Generalization of implicit and explicit adjustments to visuo-motor rotations across the workspace in younger and older adults

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Abstract

We examined the generalization of adjustment to a visuo-motor rotation across the workspace in younger and older adults. Participants practiced in the right workspace with a single target direction and were tested in both the right and left workspace with eight different target directions. A set of tests served to identify implicit and explicit components of adjustment. Explicit, but not implicit components were stronger at younger than at older adult age. Explicit components generalized across all target directions, whereas implicit components were restricted to the target direction during practice and clockwise adjacent ones. Generalization to the contralateral workspace was found only for explicit components of adjustment. These findings expand the list of functional differences between implicit and explicit components of adjustment to visuo-motor transformations.
Humans have the capability to adjust to novel visuo-motor transformations, for example when they use a computer mouse to control the position of a cursor on a monitor. Since the seminal work of Cunningham (1989), adjustment to visuo-motor rotations has become a well-established paradigm for the study of this capability (e.g., Abeele & Bock, 2001a, b, 2003; Imamizu & Shimojo, 1995, Krakauer, Pine, Ghilardi, & Ghez, 2000). Typically a start and several target locations are presented on a monitor. Participants are asked to move a cursor, whose motion is controlled by the movements of the participant’s hand, from the start to a particular target location. The direction of cursor motion is rotated (around the start position) relative to the direction of hand movement. In spite of the extensive use of this paradigm, generalization of adaptation to novel start locations has received only limited attention. In the present study, we explore the generalization of adjustment to a visuo-motor rotation across the workspace in younger and older adults.

Adjustment to a visuo-motor rotation embraces different components (e.g. Saijo & Gomi, 2010) which are likely to contribute differently to its generalization. A fundamental distinction is that between implicit and explicit adjustments (cf. Hegele & Heuer, 2010a; Heuer, Hegele, & Sülzenbrück, in press; Mazzoni & Krakauer, 2006; Sülzenbrück & Heuer, 2009; Taylor & Ivry, 2011; Taylor, Klemfuss, & Ivry, 2010). Implicit adjustments are outside conscious awareness, whereas explicit adjustments are intentional movement corrections based on explicit knowledge of the rotation. Implicit adjustments reveal themselves as after-effects, that is, as changes of movement directions in spite of the knowledge that there is no visuo-motor rotation present any more. They can be conceived as originating from an internal model of the transformation (e.g., Heuer, 1983; Wolpert & Kawato, 1998). Explicit adjustments, in contrast, should reveal themselves in (non-motor) judgements of the proper direction of arm movement given a certain target direction. Both explicit and implicit adjustments are combined to contribute to adaptive shifts of movement direction, that is, to changes of movement direction when the presence of a visuo-motor rotation is known.

Implicit and explicit adjustments to visuo-motor rotations have different characteristics. First, they differ with respect to the generalization across target directions. Adaptation to a visuo-motor rotation has been shown to be rather specific
for a particular target direction, that is, after practice with only a single target direction adaptation is restricted to this direction and adjacent ones (Krakauer et al., 2000). However, the small range of generalization is found only for implicit adjustments, whereas explicit adjustments generalize across all directions (Heuer & Hegele, 2008).

A second difference between implicit and explicit adjustments to visuo-motor rotations is that they are differently sensitive to ageing. Whereas implicit adjustments remain constant or even increase across the adult age range, explicit adjustments decline (cf. Heuer & Hegele, 2008). This pattern of results is a highly consistent one (cf. Bock, 2005; Bock & Girgenrath, 2006; Buch, Young, & Contreras-Vidal, 2003; Hegele & Heuer, 2010b; Heuer & Hegele, 2010; McNay & Willingham, 1998). Perhaps it is related to an age-related failure to engage spatial working memory efficiently during learning (Anguera, Reuter-Lorenz, Willingham, & Seidler, 2010).

In the present experiment, participants practiced a visuo-motor rotation with only a single target direction. The purpose was to explore the respective roles of implicit and explicit adjustments for the generalization across the workspace. Under the hypothesis that generalization primarily pertains to the explicit component of adjustment to the visuo-motor rotation, it should be roughly identical for practiced and non-practiced target directions, and it should be stronger in younger than in older adults. In contrast, under the hypothesis that generalization primarily pertains to the implicit component, it should be restricted to a small range of target directions, and it should be invariant across the adult age range.

In addition to examining the role of implicit and explicit adjustments to a visuo-motor rotation for its generalization across the workspace, the present experiment was designed to shed some light on the frame of reference which underlies generalization. According to the few studies that explored generalization across a limited range of the workspace, the underlying frame of reference is extrinsic or workspace-based (cf. Krakauer et al. 2000; Wang & Sainburg, 2005). This contrasts with findings on generalization of adaptation to a novel force field, which is governed by an intrinsic or effector-based frame of reference (cf. Shadmehr & Moussavi, 2000; Malfait, Shiller, & Ostry, 2002). To determine the frame of reference in the present study, participants practised with the forearm about parallel to the sagittal plane, but
in the transfer test the forearm was repositioned roughly parallel to the frontal plane. With only a single target direction during practice, in the transfer test the adapted direction should be the same in the workspace if generalization were based on an extrinsic frame of reference. In contrast, the adapted target direction should be the same relative to the orientation of the forearm if generalization were based on an intrinsic frame of reference. Of course, this rationale presupposes the generalization of directionally selective implicit adjustments across the workspace.

Method

Participants. Two groups of participants served in the experiment. All of them had given written informed consent. The younger participants, 10 male and 12 female, were 20 to 28 years old (mean: 24.0 years, SD: 1.91 years). The older participants, 10 male and 8 female, were 47 to 66 years old (mean: 57.3 years; SD: 5.12 years). All participants were self-declared right-handers and had normal colour vision according to the Ishihara test. The data of two additional participants were not included in the analyses because of extreme pointing errors in the pre-test (see below) or at the end of practice.

The older and younger participants were compared on two subtests of the German version of the Wechsler Adult Intelligence Scale (Tewes, 1991): the Digit Symbol Test, a test of perceptuo-motor processing speed, and the Vocabulary Test, a test of culturally mediated knowledge. Conforming to typical findings, younger participants performed better on the Digit Symbol Test, 61.1 vs. 51.3, t(38) = 2.7, p < .01, but not on the Vocabulary Test where their performance was even worse than that of the older participants, 26.9 vs. 31.7, t(38) = 3.6, p < .01.

Apparatus. Participants sat on a height-adjustable chair and faced a 19-inch LCD Monitor (Iiyama ProLite E1902S), which was placed on a table at a distance of about 100 cm from their eyes. Their right index finger was strapped to a sled of 50 x 30 mm (height: 6 mm), which slid with only little friction on the table surface. The sled carried a vertically oriented sensor of a miniBIRD 800 system (Ascension Technology Corporation, Burlington, VT) directly above the fingernail. The position of the fingertip
was recorded at 103.3 Hz (spatial resolution: 0.11 mm). Direct vision of the hand was prevented by an occluder 20 cm above the table surface.

**Task.** Participants were instructed to perform swift and accurate aimed movements from a start location to a target. On the monitor the start location was marked by an outline circle of 9.6 mm diameter in the centre of the screen. In each trial one of eight possible targets was presented, which was marked by a filled white circle of 5.6 mm diameter. Targets were located on an invisible circle with a radius of 100 mm around the start location, so that the target distance was always 100 mm. Target directions were 0°, 45°, 90°, 135°, 180°, 225°, 270°, and 315°, with 0° designating the right target and 90° the forward target. In visual closed-loop trials the output of the visuo-motor transformation (or the position of the right index finger when the transformation was off) was indicated by a cursor, a cyan circle of 4.8 mm diameter. In visual open-loop trials the cursor was invisible.

Whereas on the monitor all cursor motions started in the same location, hand movements started in two different locations which were laterally separated by 576 mm and by 60 mm in depth. The approximate arm configurations when the right index finger was placed in the two start positions are illustrated in Figure 1. In the right start position the shoulder angle was about 0° and the elbow angle about 90°. In the left start position both the shoulder angle and the elbow angle were about 90°. Whereas the right start position was used during both practice phases and in all tests, the left start position was used only during baseline practice and tests. In terms of an effector-based frame of reference, a movement to the right in the right start position was roughly equivalent to a forward movement in the left start position; similarly a forward movement in the right start position was roughly equivalent to a leftward movement in the left start position.

**Design and procedure.**

The experiment consisted of four phases (cf. Figure 2): baseline practice, pre-tests, practice with a visuo-motor rotation of 75° counter-clockwise, and post-tests. Baseline practice was organized in two blocks of 48 trials, one block for each start
position. In each block there were six random permutations of the eight target
directions. The experiment started with baseline practice in the right workspace,
followed by the pre-tests for the right start location. Thereafter baseline practice in
the left workspace was followed by the pre-tests for the left start location.

Pre-tests were performed in both start locations and followed the respective
baseline-practice blocks. For each start location there were a visual open-loop test
and an explicit test. The open-loop test consisted of three blocks of 8 trials each, with
each target direction occurring once. The explicit test consisted of one block of 8
trials, again with each target direction occurring once. Each test block was preceded
by a maintenance block of four visual closed-loop trials that were identical to the trials
of a baseline-practice block. The four targets were selected randomly from the set of
8 possible targets. In all baseline-practice trials and pre-test trials the start circle was
green to cue the absence of the visuo-motor rotation. Not shown in Figure 2 are
proprioceptive-shift tests as the last ones of the pre-tests and post-tests. These tests
produced only negligible after-effects that showed no meaningful pattern and will
therefore not be described in detail.

The practice phase consisted of 6 blocks of 48 trials each, with a break of 2
minutes after the fifth block. During practice only the right start position was used and
only one target, which was the target at 0° (rightward) for half of the young and old
participants and the target at 90° (forward) for the other half. All practice trials were
with visual feedback and with the visuo-motor rotation present. Thus, to reach the
target at 0°, the required direction of hand movements was 285°, and to reach the
target at 90°, the required direction of hand movements was 15°. In practice trials the
start circle was red to cue to presence of the rotation.

Post-tests consisted of a visual open-loop test with cued presence of the visuo-
motor rotation (red start circle) and an open-loop test with cued absence (green start
circle). Since no cursor was presented, these two tests differed only with respect to
the colour cue. As in the pre-tests there was an explicit test, this time with cued
presence of the transformation, and with two blocks of trials rather than only a single
block. Each of the three types of test was performed first for the right start position and thereafter for the left start position. Each test block was preceded by a maintenance block of four visual closed-loop trials which were identical to practice trials (only right start position and only one target for each participant).

Each movement trial began with the presentation of the start circle, which was green or red depending on whether the visuo-motor rotation was turned off or on. Arrows were presented at the left, right, lower or upper edge of the monitor, which pointed to the centre and thereby served to guide the participant to the start location. For example, when the hand had to be moved to the left and forward to approach the start location, arrows were presented at the right and bottom edge of the monitor. The cursor became visible when it was within 10 mm of the start location to assist in reaching it accurately.

After 500 ms in the start location, a tone (1000 Hz, 20 ms) was presented and the start circle was filled. At the end of a randomly chosen interval of 500 ms, 700 ms, 900 ms, 1100 ms or 1300 ms a target was presented, and the start circle disappeared. In visual open-loop trials the cursor disappeared as well. The end of the movement was reached when the visible or invisible cursor had left the tolerance range of 10 mm around the start location and the distances between successively sampled positions were not larger than 0.25 mm for 400 ms. In visual closed-loop trials the cursor had to be within a tolerance range of 2 mm around the target location during the 400-ms interval in addition. The end of the movement was indicated to the participants by the disappearance of the target and, only in closed-loop trials, of the cursor. There was a time limit of 5 s for the movement, otherwise the trial was ended and a time-over message appeared on the monitor.

In trials of the explicit tests start and target locations were presented together with a line of 6 pixels width and 100 mm length. The line was centred in the start location around which it could be rotated. Its initial orientation was opposite to the visual target direction. Participants instructed the experimenter to rotate the line until its orientation matched the direction of the hand movement the participants thought to be correct for the cursor to reach the target presented. The explicit tests were
identical for the two start locations except that the participants placed their right index finger in the respective position.

Data analysis. For each movement trial the terminal direction error, the initial direction error, and the movement time were computed. The time series of finger positions and cursor positions were low-pass filtered (fourth-order Butterworth, 10 Hz, dual pass) and differentiated (two-point central difference algorithm). Start and end of each movement were determined from the tangential velocity. Starting at peak velocity, those samples were identified in both a forward and a backward search at which tangential velocity was smaller than 5 mm/s and remained smaller for 250 ms thereafter. Terminal direction of the movement was defined as the direction of the vector from the start position to the endpoint of the movement, initial direction by the direction of the vector from start to the position after a movement duration of 200 ms. Terminal and initial direction errors were the deviations of these directions from the target direction in each particular trial. For the practice phase means were computed for each block of trials. For each type of open-loop test means were computed across blocks of trials for each target direction. From the direction errors adaptive shifts and after-effects were computed. Adaptive shifts are the differences between the directions of hand movements in the visual open-loop post-tests with cued visuo-motor rotation and the pre-test. After-effects are the differences between the directions of hand movements in the visual open-loop post-tests with cued absence of the visuo-motor rotation and the pre-test. For explicit tests direction errors were determined, and explicit shifts were computed in the same way as adaptive shifts were for the open-loop tests.

Movement trials were screened for irregularities. Trials were discarded when movement time was shorter than 200 ms or longer than 5000 ms. In total there were 61 invalid trials (0.6 %) in the younger group and 207 (2.7 %) in the older group. In all cases the upper time limit was exceeded.

Results

We report findings for the practice phase first, followed by pre-test data. Thereafter we present adaptive shifts, after-effects, and explicit shifts.
Practice. In the practice phase movements reached the target accurately because of the continuous availability of concurrent visual feedback. However, initial direction errors reflected the visuo-motor rotation, and their decline indicated adjustment. The mean initial direction errors are shown in Figure 3a. Corresponding to the counter-clockwise (positive) visuo-motor rotation, they were positive and declined in the course of practice. The two age groups did not differ. The data were subjected to a two-way ANOVA with the between-participant factor age and the within-participant factor block of trials. The degrees of freedom were Greenhouse-Geisser adjusted, but we report the uncorrected degrees of freedom together with the Greenhouse-Geisser epsilon. Effect sizes are given as partial eta-squared. Only the main effect of block turned out to be statistically significant, $F(5,190) = 5.0, p < .01, \varepsilon = 0.47, \eta^2 = 0.12$. Both for the main effect of age and the age x block interaction $F < 1$. Insert Figure 3 about here

Mean movement time is shown in Figure 3b. It declined in the course of practice, and it was longer for the older than for the younger participants. However, the main effect of age failed to reach statistical significance, $F(1,38) = 1.9, p > .10$, and so did the age x block interaction, $F < 1$. Only the main effect of block was significant, $F(5,190) = 75.1, p < .01, \varepsilon = 0.56, \eta^2 = 0.66$.

Pre-tests. In the tests all eight targets were presented rather than only one as during practice. For the analyses the targets were arranged relative to the practice target. The practice target was designated as 0°, and the order of relative target directions was -135°, -90°, -45°, 0°, 45°, 90°, 135°, 180°. With this arrangement the adaptive shifts and after-effects should peak at 0°. For the sake of consistency, pre-tests were analyzed with the same data organization.

Pre-test errors did not depend on age, but they depended on start location and relative target direction. Consistent with findings of Ghilardi, Gordon, and Ghez (1995), the mean direction error was clockwise (-3.5°) for the right start location and counter-clockwise (5.2°) for the left start location. A three-way ANOVA with the
between-participant factor age and the within-participant factors start location and relative target direction revealed a significant main effect of start location, \( F(1,38) = 72.3, p < .01, \eta^2 = 0.66 \). In addition the interaction of start location and relative target direction was significant, \( F(7,266) = 8.7, p < .01, \epsilon = 0.63, \eta^2 = 0.19 \). For the right start location direction errors varied between -7.4° and 1.7°, but for the left start location they varied between 0.7° and 10.7°. However, the main effect of relative target direction was not significant, \( F(7,266) = 1.4, p > .20 \), and neither was the main effect of age, \( F < 1 \), nor any of the interactions involving this factor. In the explicit pre-test the mean direction error was zero without any reliable variation across experimental conditions.

Adaptive shifts. The mean adaptive shifts are shown in Figure 4 (top row of graphs). These are the changes of hand direction after practice, tested in open-loop trials in which the presence of the visuo-motor rotation was cued by the red colour of the start circle. Adaptive shifts were strongest for the practised target direction (0°) and the adjacent clockwise one (-45°). For the younger participants relative target directions even more clockwise to the practised one (-90°, -135°) showed strong adaptive shifts as well, whereas counter-clockwise to the practised target direction there was a steep decline of adaptive shifts in both age groups. Adaptive shifts of older participants were generally smaller than those of younger participants. At the left start position, adaptive shifts were generally smaller than at the right start position, and in the older participants they were essentially absent. In the younger participants there was no indication that the new joint configuration at the left start position was associated with a shifted maximum of the adaptive shifts.

The adaptive shifts were subjected to an ANOVA with the between-participant factor age and the within-participant factors start location and relative target direction. The main effect of relative target direction was significant, \( F(7,266) = 6.4, p < .01, \epsilon = 0.47, \eta^2 = 0.14 \), and so was its interaction with start location, \( F(7,266) = 3.7, p < .10, \epsilon = 0.65, \eta^2 = 0.09 \), whereas the interaction with age fell just short of significance, \( F(7,266) = 2.3, p < .10, \epsilon = 0.47, \eta^2 = 0.06 \). Both of these interactions were due to the fact that the differences between start locations and age groups were strongest at those relative target directions near the practised one at which adaptive
shifts were strongest. In addition the main effects of start location, \( F(1,38) = 4.7, p < .05, \eta^2 = 0.11 \), and age, \( F(1,38) = 13.1, p < .01, \eta^2 = 0.26 \), were significant.

We ran separate follow-up ANOVAs with the within-participant factor relative target direction for the two age groups and the two start locations to determine more specifically the specificity of adaptive changes for the target direction used during practice. The ANOVAs revealed significant main effects of relative target direction only for the right start location, \( F(7,147) = 5.8, p < .01, \epsilon = 0.46, \eta^2 = 0.22 \), for the younger participants and \( F(7,119) = 11.8, p < .01, \epsilon = 0.61, \eta^2 = 0.41 \), for the older participants. The overall mean shifts were significantly different from zero, \( F(1,21) = 29.1, p < .01 \), and \( F(1,17) = 77.6, p < .01 \), respectively. For the left start location the main effects of relative target direction were not statistically significant, \( F(7,147) = 1.7, p > .10, \epsilon = 0.56 \), for the young participants and \( F(7,119) = 1.7, p > .10, \epsilon = 0.56 \), for the older participants. Thus, at the left start location the variation of adaptive shifts across relative target directions was no longer reliable. For both groups the overall adaptive shifts were significantly different from zero at the left start position as well, \( F(1,21) = 26.8, p < .01 \), and \( F(1,17) = 11.6, p < .01 \), respectively.

After-effects. The mean after-effects are shown in Figure 4 (middle row of graphs). Overall the pattern was similar to that observed for the adaptive shifts. However, at the right start location, which was used during practice, the age-effect was reversed in that after-effects were stronger in the older participants than in the younger ones. At the left start location the after-effects were largely absent for both age groups. The main effect of relative target direction was significant, \( F(7,266) = 9.7, p < .01, \epsilon = 0.69, \eta^2 = 0.20 \), and so was its interaction with start location, \( F(7,266) = 5.7, p < .01, \epsilon = 0.69, \eta^2 = 0.13 \). Both the main effects of start location, \( F(1,38) = 28.7, p < .01, \eta^2 = 0.43 \), and age, \( F(1,38) = 6.1, p < .05, \eta^2 = 0.14 \), were significant. In addition there was a significant interaction of start location and age, \( F(1,38) = 6.3, p < .05, \eta^2 = 0.14 \). Separate contrasts revealed a significant age-related variation only for the right start location, \( F(1,38) = 11.8, p = .01 \), but not for the left one, \( F < 1 \).
Separate follow-up ANOVAs for the two age groups and the two start locations revealed significant main effects of relative target direction only for the right start location, \( F(7,147) = 6.8, p < .01, \varepsilon = 0.49, \eta^2 = 0.24 \), for the younger participants and \( F(7,119) = 4.6, p < .01, \varepsilon = 0.48, \eta^2 = 0.21 \), for the older participants. The overall after-effects were significantly different from zero, \( F(1,21) = 68.0, p < .01, \) and \( F(1,17) = 75.4, p < .01 \), respectively. In contrast, for the left start location the main effects of relative target direction were not statistically significant, \( F(7,147) = 1.8, p > .10, \varepsilon = 0.48, \) and \( F(7,119) < 1 \) for the younger and older participants. However, the overall after-effects at the left start location were significantly different from zero in both age groups, \( F(1,21) = 19.4, p < .01, \) and \( F(1,17) = 12.1, p < .01 \).

Explicit shifts. In Figure 4 (bottom row of graphs) the mean explicit shifts are shown. In contrast to adaptive shifts and after-effects they were invariant across relative target directions. For younger participants they were slightly stronger at the right start location than at the left start location, whereas for older participants they were essentially absent at both start locations. The ANOVA revealed only a significant interaction of start location and age, \( F(1,38) = 8.9, p < .01, \eta^2 = 0.19 \); both the main effects of start location and age approached statistical significance, \( F(1,38) = 3.0, p < .10, \eta^2 = 0.07 \), and \( F(1,38) = 2.9, p < .10, \eta^2 = 0.07 \). Averaged across relative target directions the mean explicit shifts were \(-28.5^\circ \pm 6.9^\circ\) and \(-21.3 \pm 8.1^\circ\) for the younger participants at the right and left start location, respectively. Both these shifts were significantly different from zero. For the older participants the mean shifts were \(-7.5^\circ \pm 5.0^\circ\) and \(-9.5^\circ \pm 5.9^\circ\) for the two start locations. Both these mean shifts did not significantly deviate from zero.

Discussion

The present experiment had been designed to study the generalization of adjustment to a visuo-motor rotation across the workspace. We distinguished different components, implicit and explicit adjustments in particular, which are differently affected by age and which exhibit different patterns of generalization across target directions (e. g., Heuer & Hegele, 2008b). The tentative hypothesis was
that different components of adjustment might also generalize differently across the workspace. To the extent that directionally specific adaptation generalizes across the workspace, the results would also shed some light on the frames of reference which underlie generalization.

The present findings add to the list of different characteristics of explicit and implicit adjustments to visuo-motor rotations. Previously it has been shown that explicit adjustments generalize across all target directions, whereas implicit adjustments are restricted to the target direction during practice and adjacent ones (Heuer & Hegele, 2008; Krakauer et al., 2000); explicit adjustments decline across the adult age range, whereas implicit adjustments remain stable (Bock, 2005; Heuer & Hegele, 2008); explicit adjustments are insensitive to spinocerebellar ataxia, whereas implicit adjustments depend on intact cerebellar functions (Taylor et al., 2010); explicit adjustments enable dual adaptation of identical muscle synergies, whereas implicit adjustments do not (Hegele & Heuer, 2010c). To this list we add that explicit adjustments generalize across the workspace, whereas implicit adjustments do not.

Explicit shifts and after-effects. Explicit shifts served to assess explicit knowledge of the participants. Consistent with previous findings, explicit shifts were essentially absent at older age. However, in young adults explicit shifts were clearly present, and there was almost perfect generalization across the workspace. Of course there is the caveat that explicit knowledge may not always be put to use for intentional or explicit adjustments, so that explicit knowledge and explicit adjustments could be dissociated to some degree.

After-effects served to assess implicit knowledge of the participants. In the respective open-loop tests the absence of the visuo-motor rotation had been cued by the colour of the start circle. Thus, participants knew there was no rotation, and intentional or explicit corrections should be absent. After-effects were essentially restricted to the target direction used during practice and clockwise target directions. They were slightly stronger in older than in younger participants, and they did hardly or not at all generalize across the workspace. At least there was no generalization of target-selective after-effects. Therefore the prerequisites to answer the question
about the frame of reference that underlies generalization are not met, and no well-
founded answer is possible.

After-effects exhibited a notable asymmetry around the target direction used
during practice in that they were largest for the next target direction clockwise rather
than for the practiced one or of about the same size for these two target directions,
but almost absent for the next target direction counter-clockwise. This observation
contrasts with the basically symmetric generalization reported by Krakauer et al.
(2000). However, it is in line with a counter-clockwise displacement of the peak after-
effects observed by Heuer and Hegele (2008, Exp. 1b). Taken together, with single-
target practice with a counter-clockwise rotation of 75° there is a clockwise shift of
peak after-effects (present study), with single-target practice with a clockwise rotation
of 75° there is a counter-clockwise shift (Heuer & Hegele, 2008), and with single-
target practice with a (counter-clockwise) rotation of 30° there is no apparent shift
(Krakauer et al., 2000). Thus, with a sufficiently large visuo-motor rotation the peak
after-effects appear to be shifted away from the practiced target direction towards the
direction of the hand movements produced repeatedly during practice. Even though
the reasons for this shift are not fully clear, use-dependent learning of the practiced
movement direction (Diedrichsen, White, Newman, & Lally, 2010; Huang, Haith,
Mazzoni, & Krakauer, 2011) might have contributed to it.

As with our measure of explicit knowledge, there are also certain caveats about
after-effects as a measure of implicit adjustment. First, they may not capture the full
implicit change. Even though implicit adjustments are outside conscious awareness
by definition, the cue that informs about the absence of the visuo-motor rotation may
also affect the application of implicit adjustments in terms of selecting the appropriate
internal model (cf. Wolpert & Kawato, 1998). Second, even though the information
about the absence of the rotation should keep participants away from strategic
corrections, this change might be incomplete. Thus, implicit adjustments may also be
over-estimated by after-effects.

Adaptive shifts. Adaptive shifts are conceived as a combination of explicit and implicit
adjustments. As found consistently, they were larger for younger than for older
participants (Bock, 2005; Bock & Girgenrath, 2006; Buch, Young, & Contreras-Vidal,
2003; Heuer & Hegele, 2008; McNay & Willingham, 1998), and they were maximal in the target direction during practice and clockwise target directions. They were reliably present at the left start position in the transfer test, but the variation of adaptive shifts across target directions was no longer significant.

With the combination of target-selective implicit adjustments, as assessed by after-effects, and target-generalized explicit adjustments, as assessed by explicit shifts, adaptive shifts can be de-composed into target-independent components, presumably explicit ones, and target-dependent components, presumably implicit ones. Taking the clockwise shift of implicit adjustments into account, the target-dependent component was estimated as the mean adaptive shift at target directions -90°, -45°, and 0°, from which the target-independent component, estimated from the adaptive shifts at the other target directions, was subtracted. For control purposes, the same estimates were done for after-effects and adaptive shifts. For after-effects the target-independent component should be zero, indicating the absence of an effect of explicit adjustments, and for explicit shifts the target-dependent component should be zero.

As can be evidenced from Table 1, for the young participants the target-independent component was strong for the adaptive shift and explicit shift, -16.5° and -29.5°, but basically absent for the after-effect, -2.7°, and there was almost perfect transfer to the new start location. The target-dependent component was strong for the adaptive shift and - though somewhat weaker - for the after-effect, -27.3° and -7.8°, and basically absent for the explicit shift, -2.9°. Transfer to the new start location was clearly incomplete. For the old participants the target-independent component ranged between -4° and -9° in all tests, even in the after-effect, and the target-dependent component was strong in the adaptive shift and after-effect, -11.0° and -14.3°, but did not transfer to the novel start location. Thus, the de-composition of adaptive shifts in a direction-independent and a direction-dependent component is consistent with the conclusion that explicit adjustments generalize strongly across the workspace, but implicit components hardly or not at all.
Table 1 reveals two clear deviations from the assumptions, first, that there is no target-independent (explicit) component of the after-effect and, second, that there is roughly the same target-dependent (implicit) component in the after-effect and adaptive shift. The first violation is observed in older adults. It suggests that the cue, which signals the absence of the visuo-motor rotation, had only a limited effect on older participants so that they continued to make use of the little explicit knowledge they had in the after-effect test. This observation is consistent with a variety of findings according to which older adults tend to perseverate when contextual cues change and to make less use of them in various tests (e.g., Henry & Philips, 2006; Ridderinkhof, Span, & Van der Molen, 2002; Thomas & Bulevich, 2006). The second violation is observed in younger adults. The smaller estimates of implicit adjustments from after-effects than from adaptive shifts can be take to suggest that the cue that signals the absence of the visuo-motor transformation does also have some effect on the (non-)use of implicit adjustments, in addition to the (non-)employment of strategic or explicit adjustments.

In summary, the present findings reveal a strong generalization of explicit adjustments to a visuo-motor rotation across the workspace, whereas the generalization of implicit adjustments is quite limited or even absent. Consistent with previous findings, older adults acquire only poorer explicit knowledge than younger adults. Therefore, for them generalization across the workspace is largely absent. These findings add to the increasing catalogue of differences between implicit and explicit adjustments to visuo-motor transformations.
References


Table 1  Estimates of target-independent and target-dependent components of adaptive shifts, after-effects, and explicit shifts for young and old participants in the right and left workspace

<table>
<thead>
<tr>
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<th>target-independent</th>
<th>target-dependent</th>
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<tr>
<td></td>
<td>young right old left</td>
<td>young right left old</td>
</tr>
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<td>adaptive shift</td>
<td>-16.5 -17.9 -6.2 -4.5</td>
<td>-27.3 -11.2</td>
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<tr>
<td>after-effect</td>
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<td>-7.8 -2.7</td>
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<tr>
<td>explicit shift</td>
<td>-29.5 -21.3 -7.2 -9.0</td>
<td>-2.9 -0.7</td>
</tr>
</tbody>
</table>
Figure captions

Figure 1: Arm configurations in the right and left start location.

Figure 2: Sequence of baseline, test, and practice blocks of the experiment. Numbers are the numbers of trials per block.

Figure 3: Mean initial direction error (a) and mean movement time (b) in the practice blocks of trials, shown separately for the younger and older participants.

Figure 4: Mean adaptive shifts, after-effects, and explicit shifts as a function of relative target direction, shown separately for younger (left) and older (right) participants and the two start locations in the right and left workspace. (Relative target directions are relative to the target direction during practice.)
Figure 2

right start position | left start position | right start position | right-left start position

B 48 | pre-tests right | B 48 | pre-tests left | T P 48 | T P 48 | T P 48 | T P 48 | post-tests right - left

M 4 t M 4 t M 4 t M 4 e 8

T M t 8 T M t 8 T M t 8 T M t 8

right - left | right - left | right - left

B: Baseline  t: open-loop test  T: Transformation
P: Practice  e: explicit test  M: Maintenance
Figure 3

(a) Initial direction error [deg]

(b) MT [ms]

Figure 3
Figure 4