Feedback delay attenuates implicit but facilitates explicit adjustments to a visuomotor rotation

Authors: Raphael Schween, Mathias Hegele

Neuromotor Behavior Lab, Department of Psychology and Sport Science, University of Gießen, Germany

The manuscript has been published in Neurobiology of Learning and Memory (2017). 140: 124-133.
The published version can be retrieved under the following link:
https://doi.org/10.1016/j.nlm.2017.02.015

Corresponding Author:

Raphael Schween
Kugelberg 62
35394 Gießen
GERMANY
E-mail: raphael.schween@sport.uni-giessen.de
Phone: +49 641 99 25243
Fax: +49 641 99 25209

Abstract

We examined the effects of delaying terminal visual feedback on the relative contribution of explicit and implicit components of adaptation to a visuomotor rotation. Participants practiced a 30° rotation while receiving terminal visual feedback with either a short (0 ms), medium (200 ms), or long (1500 ms) delay. Explicit and implicit adjustments were dissociated by a series of posttests. While overall adaptation did not differ significantly between groups, aftereffects progressively decreased with increasing feedback delay. Moreover, explicit knowledge of the rotation increased in both the medium and high delay groups relative to the short delay group, but did not differ between the former two. This finding of feedback delay differentially affecting implicit adjustments as indexed by aftereffects and conscious strategic corrections based on explicit knowledge of the transformation substantiates the importance of distinguishing implicit and explicit components of adaptation even with rotations of smaller size and emphasizes the need to consider time delays in the interpretation of adaptation experiments and potentially in the design of training environments.

Keywords: motor learning; sensorimotor transformation; knowledge of results

Highlights

- Delaying visual feedback facilitates explicit learning of a visuomotor rotation.
- Implicit learning is attenuated by the feedback delay.
- Implicit learning decreased progressively across two delays, 200 and 1500 ms.
- Explicit learning showed a similar increase with 200 as with 1500 ms delay.

1. Introduction

Adapting to novel transformations between bodily movements and their visually perceived consequences is an intricate part of learning to master modern tools such as a computer mouse or two-sided levers involved in laparoscopy. Adaptation to such visuomotor transformations embraces different components, and a fundamental distinction can be drawn between implicit and explicit adjustments (Hegele & Heuer, 2010; Taylor & Ivry, 2011). Previous studies of adaptation to novel visuomotor transformations suggest that delays in the presentation of visual feedback modulate implicit visuomotor adaptation, but the effect on explicit visuomotor adaptation is unclear (Brudner, Kethidi, Graeupner, Ivry, & Taylor, 2016; Held, Efstathiou, & Greene, 1966; Hinder, Riek, Tresilian, de Rugy, & Carson, 2010; Hinder, Tresilian, Riek, & Carson, 2008; Honda, Hirashima, & Nozaki, 2012b; Kitazawa, Kohno, & Uka, 1995; Peled & Karniel, 2012; Schween, Taube, Gollhofer, & Leukel, 2014; Shabbott & Sainburg, 2010). In the present study, we show that feedback timing modulates the relative contribution of implicit and explicit adjustments in visuomotor adaptation.

Explicit adjustments refer to the conscious alteration of otherwise spontaneously executed movements by cognitive strategies, e.g. pointing to a location different from the visual target (Heuer & Hegele, 2008; Taylor & Ivry, 2011). These strategies rely on explicit knowledge about the transformation (Hegele & Heuer, 2013; Mazzoni, 2006), can be applied relatively flexibly (Taylor & Ivry, 2011) and have been shown to be affected by aging (e.g. Buch, Young, & Contreras-Vidal, 2003; Heuer & Hegele, 2008; McNay & Willingham, 1998). Alternatively, the motor system can adjust to novel transformations implicitly, i.e. outside of conscious awareness. Implicit adjustments have frequently been described in terms of developing an internal model that mimics the input-output-characteristics of the transformation (Heuer, 1983; Wolpert & Kawato, 1998), but also comprise additional processes such as reinforcement learning and use-dependent plasticity (Huang, Haith, Mazzoni, & Krakauer, 2011; Izawa & Shadmehr, 2011; Therrien, Wolpert, & Bastian, 2016).

An established paradigm for the experimental study of the processes underlying sensorimotor learning is adaptation to a visuomotor rotation, i.e. a rotation of the direction of a moving cursor representing hand motion. Such a rotation of cursor feedback typically results in a strong performance decrement initially that is then gradually reduced as adaptation proceeds. When the transformation is switched off after practice, participants typically display an error in the direction opposite to the rotation. This error is referred to as (negative) aftereffect and has been conceived to reflect implicit processes of adaptation. Explicit components of adaptation to these rotations have often been inferred indirectly, but can also be assessed more directly (Heuer & Hegele, 2008; Taylor, Krakauer, & Ivry, 2014).

An important factor modulating visuomotor adaptation is timing of visual feedback regarding the outcome of reaching. Several studies have compared the continuous availability of visual feedback during movement execution (concurrent feedback) to the availability of visual feedback only near the end of, or after movement execution (terminal feedback; Hinder et al., 2010, 2008; Schween et al., 2014; Shabbott & Sainburg, 2010; Taylor et al., 2014). In spite of considerable methodological differences, those studies consistently found that implicit adaptation, as indexed by aftereffects, was smaller after practice with terminal feedback (but see Bernier, Chua, & Franks, 2005). Explicit adjustments have been found to increase with terminal as compared to continuous feedback, and it has been speculated that they compensate the reduction in implicit adjustments (Hinder et al., 2010, 2008; Shabbott & Sainburg, 2010; Taylor et al., 2014).

A crucial methodological difference between these studies however pertains to the exact time point at which terminal feedback was given. In studies that did not find any significant implicit adjustments, terminal feedback was not delivered immediately but with varying delays[1] (Hinder et

[1] Specifically, Hinder et al. (2008) report that they presented terminal feedback at a fixed interval of 4 s after trial start. Considering a random delay of 1-2 s at the beginning of the trial, a reaction time (RT) of about 0.3-0.6 s and a movement time (MT) of about 1 s, we estimate a feedback delay of 0.4-1.7 s from movement termination. Hinder et al. 2010 used a fixed interval of 5 s and random delay 1-2 s and observed RTs of 0.5-0.9 s and MTs of 0.5-0.7 s, leaving feedback delays of 1.4-3 s. Shabbott and Sainburg (2010) do not report delays, but note that "The [terminal feedback] group was instructed to reach their final position and to remain there until [terminal feedback] was displayed" (p. 78), implying that there were noticeable delays. The setup of Schween and colleagues (2014) also presented feedback at a fixed point in time and therefore allowed noticeable delays depending on movement time.

al., 2010, 2008; Schween et al., 2014; Shabbott & Sainburg, 2010). Conversely, studies that report attenuated but significant aftereffects delivered terminal feedback immediately upon passage of a target amplitude (Taylor et al. 2014). This indicates that, in addition to the mere availability of error information, the timing of feedback may be a crucial determinant of the effect on implicit adjustments. This hypothesis gains support from a recent study by Brudner and colleagues (2016) who examined the impact of a 5-second-delay on visuomotor adaptation while monitoring participants' aiming strategies during practice. They found a significant attenuation of aftereffects with delayed feedback. Interestingly, in spite of comparable overall adaptation in the no-delay and the 5-s-delay groups, they did not find any effect of feedback delay on explicit aiming strategies. This finding seems at odds with the interplay of implicit and explicit learning suggested previously based on the comparison of concurrent and terminal feedback. However, the absence of a delay effect on explicit learning could be a result of the reporting paradigm itself, as being asked to report an aiming strategy on every trial may increase subjects' inclination to develop such strategies. The absence of group differences in strategy use could therefore be a result of ceiling effects in strategy use rather than indicating the absence of a delay-effect on strategy generation.

Therefore, the purpose of the current experiment was to determine the impact of feedback time delay on explicit and implicit visuomotor adaptation. In order to avoid drawing subjects' attention to the generation of aiming strategies, we assessed participants' explicit knowledge of the rotation by means of a (nonmotor) posttest where subjects judged the required direction of arm movements given a target direction (Hegele & Heuer, 2010, 2013, Heuer & Hegele, 2008, 2015). Based on previous results from prism adaptation (Kitazawa et al., 1995; Kitazawa & Yin, 2002), and the investigation of terminal feedback, we hypothesized that aftereffects would decrease across three delays. Furthermore, in line with previous reasoning that explicit learning compensates reduced implicit learning (Hinder et al., 2010, 2008; Shabbott & Sainburg, 2010; Taylor et al., 2014), we expected explicit learning to increase across these delays.

2. Materials and Methods

2.1 Participants and experimental groups

Participants were assigned to a short, medium or long-delay terminal feedback group. The short-delay group (15 women, 5 men, mean age: 22.1 years (SD 2.6), range: 19-28 years) received terminal feedback after movement termination as soon as was allowed by the internal delay of our system (see *2.4 Trials and trial types*). The medium delay group (18 women, 3 men, mean age: 21.5 years (SD 2.2), range: 19-27 years) received terminal feedback with an additional delay of 200 ms, the long-delay group (16 women, 5 men, mean age: 23.9 years (SD 4.6), range: 19-37 years) with an additional delay of 1500 ms. Data from one additional participant from the short and one from the long delay group were excluded as they could not finish testing due to scheduling constraints. Assignment to the short and long delay group was performed by block randomization balanced for sex. The medium delay group was added a posteriori and therefore not randomized. We chose this a posteriori addition to get a more complete picture of the effect of delay on adaptation. After observing the effect on explicit learning with the ″large″ 1500 ms delay, we were particularly interested if the smaller 200 ms delay would already affect explicit learning as studies have found delays in this range to affect sensory processing despite being hardly noticeable (Blakemore, Frith, & Wolpert, 1999). All participants were students of Giessen University and received course credit for their participation. Six participants (1 short, 4 medium, 1 high delay) were not right-handed according to the handedness-test from the (unrevised) German version of the lateral preference inventory (Büsch, Hagemann, & Bender, 2009, p. 18-19), but all subjects performed tests with their right hand. Written, informed consent was obtained from all participants before testing.

2.2 Apparatus

The experimental setup is illustrated in figure 1. Participants sat at a glass-covered table, facing a 22-in., 120 Hz LCD-Screen (Samsung 2233RZ) approximately at head height 1 m in front of them, and had a plastic sled (50x30 mm^2 base, 6 mm height) strapped to their right index finger that minimized both, friction and haptic feedback when moving on the glass surface. The sled carried a vertically oriented sensor (Model M800) of a trakSTAR system (Ascension Technology, Burlington, VT, USA) directly above the fingertip, that was tracked at 120 Hz. A black occluder 20 cm above the table prevented vision of the hand. Data collection and stimulus presentation were controlled by custom scripts in Matlab (2010b, RRID:SCR_001622) using the Psychophysics toolbox (RRID:SCR_002881).

2.3 Experiment overview

Participants moved towards visual targets from a common central start location by sliding the sled over the glass surface and received visual feedback about their movement by an on-screen cursor. The experiment comprised a baseline phase, a practice phase where subjects encountered a -30° visuomotor rotation (where the minus sign means counterclockwise), and a posttest phase (figure 2, see *2.5 Experimental Protocol*), containing 160 trials in total. Trials were arranged in blocks of ten with each block containing an equal number of target appearances at one of two possible positions. The sequence of target appearances was generated individually for each subject by sequentially concatenating randomly permuted pairs of two, where each pair contained each target position once, to create a sequence with a maximum of two repetitions of the same target. We chose to use two targets instead of one to make sure that subjects needed to direct some attention towards the visual targets and not just focus on moving towards a single proprioceptively perceived position. We did not include any further targets because it would have lengthened testing and we saw no benefit in it for the research question.

2.4 Trials and trial types

Each *practice trial* began with the participant gaining the start position (outline circle, 3.5 mm radius) at the center of the screen by minimizing the size of a white concentric circle whose radius depended on the participant’s distance to the start (Taylor & Ivry, 2011). On the table surface, the start was about 30 - 40 cm in front of the participant (23 cm from the edge of the table) and in the subjects’ median plane. When within the start circle, index finger position was represented by a cursor (filled cyan circle, 2.4 mm radius) and the white circle disappeared. When the cursor was in the start circle for 300 ms, a tone sounded and the target (filled white circle, 2.8 mm radius) appeared after a time interval that was randomized (500, 700, 900, 1100 or 1300 ms) in order to prevent systematic influences of anticipation on movement preparation. The two possible target locations were -22.5° or -67.5° (with 0° corresponding to horizontal rightward movements and a negative sign indicating counterclockwise rotation from 0°), at a target amplitude of 90 mm. Participants were instructed to quickly move the cursor towards the target in a single, straight, uncorrected movement and then stay in the position where the movement terminated. The cursor disappeared upon movement onset and only reappeared at the position of movement termination after the group-specific terminal feedback delay elapsed. The feedback was shown for a fixed 1 second interval. *Movement onset* was defined as the first frame where sensor position's Euclidean distance to the center of the start was greater than 1 mm. *Movement termination* was defined as the first occurrence of two identical position data points in succession (within the resolution of the trakSTAR readout, which is approximately 0.6 mm for our model according to personal correspondence with Ascension Technologies' support) at a distance of at least 45 mm from the center. This definition of movement termination together with the instruction and movement time requirements (see next paragraph) was designed to enable feedback display as quickly as possible after the end of the movement. We tested the suitability of this method by analyzing velocity at the time of the termination criterion and residual movements occurring thereafter for all valid rotation practice trials (see *2.6 Data analysis* and *3.4 Movement termination*). Furthermore, we estimated the internal delay of this termination criterion within our system by performing 50 trials in a modified setup using a synchronized response time box (Version 4, http://lobes.osu.edu/rt-box.php) with a photodiode. By this procedure, the average time from the data request that would eventually yield the first of the two identical data points for movement termination to screen cursor display was 26.6 ms (SD 3.8) in the low delay configuration.

After feedback display, the short- and medium-delay groups received 1.5 s or 1.3 s of black screen, respectively, in order to compensate the difference in trial duration that would otherwise have resulted from the feedback delay. Before the beginning of the next trial, participants saw a warning message if the movement time from onset to termination was too slow (>500 ms) or too fast (<200 ms). When a movement was not terminated within 2 s from onset, the trial was aborted and an error message was displayed. *Movement test trials* were similar to practice trials, except that participants of all groups received no position feedback during these. *Maintenance trials* were the same as corresponding practice trials, but are named differently to emphasize their function of countering memory decay between the different baseline or posttests.

Explicit judgment trials were used to assess explicit knowledge of the rotation that subjects had acquired (Heuer & Hegele, 2008). For this purpose, a straight white line of 90 mm length was displayed with one end attached to the center of the start and the other pointing in the direction opposite the current target at the beginning of each trial. The experimenter then rotated this line around the start by pressing keyboard keys, alternating the initial direction of rotation across trials. Participants were asked to verbally instruct the experimenter when to stop so that the line pointed in the direction that they thought they would hypothetically need to move their hand in, in order to aim the cursor at the target. Adjustment speed was fixed in this initial part of the explicit shift test in order to minimize unintentional influences of the experimenter's knowledge about the nature of the rotation on the participants' responses, e.g. by unintentionally slowing down the line rotation around the correct explicit shift of 30°. Participants could then instruct the experimenter to refine the chosen direction in steps of 1° by the commands "forward" (German: "weiter") and/or "backward" ("zurück") until they were content with the result and the final chosen direction was recorded. No cursor was displayed during these trials and participants rested their hand on their thigh. We chose to have participants instruct the experimenter instead of adjusting line orientation themselves to ensure that there was as little motor planning involved in the explicit judgments as possible. Further, subjects' resting their hand on their thigh instead of on the table was to prevent executed or simulated motor exploration during the explicit judgment trials.

2.5 Experimental protocol

The experimental protocol is illustrated in figure 2. Blocks (of ten trials) are named according to the type of trials they contain. During two *baseline* practice blocks, cursor feedback was veridical and the start circle was yellow. Baseline tests consisted of one movement test block and one explicit judgment block, both with a yellow start circle to indicate absence of the (not yet encountered) rotation. The explicit baseline test block was further preceded by a maintenance block with group-specific feedback (identical to the baseline practice blocks) in order to compensate memory decay occurring in the absence of feedback. *Rotation practice* consisted of five practice blocks with a -30° visuomotor rotation, i.e. the direction of cursor movement was rotated counterclockwise around the start location by 30° relative to hand movement, while the relation between amplitudes remained veridical (visuomotor gain of 1). The *posttest phase* contained two movement test blocks and an explicit judgment block, each of which was preceded by a maintenance block with rotation and group-specific terminal feedback (these maintenance blocks were thus identical to rotation practice blocks). The first test block tested for *aftereffects* in the absence of explicit strategies. Subjects consequently saw a yellow start circle, indicating that the rotation had been switched off. Trials in the second test block had a blue start circle, cuing presence of the rotation, and thus tested for overall *adaptive shifts*. The third posttest block tested for *explicit shifts* by explicit judgment trials with a blue start circle.

After the two baseline practice blocks, participants were instructed that they could now encounter trials without feedback. Before rotation practice, they were instructed that there would be trials with a rotation cued by a blue start circle, and that a yellow start circle would signal the absence of that rotation. Neither polarity nor magnitude of the rotation was provided. Participants were reminded of the start circle cuing before each of the posttests, respectively. Informing participants about the absence of the rotation allows testing aftereffects unconfounded by explicit strategies, whereas informing them about its presence provides an overall measure of combined implicit and explicit learning, which we will refer to as adaptive shifts. Participants were reminded that their primary goal was to move the cursor towards the target in all movement conditions, but they were not incentivized to generate explicit aiming strategies.

Subjects of all groups completed the movement test in one session, without specific pauses between trials, blocks, or phases. An average block took the subjects about 1.44 minutes (SD .14) in the short, 1.50 minutes (SD .17) in the medium, and 1.50 minutes (SD .19) in the long delay group, which was not significantly different between groups according to one-way ANOVA ($F_{2,59}$=.77, P=.47). Subjects received short on-screen instructions at the instances indicated in figure 2. The average time that subjects spent on the movement test was 46.75 minutes (SD: 4.12) in the short, 48.75 minutes (SD 5.67) in the medium, and 48.75 minutes (SD 5.60) in the long delay group, which was not significantly different according to a one-way ANOVA ($F_{2, 59}$=1.01, P=.37). Experiment starting times were not planned specifically, but took place between 9:00 AM and 6:15 PM. Median starting time was 1:57 PM (1st to 3rd Quartile: 12:03 AM – 2:54 PM) in the short, 2:13 PM (12:20 AM – 2:47 PM) in the medium, and 2:26 PM (12:22 AM - 4:48 PM) in the long delay group.

2.6 Data analysis

X and y coordinates of the finger movements of each trial were separately low-pass filtered (fourth-order Butterworth, 10 Hz) using Matlab's "filtfilt"-command to avoid introducing phase lags, and differentiated by two-point central difference algorithm to directional velocities. Tangential velocity was calculated as the Euclidean of the directional velocity vectors. Movements with extreme duration (>2 s) or large direction errors (< -120° or >120°) were excluded from further analyses (35 trials or 1.3% for the low, 79 trials or 2.9% for the medium and 52 trials or 1.9% for the high delay group, respectively).

Our primary outcome measure was the final hand direction, calculated as the angular difference between the vector connecting the start circle with the respective target and the vector connecting the start circle with movement-terminal hand position. For explicit judgment trials, the angular difference between target direction and participants' direction judgment was calculated. Individual block medians of these final direction measures were calculated and the posttest minus baseline test differences were determined to account for potential directional biases in subjects' baseline behavior. The main data for analysis were thus the individual, baseline-corrected block medians of the three test blocks after rotation practice, i.e. the test block with yellow start circle for aftereffects, with blue start circle for adaptive shifts and the explicit judgment test block for explicit shifts. Maintenance blocks were not included in the analysis.

As additional kinematic parameter, we calculated individual medians of trial average movement velocities for the 50 trials of the practice and 20 trials of the posttest phase, respectively. These phase medians were used for a comparison between practice and posttest velocities as such a difference could have confounded aftereffects (Kitazawa, Kimura, & Uka, 1997). For the practice phase, we furthermore analyzed the velocity at movement termination, the magnitude of residual movements within 100 ms after termination, as well as during the 1000 ms of feedback display by calculating the maximum Euclidean distance to movement terminal position during respective time windows.

Statistical analyses were done in R (Version 3.3.1, http://www.R-project.org/) and JASP (Version 0.7.5.6, https://jasp-stats.org/). Inter-group comparisons on the baseline, and baseline-corrected posttest data were done by separate one-way ANOVAs with the exception of the explicit baseline test. For the latter, no median deviations other than -0.5, 0 and 0.5 occurred, which made parametric testing unsuitable. Instead, we used Kruskal-Wallis test for median differences. Where the ANOVAs indicated a significant group effect, Bonferroni-Holm-corrected, one-sided post-hoc t-tests were performed to test our specific hypotheses, i.e. that aftereffects would be smaller with larger feedback delays and explicit shifts would be larger (see *1. Introduction* for a more detailed justification of these hypotheses). Additional tests against zero were done by Bonferroni-Holm-corrected one-sample t-tests for all groups, respectively. The practice blocks were analyzed using an ANOVA with BLOCK and GROUP as within- and between-participant factors, respectively.

We repeated the analyses of posttests while excluding seven subjects (3 low, 2 medium, 2 long delay) who displayed very low explicit knowledge (< 5° explicit shift) to ascertain that these had no disproportionate influence on our main results. Furthermore, experimental groups differed in characteristics that could potentially have influenced our results. Specifically, the medium delay group comprised more non-right-handed subjects and less males, potentially as a result of being exempt from randomization, and the long delay group was slightly older than the others. To investigate whether these differences influenced our main results, we repeated the analyses of posttests while excluding all non-right-handed, male, and above 29-years-old (1 from high delay group) subjects, to create a uniform sample of 42 “young”, right-handed women (14 per group, low delay mean age: 22.3 years (SD 2.9), range: 19-28 years; medium delay: 21.4 years (SD 2.5), range: 19-27 years; high delay: 23.2 years (SD 3.8), range: 19-29 years). If the exclusions caused alpha error probability to rise above 5%, we generated 10000 bootstrap datasets of the same size as the respective reduced dataset (i.e. 42 cases per dataset drawn randomly with replacement from all groups for ANOVAs or 28 cases drawn randomly from two subgroups in focus for t-tests), and repeated the analyses on these datasets. We then compared the test statistics of the set with specific exclusions to the distribution of test statistics for the bootstrap sets to get an intuition whether increased alpha error probability was specific to the selected exclusions or a random consequence of reduced sample size.

We further conducted an additional analysis where we tested for different learning performance on the posttests for movements to the two different targets. For this purpose, we calculated separate block averages for movements to the two targets, respectively and repeated the ANOVAs on our aftereffect and explicit shift posttest measures with an additional within-subject factor TARGET. The main purpose of this analysis was to see whether subjects used the upper right screen corner as a landmark to aim to when compensating the rotation while moving to the -62.5° target, in which case we would have expected performances towards the two targets to differ.

To test for possible differences in movement velocity between practice and movement posttests, we performed a two-way ANOVA on the phase median velocities with between-subject factor GROUP and within-subject factor PHASE. Group differences for residual movements were analyzed by separate one-way ANOVAs on the individual medians of rotation practice.

Results are labeled as significant if the respective corrected *P*-values were below 0.05, but uncorrected *P*-values are reported for clarity. For the tests of our main results, we report η^2 with 90% confidence intervals (CI_{90}) as effect size measure for ANOVAs and *Cohen's d (d)* with 95% confidence intervals (CI_{95}) for post-hoc t-tests. Note that confidence intervals on these measures are point-wise, i.e. not corrected for "multiple comparison".

3. Results

3.1 Baseline and practice phase

Baseline performance did not differ significantly between groups in either movement test ($F_{2,59}$=-.35, P=.71) or explicit test (X^2_2=.22, P=.90). The two-way ANOVA on practice data revealed a significant main effect of within-subjects factor BLOCK ($F_{1.62,95.59}$=, P=.002) but not of between-subjects factor GROUP ($F_{2,59}$=.7, P=.49) and no interaction ($F_{3.24,95.58}$=.61, P=.62), indicating that participants reduced their visual pointing error during practice irrespective of terminal feedback delay. Note that the degrees of freedom were Greenhouse-Geisser corrected (ε=.405) as data violated sphericity (*Mauchly's W*=.077, P<.001). Figures 3 and 4 show that, upon introduction of the rotation, all groups quickly adapted their reaching direction to a level close to full compensation (i.e. zero visual error) and then remained there. The fact that subjects did not reach zero visual error irrespective of practice condition is in accordance with previous observations (Haith, Huberdeau, & Krakauer, 2015; Hinder et al., 2008; Shabbott & Sainburg, 2010) and can be explained by an equilibrium between learning and forgetting (Cheng & Sabes, 2006).

3.2 Posttest results

In accordance with practice performance, baseline-corrected adaptive shifts in the posttests differed significantly from zero for all groups in the direction opposite to the rotation and almost fully compensated its size (figure 5, short delay: 26.3° (SD 6.3), t_{19}=18.6, P<.001; medium delay: 28.0° (SD 8.4), t_{20}=15.2, P<.001; long delay: 26.9° (SD 9.8), t_{20}=12.6, P<.001). The one-way ANOVA on adaptive shifts showed no group differences ($F_{2,59}$=-.21, P=.81, η^2=.007, CI_{90}: [0, .046]), indicating that all groups learned to compensate the transformation to a similar extent. Mean aftereffects were significantly different from zero in all groups (short: 11.1° (SD 5.2), t_{19}=9.6, P<.001; medium: 7.2° (SD 5.2), t_{20}=6.3, P<.001; long: 4.0° (SD 4.8), t_{20}=3.9, P<.001), and showed conspicuous differences between delay-groups ($F_{2,59}$=10.05, P<.001, η^2=.25, CI_{90}: [.09, .38]). Post-hoc t-tests revealed significant differences for all pairwise group comparisons (short vs. medium: t_{39}=2.42, P=.010, d=.76, 95% CI_{95}: [.12, 1.39]; short vs. long: t_{39}=4.54, P<.001, d=1.42, CI_{95}: [.72, 2.1]; medium vs. long: t_{40}=2.04 P=.024, d=.63, CI_{95}: [.01, 1.25]). Thus, in accordance with our hypothesis, aftereffects decreased with increasing feedback delay, which is in line with the idea of a quantitative influence of feedback delay on implicit learning.

Explicit shifts also differed significantly from zero in all delay groups (short: 15.2° (SD 9.3), t_{19}=7.29, P<.001; medium: 23.6° (SD 11.7), t_{20}=9.27 P<.001; long: 21.8° (SD 10.8), t_{20}=9.24 P<.001), and differed between groups ($F_{2,59}$=3.45, P=.038, η^2=.10, CI_{90}: [.003, .22]). The short delay group displayed significantly less explicit knowledge than the medium delay group (t_{39}=-2.52, P=.008, d=-.79, CI_{95}: [-1.42, -.15]) and the long delay group (t_{39}=-2.07, P=.023, d=-.65, CI_{95}: [-1,27, -.01]). There was no significant difference between the medium and long delay group (t_{40}=.52, P=.70, d=.16, CI_{95}: [-.45, .77]). Thus, delaying feedback did increase explicit learning, but in contrast to our expectation there was no further increase from medium to long delay.

Figure 5C shows that there were seven subjects with explicit shifts close to zero (i.e. < 5°), but exclusion of those subjects did not alter results on any of the posttests (results not shown), indicating that these "outliers" did not disproportionately affect our results. Generally, it is a known phenomenon that some individuals display low explicit knowledge on the explicit shift test after rotation practice even in a young adult population (Heuer & Hegele, 2008, 2015). Repetition of the posttest analyses while excluding non-right-handed, male and ʺolderʺ subjects yielded no qualitative differences in the relation between group average values on the explicit or implicit posttest, either, but the ANOVA on explicit shifts was no longer significant ($F_{2,39}$=2.59, P=.088), as were the post hoc t-tests for differences in explicit shifts between the short and medium (t_{29}=-2.21, P=.018) and between the short and long delay group (t_{31}=-1.69, P=.051). However, the F- and t-statistics of these tests were in the 43rd, 51st, and 47th percentile of respective test statistics on 10000 bootstrap datasets of equal sample size. It therefore appears that the above changes in significance are likely an unspecific result of reduced group size and we see no strong indication that the left-handed, male and ʺolderʺ subjectsʹ behavior may have driven the group effects in explicit shifts.

In the additional ANOVAs with within subject factor TARGET and between subject factor GROUP, the main effect of GROUP on aftereffects remained significant (P < .001) and the effect on explicit shifts persisted as a tendency (P = .053), but there were no effects of TARGET or interactions (all P > .22).

3.3 Movement velocity

Differences in movement velocity between practice and posttests have been found to affect prism adaptation (Kitazawa et al., 1997). This effect could cause group differences unrelated to feedback delays if movement velocity differed between practice and posttests in a group-specific manner. Movement velocities for the practice phase were 262 mm*s^{-1} (SD 48) for the short, 265 mm*s^{-1} (SD 41) for the medium, and 251 mm*s^{-1} (SD 43) for the long-delay group, respectively. Corresponding movement velocities for the posttest phase were 265 mm*s^{-1} (SD 53), 268 mm*s^{-1} (SD 52), and 242 mm*s^{-1} (SD 60). The two-way ANOVA indicated no significant difference between practice and posttest phase ($F_{1,59}$=.12, P=.74), or between groups ($F_{2,59}$=1.09, P=.34), or interaction ($F_{2,59}$=1.11, P=.34). Thus, it seems unlikely that effects of movement velocity provide a relevant alternative explanation for our findings.

3.4 Movement termination

The means of individual median velocities at movement termination were 3.57 mm*s^{-1} (SD .69), 3.21 mm*s^{-1} (SD .68) and 3.40 mm*s^{-1} (SD .75) for the low, medium and high delay groups, respectively. Thus, there was still movement at our termination criterion, albeit very slow (<1.5 % of average velocity). We therefore analyzed the magnitude of residual movements after the termination criterion. The 95th percentile of maximum Euclidean distance to position at movement termination was 0.5 mm within the first 100 ms after termination and 1.4 mm during feedback display, which is still considerably smaller than cursor radius. Importantly the individual subject medians did not differ significantly between groups for either of these measures ($F_{2,59}$=1.61, P=.21 and $F_{2,59}$=1.31, P=.28 on respective one-way ANOVAs) even though the longer waiting time until feedback display would have provided more opportunity for the subjects in the medium and high delay groups to execute additional movements. It therefore appears that the assessment of movement termination was adequate to the purpose and is unlikely to have biased the results.

4. Discussion

The purpose of the present study was to examine the effect of delaying terminal visual feedback on the contribution of explicit and implicit processes to visuomotor adaptation. We used a series of posttests to dissociate explicit and implicit components. While overall adaptation was of similar magnitude in all three groups, clear differences emerged for the relative contribution of explicit and implicit adaptive processes. We found a negative relationship between implicit adaptation and feedback delay as indicated by aftereffects that were progressively attenuated with the addition of two different feedback delays (200 ms and 1500 ms). Explicit shifts on the other hand increased with both delays compared to the no-delay-group. Notably, this increase was already fully present with as little as 200 ms delay and did not increase further in the 1500 ms delay group, and was thus more categorical in nature (delay present vs. absent).

The observation that implicit adaptation was attenuated with the addition of feedback delays is in line with previous findings on delayed concurrent (Honda, Hirashima, & Nozaki, 2012a; Honda et al., 2012b) and terminal feedback in visuomotor adaptation (Brudner et al., 2016; Held et al., 1966; Kitazawa et al., 1995). It further is in line with the hypothesis that differences in time delays contribute to variations in the amount of implicit adaptation observed previously in various studies providing movement-terminal feedback (Hinder et al., 2010, 2008; Schween et al., 2014; Shabbott & Sainburg, 2010; Taylor et al., 2014).

Our finding of increased explicit learning in the delayed feedback groups is at odds with the recent findings by Brudner and colleagues (2016) who did not observe such an increase in explicit learning with a 5 seconds visual feedback delay compared to no delay. As noted in the introduction, we suggest that reporting the aiming direction on every trial may have induced subjects to generate unusually large explicit strategies in that previous study, thus causing ceiling effects to mask potential delay-related differences. This assertion is supported by the fact that mean aiming strategies in the experiment by Brudner and colleagues (2016) quickly reached a size close to full compensation of the 45° rotation used, with the delay group trailing slightly above the non-delay group for most of the time. Alternatively, the difference between the present and Brudner and colleagues' (2016) study could also relate to the different magnitude of the delays under investigation. For example, the shorter delays in our present study could impair the system's response to prediction errors that presumably drive implicit adaptation (Taylor and Ivry 2011; Brudner et al. 2016), and explicit learning could increase as an indirect response. Then, with the even larger 5 seconds delay investigated by Brudner and colleagues (2016), the integration of task errors that drive explicit learning (Taylor & Ivry, 2011) could also be impaired, causing an analogous decline in explicit learning. The absence of a difference in explicit shifts between the two longer delay groups in our present study could in principle be representative of such a non-monotonic relationship but further experiments investigating more time delays are required to adequately address this issue, especially as the confidence interval on the effect size between explicit learning in the medium and in the long delay group still includes a medium-sized effect for a further increase in explicit learning.

Nevertheless, the current results demonstrate that explicit learning is increased with delays in the time-range under consideration.

In line with previous observations on delayed and terminal feedback (Hinder et al. 2008; Schween et al. 2014; Brudner et al. 2016), we suggest that at least a fraction of the differences in aftereffects in our study is mediated by the feedback delay affecting the development of an internal model of the transformation. However, with the present experimental design, we cannot definitively preclude that implicit processes other than model-based adaptation (e.g. use-dependent learning and model-free reinforcement learning; Haith & Krakauer, 2013; Huang et al., 2011; Izawa & Shadmehr, 2011; Therrien et al., 2016) contributed to the observed aftereffects. Nevertheless, previous studies on long-term depression (LTD) at synapses from parallel fibers to Purkinje cells in the cerebellum as a consequence of synchronized activity of climbing fibers and parallel fibers do suggest a potential cellular mechanism for a delay-dependent discounting of model-based adaptation. LTD at these synapses has been suggested as an important mechanism for the utilization of prediction errors that drive model-based adaptation (Miall, Weir, Wolpert, & Stein, 1993) and has further been demonstrated to peak at an inter stimulus interval (ISI) between climbing fiber and parallel fiber activation of 125 ms (Ekerot & Kano, 1989) and to decrease over a relatively long ISI range up to at least 1750 ms (Karachot, Kado, & Ito, 1994). It could thus potentially explain the decrease across the time range under consideration in our study. Conceptually, such changes may conform to a decrease in “relevance”, or an externalization in the attribution of errors (Berniker & Körding, 2011; Wei & Körding, 2009).

The increase in explicit learning on the other hand can likely at least in parts be explained by mere compensation for less implicit learning. It has been demonstrated that explicit learning can flexibly complement the more monotonous implicit learning in order to account for sensorimotor transformations of various sizes (Bond & Taylor, 2015). Therefore, it seems likely that it would behave in a similar way when implicit learning is reduced for other reasons. However, if compensation for reduced implicit learning were the sole reason for increases in explicit learning with delayed feedback, we would have expected explicit shifts to increase quantitatively across the three delays. Conversely, the absence of a difference in explicit shifts between the medium and high delay group of our study may be indicative of a more categorical mechanism contributing to the observed increase. As the analysis of movement velocity indicated that the movement was not fully terminated at our termination criterion, such a categorical cause could in principle also be related to whether the movement is still ongoing (in the low delay group) or not (in the other two groups) rather than to a temporal delay. While this null result should thus be interpreted with caution, there are reasons why the feedback delay could exert a more direct influence on explicit learning that may be more categorical in nature: In order to compare the intended/predicted movement outcome with delayed feedback, the sensorimotor system would have to actively maintain a representation of such a prediction, which may require the transfer of predictions from the cerebellum to working memory involving, among others, prefrontal cortex (see Lara & Wallis 2015 for a recent review). Whereas working memory involvement does not necessarily imply explicit processing, visuospatial working memory and (right dorsolateral) prefrontal cortical activity have previously been linked to explicit processes of visuomotor adaptation (Anguera, Reuter-Lorenz, Willingham, & Seidler, 2010; Slachevsky et al., 2001; Taylor & Ivry, 2014 for review). On a conceptual level, processing of delayed error feedback in visuospatial working memory might give rise to what has been referred to as an unexpected event (Frensch et al., 2003) or strengthening in representational quality (Cleeremans & Jiménez, 2001), leading to increased explicit processing.

Interestingly, similar roles for cerebellar and extracerebellar (and specifically prefrontal) regions have been proposed for classical eyeblink conditioning, which is cerebellum-dependent when the unconditioned and conditioned stimulus overlap (delay conditioning) but requires awareness and prefrontal cortical activity when there is a temporal separation between stimuli (trace conditioning) (Clark & Squire, 1998; McLaughlin, Skaggs, Churchwell, & Powell, 2002; Siegel, Kalmbach, Chitwood, & Mauk, 2012). Therefore, our findings on feedback delays in visuomotor adaptation may reflect a more general principle of sensorimotor learning by which cerebellar processing is sufficient to form (new) connections between signals that occur in close temporal vicinity, but (explicit) extracerebellar processing in working memory is required to associate actions with effects that are separated from them by more than a few hundred milliseconds.

Our results are subject to some potential confounders relating to differences in group characteristics, some of which may result from the a posteriori addition of the medium delay group. We specifically tested this possibility for a number of parameters: Left-handedness was considered potentially relevant because performing the movements under investigation with the non-dominant hand likely increases movement variability, which could have caused greater internal attribution of errors (Berniker & Körding, 2008) and thereby a shift towards implicit learning. Sex is considered a predictor of various cognitive ability parameters on a population level and could therefore influence explicit adaptation. Interestingly, arguments for differences in both directions can be made: males display an on average advantage in tasks requiring visuospatial transformations in working memory (Halpern, 1997), which could positively affect explicit learning of visuomotor rotations. Females on the other hand on average outperform males on the digit symbol test (Snow & Weinstock, 1990), which has been found positively correlated with early adaptation to a visuomotor rotation likely mediated by explicit adaptation (Anguera et al., 2010). Finally, older age has been shown to impair explicit learning of visuomotor rotations (Heuer & Hegele, 2008) and could therefore have influenced our results. However, our additional analyses indicate that exclusion of male, non-right-handed and "older" subjects did not impact our main results regarding group differences in aftereffects and explicit shifts beyond a reduction in power due to decreased sample size. We note that an age difference remained between the medium and long delay group even after excluding the one age outlier from the latter. The slightly older mean age in the long delay group could in principle explain the absence of a further increase in explicit learning from medium to long feedback delay. However, previous findings on age-related differences in explicit adaptation have generally been based on the comparison of much older subjects to a group in the age range of our study, whereas age effects within the latter population have, to our knowledge, not been reported. Furthermore, a large fraction of the impairment in explicit learning in older adults appears to be due to a higher portion of outliers that generate very little explicit knowledge compared to younger adults (Heuer & Hegele, 2008). The relative prevalence of such outliers in our study did not differ between groups and their exclusion did not alter our results. In summary, based on our additional analyses, we consider it unlikely that the group characteristics strongly influenced our results. Nevertheless, potential interactions between the above parameters and feedback effects on visuomotor adaptation constitute an interesting field for future investigations.

In addition to group characteristics, we cannot completely rule out that subject used additional points of orientation in the explicit test. For example, the upper right corner could have provided a near-optimal aiming target for the -67.5° location when the rotation was present. However, given that this advantage would have been specific to this target (as the compensation for the -22.5° target would have benefited more from moving towards the cardinal zero direction than towards the lower right screen corner), we would then have expected learning performance to differ between the two targets, which was not the case. This point similarly pertains to potential retinal afterimages of targets from previous trials that subjects might have used as orientation points. Here, an afterimage of the -22.5° target could have provided an approximate landmark for moving towards the -67.5° target while countering the rotation, but not vice versa.

Thus, notwithstanding the need to further clarify the underlying mechanisms, our finding of implicit adaptation being attenuated while explicit adaptation is facilitated by feedback delay provides support for the notion of a sensorimotor learning system that consists of at least two distinct mechanisms: On the one hand a (purely implicit) calibration mechanism that is directly driven by input-output relationships and requires little cognitive control, but is therefore also inflexible (Mazzoni and Krakauer 2006; Bond and Taylor 2015) and probably susceptible to time delays. On the other hand, a mechanism that utilizes cognitive control (provided that sufficient resources are available; cf. Anguera et al., 2012; Haith et al., 2015) to flexibly accommodate complex relationships of cause and effect across time, and thereby also increases the probability for participants to extract explicit knowledge about the task and apply aiming strategies (cf. Taylor and Thoroughman 2008).

Importantly, some of these learning properties appear to also pertain to the execution of respective behavior. Thus, while explicitly learned behaviors may be applied with greater flexibility, their appropriate application may also be more susceptible to breakdown under pressure (e.g. by time constraints, stress, or multiple task requirements) than behaviors that have been learned implicitly (Haith et al., 2015; Masters, 1992; Maxwell, Masters, & Eves, 2003). Furthermore, specific groups of neurological patients may be unable to apply a specific type of learning (e.g. Abbruzzese, Trompetto, & Marinelli, 2009; Gutierrez-Garralda et al., 2013). For these reasons, adjusting feedback delays to support a specific learning type may provide one parameter in creating learning environments that suit the specific goals of a training intervention or abilities of a patient. However, it is currently not clear to which extent results from sensorimotor adaptation transfer to more applied skill learning tasks. Learning mechanisms and, therefore, influences of feedback parameters involved in these tasks may differ (e.g. Telgen, Parvin, & Diedrichsen, 2014). Thus, further research investigating this relationship and feedback influences on skill learning is needed. Finally, our results emphasize the potential modulatory influences also of apparatus-inherent delays on the contribution of explicit and implicit processes to visuomotor adaptation. These constitute a potential influence on behavioral parameters like aftereffects, retention and generalization, that is rarely controlled.

Acknowledgements: This research was supported by a grant within the Priority Program, SPP 1772 from the German Research Foundation (Deutsche Forschungsgemeinschaft, DFG), grant no [He7105/1.1]. We would like to thank Scott Albert for his comments on a previous version of the manuscript.

References

Abbruzzese, G., Trompetto, C., & Marinelli, L. (2009). The rationale for motor learning in Parkinson's disease. *European Journal of Physical and Rehabilitation Medicine*, *45*(2), 209–14.

Anguera, J. A., Bernard, J. A., Jaeggi, S. M., Buschkuehl, M., Benson, B. L., Jennett, S., … Seidler, R. D.

(2012). The effects of working memory resource depletion and training on sensorimotor adaptation. *Behavioural Brain Research*, *228*(1), 107–15. https://doi.org/10.1016/j.bbr.2011.11.040

Anguera, J. A., Reuter-Lorenz, P. a, Willingham, D. T., & Seidler, R. D. (2010). Contributions of spatial working memory to visuomotor learning. *Journal of Cognitive Neuroscience*, *22*(9), 1917–1930. https://doi.org/10.1162/jocn.2009.21351

Bernier, P.-M. M., Chua, R., & Franks, I. M. (2005). Is proprioception calibrated during visually guided movements? *Experimental Brain Research*, *167*(2), 292–6. https://doi.org/10.1007/s00221-005-0063-5

Berniker, M., & Körding, K. P. (2008). Estimating the sources of motor errors for adaptation and generalization. *Nature Neuroscience*, *11*(12), 1454–61. https://doi.org/10.1038/nn.2229

Berniker, M., & Körding, K. P. (2011). Estimating the relevance of world disturbances to explain savings, interference and long-term motor adaptation effects. *PLoS Computational Biology*, *7*(10). https://doi.org/10.1371/journal.pcbi.1002210

Blakemore, S. J., Frith, C. D., & Wolpert, D. M. (1999). Spatio-temporal prediction modulates the perception of self-produced stimuli. *Journal of Cognitive Neuroscience*, *11*(5), 551–559. https://doi.org/10.1162/089892999563607

Bond, K. M., & Taylor, J. A. (2015). Flexible explicit but rigid implicit learning in a visuomotor adaptation task. *Journal of Neurophysiology*, *113*, 3836–3849. https://doi.org/10.1152/jn.00009.2015

Brudner, S. N., Kethidi, N., Graeupner, D., Ivry, R. B., & Taylor, J. A. (2016). Delayed feedback during sensorimotor learning selectively disrupts adaptation, but not strategy use. *Journal of Neurophysiology*, *115*, 1499–1511. https://doi.org/10.1152/jn.00066.2015

Buch, E. R., Young, S., & Contreras-Vidal, J. L. (2003). Visuomotor adaptation in normal aging. *Learning & Memory*, *10*(1), 55–63. https://doi.org/10.1101/lm.50303

Büsch, D., Hagemann, N., & Bender, N. (2009). Das lateral preference inventory: Itemhomogenität der deutschen version. *Zeitschrift Fur Sportpsychologie*, *16*(1), 17–28. https://doi.org/10.1026/1612-5010.16.1.17

Cheng, S., & Sabes, P. N. (2006). Modeling sensorimotor learning with linear dynamical systems. *Neural Computation*, *18*(4), 760–93. https://doi.org/10.1162/089976606775774651

Clark, R. E., & Squire, L. R. (1998). Classical conditioning and brain systems: the role of awareness. *Science*, *280*(5360), 77–81. https://doi.org/10.1126/science.280.5360.77

Cleeremans, A., & Jiménez, L. (2001). Implicit learning and consciousness: a graded, dynamic perspective. In R. M. French & A. Cleeremans (Eds.), *Implicit Learning and Consciousness: An Empirical, Computational and Philosophical Consensus in the Making* (pp. 1–40). Hove: Psychology Press.

Ekerot, C.-F., & Kano, M. (1989). Stimulation parameters influencing climbing fibre induced long-term depression of parallel fibre synapses. *Neuroscience Research*, *6*(3), 264–268. https://doi.org/10.1016/0168-0102(89)90065-5

Frensch, P. A., Haider, H., Rünger, D., Neugebauer, U., Voigt, S., & Werg, J. (2003). The route from implicit learning to verbal expression of what has been learned. In L. Jiménez (Ed.), *Attention and implicit learning* (pp. 335–66). Amsterdam: John Benjamins Publishing Company.

Gutierrez-Garralda, J. M., Moreno-Briseño, P., Boll, M.-C. C., Morgado-Valle, C., Campos-Romo, A., Diaz, R., & Fernandez-Ruiz, J. (2013). The effect of Parkinson’s disease and Huntington’s disease on human visuomotor learning. *European Journal of Neuroscience*, *38*(6), 2933–2940. https://doi.org/10.1111/ejn.12288

Haith, A. M., Huberdeau, D. M., & Krakauer, J. W. (2015). The influence of movement preparation time on the expression of visuomotor learning and savings. *Journal of Neuroscience*, *35*(13), 5109–5117. https://doi.org/10.1523/JNEUROSCI.3869-14.2015

Haith, A. M., & Krakauer, J. W. (2013). Model-based and model-free mechanisms of human motor learning. *Advances in Experimental Medicine and Biology*, *782*(585), 1–21. https://doi.org/10.1007/978-1-4614-5465-6

Halpern, D. F. (1997). Sex differences in intelligence. Implications for education. *The American Psychologist*, *52*(10), 1091–1102. https://doi.org/10.1037/0003-066X.52.10.1091

Hegele, M., & Heuer, H. (2010). The impact of augmented information on visuo-motor adaptation in younger and older adults. *PLoS One*, *5*(8), e12071. https://doi.org/10.1371/journal.pone.0012071

Hegele, M., & Heuer, H. (2013). Age-related variations of visuomotor adaptation result from both the acquisition and the application of explicit knowledge. *Psychology and Aging*, *28*(2), 333–9. https://doi.org/10.1037/a0031914

Held, R., Efstathiou, A., & Greene, M. (1966). Adaptation to displaced and delayed visual feedback from the hand. *Journal of Experimental Psychology*, *72*(6), 887–891. https://doi.org/10.1037/h0023868

Heuer, H. (1983). *Bewegungslernen*. Stuttgart: Kohlhammer.

Heuer, H., & Hegele, M. (2008). Adaptation to visuomotor rotations in younger and older adults. *Psychology and Aging*, *23*(1), 190–202. https://doi.org/10.1037/0882-7974.23.1.190

Heuer, H., & Hegele, M. (2015). Explicit and implicit components of visuo-motor adaptation: An analysis of individual differences. *Consciousness and Cognition*, *33*, 156–169. https://doi.org/10.1016/j.concog.2014.12.013

Hinder, M. R., Riek, S., Tresilian, J. R., de Rugy, A., & Carson, R. G. (2010). Real-time error detection but not error correction drives automatic visuomotor adaptation. *Experimental Brain Research*, *201*(2), 191–207. https://doi.org/10.1007/s00221-009-2025-9

Hinder, M. R., Tresilian, J. R., Riek, S., & Carson, R. G. (2008). The contribution of visual feedback to visuomotor adaptation - How much and when? *Brain Research*, *1197*(1), 123–134. https://doi.org/10.1016/j.brainres.2007.12.067

Honda, T., Hirashima, M., & Nozaki, D. (2012a). Adaptation to visual feedback delay influences visuomotor learning. *PloS One*, *7*(5), e37900. https://doi.org/10.1371/journal.pone.0037900

Honda, T., Hirashima, M., & Nozaki, D. (2012b). Habituation to feedback delay restores degraded visuomotor adaptation by altering both sensory prediction error and the sensitivity of adaptation to the error. *Frontiers in Psychology*, *3*(December), 540. https://doi.org/10.3389/fpsyg.2012.00540

Huang, V. S., Haith, A. M., Mazzoni, P., & Krakauer, J. W. (2011). Rethinking motor learning and savings in adaptation paradigms: model-free memory for successful actions combines with internal models. *Neuron*, *70*(4), 787–801. https://doi.org/10.1016/j.neuron.2011.04.012

Izawa, J., & Shadmehr, R. (2011). Learning from sensory and reward prediction errors during motor adaptation. *PLoS Computational Biology*, *7*(3), e1002012. https://doi.org/10.1371/journal.pcbi.1002012

Karachot, L., Kado, R. T., & Ito, M. (1994). Stimulus parameters for induction of long-term depression in in vitro rat Purkinje cells. *Neuroscience Research*, *21*(2), 161–168. https://doi.org/10.1016/0168-0102(94)90158-9

Kitazawa, S., Kimura, T., & Uka, T. (1997). Prism adaptation of reaching movements: specificity for the velocity of reaching. *Journal of Neuroscience*, *17*(4), 1481–1492. https://doi.org/citeulike-article-id:437225

Kitazawa, S., Kohno, T., & Uka, T. (1995). Effects of delayed visual information on the rate and amount of prism adaptation in the human. *The Journal of Neuroscience*, *15*(November), 7644–52. https://doi.org/10.3389/fpsyg.2012.00061

Kitazawa, S., & Yin, P.-B. (2002). Prism adaptation with delayed visual error signals in the monkey. *Experimental Brain Research*, *144*(2), 258–61. https://doi.org/10.1007/s00221-002-1089-6

Lara, A. H., & Wallis, J. D. (2015). The role of prefrontal cortex in working memory: a mini review. *Frontiers in Systems Neuroscience*, *9*(December), 1–7. https://doi.org/10.3389/fnsys.2015.00173

Masters, R. S. W. (1992). Knowledge, knerves and know-how: The role of explicit versus implicit knowledge in the breakdown of a complex motor skill under pressure. *British Journal of Psychology*, *83*(3), 343–358. https://doi.org/10.1111/j.2044-8295.1992.tb02446.x

Maxwell, J. P., Masters, R. S. W., & Eves, F. F. (2003). The role of working memory in motor learning and performance. *Consciousness and Cognition*, *12*(3), 376–402. https://doi.org/10.1016/S1053-8100(03)00005-9

Mazzoni, P. (2006). An implicit plan overrides an explicit strategy during visuomotor adaptation. *Journal of Neuroscience*, *26*(14), 3642–3645. https://doi.org/10.1523/JNEUROSCI.5317-05.2006

McLaughlin, J., Skaggs, H., Churchwell, J., & Powell, D. a. (2002). Medial prefrontal cortex and pavlovian conditioning: trace versus delay conditioning. *Behavioral Neuroscience*, *116*(1), 37–47. https://doi.org/10.1037/0735-7044.116.1.37

McNay, E. C., & Willingham, D. B. (1998). Deficit in learning of a motor skill requiring strategy, but not of perceptuomotor recalibration, with aging. *Learning & Memory*, *4*(5), 411–420. https://doi.org/10.1101/lm.4.5.411

Miall, R. C., Weir, D. J., Wolpert, D. M., & Stein, J. F. (1993). Is the cerebellum a smith predictor? *Journal of Motor Behavior*, *25*(3), 203–216. https://doi.org/10.1080/00222895.1993.9942050

Peled, A., & Karniel, A. (2012). Knowledge of performance is insufficient for implicit visuomotor adaptation. *Journal of Motor Behavior*, *44*(3), 185–194. https://doi.org/10.1080/00222895.2012.672349

Schween, R., Taube, W., Gollhofer, A., & Leukel, C. (2014). Online and post-trial feedback differentially affect implicit adaptation to a visuomotor rotation. *Experimental Brain Research*, *232*(9), 3007–3013. https://doi.org/10.1007/s00221-014-3992-z

Shabbott, B. A., & Sainburg, R. L. (2010). Learning a visuomotor rotation - simultaneous visual and proprioceptive information is crucial for visuomotor remapping. *Experimental Brain Research*, *203*(1), 75–87. https://doi.org/10.1007/s00221-010-2209-3

Siegel, J. J., Kalmbach, B., Chitwood, R. A., & Mauk, M. D. (2012). Persistent activity in a cortical-to-subcortical circuit: bridging the temporal gap in trace eyelid conditioning. *Journal of Neurophysiology*, *107*(1), 50–64. https://doi.org/10.1152/jn.00689.2011

Slachevsky, A., Pillon, B., Fourneret, P., Pradat-Diehl, P., Jeannerod, M., & Dubois, B. (2001). Preserved adjustment but impaired awareness in a sensory-motor conflict following prefrontal lesions. *Journal of Cognitive Neuroscience*, *13*(3), 332–40. https://doi.org/10.1162/08989290151137386

Snow, W. G., & Weinstock, J. (1990). Sex differences among non-brain-damaged adults on the Wechsler Adult Intelligence Scales: a review of the literature. *Journal of Clinical and Experimental Neuropsychology*, *12*(6), 873–86. https://doi.org/10.1080/01688639008401028

Taylor, J. A., & Ivry, R. B. (2011). Flexible cognitive strategies during motor learning. *PLoS Computational Biology*, *7*(3), e1001096. https://doi.org/10.1371/journal.pcbi.1001096

Taylor, J. A., & Ivry, R. B. (2014). Cerebellar and prefrontal cortex contributions to adaptation, strategies, and reinforcement learning. *Progress in Brain Research*, *210*, 217–53. https://doi.org/10.1016/B978-0-444-63356-9.00009-1

Taylor, J. A., Krakauer, J. W., & Ivry, R. B. (2014). Explicit and implicit contributions to learning in a sensorimotor adaptation task. *Journal of Neuroscience*, *34*(8), 3023–3032. https://doi.org/10.1523/JNEUROSCI.3619-13.2014

Taylor, J. A., & Thoroughman, K. A. (2008). Motor adaptation scaled by the difficulty of a secondary cognitive task. *PLoS ONE*, *3*(6), e2485. https://doi.org/10.1371/journal.pone.0002485

Telgen, S., Parvin, D., & Diedrichsen, J. (2014). Mirror reversal and visual rotation are learned and consolidated via separate mechanisms: recalibrating or learning de novo? *Journal of Neuroscience*, *34*(41), 13768–79. https://doi.org/10.1523/JNEUROSCI.5306-13.2014

Therrien, A. S., Wolpert, D. M., & Bastian, A. J. (2016). Effective reinforcement learning following cerebellar damage requires a balance between exploration and motor noise. *Brain*, *139*(1), 101–114. https://doi.org/10.1093/brain/awv329

Wei, K., & Körding, K. P. (2009). Relevance of error: what drives motor adaptation? *Journal of Neurophysiology*, *101*(2), 655–664. https://doi.org/10.1152/jn.90545.2008

Wolpert, D. M., & Kawato, M. (1998). Multiple paired forward and inverse models for motor control. *Neural Networks*, *11*(7–8), 1317–1329.

Figure Captions

Figure 1: Illustration of our experimental design. A) Apparatus. B) Baseline practice condition. Black outline circle is start, grey filled circle is target, black filled circle is cursor. Hand position is depicted but was not seen by subjects. C) Rotation practice condition. Here, grey filled vs. outline start circle indicates presence vs. absence of the rotation. In the actual experiment it was blue vs. yellow start circle. D) Explicit judgment trial. The subject verbally instructs for the line to indicate the required hand direction.

Figure 2: Overview of the experimental protocol. Each box represents a block of ten trials.

Figure 3: Group means (lines) and standard deviations (shaded areas) of single trial data (not baseline-corrected) across the whole experiment. Dark-shaded x-sections are trials with visual feedback. Light-shaded sections are test trials without visual feedback or explicit shift tests. Dotted lines indicate hypothetical ideal hand direction in blocks with or without rotation, respectively.

Figure 4: Means of block median hand directions for baseline and practice blocks (not baseline-corrected). X-axis are blocks named according to the logic of figure 2. E.g. bp1 is the first practice block during baseline phase and without rotation and P2 is the second practice block during practice phase and with rotation. Y-axis position of filled symbols indicates mean hand movement direction for the respective group on the respective block. Whiskers indicate standard deviations of these means. Dotted horizontal lines indicate hypothetical complete compensation of the visuomotor rotation.

Figure 5: Results of posttests without visual feedback (baseline-corrected). Panels A, B, and C represent adaptive shifts, aftereffects, and explicit shifts, respectively. X-axes are delay groups; Y-axes are baseline-corrected hand directions. Horizontal lines and whiskers represent group means and standard deviations of individual block medians. Filled symbols' Y-positions represent individual subjects' block medians, while X-positions are randomly scattered within the respective group.

Dotted horizontal lines indicate hypothetical complete compensation of the active visuomotor rotation.

Figures

Figure 1

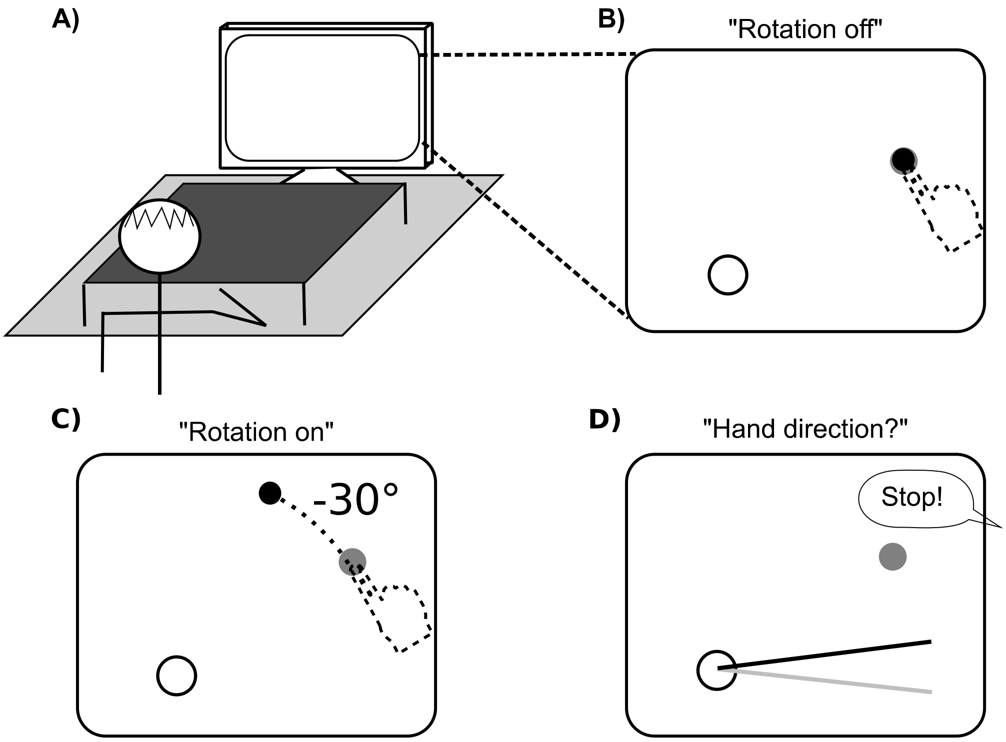


Figure 2

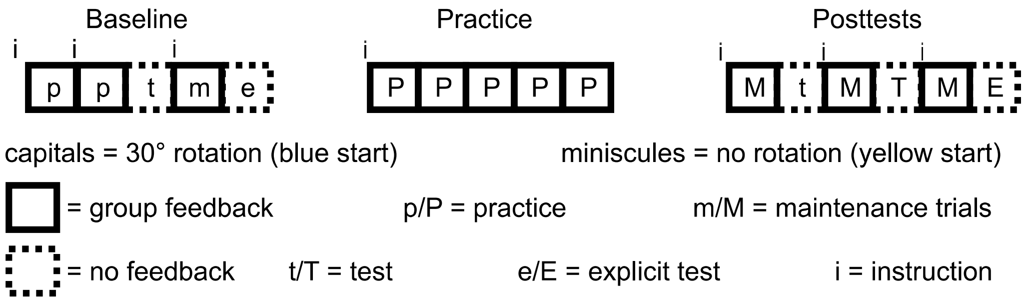


Figure 3

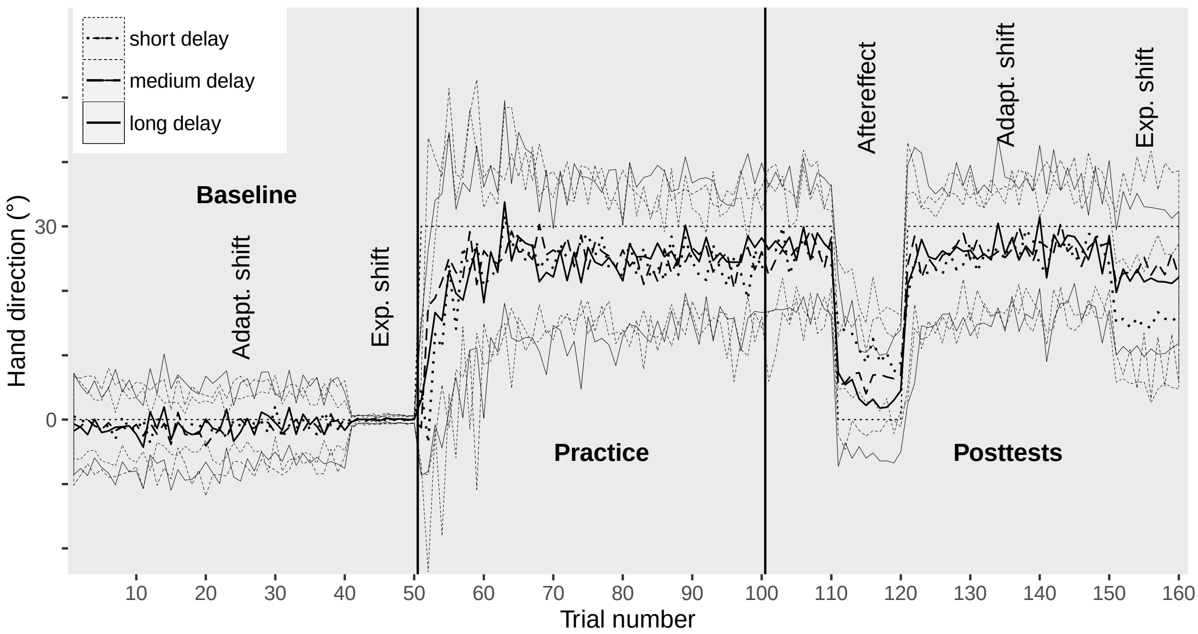


Figure 4

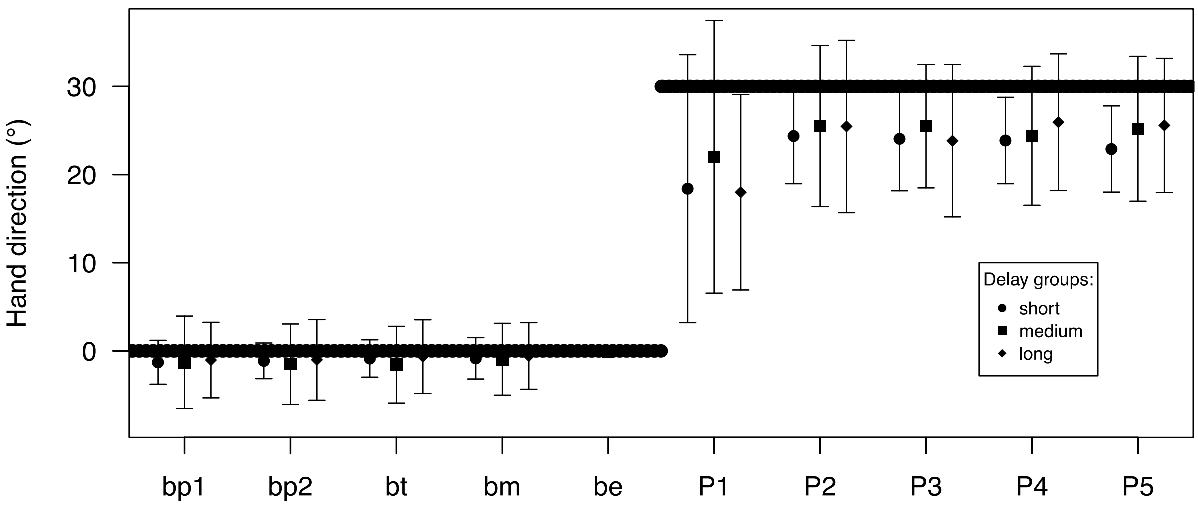
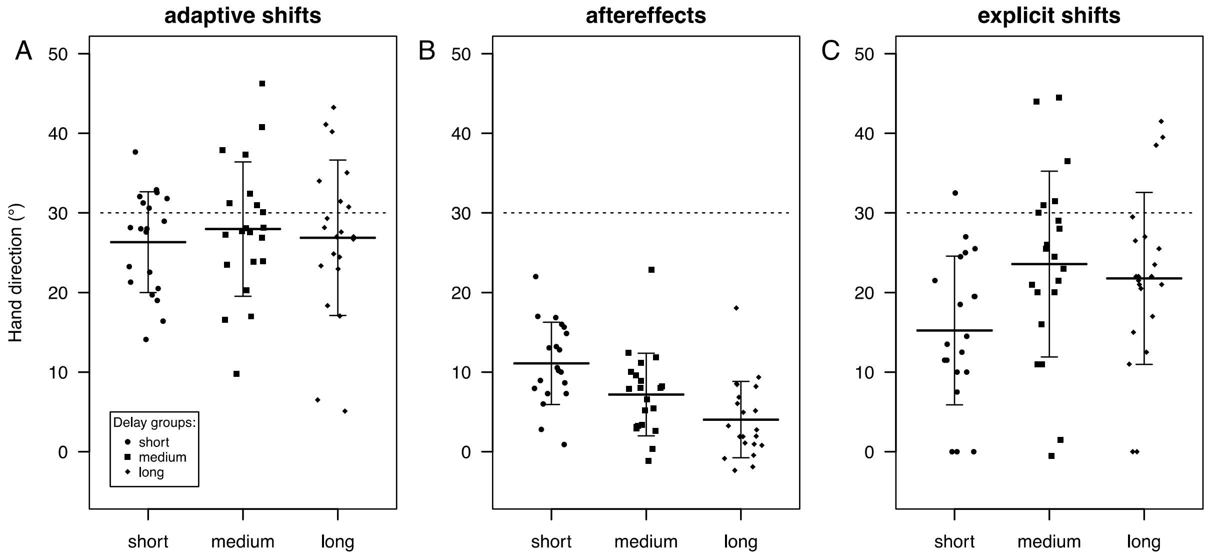


Figure 5



adaptive shifts
aftereffects
explicit shifts
A
B
C
Hand direction (°)
50
40
30
20
10
0
Delay groups:
short
medium
long
short
medium
long