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Adaptation to a direction-dependent visuomotor gain in the young and elderly

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Abstract Consistent with the widely accepted notion of separate specification of movement amplitude and direction, it has been argued that there is also a categorical difference between adaptation to novel visuomotor rotations and to novel visuomotor gains. In line with this view, ageing seems to affect rotation and gain adaptation differently in that age-related impairments are consistently found for the former, but not for the latter. In this study we ask whether the contrasting findings could also be ascribed to differences in the level of difficulty of gain and rotation adaptation tasks, respectively. In order to increase the difficulty of gain adaptation, younger and older participants had to adapt to a direction-dependent gain transformation. Results revealed direction-dependent adaptation in both groups. More importantly, we replicated the typical findings of age-related impairments of adaptation, but not of aftereffects, that were previously only reported for rotation adaptation. Younger participants also showed superior explicit knowledge regarding the novel visuomotor mapping as compared to the older participants. We show that this knowledge was used by younger participants to selectively augment adaptive shifts. Finally, our findings suggest that the difficulty of the novel visuomotor transformation and, related to this, the involvement of explicit knowledge in adaptation is critical for age-related changes to show up, but not the type of adaptation task, rotation and gain adaptation, respectively.

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Introduction

Research on visuomotor adaptation of goal-directed movements has shown that the human sensorimotor system is capable of adapting to a variety of visuomotor transformations. Classical studies dealt with changes in intrinsic visuomotor mappings between visually perceived locations and body movements (for a review, see Welch, 1978). More recent research focused on variations in extrinsic visuomotor mappings, where the end effector is no longer a part of the body, but of a tool that is controlled by bodily movements (e.g. Buch, Young, & Contreras-Vidal, 2003; Flanagan & Rao, 1995; Krakauer, Pine, Ghilardi, & Ghez, 2000). Adjustments to such novel extrinsic visuomotor transformations can be conceived as instances of the plasticity of the human brain. Even though neural plasticity declines with increasing age in general, age-related impairments of adjustments to extrinsic visuomotor transformations are not invariantly found. In the present study, we ask whether variations of age-related differences in visuomotor adaptation are based on variations in the level of difficulty of the extrinsic visuomotor transformation or reflect a fundamental difference between adaptive changes of different movement parameters, amplitude and direction in particular.

The question whether or not variations of age-related differences in visuomotor adaptation reflect a basic difference between types of adaptation tasks, amplitude and direction adaptation in particular, is related to different concepts of motor control. Previous work on the control mechanisms underlying goal-directed reaching has led to the formulation of different hypotheses regarding the variables used by the motor system in planning and control. According to the vector-coding hypothesis (Vindras & Viviani, 1998), movement planning is conceived as a

parametric process where hand movements are planned in terms of a start-target vector with independent specification of movement amplitude and direction (e.g., Bock, 1992; Favilla, Hening, & Ghez, 1989; Ghez et al., 1997). This notion gained support from several findings. For example, there is a covariation of the direction of population vectors derived from directionally tuned neurons in the motor cortex of behaving monkeys and the direction of movements (Georgopoulos, Schwartz, & Kettner, 1986). Further, independence of the variability of direction and amplitude of movements aimed at visually presented targets has been shown (Desmurget, Jordan, Prablanc, & Jeannerod, 1997; Desmurget, Prablanc, Jordan, & Jeannerod, 1999; Gordon, Ghilardi, & Ghez, 1994; Messier & Kalaska, 1997; Vindras & Viviani, 1998) Finally, several studies showed a decrease in reaction time when either amplitude or direction of an upcoming goal-directed hand movement had been cued prior to movement initiation (Bock & Arnold, 1992; Bock & Eversheim, 2000; Rosenbaum, 1980).

In spite of the available evidence, the vector-coding hypothesis is not without alternatives. The joint-coding hypothesis, for example, holds that planning is in joint space. The crucial planning variables are assumed to be joint-related, such as angles or muscle activity (Hollerbach & Atkeson, 1987; Todorov, 2000). In support of this hypothesis, it was shown that the direction of population vectors and individual cells in the motor cortex of behaving monkeys are sensitive to the starting postures of reaching movements (Scott & Kalaska, 1995).

In order to accommodate these diverging theoretical accounts along with their supporting empirical results, it has been suggested that vector-coding applies only to movements that are constrained to two dimensions whereas unconstrained movements in three dimensions are planned in joint space (Desmurget et al., 1997; Magescas & Prablanc, 2006a; Palluel-Germain, Boy, Orliaguet, & Coello, 2004). Moreover, it was demonstrated that the choice of variables for motor control is sensitive to the type of visual control exerted during movement execution such that a remotely controlled end effector yielded vector-coding even for unconstrained movements in three dimensions (Palluel-Germain et al., 2004).

Regarding visuomotor adaptation to extrinsic transformations (e.g. Flanagan & Rao, 1995; Heuer & Hegele, 2007; Krakauer et al., 2000), the nature of the task suggests that vector-coding might be involved. First, there is a spatial separation of movement execution and observation, and second, there is a lack of identity of the observed object and the moving limb. A likely way to specify a movement to a target is in form of a vector from initial location to target location defined for visually perceived locations and shifted to the start location of the hand. Consistent with the vector-coding hypothesis there is

indeed evidence for a categorical distinction between adaptation to a novel visuomotor gain, i.e. to a novel transformation of the ratio of the amplitudes of visually perceived motion of the end effector and the associated body movement (e.g., Bock, 1992; Bock & Burghoff, 1997; Krakauer et al., 2000), and to a visuomotor rotation, i.e. to an altered relation between the directions of body movement and the associated motion of the end effector (e.g., Abeele & Bock, 2001a, b, 2003; Cunningham, 1989; Imamizu & Shimojo, 1995; Krakauer et al., 2000; Pennel, Coello, & Orliaguet, 2002).

These two types of adaptation have been shown to have different behavioral characteristics (e.g. Krakauer et al., 2000). Adaptation to a novel visuomotor gain is rapid and generalizes across different target amplitudes and target directions (cf. Bock, 1992; Bock & Burghoff, 1997; Krakauer et al., 2000, Vindras & Viviani, 2002), whereas generalization of rotation adaptation is limited to the target directions encountered during practice and nearby directions (Krakauer et al., 2000; Pine, Krakauer, Gordon, & Ghez, 1996). The differences on the behavioral level are paralleled by activations of different areas of the brain. Gain adaptation involves primarily bilateral subcortical structures (Krakauer et al., 2004) whereas rotation adaptation is associated with enhanced activity of cortical regions (Ghilardi et al., 2000; Inoue et al., 2000) and the cerebellum (Imamizu et al., 2000).

The findings on age-related variations of visuomotor adaptation seem to be consistent with the claim of a categorical difference between visuomotor adaptation of amplitude and direction, respectively. Regarding adaptation to novel directional mappings, an age-related decline of visuomotor plasticity is consistently found (Bock, 2005; Bock & Girgenrath, 2006; Buch et al., 2003; Heuer & Hegele, 2008a; McNay & Willingham, 1998; Seidler, 2006). In contrast, findings on age-related variations of gain adaptation are rather inconsistent. For example, Heuer and Hegele (2007) did not find an age-related decline of adjustment to novel visuomotor gains at age 51–65 years; only for older persons Seidler (2006) reported such a decline. Whereas gain adaptation could be based on a rescaling of visual information to already existing schemata, direction adaptation could require the construction of a novel reference axis for movements, a process that might be computationally more demanding and therefore be more affected by ageing (cf. Bock & Schneider, 2002; Krakauer et al., 2000; Pine et al., 1996).

Closer scrutiny reveals that there are boundary conditions for the age-related decline of adaptation to visuomotor rotations. In particular a certain level of difficulty in terms of the size of the rotation seems to be required for age-related differences to show up. When the visuomotor rotations were small (45° and less rather than

60° and more), the age-related decline of visuomotor plasticity could not always be found. Heuer and Hegele (2008a) reported age-related impairments of adaptation to rotations of 75° CW and CCW, but not to a rotation of 30° CCW. Seidler (2006), on the other hand, found age-related differences for adaptation to visuomotor rotations of 30° and 45° CCW. However, Seidler's participants were considerably older than the participants studied by Heuer and Hegele. A rotation of 30° CCW might have been difficult enough to induce age-related deficits in seniors at post-retirement age (mean age: 73.3; Seidler, 2006), but failed to induce those changes in older adults at pre-retirement age (mean age: 56.8; Heuer & Hegele, 2008a).[1] A similar reasoning can be applied to gain adaptation (cf. Seidler, 2006; Heuer & Hegele, 2007).

The absence of age-related deficits for adaptation to both, rotations of a smaller size and novel visuomotor gains, at pre-retirement age but not necessarily at post-retirement age suggests that age-related differences of rotation adaptation may not reflect a specific impairment of direction adaptation but rather a specific impairment of adaptation to difficult visuomotor transformations independent of the particular parameter involved. If it is indeed the difficulty of the transformation that modulates age-related changes in visuomotor adaptation and not a categorical difference between rotation and gain adaptation, age-related deficits should also show up at pre-retirement age when the visuomotor gain transformation has a sufficient level of difficulty. A critical role of the difficulty of the visuomotor transformation would be consistent with the observation that age effects in general are smaller when motor tasks are less difficult (e.g., Ketcham, Seidler, van Gemmert, & Stelmach, 2002), but no longer provide additional evidence for vector coding.

Based on these considerations, the purpose of the present study was to investigate whether the typical findings of age-related deficits in rotation adaptation at pre-retirement age could also be found with a more difficult kind of gain adaptation. In order to increase the level of difficulty, we had participants adapt to a visuomotor gain that varied with movement direction. Whereas increasing the number of target directions raises the level of difficulty of rotation adaptation, the difficulty of gain adaptation has been shown to be insensitive to the number of target directions. This is

presumably due to the fact that a novel visuomotor gain is typically found to generalize across all directions, so that subjects simply have to adjust a single scaling factor for movements within the whole visuomotor workspace (cf. Bock, 1992; Krakauer et al., 2000; Heuer & Hegele, 2007). With a direction-dependent gain this strategy of the visuomotor system is maladaptive. Instead of a uniform shift of movement amplitudes (and thus visuomotor gains), participants are required to adjust their movement amplitudes depending on movement direction. According to Bock (1992), a direction-dependent visuomotor gain is so difficult that it is not learned but only approximated by a direction-independent, and thus uniform gain shift. Only recently it has been shown that younger participants can adapt to a direction-dependent gain, but only under certain conditions of practice, namely with terminal instead of continuous visual feedback (Heuer & Hegele, 2008b). Thus, if the different findings for rotation and gain adaptation at pre-retirement age were due to an insufficient level of difficulty of the gain transformation, age-related differences should show up for adaptation to a direction-dependent visuomotor gain.

Visuomotor adaptation is not a unitary process (cf. Bock, 2005; McNay & Willingham, 1998; Redding, Rossetti, & Wallace, 2005; Welch, 1978). In order to disentangle different explicit and implicit components of adaptation (e.g. Jakobson & Goodale, 1989; Uhlarik, 1973), we used a series of tests designed to assess the contribution of different sets of processes.

Proper adaptation to a novel visuomotor transformation is commonly conceptualized in terms of an internal model of the transformation that is acquired implicitly (Bock, 2005) and has been demonstrated in a variety of experimental paradigms such as force field (Malfait & Ostry, 2004), gain (Magescas & Prablanc, 2006b) and prism (Michel, Pisella, Prablanc, Rode, & Rossetti, 2007) adaptation. However, in addition there may be cognitive responses to consciously perceived changes in the visuomotor mapping (cf. Malfait & Ostry, 2004). Here we conceive those cognitive responses as strategic corrections that are based on explicit knowledge of the visuomotor transformation. Whereas the acquisition of an internal model implicitly establishes a new visuomotor mapping, strategic corrections are conceived as intentional modifications of the movements. For example, one can point intentionally to a location that is further, nearer, to the left or to the right of the location of the visual target.

Measures of aftereffects, which are obtained in visual open-loop tests without the visuomotor transformation, are generally thought of as measures of adaptation, which are unconfounded by strategic corrections. In the present study, therefore, we used open-loop tests both with the presence and the absence of the transformation. Of course,

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[1] The dependent variables used in the studies differed. Whereas Heuer and Hegele assessed the directional errors at the end of visually open-loop movements, Seidler measured directional errors only at the time of peak velocity (and found no age-related group differences) and final movement errors in terms of the total distance from movement end point to visual target. The latter measure includes amplitude as well as directional errors and might thus be fallible to systematic differences in movement amplitude between the age groups (Heuer & Hegele, 2007). Thus it does not reflect genuine adaptation to directional errors as induced by the visuomotor rotation.

participants must be aware of presence or absence of the transformation, otherwise strategic corrections are unlikely to be present or absent as well. Therefore, we provided participants with a color cue indicating the presence or absence of the visuomotor transformation. Even though differences between open-loop tests with and without the transformation can be attributed to strategic corrections, there is also the possibility that an internal model of the transformation is switched on or off depending on the color cue. So we also included a test of explicit knowledge in which we collected explicit judgments of the movement amplitudes believed to be appropriate to reach the visual targets in the presence of the visuomotor transformation. Their amplitudes were indicated by the length of a visually perceived line. Finally, we used an extended period of visual open-loop performance to compare the stability of adaptive changes in the two age groups. (cf. Heuer & Hegele, 2008a).

The use of different test procedures also serves to make the present results comparable with those observed for direction adaptation. Under the hypothesis that the difficulty of the visuomotor transformation is critical for age-related impairments to show up, we would expect the same pattern of results for adaptation to direction-dependent visuomotor gains as has been reported for rotation adaptation, i.e. an age-related impairment of adaptive changes observed in the presence of the visuomotor transformation and of changes of explicit knowledge, but no age-related impairment of aftereffects (cf. Bock, 2005; McNay & Willingham, 1998). In contrast, if age-related impairments would be restricted to rotation adaptation and not show up for gain adaptation, they should be absent in all tests even for the difficult gain adaptation task of the present study.

Method

Participants

The younger participants, 7 men and 14 women, were 20–29 years old (mean: 23.6 years; SD: 2.4 years). The older participants, 14 men and 7 women, were 50–67 years old (mean: 58.5 years; SD: 5.0 years). The younger participants were students of Dortmund University, whereas most of the older participants responded to a newspaper ad. All participants were self-declared right-handers with normal color vision according to the Ishihara test (Ishihara, 2005) and had given informed consent prior to the start of the experiment.

The older and younger participants were compared on a number of cognitive and sensorimotor tests prior to the experiment in order to establish that they were representative for their respective age groups in terms of typical

Table 1 Comparison of the younger and older adults on a set of control variables

Variable	Young	Old	U (21,21)
Mental rotation (IST)	12.0 (4.2)	9.3 (3.8)	122.5, $p < 0.05$
Digit symbol	65.1 (8.1)	46.9 (10.5)	41.5, $p < 0.01$
Vocabulary	25.5 (3.6)	23.9 (4.8)	178.5
Steadiness: errors	8.5 (7.9)	28.9 (26.3)	104, $p < 0.01$
Tracing: errors	21.1 (14.8)	32.0 (20.4)	114.5, $p < 0.01$
Tracing: duration	41.0 (18.5)	28.4 (13.9)	134, $p < 0.05$
Aiming: errors	0.6 (1.2)	0.2 (0.7)	178
Aiming: duration	8.3 (2.2)	10.7 (2.8)	95, $p < 0.01$
Tapping: number of taps	203.1 (23.2)	198.4 (17.1)	202
Pegboard: duration	36.3 (4.6)	41.5 (5.2)	102, $p < 0.01$

For each group the means and the standard deviations (in brackets) are given, and for each variable the result of a Mann–Whitney U test (durations are in s), In the cognitive tasks, higher values indicate better performance

age-related variations and invariances. The means and standard deviations are shown in Table 1. Conforming to typical findings (e.g., Salthouse, 2006), performance of the older participants was worse than that of the younger participants on the Digit Symbol Test of the German version of the WAIS (Tewes, 1991), reflecting an age-related decline in fluid intelligence, but not on the Vocabulary Test, indicating age-related invariances of crystallized intelligence. In order to scan our participants for visuospatial and motor deficits that could influence the results on the adaptation task, we used a test of mental rotation ("Würfelaufgaben" of the IST, a German test of intelligence, Amthauer, 1953), and a series of motor tests (subtests of the "Motorische Leistungsserie", Schoppe, 1974, all performed with the right hand; Schuhfried GmbH, Mödling, Austria). Among those tests, some significant age differences appeared. Older participants exhibited poorer performance in the mental rotation test and slower performance in the aiming and the pegboard test. They produced more errors both in the steadiness and the tracing test. Contrary to typical findings (cf. Vercruyssen, 1997) however, the tracing test was also performed faster by the older than by the younger group.

Apparatus

Participants sat on a height-adjustable chair. They faced a 15-inch LCD monitor (EIZO FlexScan L365), which was placed in about 100 cm distance from their eyes on a table platform. Between the monitor and the participants a glass plate was placed on the table on which the movements were performed. The right index finger of the participants

was strapped to a slide of 50 mm × 30 mm (6 mm height), which ran on the glass plate with only little friction. Located directly above the finger nail, the slide carried a vertically oriented sensor of a miniBIRD system (mini-BIRD 800, Ascension Technology Corporation). The position of the finger was recorded at 103.6 Hz (spatial resolution: 0.11 mm). An occluder 20 cm above the table platform prevented vision of the hand. To assist in finding the start location, a disc of 54 mm height and 13 mm diameter was placed on the glass plate. The start location was just in front of this disk.

Task

Participants had to produce aimed movements from a common start location in the lower left of the monitor to targets in different directions, ranging from 0° (to the right) to 90° (forward). They were instructed to move swiftly and as accurately as possible. Both groups received visual feedback after the end of the movement by means of a cursor on the monitor showing the final position of the movement in relation to the respective target. In open-loop test trials, no visual feedback was given.

In the present study the visuomotor gain was varied across experimental conditions. In the baseline condition the amplitude of the cursor motion was the same as the amplitude of the hand movement, $d_v = d_h$. Thus the visuomotor gain was $g = 1.0$. In the adaptation condition, the visuomotor gain changed across movement directions. The direction-related visuomotor gain was

$$g(\theta) = \frac{0.75 \times 1.25}{\sqrt{1.25^2 \sin^2 \theta + 0.75^2 \cos^2 \theta}} \tag{1}$$

Thus, in adaptation trials with visuomotor transformation, that is, with the direction-dependent visuomotor gain, the amplitude of cursor motion was $d_v = g(\theta) \times d_h$, and the amplitude of hand movement appropriate for a desired visual amplitude d_y^* was $d_h = \frac{1}{g(\theta)} d_v^*$. In Table 2 the correct hand movement amplitudes for the visual target amplitudes used in the experiment are given, also the errors of the amplitudes

of cursor motion under the assumption that the hand amplitudes match the visual amplitudes. In practice trials target directions of 0, 22.5, 45, 67.5, and 90° with a target amplitude of 80 mm were used; in test trials target directions were 0, 34, and 90° with target amplitudes of 40, 80, and 120 mm. In practice trials the direction-dependent visuomotor gains were 1.25, 1.11, 0.91, 0.79, and 0.75 for the five target directions, and in test trials they were 1.25, 1.00, and 0.75.

Throughout the experiment, participants were instructed that there were trials with and without a novel visuomotor gain, but the exact nature of the transformation (magnitude, direction dependence) was not explained. The absence or presence of the transformation was cued by the color of the circle which marked the start location, red meaning *gain on* and green indicating *gain off*, respectively.

Design and procedure

The experiment started with six blocks of baseline practice, each block consisting of five trials with a target amplitude of 80 mm. Target directions of 0, 22.5, 45, 67.5, and 90° were pseudorandomized, so that within each block each target direction occurred once and between blocks no target direction was repeated. Terminal visual feedback was presented after the end of each movement.

Baseline practice was followed by a series of baseline tests. The open-loop test consisted of three blocks of nine trials each. In each block all combinations of target directions 0, 34, and 90° and target amplitudes 40, 80, and 120 mm were presented and no visual feedback was provided. In-between the two blocks there were five maintenance trials that were identical to a baseline practice block. The open-loop test was followed by a test of explicit knowledge consisting of nine trials, each combination of three target directions and three target amplitudes being presented once in a pseudorandom order. In all trials of baseline practice and baseline tests, the start circle was green, informing participants about the absence of the novel visuomotor gain.

Table 2 Correct amplitudes of hand movements for different target distances and target directions, $d_h(d_v^*)$, and amplitude errors of cursor motions when amplitude of hand movements match the visual target amplitudes, $d_v(d_h = d_v^*) - d_v^*$

Target direction (°)	Visuomotor gain	$d_h(d_v^*)$ target amplitude (mm)			$d_v = (d_h = d_v^*) - d_v^*$ target amplitude (mm)		
		40	80	120	40	80	120
0	1.25	32.0	64.0	96.0	10.0	20.0	30.0
22.5	1.11	–	71.8	–	–	9.1	–
34.0	1.00	39.9	79.8	119.7	0.1	0.2	0.3
45.0	0.91	–	88.0	–	–	−7.2	–
67.5	0.79	–	101.5	–	–	−17.0	–
90.0	0.75	53.3	106.7	160.0	−10.0	−20.0	−30.0

In the explicit baseline test each trial began with the presentation of the start circle, a target, and a white line of 2.3 mm width. It was parallel to the imaginary line connecting start and target, but shifted upward or to the left by 11 mm. The experimenter increased its length by way of pressing a key, beginning at zero length. The task of the participant was to instruct the experimenter to increase or decrease the length of the line until it matched the amplitude of the hand movement he or she thought appropriate to move the cursor from the start circle to the target circle.

Subsequent to the baseline phase, the visuomotor transformation was practiced for 15 blocks, each with 25 terminal-feedback trials. In all trials the start circle was red, cueing the presence of the visuomotor transformation. Target amplitude was 80 mm; target directions were 0, 22.5, 45, 67.5, and 90°, presented five times each in a pseudorandom sequence without repetitions during each block.

The practice phase was followed by three different posttests, an open-loop test with cued presence of the transformation, an open-loop test with cued absence of the transformation, and an explicit test with cued transformation. The open-loop test with cued presence of the transformation differed only with respect to the color of the start circle from the open-loop test without transformation. The open-loop test with cued absence of the transformation was identical to the open-loop baseline test. Of course, in the maintenance trials in-between the blocks of test trials, the transformation was present and the start circle was red. In the explicit test, which was otherwise identical to the explicit baseline test, the presence of the transformation was also cued by the red start circle.

The experiment ended with an extinction period of five blocks of 25 trials each. These were identical to the practice period except that no visual feedback at all was presented. The extinction period served to assess the stability of an eventual adaptation to the direction-related visuomotor gain. In order to refresh adaptation to the direction-dependent gain, the extinction period was preceded by a block of 25 trials with terminal visual feedback.

Each single trial started with the presentation of the start circle, an outline circle of 7.6 mm diameter. Its color was red or green depending on whether the presence or absence of the visuomotor transformation was cued. Its location on the monitor was 55 mm from the left edge and 21 mm from the bottom edge, that is, in the lower left sector. On the table the start location was about 30–40 cm in front of the participant and displaced to the right of his or her median plane by about 15 cm. The cursor, a filled cyan circle of 4.6 mm diameter, appeared on the monitor when it entered a tolerance range of 15.2 mm around the center of the start circle. It was presented to assist participants in homing-in on the start position. During homing-in the

visuo-motor gain was 1.0 in all trials. When the cursor was within a tolerance range of 0.8 mm around the center of the start circle for 500 ms, a tone (1,000 Hz, 26 ms) was presented and the start circle was filled. For a randomly chosen period of 500, 700, 900, 1,100, or 1,300 ms the finger had to remain in the start location, otherwise the trial was reset. At the end of this waiting period a target appeared, a filled white circle of 5.3 mm diameter. Simultaneously the start circle and the cursor disappeared.

The end of the movement was determined online by a velocity criterion, provided that the cursor had left the tolerance range of 15.2 mm around the center of the start circle. The velocity criterion required that the distance between successively sampled positions was not larger than 0.25 mm for more than 400 ms. The cursor was presented in its final position for 1,000 ms after the end of the movement, together with the target, and thereafter both the cursor and the target circle disappeared. The movement back to the start location was always open-loop except for the final homing-in.

Data analysis

For each trial the x and y positions both of the finger on the table and the cursor on the monitor were recorded, with the start positions as the origins of the respective Cartesian coordinate systems. Each of the resulting time series was low-passed filtered (fourth-order Butterworth, 10 Hz, dual pass) and differentiated (two-point central difference algorithm). Tangential velocities were computed as well as the positions in polar coordinates, both for the table and for the monitor. Start and end of the movements were determined based on tangential velocity of the finger. Starting from peak tangential velocity, both in a forward and a backward search those samples were determined at which tangential velocity was less than 5 mm/s for the first time and remained smaller for 200 ms thereafter.

Movements with extreme durations (<200 ms or >5,000 ms) as well as movements with extremely long trajectories (longer than 5 times the distance between initial and final hand position) were not included in subsequent analyses. In total these were 10 of 29,022 trials (0.04%).

Practice trials and extinction trials were analyzed in terms of amplitude errors. Amplitude errors were determined for the cursor position relative to the target. Means were computed for each target direction and each block of trials. Each mean was thus based on five trials. These individual means were entered into the statistical analyses. For the visual open-loop tests and the explicit tests amplitudes of hand movements were analyzed. Means were computed again for each combination of three target directions and three target amplitudes, except for the explicit test, in which each target was presented only once.

Both for open-loop tests and for explicit tests posttest minus baseline test differences of amplitudes were computed. For the tests with cued visuomotor transformation (red start circle) these differences are designated as adaptive shifts, for the tests without transformation they are referred to as aftereffects, which should reflect implicit modifications of the internal model of the visuomotor transformation. For the explicit tests, these differences are referred to as explicit shifts.

The individual means of amplitude errors, amplitudes of hand movements, posttest-pretest differences as well as of movement times were analyzed with a series of ANOVAs. In addition to the between-participant factor age and the relevant within-participant factors (target direction and target amplitude, respectively), the between-participant factor gender was included in order to give equal weights to the male and female subgroups and thus to avoid biasing of the differences between age groups by the different proportions of male and female participants in the two groups.

Results

Results will be reported for the various phases of the experiment, first for the practice phase, second for the baseline-to-posttest changes, and third for the extinction phase. The Huynh–Feldt epsilon (Huynh & Feldt, 1970) was evaluated to determine whether the repeated measures data met the assumption of sphericity ($\Sigma > 0.75$). In cases where sphericity was not met, the F statistic was evaluated for significance using the Huynh–Feldt adjusted degrees of freedom, though the uncorrected degrees of freedom are reported.

Practice phase

In Fig. 1 the means of the individual mean amplitude errors in the practice phase are shown for both age groups. Amplitude errors were subjected to a four-way ANOVA with the between-participant factors age and gender and the within-participant factors target direction and block of trials. Both age groups produced overshoots for those directions (0°, 22.5°) for which visuomotor gains were largest (1.25, 1.11), whereas for those directions (67.5°, 90°) for which visuomotor gains were smallest (0.79, 0.75) amplitude errors were undershoots. Both overshoots and undershoots declined in the course of practice without vanishing completely. The differences between the two target directions 0 and 22.5° as well as between the two target directions 67.5 and 90° disappeared in the course of practice. For the target direction of 45°, for which the visuomotor gain was 0.91, amplitude errors remained close to zero and did not vary systematically across blocks.
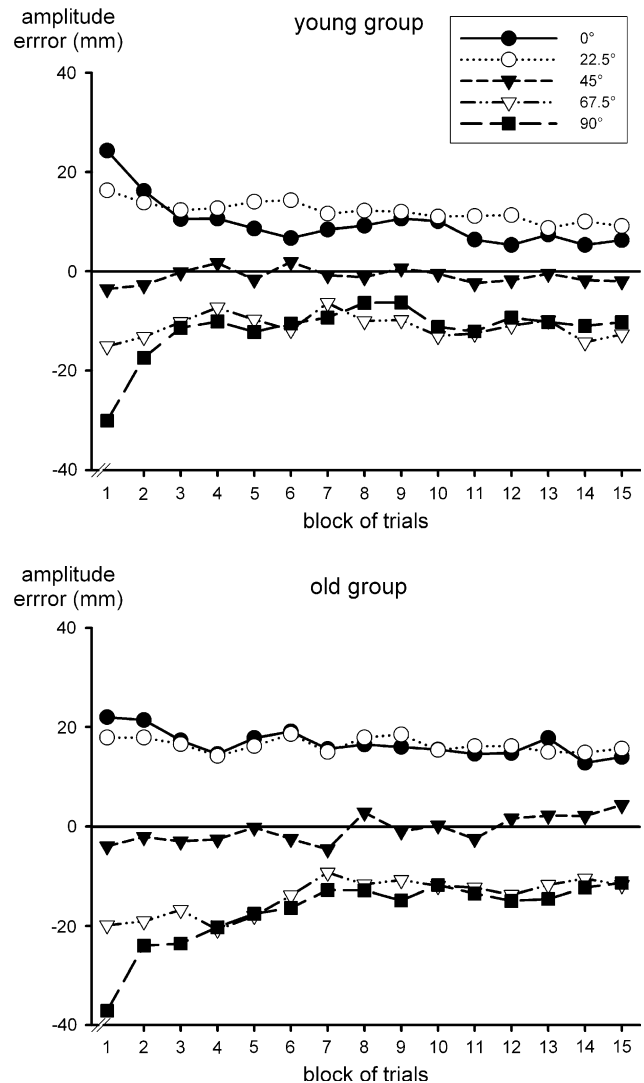
Fig. 1 Mean error of cursor amplitude during practice of the young and the old group as a function of target direction and block of trials

The convergence of overshoots and undershoots in both age groups was reflected in a significant interaction of target direction and block, $F(56,2128) = 7.1$, $p < 0.01$, $\eta^2 = 0.16$. Furthermore, both the overshoots and undershoots were smaller for the younger than for the older participants. This was reflected in a significant interaction of group and target direction, $F(4,152) = 4.2$, $p < 0.05$, $\eta^2 = 0.10$. The interaction of age group, target direction, and block failed to approach statistical significance.

The means of the individual mean movement times in the practice phase are shown in Fig. 2. The ANOVA of movement times revealed a significant difference between movements with different target directions for both groups, with longer movement times for those directions at which visuomotor gains were smaller. This gave rise to a significant main effect of target direction, $F(4,152) = 11.4$,
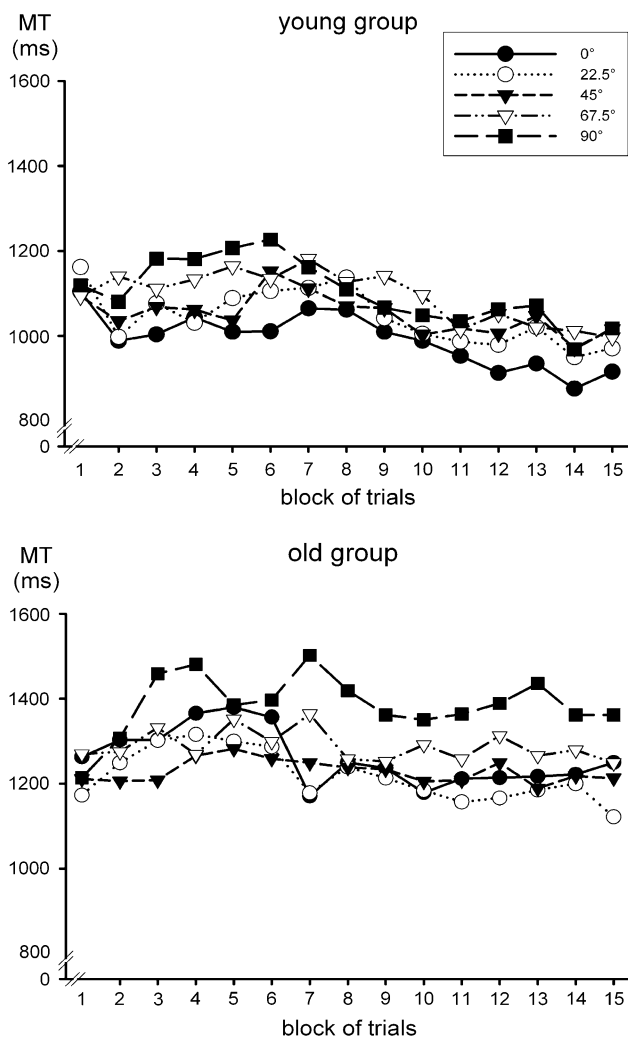
Fig. 2 Mean movement time during practice of the young group and the old group as a function of target direction and block of trials

$p < 0.01$, $\eta^2 = 0.23$. The association of a smaller visuomotor gain with longer movement time was more pronounced for the older participants, as evidenced by a significant interaction of age and target direction, $F(4,152) = 3.1$, $p < 0.05$, $\eta^2 = 0.08$. The three-way interaction of age group, target direction, and block, $F(56,2128) = 1.5$, $p < 0.05$, $\eta^2 = 0.04$ reflected the observation that in the old group movement times for the different target directions diverged in the course of practice, whereas in the young group there was a general decline of movement time with a less pronounced divergence. Finally, the overall decline of movement times across blocks of trials gave rise to a significant main effect of block, $F(14,532) = 13.8$, $p < 0.01$, $\eta^2 = 0.09$, and the overall longer movement times for older than for younger participants to a significant main effect of age group, $F(1,38) = 5.5$, $p < 0.05$, $\eta^2 = 0.13$.

Adaptive shifts and aftereffects

For the target direction of 34°, for which the visuomotor gain was always 1.0 regardless of experimental condition, no adaptive shifts would be expected. For the target direction of 0°, for which the visuomotor gain had been 1.25 during practice, movement amplitudes should be reduced compared to baseline, and they should be increased for the target direction of 90°, for which the visuomotor gain had been 0.75. Both the increase and the reduction should be the stronger the larger the target amplitude is. These ideal adaptive shifts are illustrated in Fig. 3a. They comprise two core features, first, a gradation of the shifts according to target directions, and thus according to the direction-related visuomotor gain, and, second, the divergence of the adaptive shifts with increasing target amplitude.

For the statistical analysis of the adaptive shifts, aftereffects, and explicit shifts, a series of ANOVAs was run. For each type of test, open-loop with cued transformation, open-loop with cued absence of the transformation, and explicit with cued transformation, the ANOVA included the between-participant factors age and gender and the within-participant factors target direction and target amplitude. The main focus in these analyses was, first, on the main effect of target direction and its interaction with age, and, second, on the interaction of target direction and target amplitude and its interaction with age as the third factor. These effects capture the core characteristics of the ideal adaptive shifts (cf. Fig. 3a) and their eventual dependence on age.

As can be seen in Fig. 3b, younger and older participants showed adaptive shifts that were appropriate for the direction-related visuomotor gain. Both groups showed increased movement amplitudes at the target direction of 90°, decreased movement amplitudes at 0°, and rather unchanged amplitudes at 34°. The main effect of target direction was significant, $F(2,76) = 62.1$, $p < 0.01$, $\eta^2 = 0.62$. Furthermore, the statistical analysis revealed a marginally significant interaction of target direction and age, $F(2,76) = 2.9$, $p < 0.10$, $\eta^2 = 0.07$, indicating that direction-dependent visuomotor adaptation was more pronounced for the younger than for the older participants. A significant interaction of target direction and target amplitude, $F(4,152) = 14.7$, $p < 0.01$, $\eta^2 = 0.28$, reflected the divergence of the direction-related adaptive shifts with increasing target amplitude, but the three-way interaction involving age failed to reach statistical significance, $F(4,152) = 1.13$, $p > 0.20$.

A similar, though smaller main effect of target direction was also found for the aftereffects (Fig. 3c), $F(2,76) = 35.9$, $p < 0.01$, $\eta^2 = 0.47$, but this time, there was no interaction of target direction and age ($F < 1$). The

Fig. 3 Pretest-to-posttest changes of hand amplitude as a function of target amplitude and target direction. (**a**) Expected changes in the case of perfect adaptation (for the direction of 34° no change was expected), (**b**) observed changes in the open-loop test with transformation (adaptive shifts) in younger and older subjects, (**c**) observed changes in the open-loop test without transformation (aftereffects) in younger and older subjects, (**d**) observed changes in the explicit test with transformation (adaptive shifts of explicit judgment) in younger and older subjects
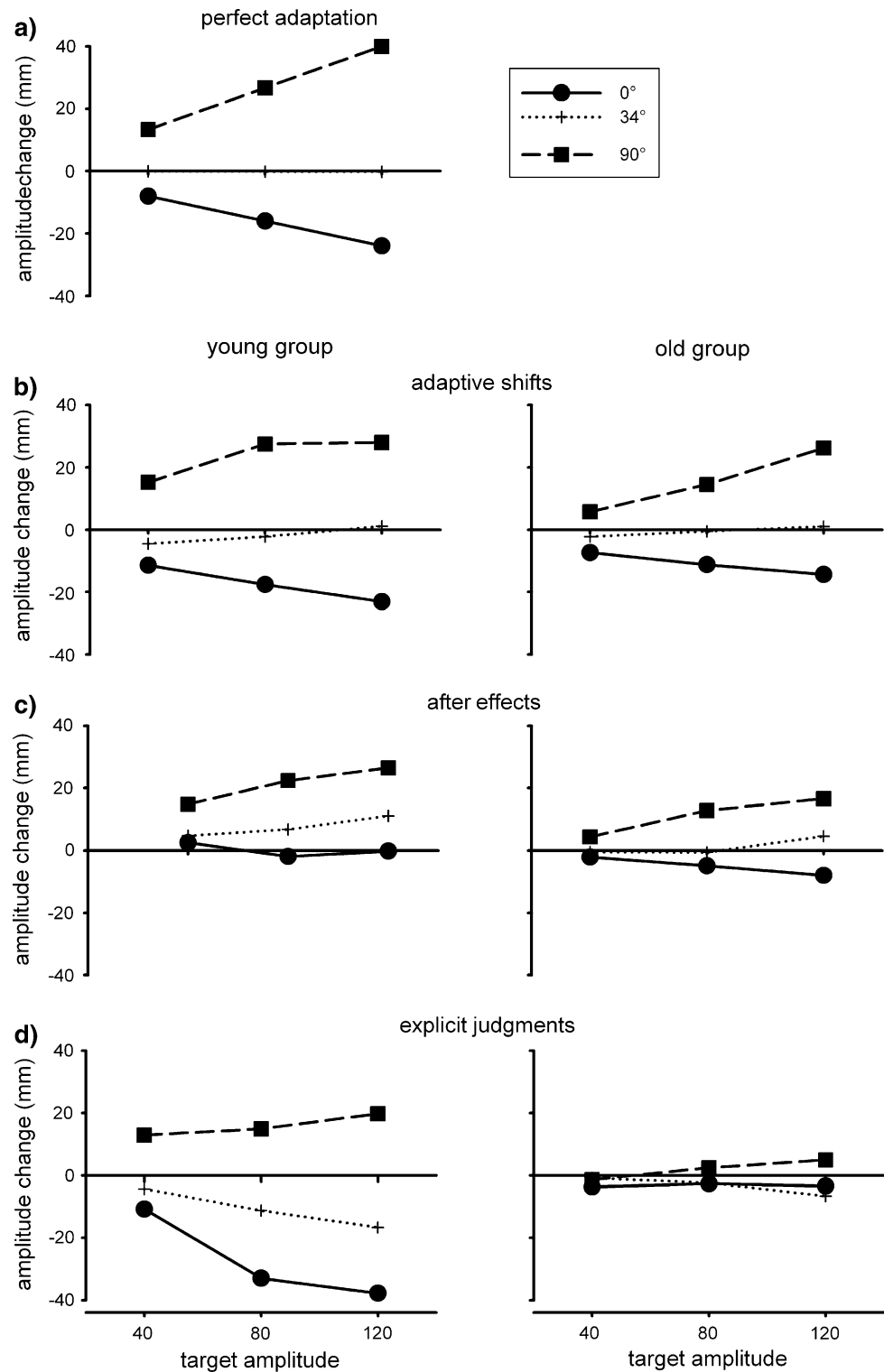
interaction of target direction and target amplitude was also significant, $F(4,152) = 6.5$, $p < 0.01$, $\eta^2 = 0.15$, but the interaction with age as a third factor again failed to reach statistical significance, $F < 1$.

From Fig. 3d it is evident that for the older group the shifts of explicit judgments did not conform to the basic pattern of adaptive changes appropriate for the direction-related visuomotor gain. Participants of the younger group, in contrast, showed a remarkable amount of explicit knowledge. The statistical analysis revealed significant main effects of target direction and target amplitude, $F(2,76) = 31.5$, $p < 0.01$, $\eta^2 = 0.45$, and $F(2,76) = 4.6$,

$p < 0.05$, $\eta^2 = 0.11$, respectively, as well as significant interactions of those variables with the between-subject factor age, $F(2,76) = 18.9$, $p < 0.01$, $\eta^2 = 0.33$ and $F(2,76) = 5.7$, $p < 0.01$, $\eta^2 = 0.13$, respectively. Furthermore, the interaction of target amplitude and target direction became significant, $F(4,152) = 7.1$, $p < 0.01$, $\eta^2 = 0.16$, and so did the triple interaction of target amplitude, target direction and age, $F(4,152) = 3.6$, $p < 0.05$, $\eta^2 = 0.09$. Separate ANOVAs for both age groups showed that main effects of target direction and target amplitude as well as their interaction could only be found in the younger age group, whereas no significant effects were found in the older group.

Extinction phase

The mean cursor amplitude errors in the five blocks of trials of the extinction phase are shown in Fig. 4. Those errors were produced in the presence of the visuomotor transformation as cued by the red start circle, i.e. they are comparable to the amplitude errors found in the practice phase (Fig. 1) though there was no visual feedback at all in the extinction phase. Errors were overshoots for the target directions of 0 and 22.5° and undershoots for the target directions of 67.5 and 90°. In the older group, over- and undershoots were more pronounced than in the younger group. In fact, the mean amplitudes of hand movements for the target directions 0, 22.5, 45, 67.5, and 90° varied only little in the older group, 78, 83.8, 86, 84.5, and 87 mm, respectively. In contrast, in the younger group the variation of mean hand amplitudes across target directions was considerable, 78, 87, 91, 97, and 103 mm, respectively. Thus, whereas both groups continued to exhibit a direction-dependent specification of movement amplitude, this was more pronounced in the younger participants.

The amplitude errors of Fig. 4 were subjected to a four-way ANOVA with the between-participant factors age and gender and the within-participant factors target direction and block. The overall difference between the two age groups was significant, $F(1,38) = 4.5, p < 0.05, \eta^2 = 0.11$, reflecting the tendency of younger participants to overshoot the target and of older participants to undershoot it. Second, the effect of target direction was different in the two groups as indicated by a significant group × target-direction interaction, $F(4,152) = 3.6$, $p < 0.05$, $\eta^2 = 0.09$. Third, the changes across the five blocks of trials were different, giving rise to a significant interaction of age group and block, $F(4,152) = 4.3, p < 0.01, \eta^2 = 0.10$ When analyzed separately, for the younger group there was only a significant main effect of target direction, $F(4,76) = 16.9$, $p < 0.01$, $\eta^2 = 0.47$, whereas for the older group both the main effects of target direction, $F(4,76) = 35.2, p < 0.01$,
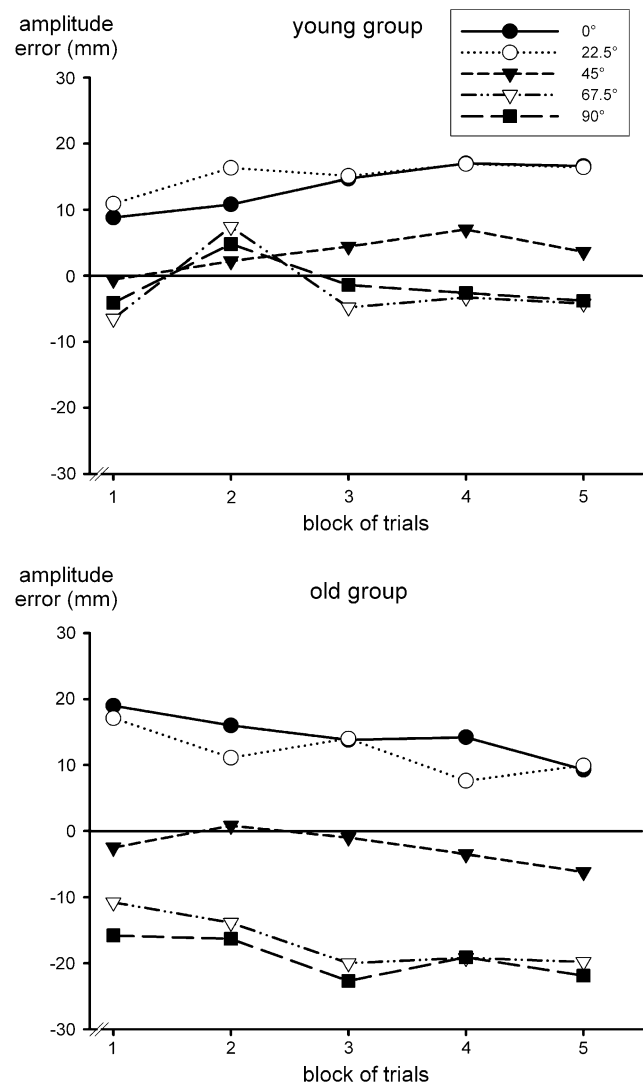
Fig. 4 Mean errors of cursor amplitudes in extinction trials (in which the cursor was also invisible at the end of each movement) as a function of target direction and block of trials

$\eta^2 = 0.65$, and block, $F(4,76) = 3.0, p < 0.05, \eta^2 = 0.14$ were significant.

Movement times in the extinction phase were 1,013, 1,029, 1,056, 1,098, and 1,127 ms for the target directions of 0, 22.5, 45, 67.5, and 90°, respectively, giving rise to a statistically significant variation across target directions, $F(4,152) = 7.8, p < 0.01, \eta^2 = 0.17$. No effects involving the factor age were significant. Movement times for the young and old group were 1,009 and 1,119 ms, respectively, $F(1,38) = 1.9, p > 0.10$.

Adaptive shifts, aftereffects, extinction, and explicit knowledge

In order to examine the potential modulation of age-related differences in performance measures of adaptation by age-

related variations in explicit knowledge, we classified participants according to their explicit shifts as having no, intermediate, or full explicit knowledge of the transformation. To be classified as having full explicit knowledge, the explicit shifts of the participant had to exhibit both core characteristics, the correct gradation of adaptive shifts by target direction and the increase of the directional differences with increasing target amplitude. Participants classified as having no explicit knowledge exhibited none of the two core characteristics. All other participants who had noticed some change from baseline-to practice, but did not modify their judgements in a consistent fashion according to the direction-dependent gain, were classified as intermediate. Under the hypothesis that the age-related impairment of adaptation is due to an age-related decline of explicit knowledge, the age-related differences in practice, adaptive shifts, and extinction should disappear when comparing young and old subjects with a similar amount of explicit knowledge.

Seventeen older and six younger participants with no explicit knowledge of the direction-dependent gain were compared. The interaction of age and target direction, which reflects age-related differences in direction-sensitive adaptation, disappeared for the adaptive shifts and the amplitude errors in the extinction phase, both $F < 1$, as well as for the amplitude errors during practice, $F_{(4,84)} = 1.7$, $p > 0.20$, while the main effects of target direction remained significant within both groups (all $p < 0.01$). In order to exclude the possibility of non-significant interactions due to diminished statistical power, we did a second set of ANOVAs involving the 17 older participants without explicit knowledge and the five younger participants with perfect explicit knowledge. These ANOVAs involved almost the same group sizes, but the two age groups differed in explicit knowledge rather than being comparable in this respect. The results showed a marginally significant age × target-direction interaction for the amplitude errors during practice, $F_{(4,80)} = 2.2$, $p < 0.10$, $\eta^2 = 0.10$, and highly significant interactions of age and target direction for adaptive shifts as well as for the amplitude errors in the extinction phase, $F_{(2,38)} = 9.2$, $p < 0.01$, $\eta^2 = 0.31$, and $F_{(4,80)} = 2.7$, $p < 0.05$, $\eta^2 = 0.12$, respectively. In contrast, the beneficial effect of explicit knowledge on performance measures was not found for the aftereffects, $F_{(2,38)} = 2.6$, $p > 0.10$, consistent with the view that adaptive shifts, but not aftereffects, are affected by explicit knowledge.

To further probe the assumption that adaptive shifts comprise both types of adjustments, explicit strategic corrections and implicit modifications of an internal model, we calculated the partial correlations between explicit shifts and adaptive shifts with aftereffects being partialled out. In order to assess both core characteristics, we computed for each participant the mean difference between shifts at 0 and 90° averaged across all target distances to assess their correct gradation by target direction and the increase of shifts with target amplitude. Partial correlations for the younger group were 0.67, $p < 0.01$, for the direction dependence and 0.57, $p < 0.01$, for the modulation of to the direction dependence by the target amplitude. Correlations in the older group were 0.49, $p < 0.05$, and 0.42, $p < 0.1$, respectively. No correlation of explicit knowledge and aftereffects, i.e. between measures of explicit strategic corrections and implicit adjustments approached statistical significance. Note that these correlations were computed within each age group and are smaller than correlations computed for samples with larger age ranges and thus unrestricted variances.

Discussion

The purpose of the present study was to examine age-related variations of adaptation to a complex, direction-dependent visuomotor gain transformation at pre-retirement age in order to gain further insights into the relation between amplitude and direction adaptation. Participants were required to rescale their movements to a direction-dependent gain ranging from 1.25 for movements to the right (0°) to 0.75 for forward movements (90°). Additionally, we used different test procedures to assess the influence of age on implicit and explicit components of visuomotor adaptation. This served to determine whether the typical pattern of age-related declines in direction adaptation could also be found for adaptation to a sufficiently difficult visuomotor gain. If difficulty rather than type of adaptation task were critical for different age-related variations observed in previous studies, with a more complex gain transformation a similar pattern of age-related effects on visuomotor adaptation should show up as it is commonly observed for adaptation to visuomotor rotations of a sufficient size (cf. Bock, 2005; McNay & Willingham, 1998; Heuer & Hegele, 2008a).

All in all, adaptive shifts in both age groups revealed adaptation to a direction-dependent visuomotor gain. Of course, practice for both groups was with terminal visual feedback because continuous visual feedback had been shown to produce no adaptation to a direction-dependent gain (Bock, 1992; Heuer & Hegele, 2008b). Whereas age-related deficits could be found in the explicit component of adaptation, the implicit modification of an internal model of the transformation seems to be independent of age. This is strongly suggested by the pattern of findings.

First, the implicit modification of an internal model of the visuomotor transformation is indicated by the aftereffects which in both age groups were graded according to

target direction, with the directional variation increasing with increasing target amplitude. The same pattern of results was observed for the adaptive shifts in both age groups, but it was more pronounced in the younger group. Second, for the explicit shifts the gradation by target direction and its divergence with increasing target amplitude was found only for younger participants, but not for older ones. The behavioral consequences of the age-related differences in explicit knowledge became apparent when younger and older participants without explicit knowledge were compared: without explicit knowledge the age-related variations of adaptive shifts and of amplitude errors during practice and extinction disappeared. Thus, behavioral consequences of explicit knowledge were superposed on implicit performance modifications in order to improve visuomotor performance whenever the presence of the direction-dependent gain was cued, but only in the younger participants, whereas in the older participants explicit knowledge was generally absent.

The present results extend the body of findings which overall reveal a remarkably consistent pattern of age-related changes in adapting to novel visuomotor rotations (Buch et al., 2003; Bock, 2005; Bock & Girgenrath, 2006; McNay & Willingham, 1998; Seidler, 2006) to adaptation to a novel and difficult visuomotor gain. They are consistent with the hypothesis that adaptive changes in the implicit mapping of visual input to motor output, referred to as adaptive recalibration (Bock, 2005) or spatial realignment (Redding & Wallace, 1996), remain largely unaffected by age at least up to about 65 years. In contrast, overall visuomotor adjustment is stronger in younger than in older adults, supposedly due to age-related differences in the formation and/or application of deliberate strategic corrections during adaptation (cf. Heuer & Hegele, 2008a).

Perhaps the particular pattern of age-related changes in visuomotor adaptation is related to different effects of ageing on frontal areas and the cerebellum. In the past, regions within the frontal cortex have been associated with conscious processes that can improve visuomotor performance by selecting more appropriate spatial targets (cf. Willingham, 1998; see also Frith, Friston, Liddle, & Frackowiak, 1991), and the cerebellum has been associated with the acquisition and modification of internal models (e.g. Imamizu et al., 2000; Wolpert, Miall, & Kawato, 1998).

The different effects of ageing on implicit and explicit components of adaptation suggest that the frontal contribution to adaptation declines earlier with age than the cerebellar contribution. This is supported by neurobiological findings that show differences in ageing between cortical and cerebellar regions of the human brain. Gene activity levels in the cerebellum remain stable in the course of ageing, which indicates that this region of the brain

experiences less oxidative stress and damage (Fraser, Khaitovich, Plotkin, Pääbo, & Eisen, 2005). Also consistent with differential ageing of cerebellar and frontal regions, extrastriatal dopamine receptor density was reported to remain rather stable over time in the cerebellum, whereas it decreased in the frontal cortex (Inoue et al., 2001; Volkow et al., 1998). Actually, the decrease was even more pronounced in the frontal cortex as compared to other regions of the brain (Kaasinen et al., 2005). There is also converging evidence from neuroimaging studies of a selective reduction of blood flow to the frontal cortex with increasing age (for a review, see West, 1996).

A prominent behavioural characteristic of normal ageing is generalized slowing, e.g. in terms of the time needed to perform cognitive operations (cf. Welford, 1981; Myerson, Hale, Wagstaff, Poon, & Smith, 1990; Li, Lindenberger, & Sikström, 2001) or the time needed to initiate and produce simple or complex movements (cf. Proctor, Vu, & Pick, 2005; Seidler & Stelmach, 1995). Even though motor slowing becomes prominent in every day life mainly at an age beyond retirement, it is a gradual process that begins in early adulthood and continues throughout working age (e.g., Szafran, 1951; Teeken et al., 1996; Yan, Thomas, & Stelmach, 1998). Based on the observation that the incidence of age-related changes in older adults at pre-retirement age (50–67) depends on the level of difficulty of the visuomotor transformation, it seems that the principle of a gradual change throughout adulthood most likely also holds for of the explicit component of visuomotor adaptation. Explicit processes are likely to become involved with visuomotor transformations of sufficient levels of difficulty and perhaps sufficient amount of practice. Whenever they become involved, age-related impairments of visuomotor adaptation will show up. If the visuomotor transformation is more difficult, those impairments will be observable earlier in the course of ageing.

Finally, some remarks on the notion of vector-coding are in order. According to the present results, age-related impairments of visuomotor adaptation are not categorically different for amplitude and direction adaptation, but show up with sufficient difficulty of the transformation for both movement parameters. Age-related impairments disappear when visuomotor rotations are only small (Heuer & Hegele, 2008a), and, as we show here, they appear when gain changes become sufficiently complex. These findings do not support the notion of a categorical difference between amplitude and direction adaptation (e.g., Bock, 1992; Krakauer et al., 2000, 2004; Pine et al., 1996). Consequently, they also provide no additional evidence for vector-coding. On the other hand, even though the present findings do not support the notion of separate mechanisms of amplitude and direction adaptation, they are not inconsistent with it because different mechanisms associated

with different neural structures do not necessarily imply different age-related variations.

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