecutive trials were performed as blocks with one of five movement times (movement time in ms: 800, 1000, 1200, 1400, and 1800) and these blocks were randomly ordered with 15 s breaks in between. Ten familiarization trials were allowed prior to the very first test session (ie, pretraining test) and, as already mentioned, a demonstration of the movement time was shown at the beginning of each movement time block. All in all, participants performed 35 trials per test session.

The training, on the other hand, was composed of five blocks of 50 trials each with 15 s breaks after 25 movements (within blocks) and 2 min breaks between the blocks. All 250 training trials were performed at one single movement time (ie, 1200 ms). After a movement, subjects received a terminal feedback by ~50% chance. Here, the three groups differed in terms of the selection of feedback trials

FIG. 2

(A) During the movement, the position of the cursor was indicated with a *white circle* (online feedback) and a clock hand continuously pointed at the current nominal position, which was defined to be in the middle of the semicircular channel. (B) A knowledge of performance feedback was presented after feedback trials, including the trajectory traveled by the cursor (series of *green* (inside of channel) or *red* (outside of channel) *colored circles*), as well as the nominal trajectory (series of uniformly distributed *white circles*). A *red line*

and in terms of the type of feedback they were given. While the first group received knowledge of performance after randomly selected trials (KP_{random}), the other groups got either knowledge of performance only (KP_{good}) or knowledge of performance signifying a monetary reward ($KP_{good}+MR$) after relatively good performance, ie, when they performed better than the moving median over their performance in the last 10 trials. As described earlier, the tip of the clock hand pointed at the nominal position for each frame during a trial and the cursor's mean distance ($\bar{d}$) to the corresponding nominal position over all 72 frames per training trial (1200 ms at 60 frames per second) was used as measure to quantify performance.

$$\bar{d}_t = \frac{\sum_{f=1}^{72} d_f}{72},$$

where t is the number of the current trial and f stands for frame number. For members of KP_{good} and $KP_{good}+MR$, hence, a feedback was delivered from the 11th trial on, if $\bar{d}_t < \tilde{d}\left\{\bar{d}_{t-1}, \bar{d}_{t-2}, \ldots \bar{d}_{t-10}\right\}$, where $\tilde{d}$ is the median value. If selected as feedback trial, the feedback included, as a still image, the presentation of the trajectory traveled by the cursor as a series of circles that were colored according to their positions with respect to the channel (green if inside and red if outside of the channel). Moreover, the nominal trajectory was drawn as a series of equally spaced white circles along the middle of the channel and circles of the trajectory traveled by the cursor were linked to the corresponding nominal position by red lines (line width $= 2$ pixels ≈ 0.02 degree visual angle) to visualize d_f (Fig. 2B). Additionally, a score-feedback, for KP_{random} and KP_{good}, and a monetary reward, for $KP_{good}+MR$, was calculated based on $\bar{d}_t$. The relation between $\bar{d}_t$ and the monetary reward was chosen, based on pilot measurements, to allow members of $KP_{good}+MR$ to earn approximately 50 Swiss Francs (CHF; approx. 50 US Dollars) over the course of the experiment, since their minimal financial compensation was fixed to be 50 CHF less than that of KP_{random} and KP_{good}, if performance-related monetary rewards are not considered. Therefore, the monetary reward in Rappen (1 Rappen $= 0.01$ CHF; approx. 0.01 US Dollars) was set to be equal to $100 - \bar{d}_t/2$, if $\bar{d}_t < 200$ pixels, and 0 if $\bar{d}_t \geq 200$ pixels. Accordingly, a maximum of 1 CHF per trial could be won in the unrealistic case of perfect performance (ie, $\bar{d}_t = 0$). Note that no money was deducted after poor

linked each point of the cursor's trajectory to its corresponding nominal position and the average length of these lines was used to determine a score (for KP_{random}- and KP_{good}-groups) or a monetary reward (for $KP_{good}+MR$). "In diesem Versuch gewonnen: 45 Punkte" is the German expression explaining that the subject has won 45 points in the preceding trial, which, in this example, sums up to a total score of 137 over the whole experiment (Gesamtpunktzahl: 137). The neutral visual control stimulus presented after no-feedback trials is shown in (C). Note that the traveled trajectory was omitted and numbers specifying the score or monetary reward were replaced by question marks.

performance. Knowledge of performance for KP_{random} and KP_{good} was equally calculated, but its unit was points instead of Rappen, and for all groups the result of the current trial as well as the sum over the whole course of the experiment (money in CHF) was presented after feedback trials (all in letters and digits of $\approx 0.38°$ visual angle; Fig. 2B). In case of no-feedback trials, subjects were shown a similar screen in which scores or monetary rewards were replaced by question marks and only the nominal trajectory was presented. This ensured a comparable visual stimulus to the feedback conditions (no-feedback screen; Fig. 2C).

2.4 fMRI MEASUREMENTS

During the experiment, subjects lay supine in the MR scanner having their left forearm fixated with a customized armrest that was screwed on to the scanner table. A spherical reflective marker was attached to the proximal interphalangeal joint (knuckle) of their left index finger using surgical double-sided adhesive tape. An MRI-compatible motion capture camera set (Oqus MRI, Qualisys AB, Gothenburg, Sweden) consisting of eight cameras was used to continuously track the marker position at a frequency of 400 Hz. This information was imported online into Matlab R2012b (Mathworks Inc., Natick, MA, USA) using the Qualisys Matlab plug-in. A computer program written in "Presentation 16.3" software (Neurobehavioral Systems, Inc., Albany, USA) sampled the Qualisys-marker position via Matlab interface and transformed it into screen coordinates. To do so, in a calibration step, subjects were asked to move their wrist maximally in all directions having arm movements prevented by the aforementioned armrest. During this step, extreme x- (left-right) and y-positions (up–down) were logged and the screen was adjusted to display, in x- and y-direction, the middle 60% of each subject's individual range of motion. This procedure ensured that all participants were able to perform the required movements within a comfortable movement range.

The computer program also controlled stimulus presentation. While moving within the calibrated area, the marker position was displayed as a circle ($\approx 0.13°$ visual angle) on a screen (0.64×0.4 m; 1920×1200 pixels) visible via mirrors to the subject inside the scanner (distance mirror $-$ screen ≈ 1.90 m). The arc was centered around the middle of the screen (origin of ordinates) with an inner and outer radius of 384 ($\approx 3.86°$ visual angle) and 456 pixels ($\approx 4.58°$ visual angle), respectively. However, only the upper arc was used for task execution and all task movements were performed in clockwise direction. To indicate the start position, a red square with the side length equaling the width of the channel (72 pixels $\approx 0.72°$ visual angle) was placed at the beginning of the arc (box-center coordinates: $x = -420$ pixels, $y = 0$ pixels). Finally, a clock hand used to point at the nominal position for each frame during a trial, starting at the origin of ordinates with a length of 384 pixels ($\approx 3.86°$ visual angle) and a width of 10 pixels (≈ 0.10 degree visual angle), completed the visual stimulus presented during each trial.

A Philips Ingenia 3.0T MRI scanner (Philips Healthcare, Best, The Netherlands) equipped with a Philips 32-channel dS head coil was used. During scanning sessions,

head movement was minimized using a cushion and foam material parts. Three-dimensional anatomical images of the entire brain were obtained by using a T1-weighted three-dimensional spoiled gradient echo pulse sequence (180 slices, TR = 20 ms, TE = 2.3 ms, flip angle = 20°, FOV = 220 mm × 220 mm × 135 mm, matrix size = 224 × 187, voxel size = 0.98 mm × 1.18 mm × 0.75 mm). Functional data were obtained in 150 scans per testing session and 317 scans per training block, all consisting of 40 slices (slice thickness 3.5 mm, ascending acquisition order, no interslice-gap) covering the whole brain in oblique acquisition orientation. We used a sensitivity encoded (SENSE, factor 1.8) single-shot echo planar imaging technique (FEEPI; TR = 2.35 s; TE = 32 ms; FOV = 240 mm × 240 mm × 140 mm; flip angle = 82°; matrix size = 80 × 80; voxel size = 3 mm × 3 mm × 3.5 mm) with three dummy scans acquired at the beginning of each run and discarded in order to establish a steady state in T1 relaxation for all functional scans to be analyzed. Moreover, cardiac and respiratory cycles were continuously recorded (Invivo Essential MRI Patient Monitor, Invivo Corporation, Orlando, FL, USA) to allow correction of fMRI data for physiological noise (see Section 2.5).

2.5 ANALYSIS OF IMAGING DATA

Artifact minimization and MRI data analysis were performed using Matlab R2013b and the SPM8 software package (Institute of Neurology, London, UK; http://fil.ion.ucl.ac.uk/spm). All images were realigned to the first volume, normalized into standard stereotactic space (using the EPI-template provided by the Montreal Neurological Institute, MNI brain), resliced to 3 mm × 3 mm × 3 mm voxel size and smoothed using a 6 mm full-width-at-half-maximum Gaussian kernel. Since the interest of this study lay in the activation of rather small brain areas, a 6-mm rather than a larger Gaussian kernel was chosen, providing higher spatial resolution of resulting images and thus smaller partial volume effects in region of interest (ROI) analyses. Correction for physiological noise was performed via RETROICOR (Glover et al., 2000; Hutton et al., 2011) using Fourier expansions of different order for the estimated phases of cardiac pulsation (third order), respiration (fourth order), and cardio–respiratory interactions (first order) (Harvey et al., 2008). The corresponding confound regressors were created using the Matlab physIO Toolbox (Kasper et al., 2009, open source code available as part of the TAPAS software collection: http://www.translationalneuromodeling.org/tapas/). For first level data analysis of the arc-pointing task training, after highpass filtering (cut-off 128 s), an individual statistical general linear model was set up for each subject (Friston et al., 1995) by defining six regressors, corresponding to six recurring conditions per training block. Onsets and durations (in seconds) for each condition were extracted from Presentation-log-files using custom Matlab routines. The first regressor defined, for each trial, the time interval needed to place the cursor into the start box. The second condition started immediately after reaching the box and thus the corresponding regressor included both the planning and the execution of the complete movement (movement phase). This was followed by a period of variable length where subjects

were looking at a still image of the arc waiting to either be shown the feedback screen after feedback trials or the no-feedback screen after no-feedback trials. Feedback screens then have been presented for 3 s and were modeled as separate regressors (feedback presentation and no-feedback presentation). The sixth regressor was a parametric modulation of the feedback regressor by the number of points (when KP_{random} or KP_{good} was presented) or the magnitude of the monetary reward (when $KP_{good}+MR$ was presented) presented on the feedback screen in case of a feedback trial. Delays were not modeled and thus were used as baseline.

Based on our hypothesis of improving motor skill learning by reward-induced striatal upregulation, we focused the fMRI analysis on the striatum. To separate the signal change due to knowledge of performance and monetary reward from irrelevant visual input, the linear contrast "feedback vs no-feedback presentation" was specified. Thus, the relative signal increase during reward presentation after feedback trials relative to the signal elicited when looking at a visual control stimulus after no-feedback trials (both with respect to baseline signal during break periods) was calculated and represented as beta weights. These contrast values were then averaged over two ROIs (ventral and dorsal striatum) using an in-house Matlab ROI analysis routine. The striatum was partitioned into ventral and dorsal parts according to Lutz et al. (2012). To test for significant activation of the ROI, average effect sizes per participant were tested against null by one-tailed one-sample t-tests. All statistical analyses (imaging and behavioral data) were performed using SAS Enterprise Guide (5.1, SAS Institute, Cary, NC, USA). Moreover, beta values from the contrast "feedback vs no-feedback presentation" were subjected to a one-way ANOVA with the between-subject factor "group" (KP_{random}, KP_{good}, and $KP_{good}+MR$), and results were Bonferroni-corrected for performing multiple ANOVAs (two ROIs). Dunnett's two-tailed t-tests were then used to locate eventual influences of reward type ($KP_{good}+MR$ vs KP_{good}) and/or feedback schedule (KP_{random} vs KP_{good}), where applicable (ie, in case of a significant main effect "group").

2.6 ANALYSIS OF BEHAVIOR

Boolean cursor position with respect to the arc-channel and d_f were calculated online for each frame and logged together with all other relevant experimental information. Data were extracted and $\bar{d}_t$ (according to the formula presented earlier) and ratios of data points lying within the arc-channel were determined using custom Matlab routines. Data were then corrected for outlier trials ($\bar{d}_t >$ average $\bar{d}_t$ of the corresponding block of trials $+2$ standard deviations (SDs) or $\bar{d}_t >$ average $\bar{d}_t$ of the corresponding block of trials -2 SD) using SAS Enterprise Guide 5.1. For statistical analysis of absolute movement errors during arc-pointing task training, the absolute error was logarithmically transformed in order to fulfill requirements for statistical tests. Performance changes between sessions were calculated, for each subject and movement time, as percentage changes relative to the corresponding baseline. That is, relative to the individual pretraining $\bar{d}_t$ for task acquisition and relative to post-training $\bar{d}_t$ for quantification of task consolidation. Generalized linear mixed models

(GLMM) for repeated measures were applied using SAS proc mixed. GLMM1: Analysis of absolute errors during training included the main factors "group" (levels: KP_{random}, KP_{good}, and $KP_{good}+MR$) and "training block" (levels 1–5). GLMM2: Analysis of percentage change in performance comprised the main factors "group" (levels: KP_{random}, KP_{good}, and $KP_{good}+MR$), "learning phase" (levels: acquisition and consolidation) and "movement time" (levels: 0.8, 1.0, 1.2, 1.4, and 1.6 ms). For posthoc analysis, Dunnett's t-tests, with KP_{good} acting as control condition, were used to locate whether differential skill development can be attributed to either the usage of different feedback schedules (KP_{random} vs KP_{good}) or different types of reward ($KP_{good}+MR$ vs KP_{good}). One-tailed (hypothesis driven) Dunnett's t-tests were performed, where differences in striatal activations between two conditions reached significance. Moreover, one-sample t-tests were used to examine whether the groups' skill level changed during either of the learning phases, ie, whether percentage changes were significantly different from zero.

3 RESULTS

Data from one subject had to be excluded due to a software crash during the training of the task, which required recalibration and a restart of the experiment thus hampering comparability to the data of other participants.

3.1 fMRI

Using the contrast "feedback vs no-feedback presentation," one-tailed one-sample t-tests revealed significant activations of the ventral striatum for KP_{random} and $KP_{good}+MR$ ($t=2.40$, $p=0.0153$ and $t=4.57$, $p=0.0002$, respectively) and of the dorsal striatum for $KP_{good}+MR$ exclusively ($t=3.11$, $p=0.0077$; Fig. 3). The reward condition (main effect "group") significantly influenced the relative signal increase in the ventral striatum ($F=5.04$, $p=0.0220$), but less clearly in the dorsal striatum ($F=2.56$, $p=0.179$). In the ventral striatum, $KP_{good}+MR$ showed significantly higher activation than KP_{good} ($t=2.98$, $p_{Dunnett}=0.0093$).

3.2 BEHAVIORAL RESULTS

Task performance is expressed as $\bar{d}_t$, which was the measure determining knowledge of performance and monetary rewards. As a result of our experimental manipulation (ie, selecting well-solved trials for feedback), average performance during feedback trials was better ($\bar{d}_t$ was smaller) in KP_{good} (54.16 ± 18.12 pixels, $t=3.77$, $p=0.0005$) and $KP_{good}+MR$ (50.07 ± 8.851 pixels, $t=4.47$, $p<0.0001$) compared with KP_{random} (75.11 ± 17.22 pixels; GLMM1: main effect "group": $F=11.58$, $p<0.0001$). As a consequence, these subjects were shown higher average scores per feedback trial (41.03 ± 7.158 points and 42.59 ± 13.97 Rappen vs 32.98 ± 5.421 points) and reached higher total scores over the course of the experiment
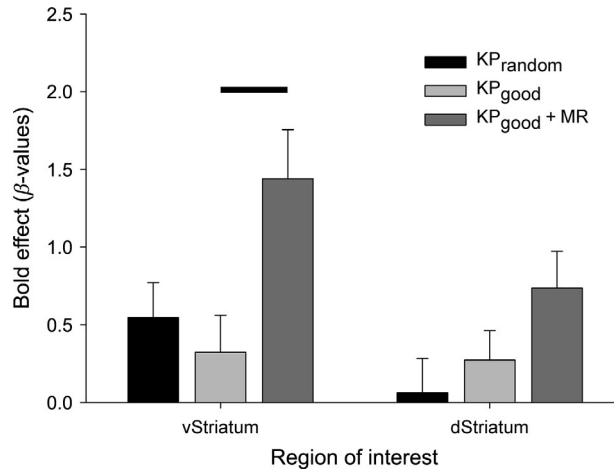
FIG. 3

Striatal activations (β-values) for the "feedback vs no-feedback presentation" contrast. Group effects were found to be significant in the ventral Striatum (vStriatum), but not significant in the dorsal Striatum (dStriatum). Means $\pm$ standard error of the mean (SEM). —, Significant pairwise comparison ($p < 0.05$). $N = 44$.

(5203 ± 908.7 points and 5358 ± 572.5 Rappen vs 4122 ± 677.6 points), all KP_{good} and $KP_{good} + MR$ vs KP_{random}.

Considering all trials, including no-feedback trials, overall performance increased (ie, $\bar{d}_t$ decreased) over the course of training (Fig. 4; GLMM1: main effect "training block": $F = 28.02$, $p < 0.0001$). No difference in overall $\bar{d}_t$ was found between groups (GLMM1: main effect "group": $F = 0.58$, $p = 0.5599$), but performance development over the course of the training was influenced by the group-specific reward condition (GLMM1: interaction "group*training block": $F = 2.20$, $p = 0.0247$).

Performance in our version of the arc-pointing task has been assessed before, right after and 24 h after the training of the arc-pointing task without providing additional terminal feedback in these testing sessions. The evolution of absolute errors, ie, of $\bar{d}_t$, across the different test sessions is presented in Fig. 5 (top). Of greater relevance than absolute error values, however, are performance changes between pre- and post- (due to task acquisition), as well as between post- and 24 h posttraining tests (due to task consolidation processes). Fig. 5 (bottom) displays percentage changes relative to the corresponding baseline value (ie, relative to pretraining $\bar{d}_t$ for acquisition and relative to posttraining $\bar{d}_t$ for consolidation). Online learning and consolidation differentially influenced performance (GLMM2: main effect "learning phase": $F = 81.80$, $p < 0.0001$), with greater changes caused by online learning. This change was influenced by task difficulty (GLMM2: interaction "learning phase*movement time": $F = 11.15$, $p < 0.0001$). Performance improved
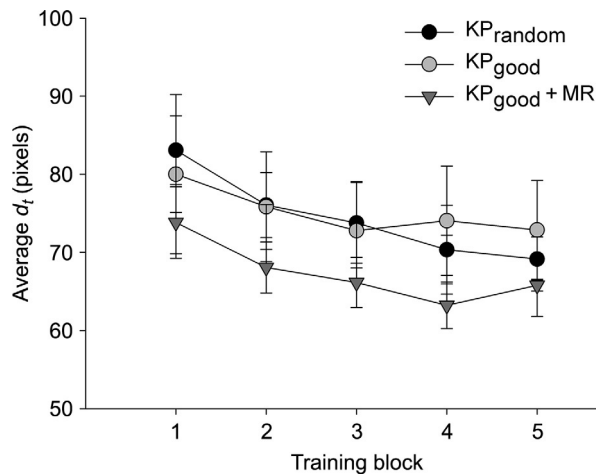
FIG. 4

Development of absolute errors ($\bar{d}_t$) in pixels for all trials (feedback and no-feedback trials) averaged over each training block (1–5) for all three study groups. Means $\pm$ SEM. $N=44$.
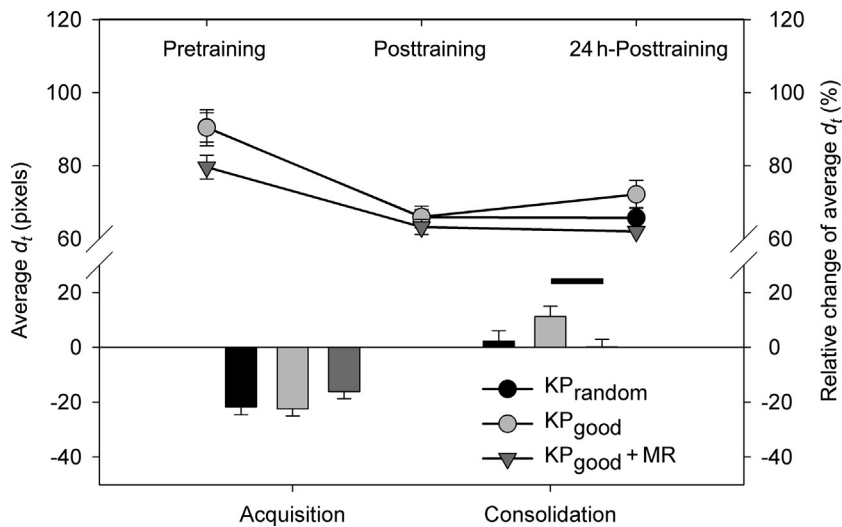

FIG. 5

Absolute performance ($\bar{d}_t$) during test sessions (*top*, upper *x*-axis, left *y*-axis) and relative performance change (in %) compared to the preceding test session (*bottom*, lower *x*-axis, right *y*-axis), ie, to pretraining $\bar{d}_t$ for task acquisition and to posttraining $\bar{d}_t$ for consolidation. All data are presented as Means $\pm$ SEM. ▬, Significant posthoc comparison ($p<0.05$). $N=44$.

due to online learning at all movement times, while, on the other hand, performance at 24 h could be maintained for movement times ≥ 1.2 but significantly suffered from "forgetting" at shorter movement times (ie, at higher task difficulty). Furthermore, "learning phase" significantly interacted with the "group" factor (GLMM2: $F = 3.69$, $p = 0.0259$). While all groups profited similarly from arc-pointing task training, only KP_{random} and $KP_{good} + MR$ consolidated their performance overnight. KP_{good}'s performance decreased significantly ($t = 3.39$, $p = 0.0008$) and this worsening was significantly different compared with $KP_{good} + MR$ ($t = 2.42$, $p_{Dunnett} = 0.0324$), and by tendency different compared with KP_{random} ($t = 2.09$, $p_{Dunnett} = 0.1399$).

4 DISCUSSION

Our results demonstrate that both striatal response and motor skill learning, measured as relative change of error from pre- to posttraining (=acquisition) and from posttraining to 24 h thereafter (=consolidation), are influenced by manipulations of the schedule for performance feedback and/or the type of reward. Specifically, adding an extrinsic (monetary) reward increases ventral striatal activation to performance feedback, which is associated with better motor skill consolidation overnight.

4.1 TRAINING AND MOTOR SKILL ACQUISITION

All groups practiced in identical intensity. Interventions only differed in terms of which trials were selected for KP and whether performance had monetary consequences or not. Higher subjective benefit through additional extrinsic (monetary) reward at stable cost should raise the motivation for a specific exercise. Motivation may rely on dopaminergic activity in the nucleus accumbens, as animal studies have shown that dopamine depletion in nucleus accumbens or low doses of dopamine antagonists reduce the willingness to work for extrinsic rewards (reviewed by Salamone and Correa, 2002). Enclosing nucleus accumbens, ventral striatum activations observed during our experiment (Fig. 3) could thus be an indication that groups invested varying amounts of effort into training. But, MR neither improved performance during training nor skill acquisition. This supports the results from Abe et al. (2011), who also found no difference in acquisition between reward, punishment, and control groups. However, other studies showed that punishment, but not reward improved the acquisition of a motor adaption paradigm (Galea et al., 2015) and induced a performance effect in a procedural motor task (Wachter et al., 2009). But, Wachter et al. (2009) also found that the acquisition of an implicit motor learning task profited from reward but not from punishment. This apparent inconsistency should be taken as indication that conclusions across different (motor) learning modalities like procedural, skill, or adaption learning must be drawn with caution (Shmuelof et al., 2012).

4.2 CONSOLIDATION

Our study design allows investigating the influence of using different schedules for intrinsic reward on neural activity and motor skill learning by comparing KP_{good} and KP_{random} conditions. While feedback trials were randomly selected in case of KP_{random}, subjects in KP_{good} were only informed about trials with good performance. Interestingly and against our hypothesis, striatal activation was only observed in KP_{random} but not KP_{good}. Behaviorally, this resulted in successful task consolidation for KP_{random} and significant overnight forgetting in KP_{good} with a between-group difference close to significance. Thus, ventral striatal activation during training supports successful consolidation of a newly learned motor skill.

Poor performance and striatal underactivation in KP_{good} were unexpected. This result is in contrast to findings from Chiviacowsky and Wulf (2007), who studied two experimental groups, one receiving knowledge of result after good (KR_{good}) and the other after bad performance (KR_{poor}), in a ballistic task that required subjects to throw beanbags at a target with their eyes covered. In their experiment, the KR_{good}-group significantly outperformed the KR_{poor}-group when subjects repeated the task 1 day after the training without knowledge of result. Therefore, the authors proposed motivational properties of positive feedback to have a direct effect on learning. On the contrary, the guidance hypothesis of feedback suggests that feedback is more beneficial if presented after larger rather than smaller errors because it then better guides the learner to the correct response (Salmoni et al., 1984; Schmidt, 1991). Relating this controversy to our finding of a tendency towards better consolidation in KP_{random} compared with KP_{good}, it appears that KP_{random} combines the best of both theories. That is, adequate error information guiding subject's response towards better performance, but still keeping subjects motivated by frequently including knowledge of performance after good performance. A positive motivational status might be indicated by the observed activation of the ventral striatum in KP_{random}, as motivation may rely on dopaminergic activity in the nucleus accumbens (Salamone and Correa, 2002). However, the question remains why knowledge of performance after average performance (KP_{random}) lead to striatal activation, while knowledge of performance after good performance did not. Attentively steering the cursor along the arc-channel under visual control may have enabled subjects to evaluate their performance online and thus to make predictions about the feedback. This, in turn, may have allowed KP_{good}-group to predict the reception of knowledge of performance, as for them the selection of feedback trials depended on performance. We know from experiments in primates that dopamine neurons appear to emit an alerting message about the surprising presence or absence of rewards and that response to rewards and reward-predicting stimuli depend on event predictability (Schultz, 1998). It therefore seems to be the unpredictable selection of feedback trials in KP_{random}, rather than the magnitude of the score that made up the activation in the ventral striatum. This finding is supported by the absence of significant activations to a parametric modulation of the "feedback presentation" contrast by the amount of points won during a trial.

Interestingly, although KP_{good} failed to induce any striatal activation and was accompanied by overnight forgetting, knowledge of performance after good performance lead to highest ventral striatum response and also activated the dorsal striatum when knowledge of performance signified a monetary outcome. Both ventral striatum activation and overnight task consolidation were significantly higher/better in $KP_{good}+MR$ compared with KP_{good}. A beneficial influence of increased motivation due to higher subjective benefit (induced by extrinsic reward) on the consolidation component of motor skill learning thus emerges from our results. This corroborates previous findings on motor skill learning (Abe et al., 2011) and motor adaption (Galea et al., 2015). The former experiment used an isometric pinch force tracking task to investigate motor skill learning under either monetarily rewarded, punished, or neutral control training conditions. While at 24 h posttraining, punishment, and control groups performed at a similar level as immediately after the training, the rewarded group experienced significant offline gains, which remained present at 30 days posttraining. In contrast, the neutral and punished groups showed substantial performance loss at 30 days. When comparing to the experiment of Abe et al. (2011), the beneficial effect of reward could be similarly demonstrated in the present study. Although, for practical reasons, we did not test further than 24 h posttraining. Some remaining discrepancies of performance changes at 24 h posttraining may be attributed to differential influences of task complexity or difficulty between the pinch force task and the arc-pointing task, as indicated by our finding of a significant "learning phase*movement time" interaction. That is, changes due to task consolidation highly depended on task difficulty (ie, movement time).

However, regarding the comparison between $KP_{good}+MR$ and KP_{good}, observed striatal activations are in line with previous work, revealing that feedback related activity in the ventral striatum is increased if knowledge of performance has monetary consequences and that a monetary incentive is needed to elicit a neural response in the dorsal striatum (Lutz et al., 2012). The absence of a response of the dorsal striatum to performance feedback is, on the other hand, in contrast to findings from other studies (Poldrack et al., 2001; Tricomi and Fiez, 2008; Tricomi et al., 2004, 2006). Unfortunately, different approaches for defining striatal subdivisions hamper comparability between these results.

To summarize, training under a feedback condition, which elicited higher activation of the ventral striatum, positively influenced skill development via better task consolidation. Overall, it seems that training under a feedback condition that induces activation in the ventral striatum helps for successful task consolidation. It is known that, in a rewarded task, hemodynamic ventral striatal response correlates with dopamine release in the ventral striatum, which as well correlates with the reward-related neural activity in the substantia nigra/ventral tegmental area, the origin of the dopaminergic projection (Schott et al., 2008). Reward-related ventral striatal activity may thus be an indication for increased dopaminergic function in the midbrain. In rodents, the existence of direct pathways linking midbrain reward centers to the motor cortex has been demonstrated (Hosp et al., 2011). In the motor cortex, dopamine facilitates long-term potentiation (Molina-Luna et al., 2009), a form of synaptic

plasticity discussed to be critically involved in skill learning (Rioult-Pedotti et al., 2000; Ziemann et al., 2004). In their experiment, Hosp et al. (2011) could demonstrate that destroying dopaminergic neurons in the ventral tegmental area prevented improvements in forelimb reaching, a state that was abolished on administration of levodopa into the primary motor cortex. Dopamine-dependent long-term potentiation develops gradually over hours (Huang and Kandel, 1995) and persists for days to weeks (Abraham, 2003). We thus propose increased dopamine release into the primary motor cortex in feedback conditions with significant activation of the ventral striatum to be the key factor facilitating motor skill learning via better task consolidation.

4.3 LIMITATIONS

The striatum is involved in fine motor control. Therefore, it is not surprising that both ventral and dorsal striatum activation was observed during movement execution in this experiment. These activations, however, did not differ between groups (data not shown) and the movement phase was well separated from feedback/no-feedback presentation through a variable delay period (Fig. 1). Hence, we do not expect striatal involvement in movement control to have an influence on our imaging results observed during reward processing.

Furthermore, the present study does not yield a double dissociation between the influence of feedback schedule (random selection/good performance) and type of reward (knowledge of performance only/knowledge of performance plus monetary reward), because we have not fully balanced the possible conditions (KP_{random}, KP_{good}, $KP_{random}+MR$, and $KP_{good}+MR$). Nevertheless, we can corroborate influences of monetary reward on striatal activity and can link these to consolidation of a motor skill. It also allows to discuss effects of performance feedback schedules on striatal activity and motor skill learning, but it does not allow to investigate interactions between these two factors.

Moreover, generalization of these findings to other types of motor or nonmotor learning is limited. In motor skill learning, motor learning is investigated in the absence of a perturbation and the main goal is to reduce a variable error (Deutsch and Newell, 2004; Guo and Raymond, 2010; Hung et al., 2008; Liu et al., 2006; Muller and Sternad, 2004; Ranganathan and Newell, 2010). Task difficulty limits performance, usually in the form of a trade-off between speed and accuracy. Learning consists of breaking through this limit (ie, improving the speed-accuracy trade-off) (Reis et al., 2009). In the original work introducing the arc-pointing task, the authors well defined and checked for fulfillment of speed requirements (ie, the movement time) and then investigated an isolated measure of accuracy (Shmuelof et al., 2012). In contrast, our main outcome measure, $\bar{d}_t$, is influenced by both speed and accuracy. A reduction in $\bar{d}_t$ can thus occur by improved accuracy, more accurate timing, or a combination of both. Although we refrained from defining a target zone and thus from strictly checking for observance of the movement time, we excluded outlier trials, where, for example, the trial was accidentally started. In conclusion, although

we can demonstrate a shift in the speed-accuracy trade-off function for the entire subject population, comparing groups by means of a separable measure of either speed or accuracy is in our case not valid, as it was the combined measure $\bar{d}_t$ that determined group-specific feedback conditions. This might be viewed as a shortcoming, hampering clear definition of the behavior observed during our study as motor skill learning, but on the other hand it allowed effective investigation of learning of goal-oriented movements with clearly set goals and well-defined feedback on goal achievement.

5 CONCLUSION

Our results demonstrate that motor skill learning is influenced by different reward conditions applied during the training of a motor task. Particularly, linking performance feedback to a monetary outcome efficiently raises ventral striatum activation, which comes along with better overnight task consolidation of the corresponding study group. Notably, all groups showing a significant response of the ventral striatum to feedback during training could retain their performance from the first day at the 24 h posttraining test, whereas a lack of ventral striatal response in the other group was accompanied by significant overnight forgetting. This leads us to conclude that increasing ventral striatal activity during acquisition of a motor skill by using appropriate reward improves consolidation of the acquired skill.

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