

# Concurrent adaptation to opposite visual distortions: impairment and cue

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**Abstract** The present study compared single and dual adaptation to visuomotor rotations in different cueing conditions. Participants adapted either to a constant rotation or to opposing rotations (dual adaptation) applied in an alternating order. In Experiment 1, visual and corresponding postural cues were provided to indicate different rotation directions. In Experiment 2, either a visual or a postural cue was available. In all cueing conditions, substantial dual adaptation was observed, although it was attenuated in comparison to single adaptation. Analysis of switching costs determined as the performance difference between the last trial before and the first trial after the change of rotation direction suggested substantial advantage of the visual cue compared to the postural cue, which was in line with previous findings demonstrating the dominance of visual sense in movement representation and control.

## Introduction

In everyday life, the human sensorimotor system has to deal with a wide range of environmental conditions during goal-directed movements—especially in the context of tool use, which frequently causes a changed movement dynamic or an idiosyncratic sensorimotor mapping (for overviews see, e.g. Massen, 2012; Sutter, Sülzenbrück, Rieger, & Müsseler, 2013). A number of studies focusing on adaptive motor control, using either viscous curl force fields (changing movement dynamics by applying

additional forces on body effectors) or visuomotor rotations (changing movement kinematics by transforming visual movement feedback), showed evidence of adaptation (Gandolfo, Mussa-Ivaldi, & Bizzi, 1996; Kagerer, Contreras-Vidal, & Stelmach, 1997; Karniel & Mussa-Ivaldi, 2002; Krakauer, Ghez, & Ghilardi, 2005; Krakauer, Pine, Ghilardi, & Ghez, 2000). The participants learned to counteract the perturbation by establishing a model to mimic the sensorimotor process in the novel environment. This model, termed an “internal model”, has two varieties: forward models (or predictors), which predict the movement consequences of motor commands; and inverse models (or controllers), which determine the commands needed to achieve a desired movement effect (Gordon, Westling, Cole, & Johansson 1993; Miall & Wolpert, 1996; Wolpert, Ghahramani, & Jordan, 1995).

Withdrawing the perturbation after adaptation results in movement errors in the opposite direction of the perturbation, which are referred to as “aftereffects” (Krakauer et al., 2000; Shadmehr & Mussa-Ivaldi, 1994; Tong, Wolpert, & Flanagan, 2002). The performance of re-adaptation, which means the relearning of an earlier adapted perturbation following a period of de-adaptation after the original exposure, is better than it had been during the first exposure phase (Krakauer, 2009; Miall, Jenkinson, & Kulkarni, 2004), suggesting the retention of the acquired internal model in long-term memory, which could be recalled on a later occasion.

In a study by Bock, Schneider, and Bloomberg (2005), participants performed center-out pointing tasks with rotated visual feedback. In the adaptation blocks participants performed with the left arm facing a clockwise (cw) rotation or with the right arm a counterclockwise (ccw) rotation in an alternating manner. Results showed significant increase of movement accuracy suggesting concurrent

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adaptation in both arms, which means adaptation to discordant rotations. Post-adaptation measures without visual feedback showed discernable aftereffects in both unimanual and bimanual tasks. Though the data do not establish whether the adaptation states are hard-wired to each arm, which means with two adaptive states implemented within arm-specific segments of the sensory-to-motor pathways, or whether the linkage is functional, with the usage of a given arm as a cue for contextual switching between both states. As suggested by Galea and Miall (2006), the latter assumption corresponds better with other dual adaptation studies using contextual cues. Hence, the motor system can simultaneously adapt to opposing force fields (Gandolfo et al., 1996; Krouchev & Kalaska, 2002; Rao & Shadmehr, 2001) or opposing visuomotor rotations (Bock, Worringham, & Thomas, 2005; Imamizu et al., 2007; Woolley, Tresilian, Carson, & Riek, 2007), and was able to switch between these states in a context-dependent fashion. Similar dual adaptation effects could be shown with a trained rhesus monkey, which was allowed to distinguish the perturbation conditions with the help of color cues (Krouchev & Kalaska, 2002).

Explanations are provided by computational approaches. For instance, Lee and Schweighofer (2009) assumed a parallel architecture with a fast process containing a single state and a slow process containing multiple states switched via contextual cues. A more elaborated contextual switching mechanism is implemented in the modular-selection-and-identification-for-control model (MOSAIC, cf. Haruno, Wolpert, & Kawato, 2001; Imamizu, Kuroda, Yoshioka, & Kawato, 2004), which employs a probability distribution of responsibility estimates for each control module for a context-dependent control module selection. Taken together, multiple internal models could be acquired and retained in long-term memory, if interferences between task requirements are precluded (Bock et al., 2001) or if sufficient contextual cues were given.

Since the dual adaptation studies mentioned above made no direct comparison between opposing conditions and conditions with constant perturbations as control, performance losses due to possible interference still cannot be completely excluded despite substantial dual adaptation. Therefore, it remains open if the context cues in those studies, which enabled dual adaptation, also completely prohibited mutual interference of discordant transformations or not.

Based on these considerations, the present paper addresses two questions regarding dual adaptation with context cues. The first question is, whether the adaptation to discordant sensorimotor rotations is compromised by their interference, when context cues are available. The second question is related to the effectiveness of different contextual cues, which are frequently used in dual adaptation studies. These cues can be roughly classified as

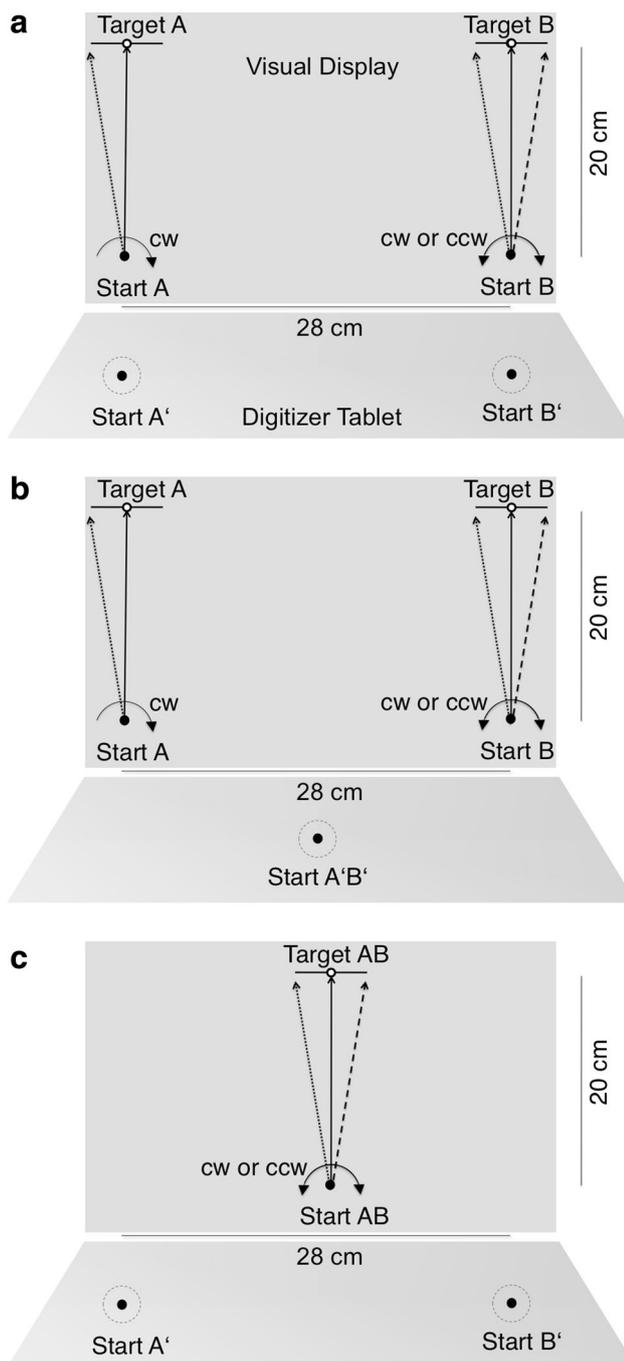
visual cues (Karniel & Mussa-Ivaldi, 2002; Krouchev & Kalaska, 2002; Rao & Shadmehr, 2001), somatosensory cues (i.e. postural cue; cf. Bock et al., 2005; Gandolfo et al., 1996)<sup>1</sup> or a combination of both (Woolley et al., 2007). Hence, the second question is whether a visual cue, a somatosensory cue, or a combination of both can facilitate dual adaptation most effectively.

To this end, two experiments comparing single and dual adaptation in different cue conditions were conducted using a sliding-paradigm, in which a computer cursor was flicked to a target with a rapid and short-ranged hand movement. Such movements enable more reliable analysis of the initial ballistic movement control by precluding any online corrections (cf. Wang & Müsseler, 2012).

## Experiment 1

Experiment 1 addresses the question whether the process of adaptation to opposing rotations comes along with impairment in performance despite sufficient context cues. Two groups of participants performed aimed sliding movements with their dominant right hand while switching in alternating blocks between two regions (left and right) of the workspace (Fig. 1a). They adapted either to 30° cw rotations in both regions of the workspace or to a 30° cw rotation in the left region and to a 30° ccw rotation in the right region of the workspace, respectively. Thus, the opposing rotations were differentiated through visual workspace separation on the one hand and accordingly through different hand postures at different start locations on the other. In other words, combined visual and postural cues were available. The performance during the adaptation and the adaptive shift as the difference between the movement directions in the visual open-loop posttest (with cued visuomotor rotation) and the pre-test (Heuer & Hegeler, 2011) were compared between both groups. We suppose that dual adaptation would be attenuated in comparison to single rotation adaptation, even when context cues are provided. In other words, single rotation condition would confer better performance during adaptation and larger adaptive shift. Furthermore, in case of dual adaptation, participants transitioned not from an unrotated baseline but from a counter-rotation due to the alternating rotation conditions. Miall et al. (2004) argued that it is important to take the magnitude of the absolute directional shift into account. Consequently, participants in the dual adaptation group had to deal with a shift of 60° after each alternation, which might cause larger aiming errors in the initial movements (switching costs) after the alternations.

<sup>1</sup> A further class of abstract instructional cues (Imamizu et al., 2007) will not be discussed here.



**Fig. 1** Schematic view of the manual and visual workspace in the experiments. Participants aimed at targets 20 cm perpendicularly from the respective start locations. Visual feedback was clockwise (*cw*) or counterclockwise (*ccw*) rotated. Hand paths to produce straight up cursor movements despite visual distortion are shown as *dotted lines* (for *cw* rotation) or *dashed lines* (for *ccw* rotation). **a** Setup of Experiment 1: Targets A and B were located on the left and the right side of the display, respectively. The horizontal distance between both targets was 28 cm. Manual start locations A' and B' correspond spatially to the start locations A and B on the display, so that their horizontal separation was 28 cm as well. **b** Setup of Experiment 2a: display elements in Experiment 2a were completely identical with those in Experiment 1. However, start location A and B shared one manual start location (Start A'B'), which was located in the middle of the digitizer tablet. **c** Setup of Experiment 2b: only one start location (Start AB) and one target (Target AB) were presented in the middle of the display. However, the task was either carried out on the left (Start A') or on the right (Start B') manual start location

Macintosh computer with Matlab software and the Psychophysics Toolbox (Brainard, 1997; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997). The room lights were dimmed throughout the experiment.

Participants were seated at a table. The height of the chair was adjusted individually to ensure comparable viewing and action conditions across participants. A DIN-A3 digitizer tablet (Wacom Intuos2) with a sampling rate of 200 Hz resting horizontally on the table was covered by a fiberboard to block participants' view of their hand on the tablet. The digitizer tablet was configured in absolute position-matching mode. In this mode, each dot on the tablet was assigned to a dot on the display screen in a fixed manner.

Participants controlled the cursor movement (a small blue disk with 4 mm in diameter) on the computer display with a stylus held in their right hand. The cursor movement was displayed on a 22-in. CRT color monitor (model: Iiyama Vision Master Pro514; resolution,  $1,024 \times 768$  pixels; refresh rate, 100 Hz) placed upright on the table with its center at the participants' eye level and with a distance of about 65 cm in front of the participants.

Two start locations and their corresponding targets were located on the left or the right part of the visual display (Fig. 1a). They were marked with gray dots (5 mm in diameter) visible throughout the experiment. A gray line of 50 mm at each side of the target's horizontal periphery served as target line.

Hence, the switching costs have been supposed to be larger in the opposing group.

## Method

### Apparatus and stimuli

The apparatus and the setup were the same in all experiments. The apparatus was controlled by an Apple

### Procedure

At the beginning of each trial, the start location was illuminated in yellow signaling the valid start location, while the other start location stayed gray. After participants held the cursor exactly on the valid start location for 500 ms, a pure tone (840 Hz) was released for 100 ms. This tone signaled that the trial was unlocked and the participants were instructed to initiate a sliding movement with their

right hand as soon as possible. At this moment, the stylus is exactly on either Start A' or Start B', depending on whether Start A or Start B was the valid start location on the display. Participants should slide the cursor to a given target as precisely as possible, by accelerating the cursor with a short straight flicking movement, which determines the approximate direction of the cursor. The area within a radius of 2 cm around the start location served as the area for movement initiation, inside of which the cursor was under control of stylus motion on the tablet. Once the cursor left this area, it began to slide in a straight line on a constant velocity of 17 cm/s. After the cursor hit the target line, the score was displayed immediately next to the final cursor location. Depending on the deviation from target middle, the (hit) score varied from 10 (maximum score with target middle) to 0 (minimum score 50 mm or more out of range).

All experiments used the same schedule, which consisted of three phases. At the very beginning of each experiment there was a short practice of 10 trials with veridical visual feedback. This pre-experimental part was introduced in order to get the participants acquainted with the apparatus and the flicking movement and to ensure that they have understood the task requirements. Following the pre-experimental preparation, participants performed the sliding task in 48 consecutive blocks (with 5 trials each). The start location switched after each block and the start location in block 1 was counterbalanced between participants.

*Phase 1 (pre-measure)* with block 1–block 8 served as baseline measure and was the same for both groups. It was further subdivided in to a baseline measure (block 1–block 4) with veridical feedback followed by a baseline measure without visual feedback (block 5–block 8). In trials without visual feedback, the cursor vanished as soon as the trial was unlocked. The movement was performed in a “blind flight” and no (hit) score was presented at the end of the trial. The measures with and without visual feedback served as baseline for the adaptation and the post-adaptation, respectively.

*Phase 2 (exposure)* contained block 9–block 38. Participants were exposed to a 30° visuomotor rotation, which they had to adapt to. Group 1 constantly received a cw rotation at both start locations (constant group). For group 2, the rotation at the left start location was cw and ccw at the right start location, which means that group 2 had to adapt to opposing rotations in an alternating sequence (opposing group). After each block a summary of hit score was provided and the participants could take a short break before beginning the next block.

*Phase 3 (post-measure)* contained the last 10 blocks (block 39–block 48). It served as a post-adaptation measure without visual feedback and was the same for both groups. Participants were instructed that all conditions remained the same as in the exposure with the exception that no

visual feedback was provided. The entire experiment lasted about 45 min.

### *Design and data analysis*

As dependent variable aiming errors were gathered as angular deviations  $\alpha$  (°) from the ideal trajectory, which is defined as the direct path from the visual start location to the visual target. Generally,  $\alpha$  was 0, if the actual cursor trajectory fitted the ideal trajectory exactly. In the baseline phase, a positive  $\alpha$  value indicates a clockwise deviation relative to the ideal trajectory and a negative  $\alpha$  value indicates a counterclockwise deviation relative to the ideal trajectory. Individual performances in the adaptation were adjusted by subtracting the aiming errors obtained in the pre-measure with visual feedback. Adaptive shifts were calculated as the differences between the post-measure and the pre-measure without visual feedback. The adjusted aiming errors in the adaptation and the adaptive shifts were signed relative to the rotation direction: a positive  $\alpha$  value indicates a deviation in accordance with the direction of the rotation and a negative  $\alpha$  value indicates a deviation opposite to the rotation.

These data were analyzed using mixed-factor ANOVAs. The different adaptation conditions between groups represented the first independent factor of the experiment. Within each critical experimental phase, the amount of consecutive blocks was realized as a within-subject factor. Since both groups received different rotations at the right start location (cw for constant group and ccw for opposing group), a bias due to this group-specific location and rotation combination could occur and confound the between-group comparison, if the ccw rotation was generally more difficult to be adapted. Hence, the side (left vs. right) was taken as another within-subject factor (and accordingly the experimental blocks were sorted by side). It resulted in a 2 (groups)  $\times$  2 (sides)  $\times$  15 (blocks a side) mixed design for the adjusted adaptation performance and a 2 (groups)  $\times$  2 (sides)  $\times$  5 (blocks a side) for the adaptive shifts. Additionally, mean aiming errors over all adaption blocks were computed for each start location and compared between both groups.

Switching costs due to the alternating transition between both start locations and the corresponding rotations (in the dual adaptation group) were computed as the difference between the aiming error in the last trial prior to the switching and the error in the first trial after the switching.

### *Participants*

Sixteen right-handed students (12 females) from RWTH Aachen University volunteered to take part in Experiment 1. The mean age of participants was 22.3 years (ranging

from 19 to 30 years) with a standard deviation (SD) of 2.7 years. Handedness was ensured with the Edinburgh Handedness Inventory (mean lateralization quotients of 80; Oldfield, 1971). All participants were naïve to the purpose of the study.

Participants were randomly assigned to two groups. As aforementioned, group 1 constantly received a cw rotation at both start locations, whereas group 2 had to adapt to opposing rotations in an alternating sequence.

**Results**

Figure 2a shows the plot of mean aiming errors of all experimental blocks as a function of block number. All participants were able to aim successfully for the target in both baseline conditions, in which the performance did not differ between groups.

*Adaptation phase*

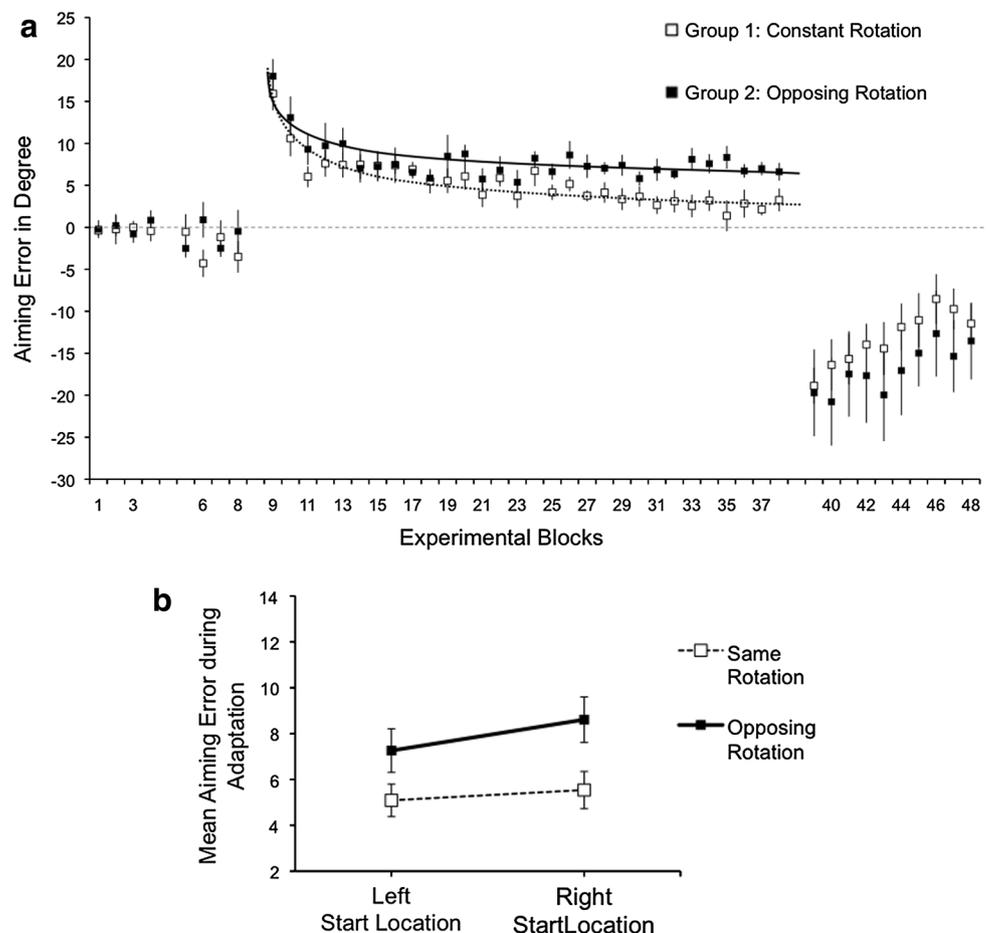
The aiming errors, caused by visuomotor rotation, declined continuously in both groups before it stagnated at a lower error level. The  $2 \times 2 \times 15$  ANOVA yielded a significant

main effect of block [ $F_{(14,196)} = 8.14, p < 0.001$ , partial  $\eta^2 = 0.47$ ], and a significant main effect of group [ $F_{(1,14)} = 5.51, p < 0.034$ , partial  $\eta^2 = 0.28$ ]. As illustrated by the power function curves (Fig. 2a) computed for the mean aiming errors of each group, the constant group showed better adaptation performance than the opposing group. The ANOVA showed neither main effect of side ( $p > 0.11$ ) nor interaction between side and group ( $p > 0.42$ ). In line with the ANOVA, mean aiming error over adaptation blocks showed similar group differences at both start locations. As illustrated in Fig. 2b, the opposing group showed larger aiming error at both left [ $t_{14} = 1.83, p < 0.045$ , one-tailed] and right [ $t_{14} = 2.39, p < 0.016$ , one-tailed] start locations. Hence, the suspicion that the group difference would have been caused merely by the assumingly more difficult ccw rotation on the right start location in the opposing group has been excluded.

*Adaptive shift*

The adaptive shift diminished with repeated movements without visual feedback. Accordingly, a  $2 \times 2 \times 5$  group-

**Fig. 2 a** Mean aiming errors (with standard errors) in degree in the three experimental phases of Experiment 1 broken down into 48 blocks. Every data point represents the average of five consecutive trials across all participants within the experimental groups. Block 1–block 8 was baseline measure; Block 9–block 38 was the adaptation phase; Block 39–block 48 served as post-adaptation measure. A single power function was fitted to the adaptation performance for each group using a least-square fit criteria (*dotted line* for the constant group and *solid line* for the opposing group). **b** Average aiming error (with standard error bars) over all adaptation blocks for each group at each start location



block mixed ANOVA showed a significant main effect of block [ $F_{(4,56)} = 3.56$ ,  $p < 0.012$ ,  $\eta^2 = 0.20$ ]. Neither a main effect of group ( $p > 0.42$ ) nor a group by block interaction ( $p > 0.91$ ) was observed, which indicates that both groups showed nearly identical adaptive shifts regarding both the size and the pattern of decay over time.

## Discussion

In accordance with our hypotheses better adaptation performance in the constant group was corroborated by the statistical analysis. The participants of the opposing group showed slower adaptation rate (the speed of aiming error decline) indicated by the less steep power curve and larger mean aiming error over the adaptation blocks. This compromised adaptation performance could be caused either by mutual interactions between the opposite rotations or merely by repeated switching between two different visual distortions. If the latter case is true, group difference must be primarily determined in the very first trial after each switching. Therefore, we eliminated the first trial of each adaptation block and repeated the ANOVA with the average of the four remaining trials in each block separately. The outcome was similar to the results reported above. Analysis of the switching costs confirmed this finding by showing comparable switching costs in both groups. Hence, the group difference can only be explained by mutual interference of discordant rotations and—most importantly—dual adaptation can succeed in spite of presence of interference. Since efficient adaptation depends on the ability to inhibit previously learned but now inappropriate visuomotor associations (Shadmehr & Holcomb, 1999), the movement initiation in dual adaptation will be slowed down due to additional inhibition processes (Heuer & Hegele, 2011). However, an additional group comparison regarding the time of movement initiation showed no discernable difference between the groups. We suppose that the single-target scenario in the present study lacks complexity compared to previous studies using multiple targets in a circular array around a start location (e.g. Bock et al., 2005; Krakauer et al., 2005). This simplified motor task may have minimized the cognitive demand of inhibition in dual adaptation, so that the movement planning and execution were not slowed down.

In the post-measure, both groups showed initially substantial adaptive shift (approximately  $19^\circ$  in the constant group and  $20^\circ$  in the opposing group), which declined with repeated movements. Astonishingly, there was no group difference regarding adaptive shift despite clearly compromised adaptation in the opposing group. Considering the fact that the switching costs was quite similar in both constant and opposing groups, it can be assumed that the explicit control performance in both rotation conditions

was broadly comparable. Consequently, the observed group difference was probably caused by compromised implicit adaptation in the opposing group. The lack of group difference in adaptive shift was likely due to the fact, that adaptive shift as a product of both implicit adaptation and explicit control was not precise enough to show the difference in implicit adaptation. Aftereffect as change of movement direction in spite of the knowledge that no visuomotor rotation is present any more (Hegele & Heuer, 2010; Heuer & Hegele, 2011) would be certainly a better indicator in this aspect. More detailed discussion concerning this issue is made in the “General discussion” by taking also the findings of Experiment 2 into account.

## Experiment 2a and 2b

Despite larger aiming errors during exposure, the opposing group in Experiment 1 showed substantial dual adaptation suggesting the effectiveness of contextual cues, which enabled the performer to distinguish between two rotation conditions during both adaptation and recall. Since the alternating schedule and its regularity per se have been proved to be no effective cue (Karniel & Mussa-Ivaldi, 2002; Woolley et al., 2007), two sensory inputs remained under suspicion. For the opposing group in Experiment 1, rotations were aligned to different regions of the workspace, which were associated with distinct visual elements on the display (visual cue) and—at the same time—with different hand postures (postural cue). Due to this confounding cueing-effect in Experiment 1, Experiment 2 aimed to dissociate visual and postural cues regarding their effectiveness for dual adaptation. In other words, dual adaptation was re-examined when either the visual cue (Experiment 2a) or the postural cue (Experiment 2b) was available. It is worth noting that both visual and postural cues in the current study were not only used to differentiate between rotation conditions, they also directly provided sensory input to specify movement plans. At this point both kinds of cues were comparable regarding the relevance for movement control—in contrast to a color cue, for example, which provides per se no sensory information for movement control. Taking into account previous findings, which indicated a more dominant role of visual representation in movement control and limited capability of proprioception in movement monitoring (c.f. Müsseler & Sutter, 2009; Rand, M. K., Wang, L., & Müsseler, 2013; Sutter et al., 2013), visual cue should be even more effective than postural cue. From another perspective, Ladwig, Sutter, & Müsseler, (2012) have shown that the reproduction of proximal action effects was biased by transformed distal action feedbacks in preceding movements. In previous studies focusing on sensorimotor learning, the visually

represented spatial structure of the distal workspace has turned out to be crucial for visuomotor adaptation and its transfer (Wang & Müsseler, 2012; Wang, Rand, & Müsseler, 2013). In other words, the visuomotor rotations obviously were perceived, understood and learned in accordance with the spatial character of the distal workspace. These findings were in line with the idea that goal-directed movements, as suggested by Mechsner, Kerzel, Knoblich and Prinz (2001) are organized by way of a representation of their distal effects, which are visually encoded and contain some same elements as the visual cue (e.g. the visually represented target location). Hence, we assume superiority of the visual cue (visual discrimination of task requirements) over the postural cue (postural discrimination of task requirements), and consequently, expect better dual adaptation performance (e.g. lower switching costs) with visual cues compared to postural cues. As it has been reasoned earlier, the opposing groups are expected to show larger switching costs. Moreover, the actual amount of the switching costs in opposing groups should depend on the effectiveness of the context cues, which facilitate dual adaptation. According to the assumed superiority of the visual cue, we expect smaller switching costs in opposing groups with visual cue (Experiment 2a) and combined cues (Experiment 1) than with postural cue (Experiment 2b).

## Method

### Setup and procedure

These were the same as in Experiment 1, except for the following changes. The experimental setups of Experiment 2a and 2b are illustrated in Figs. 1b and 2c. In Experiment 2a, the visual workspace was the same as in Experiment 1. Two start locations (Start A and Start B) with their corresponding targets were located on the left and right side of the display. The start location for the sliding task switched after each block. However, in contrast to Experiment 1 the manual start location (Start A'B') was located in the middle of the digitizer tablet and remained stationary throughout the experiment. Again, two groups differing in the rotation conditions during adaptation phase performed the experiment. Group 1 was exposed to a constant cw rotation, whereas for group 2 the rotation at the left start location (Start A) was cw and ccw at the right start location (Start B), which means group 2 had to adapt to opposing rotations in an alternating sequence.

In Experiment 2b, only one start location (Start AB) and one target (Target AB) were presented in the middle of the visual display. However, the manual start location switched after each block as in Experiment 1. In the adaptation phase a cw rotation was induced if the task was performed at the

left start location on the tablet (Start A') and a cw rotation for group 1 and, respectively, a ccw rotation for group 2 were applied at the right start location (Start B').

### Participants

Sixteen (13 females) and 14 (12 females) students of RWTH Aachen University volunteered to take part in Experiment 2a and 2b, respectively. The mean age of participants was 23.1 years (ranging from 18 to 30 years) with a SD of 3.6 years in Experiment 2a and 22.6 years (ranging from 19 to 32 years) with a SD of 3.6 years in Experiment 2b. All participants were right-handed, which was ensured again using the Edinburgh Handedness Inventory (mean lateralization quotients of 75 for Experiment 2a and 82 for Experiment 2b; Oldfield, 1971). All participants were naïve to the purpose of the study.

## Results and discussion

### Experiment 2a

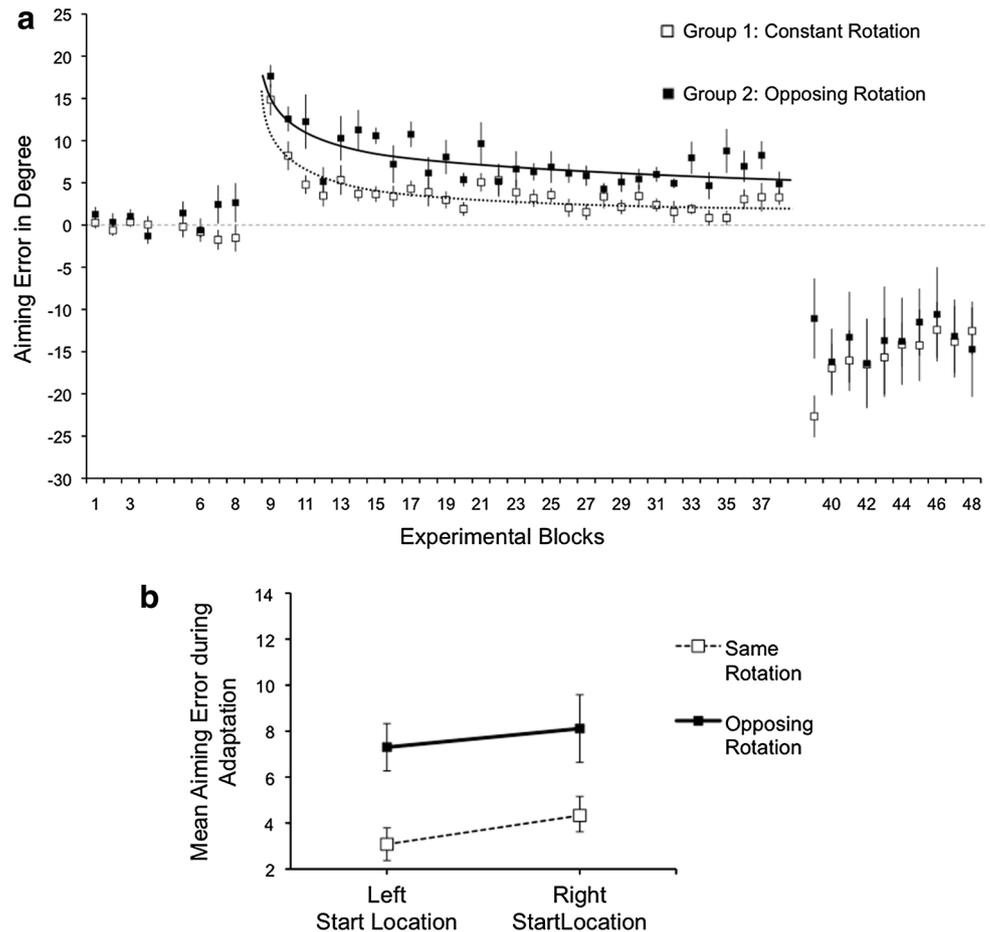
Figure 3a shows the plot of mean aiming errors of all experimental blocks as a function of block number. The fitted power function curves indicate better adaptation performance in the constant group than in the opposing group. Accordingly, the  $2 \times 2 \times 15$  ANOVA yielded a significant main effect of block [ $F_{(14,196)} = 15.06$ ,  $p < 0.001$ , partial  $\eta^2 = 0.52$ ], and a significant main effect of group [ $F_{(1,14)} = 9.13$ ,  $p < 0.009$ , partial  $\eta^2 = 0.39$ ]. Neither main effect of side ( $p > 0.19$ ) nor interaction between side and group ( $p > 0.18$ ) was found. In accordance with these findings, the opposing group showed larger aiming error averaged over the adaptation blocks at both left [ $t_{14} = 3.39$ ,  $p < 0.002$ , one-tailed] and right [ $t_{14} = 2.24$ ,  $p < 0.021$ , one-tailed] start locations (Fig. 3b).

In the post-adaptation measure, a  $2 \times 2 \times 5$  group-block mixed ANOVA showed a significant main effect of block [ $F_{(4,56)} = 1.93$ ,  $p < 0.015$ ,  $\eta^2 = 0.20$ ], but no effect of group ( $p > 0.72$ ) or group by block interaction ( $p > 0.14$ ). Additionally, no main effect of side or any other effect related to it was found to be significant. The results indicate temporal decay of adaptive shifts in both groups.

### Experiment 2b

The mean aiming errors of all experimental blocks are presented in Fig. 4a. The  $2 \times 2 \times 15$  ANOVA showed a significant main effect of block [ $F_{(14,168)} = 10.26$ ,  $p < 0.001$ , partial  $\eta^2 = 0.46$ ], and a significant main effect of group [ $F_{(1,14)} = 5.16$ ,  $p < 0.042$ , partial  $\eta^2 = 0.30$ ]. As illustrated by the power function curves computed for the

**Fig. 3 a** Mean aiming errors (with standard errors) in degree in the three experimental phases of Experiment 2a broken down into 48 blocks. Every data point represents the average of five consecutive trials across all participants within the experimental groups. Block 1–block 8 was baseline measure; block 9–block 38 was the adaptation phase; block 39–block 48 served as post-adaptation measure. A single power function was fitted to the adaptation performance for each group using a least-square fit criteria (*dotted line* for the constant group and *solid line* for the opposing group). **b** Average aiming error (with standard error bars) overall adaptation blocks for each group at each start location



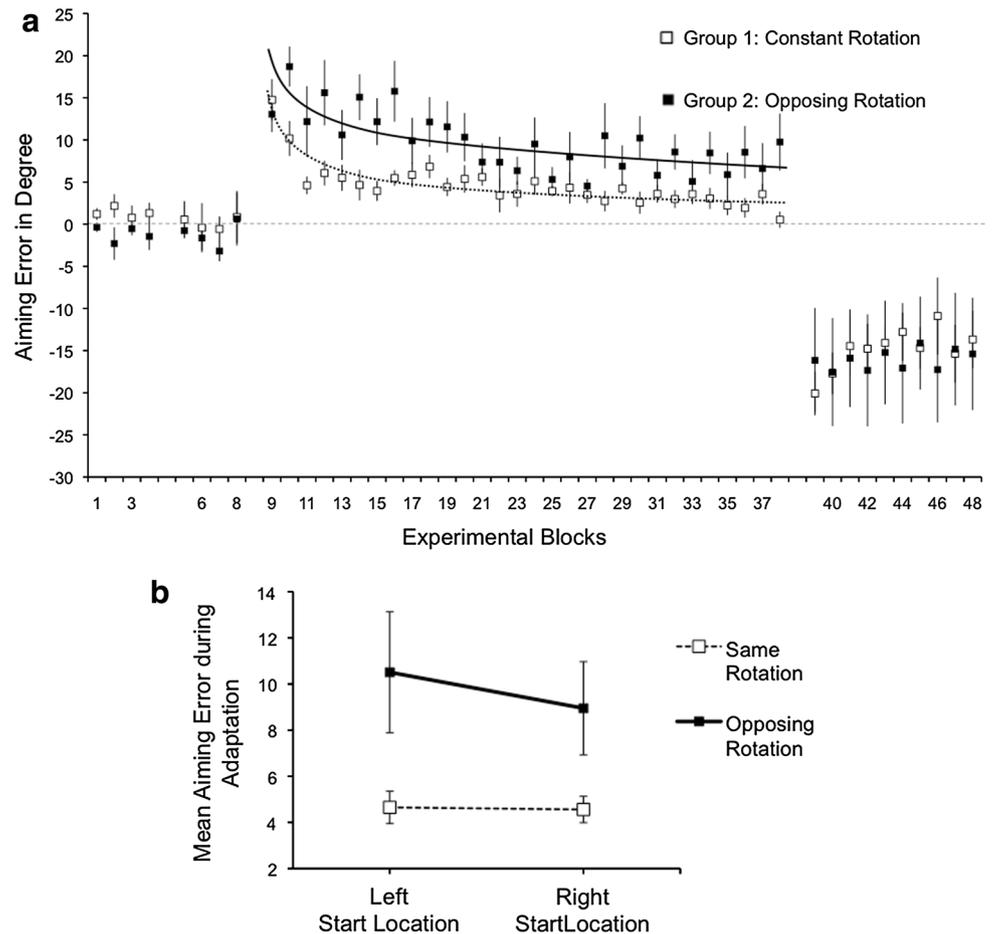
mean aiming errors of each group, the constant group showed substantially better adaptation performance than the opposing group. In contrast, the ANOVA showed neither main effect of side ( $p > 0.39$ ) nor group by side interaction ( $p > 0.35$ ). Group comparison regarding average aiming error over adaptation blocks corroborated the homogeneity of both start locations. In other words, the opposing group showed larger aiming error averaged over the adaptation blocks at both left [ $t_{12} = 2.16$ ,  $p < 0.026$ , one-tailed] and right [ $t_{12} = 2.10$ ,  $p < 0.029$ , one-tailed] start locations (Fig. 4b).

In the post-adaptation measure, a  $2 \times 2 \times 5$  group-block mixed ANOVA yielded no significant results—neither main effects nor any interactions.

In order to examine the effectiveness of different cues for dual adaptation separately, the multiple contextual cues in Experiment 1 were decomposed and the components were evaluated in Experiment 2. Hence, in Experiment 2a only the visual cue and in Experiment 2b only the postural cue was available. The findings with respect to dual adaptation were quite comparable to those in Experiment 1. In Experiments 2a and 2b, substantial adaptation in the

opposing group was found, even though the adaptation was compromised compared to the constant group. And again, no discernable group difference was found regarding adaptive shifts. It is quite unexpected that in all experiments the group differences in the adaptation phase did not translate to group differences in the posttest. Since the only difference between adaptation and the posttest was the presence or absence of visual feedback, it is likely that the presence of visual feedback was critical for the group difference, which thus disappeared in the posttests. During adaptation, the visually represented final cursor position relative to the target could be exploited to correct the movement in the subsequent trial. If the cursor hit the target to the right of the center, an appropriate correction for the next trial would be aiming stronger to the left. Although this correction would be independent of the current visuomotor rotation, it might require different consequences for an internal representation of the visuomotor rotation. In other words, internal representation of the rotation has to be attenuated if the appropriate correction and the rotation are in the same direction; otherwise, it has to be enhanced. These corrections would be especially

**Fig. 4 a** Mean aiming errors (with standard errors) in degree in the three experimental phases of Experiment 2b broken down into 48 blocks. Every data point represents the average of five consecutive trials across all participants within the experimental groups. Block 1–block 8 was baseline measure; block 9–block 38 was the adaptation phase; block 39–block 48 served as post-adaptation measure. A single power function was fitted to the adaptation performance for each group using a least-square fit criteria (*dotted line* for the constant group and *solid line* for the opposing group). **b** Average aiming error (with standard error bars) over all adaptation blocks for each group at each start location



confusing during adaptation to opposing rotations and have resulted in the interference in dual adaptation, since internal representations about two different rotations were concurrently available. This terminal feedback determined group difference would vanish gradually in the posttest. If this assumption is true, group differences must still be present at the very beginning of the posttest. Hence, the adjusted performance in the first trial of posttest was compared between constant and opposing groups over all experiments. The related results are reported in the following section.

#### Initial adaptive shifts across all experiments

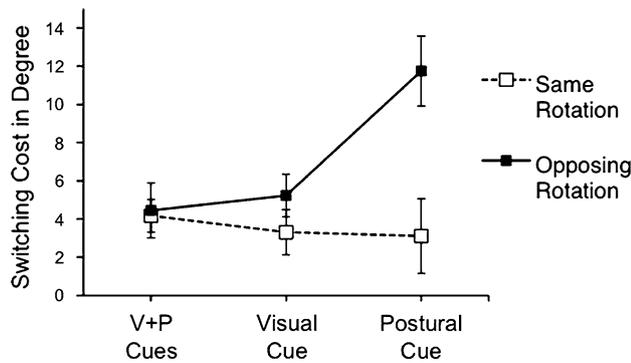
In line with the assumption, group difference regarding adaptive shifts in the first posttest trial was found to be significant with  $-23.3^\circ \pm 1.9^\circ$  in the constant group and  $15.0^\circ \pm 3.4^\circ$  [ $t_{44} = 2.11$ ,  $p < 0.021$ , one-tailed].

Finally, results based on analysis of switching costs in different cueing conditions were in line with our assumption that participants provided with the visual cue were able to switch between discordant mappings more effectively, compared to those who could only use the

postural cue. Hereby, the switching costs in the combined cue condition (Experiment 1) and in the visual cue condition (Experiment 2a) did not differ between the constant and opposing groups, whereas remarkable group difference was found in the postural cue condition (Experiment 2b). The statistics are reported in the following section.

#### Comparing switching costs across all experiments

Switching costs during adaptation was compared between the constant and the opposing groups for all experiments (visual + postural cue in Experiment 1 vs. visual cue in Experiment 2a vs. postural cue in Experiment 2b) using a 3 (cueing conditions)  $\times$  2 (rotation groups) ANOVA. This analysis served as a direct comparison of all three cueing conditions respecting their effectiveness. The main effect of the group [ $F_{(1,40)} = 9.93$ ,  $p < 0.003$ ,  $\eta^2 = 0.20$ ] and the cue  $\times$  group interaction [ $F_{(2,40)} = 4.77$ ,  $p < 0.014$ ,  $\eta^2 = 0.19$ ] were found to be significant. In accordance with these results, post hoc group comparisons for respective cue conditions yielded only a significant group difference in the postural cue condition indicating higher switching



**Fig. 5** Mean switching costs (with standard errors) in degree during adaptation. Every data point represents the average of a rotation group (*open squares* for the constant group and *filled squares* for the opposing group) in a certain cueing condition

costs in the opposing group when only postural cue was available [ $t_{12} = 3.23$ ,  $p < 0.004$ , one-tailed] (Fig. 5).

## General discussion

The present study aimed to evaluate dual adaptation to discordant visuomotor rotations in an alternating sequence. We focused on the impairment arising from dual adaptation and its consequence in distinct cueing conditions.

It is commonly accepted that learning opposing visuomotor rotations usually encounters difficulties because of mutual interference as shown by previous studies focusing on the sequential adaptation to different sensorimotor transformations. For instance, Miall et al. (2004) demonstrated anterograde interference from an original adaptation Task A<sub>1</sub> to the subsequent discordant Task B; conversely, performance was equivalent in Task A<sub>1</sub> and the retest A<sub>2</sub>, suggesting no significant retention of Task A<sub>1</sub>. Apart from the debate whether the latter case is due to retrograde interference, similar phenomena of prevented saving of original adaptation through subsequent exposure to a counter-rotation were reported in other studies as well (Krakauer, Ghilardi, & Ghez, 1999; Wigmore, Tong, & Flanagan, 2002). However, numerous studies reported evidently successful dual adaptation, i.e. the concurrent adaptation to different sensorimotor transformations (Bock et al., 2005; Gandolfo et al., 1996; Imamizu et al., 2007; Krouchev & Kalaska, 2002; Rao & Shadmehr, 2001; Woolley et al., 2007). One essential feature these studies had in common were effective contextual cues, which were not provided in those failing to show dual adaptation. Thus, the findings arouse the impression that contextual cues must have prevented interference so that dual adaptation could succeed. Bock et al. (2005) have conceded that the fact, that discordant adaptive states are established in

parallel, does not exclude the possibility that each interferes with the formation of the other. The present study examined this possibility by comparing groups adapting either to a constant rotation or to alternating discordant rotations. Our data showed indeed noticeable disadvantage of adaptation to discordant rotations regarding both the adaptation rate and the overall performance during adaptation. Apparently, contextual cues did not eliminate the mutual disruption due to discordant sensorimotor rotations. They rather provide the performer with an instrument to distinguish between distinct action contexts associated with different sensorimotor requirements, so that multiple adaptations can be performed simultaneously.

The open question is whether the compromised adaptation performance in the dual adaptation groups was caused by enhanced difficulty in explicit control or by attenuated implicit adaptation. Increased cognitive load in explicit control due to discordant task requirements appears reasonable. Shadmehr and Holcomb (1999) monitored the neural activity of participants during adaptation to opposing force fields. The authors observed changes in ventral prefrontal cortex indicating an extra inhibitory process in order to suppress the perseveration. This finding is in line with the study by Larssen, Ong, and Hodges (2012) showing that a more strategic type of learning aids dual task adaptation. Considering the alternating schedule in the present study, the demand for explicit control should have been particularly high, since the inhibitory mechanism was switched on by every alternation. The increased demand on for explicit control probably has two consequences for the aiming movements: increased time for movement initiation, larger movement error, or both. In our case, enhanced difficulty in explicit control at each alternation (or switching) should result in larger switching costs, which were computed as the difference between the aiming error in the last trial prior to the switching and the error in the first trial after the switching. However, we did not observe any discernable increase in switching costs through opposing rotations in Experiment 1 and Experiment 2a. It suggests that in Experiments 1 and 2a both constant and opposing groups would have employed similar control strategy. While the constant rotation might yield a bias to aim leftwards of the target at both start locations, the opposing rotations simply yielded a bias to aim outwards relative to the target locations (i.e. leftwards at the left and rightwards at the right start location). Since the suspected strategy in the opposing condition relied on the visual separation of two start-target units, which was not given in Experiment 2b, it also explains the significantly increased switching costs in the opposing group in that experiment. Anyway, comparable explicit control performance in both groups in Experiments 1 and 2a indicate that the group difference in the adaptation phase can only be explained by

difference in implicit adaptation. Hereby, the terminal feedback about the final cursor position and the correction in the subsequent trial seem to be crucial for the group differences. Corrections determined by the terminal feedback, which were independent of the current rotation, probably had attenuated the concurrent learning of the internal models for opposing rotations. Consequently, the missing terminal feedback would account for the finding that the group differences during adaptation were only observed in the initial trial of the posttests. Furthermore, the lack of trial-by-trial correction would also account for the remarkably increased variance in movement direction in the posttests.

Since in both Experiments 2a and 2b substantial adaptation and adaptive shift were observed, it could be concluded that dissociation between visual and manual workspace did not impair the adaptation. Furthermore, the data show that significantly lower switching costs were enabled by visual cue compared to the postural cue. This finding seems to contradict a previous study by Woolley et al. (2007) that favored motor over visual contextual cues. However, as pointed out by Hegele and Heuer (2010), that the study by Woolley et al. (2007) comprised a potential confound. Their setup was unable to dissociate the relative contribution of distinct motor requirements and of the visual separation of movement targets in dual adaptation. Hence, our results present actually an extension to their findings rather than a contradiction.

Finally, it still remains interesting to review the present findings in a future study using a multiple-target scenario to enhance the task complexity and a more elaborated post-measure to separate implicit and explicit components in adaptation.

## Conclusion

In case of dual adaptation, visual, postural, or a combination of cues allowed anticipation of different visuomotor mappings and therefore enabled dual adaptation. However, contextual cues did not eliminate the mutual impairment between conflicting visuomotor rotations. Consequently, dual adaptation was attenuated in comparison to single adaptation. Comparison between visual and postural cues showed that visual cue was more powerful in reducing switching costs during dual adaptation.

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