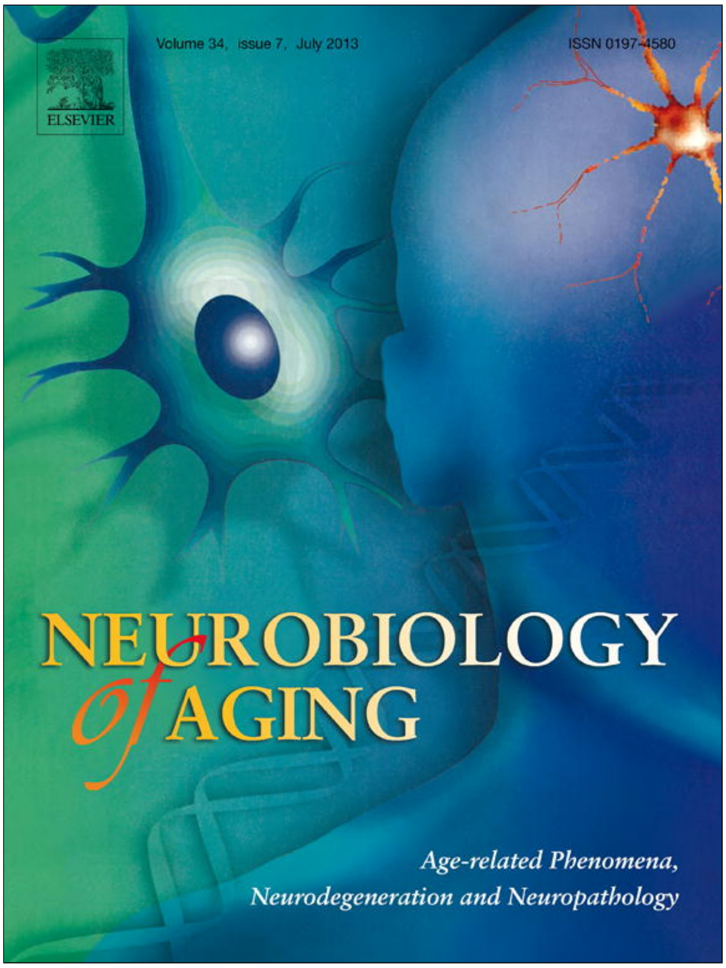
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# Vision and proprioception in action monitoring by young and older adults

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ABSTRACT

Discrimination of proprioceptive and visual spatial information is a prerequisite for the learning of visuo-motor transformations. This study investigated the individual's capability to discriminate the directions of seen cursor motions and felt hand movements under a visuo-motor rotation paradigm and its age-related variation. Young and older participants performed 3-stroke arm movements on a digitizing tablet without seeing their arm. The visual feedback of the second stroke was rotated randomly by various angles ranging from $-30^\circ$ to $30^\circ$ and displayed on a monitor. Older adults were poorer in discrimination than young adults. In both age groups, the felt hand direction was shifted toward the seen cursor direction (i.e., visual capture) by approximately 25% to 30% of the rotation of the visual feedback. Older adults also showed an enhanced visual capture. The results suggest that both the increased sensory noise and the increased assimilation of the bimodal information cause the reduction of discrimination capability in older adults. These findings provide underlying reasons for age-related changes in learning a new visuo-motor transformation.



## 1. Introduction

Humans monitor their own actions multimodally. For example, visual and proprioceptive information is used to monitor the movements of the hand. However, when actions involve the use of tools such as a lever or a computer mouse, vision typically refers to the effective part of the tool (the tip of the lever or the cursor on the monitor), and proprioception to the hand, both operating at different locations. Here we investigate the individual's capability in discriminating movement directions of the hand and a cursor presented on a monitor, indicated by the 2 sensory modalities, and their age-related variation.

Typically, visual and proprioceptive signals about the hand-position are not identical, but tend to drift apart (Smeets et al., 2006). Nevertheless, they are integrated to obtain a single estimate of the position of the hand (Van Beers et al., 1999). In case of discrepancy (e.g., due to a visual perturbation), adaptive changes bring the 2 sources in line again (Van Beers et al., 2002). Integration is obviously an appropriate way of dealing with bimodal spatial information as long as it refers to the same object (Bedford, 1995).

When a tool is used, proprioception and vision signal different positions of different objects. The relation between them reflects the kinematic transformation of the tool. An example is the control of the cursor position on a monitor by moving the hand appropriately. Actions of this type require discrimination rather than integration of bimodal spatial information as a prerequisite to acquiring an internal representation of the kinematic transformation of the tool. To study this type of adaptation, visuo-motor rotations have become a well-established paradigm (Cunningham, 1989).

Recent evidence reveals that older adults are poor in adaptation to such visuo-motor rotations (Bock, 2005; Heuer and Hegele, 2008; Heuer et al., in press). Especially, their capability to acquire explicit knowledge of the visuo-motor rotation declines. What underlies these age-related changes, however, is not well understood. In an attempt to explore their underlying mechanisms, we modify the visuo-motor rotation paradigm to study the discrimination of the directions of hand and cursor movements. In particular, we test the hypothesis that this particular discrimination is poorer at older adult age. As a consequence, acquisition of explicit knowledge of directional differences would be impeded.

The hypothesis of poor discrimination of hand and cursor directions at older age is suggested by both psychophysical and neurophysiological findings. More specifically, these findings suggest that visual and proprioceptive spatial information lose distinctiveness for at least 2 reasons. First, declining sensitivity in elderly subjects has been shown psychophysically both for visual perception (Betts et al., 2007) and proprioception (Goble et al., 2009). This is consistent with the hypothesis of increasing noise in neural functioning (Welford, 1981). Second, there is strong

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evidence of neural dedifferentiation in aging, so that different mental operations come to rely more and more on common neural substrates (e.g., Carp et al., 2011; Liang et al., 2010). Thus, with concurrent bimodal spatial information assimilation could contribute to an age-related decline of discrimination capability. In particular for visual and proprioceptive information, an attractive effect of vision is known as visual capture (Hay et al., 1965). Visual capture is not necessarily restricted to situations in which vision and proprioception refer to the same object. For example, a seen hand optically superposed on an amputated arm results in felt movement of the phantom when the healthy arm is moved (Ramachandran et al., 1995). Thus, visual capture might also shift the felt direction of hand movement toward the seen direction of cursor motion.

Therefore, we assessed the general discrimination performance by means of standard psychophysical methods on one hand, and quantified the effect of the visual capture by means of a new indirect measure on the other hand.

## 2. Methods

### 2.1. Participants

Twenty young adults (mean ± SD, 26.0 ± 3.6 years; range, 18–31 years; 8 males and 12 females) and 20 older adults (mean ± SD, 60.0 ± 4.4 years; range, 53–67 years; 10 males and 10 females) participated in the study. All participants were right-handed. They filled in a health history questionnaire to exclude those with a history of stroke, arthritis, or other neurological or movement impairments, and gave written informed consent before participation. The study was conducted in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki and with general approval of the Institutional Review Board of Leibniz Research Centre for Working Environment and Human Factors.

Young and older participants were compared on 2 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. Consistent with typical findings, the average score on the Digit Symbol Test was higher for the young adults (mean ± SD, 61.2 ± 13.5) than for the older adults (53.4 ± 13.7), but the difference only approached statistical significance [$t(38) = 1.8$, $p < 0.1$]. The results of the Vocabulary Test were similar in the 2 groups [young, 22.9 ± 4.8; old, 21.1 ± 3.3, $t(38) = 1.3$, $p > 0.1$].

### 2.2. Apparatus

The experimental setting is shown in Fig. 1A. Participants were seated at a table on which a 22-inch liquid crystal display monitor (Samsung SyncMaster2233, refresh rate 100 Hz) was placed in approximately 60 cm distance from their eyes. The monitor was covered by a large black circular screen (72 cm in diameter) with a semi-circular window (32 cm in diameter) in its center, through which the participants could see the computer monitor.

A digitizer tablet (Wacom Intuos 4XL) was placed on the table between the participants and the monitor. The participants held a stylus in a manner similar to holding a pen for handwriting. Movements of the stylus on the tablet and those of a cursor displayed on the monitor had a 1-to-1 ratio with respect to distance. An opaque board placed above the participants' arm blocked their view of the hand movements. The starting position of the cursor on the monitor was aligned with the participants' median plane. The *X*- and *Y*-positions of the tip of the stylus were recorded at 133 Hz with a spatial resolution of 0.005 mm.

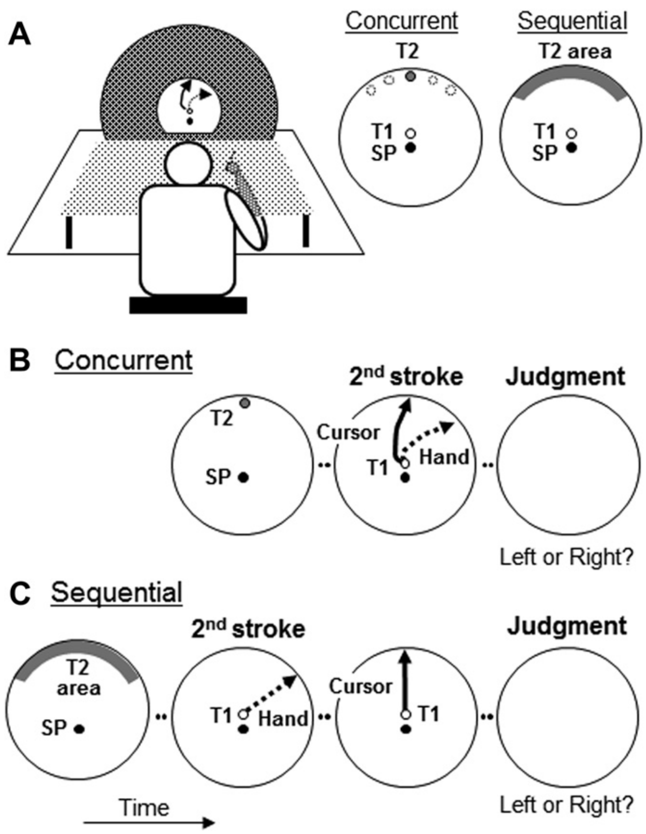


**Fig. 1.** The experimental setup and target locations are shown in (A). SP, starting position; T1, first target; T2, second target. The visual feedback of the second-stroke movement was displayed simultaneously with hand movements in the concurrent condition (B) or after the movement in the sequential condition (C).

### 2.3. Design and procedure

Participants performed 3-stroke arm movements with their right hand in the horizontal plane. To examine the effect of concurrent processing of the 2 sensory modalities (vision and proprioception) on the discrimination of hand and cursor directions, participants underwent a concurrent condition (Fig. 1B), in which the visual feedback was presented simultaneously with the hand movement. As a control to the concurrent processing of visual feedback, a sequential condition was also introduced (Fig. 1C), in which the visual feedback was presented after the hand movement.

#### 2.3.1. Starting position and targets

Target locations for both concurrent and sequential conditions are illustrated in Fig. 1A. The first target (T1, 1.4 cm in diameter) was located in the center of the semi-circular window. The starting position (SP; 1.2 cm in diameter) was located 3 cm below the T1. The locations of the SP and T1 were the same for both the concurrent and sequential conditions.

In the concurrent condition, 1 of 5 possible second targets (T2, 1 cm in diameter) was presented. The targets were located 15 cm from T1, just above it (the gray circle in Fig. 1A) and at 15° and 30° left or right of the center (open circles in Fig. 1A). The participants made 3-stroke movements from the SP to T1 (first stroke), then to T2 (second stroke), and subsequently back to T1 (third stroke).

In the sequential condition, no specific T2, but an area to which second strokes were to be made, was displayed (Fig. 1A, T2 area). The T2 area was on an invisible circle with a radius of 15 cm around T1, and the area spanned from 45° left to 45° right of the central location. The participants made 3-stroke movements from the SP to

T1 (first stroke), then to any location within the T2 area (second stroke), and subsequently back to T1 (third stroke). They were instructed to choose different directions across trials for the second strokes. To stop the movements mechanically at the end of the second strokes in both conditions, a semi-circular plastic ring (stopper ring) with a radius of 15 cm around T1 and a height of 3 mm was placed on the surface of the digitizer.

The T2 target area of the sequential condition (±45° from the center) was wider than the maximum T2 eccentricity of the concurrent condition (±30°). This difference was applied in order to equalize the spatial variability of hand positions at the end of the second stroke among the 2 conditions. When within-participant standard deviations of that hand position were measured for all participants, the mean standard deviation (±SE) across participants was only slightly but significantly smaller for the concurrent condition (31.6 ± 0.6 degrees for the young and 31.0 ± 0.6 degrees for the older group) compared to the sequential condition (34.4 ± 1.6 and 33.4 ± 1.9 degrees, respectively) as indicated by a 2 (concurrent vs. sequential) ×2 (young vs. old) ANOVA ($F_{1,38} = 4.59$, $p < 0.05$). The difference between the 2 age groups was not significant ($F_{1,38} = 0.30$, $p > 0.10$).

### 2.3.2. Three-stroke movement

At the beginning of each trial, the participants were guided to the SP. For this purpose, 1 or 2 of 4 arrows pointing to the left, right, up, and down were presented in the center of the monitor. The participants followed the guidance of these arrows and moved the stylus first to an invisible random location within an invisible rectangular area (16 × 12 cm centered around the SP), and then to the invisible SP. The random location was added to interfere with memory of the final hand position of the previous trial. The feedback cursor (a dot, 1 cm in diameter) and the circle that marked the SP became visible when the stylus was within a radius of 2 cm from the SP to assist the participants in reaching the SP accurately.

One second after the stylus was in the SP, T2 (or T2 area) was displayed for 1 second (Fig. 1B and C, first panel). Subsequently, T1 was displayed. After a delay of 0.5 second, an auditory go-signal was delivered. In response to it, the participants made 3-stroke movements at a comfortable speed. Once the participant had made the first stroke to T1, this target disappeared. The first stroke to T1 was introduced because the participants would naturally look at T1 during this movement (Neggers and Bekkering, 2000; Rand and Stelmach, 2011), which prevented them from keeping their gaze on T2 (or the T2 area) to remember those locations. Because T2 (or T2 area) was no longer visible after the initial presentation, the participants made the second stroke to the remembered T2 (or T2 area), until the movement was stopped by the stopper ring. As T1 was also no longer visible, the participants made the third stroke to the remembered T1 location. They were instructed to make a brief stop at the end of each stroke.

### 2.3.3. Feedback conditions and task

In both conditions, the feedback cursor was displayed concurrently with the hand movements for the first stroke, whereas no visual feedback was presented for the third stroke. For the second stroke, the motion of the cursor was rotated to different directions relative to the actual hand movement in both conditions. There were 12 rotation angles, half of which were in clockwise (CW) direction (−30°, −25°, −20°, −15°, −10°, and −5°), and the other half in counterclockwise (CCW) direction (5°, 10°, 15°, 20°, 25°, and 30°). These angular rotations were randomized across trials. Ten trials were collected for each of the 12 angular rotations, resulting in a total of 120 trials for each condition. The concurrent and sequential conditions differed with respect to the execution of the second stroke and the presentation of visual feedback of that stroke.

In the concurrent condition, the cursor was displayed during the second stroke, but the motion of the cursor was rotated relative to the direction of hand movement (see above). Thus, participants had to modify their hand movement so that the cursor on the monitor would move toward the remembered T2 location (Fig. 1B, second panel). The remembered T2 was introduced instead of a visible T2 in the concurrent condition, so that the participants focused on the visual feedback cursor during the second stroke. After the hand had reached the stopper ring (i.e., after the end of the second stroke), the participants moved back to the remembered T1 location (third stroke) without visual feedback. One second after completing the third stroke, participants were asked whether their second hand stroke was on the right side or the left side of the cursor motion (Fig. 1B, third panel). The participants made the judgment by answering “right” or “left.” They had to choose 1 side even when they were uncertain about the correct side. The remembered rather than visible T2 should prevent the participants from directly comparing the visible T2, instead of the feedback cursor motion, with the felt final hand position.

In the sequential condition, the participants made the second stroke into a direction of their choosing within the range of the T2 area, and the movement was stopped by the stopper ring (Fig. 1C, second panel). Then, the participants made the third stroke back to the remembered T1 location. One second after completing the third stroke, the cursor motion of their second stroke was displayed with the same velocity characteristics, but with a rotation relative to the direction of hand movement (Fig. 1C, third panel). After the completion of the visual feedback display, the participants were required to perform the same judgment task as in the concurrent condition (Fig. 1C, fourth panel).

Despite the different planes of hand movements and cursor motions, the judgment task was easily understood by the participants and required no detailed explanation regarding what “right” or “left” meant when dealing with 2 different planes. At least as far as directions are concerned, there is a natural compatibility between the 2 planes, in that forward movements of the hand are naturally related to upward motions of the cursor and right movements of the hand to right movements of the cursor. Deviations from this natural mapping result in systematic movement errors (Cunningham, 1989).

The experiment consisted of a block of 5 familiarization trials, a block of 8 practice trials of the concurrent condition, a first set of the concurrent condition (61 trials), a block of 4 practice trials of the sequential condition, a first set of the sequential condition (61 trials), a second set of the concurrent condition (61 trials), and a second set of the sequential condition (61 trials). The familiarization trials included the procedure of the concurrent condition without rotation of the visual feedback and without the judgment part. Each set of trials of the concurrent or the sequential condition included 1 warm-up trial and 60 (5 trials for each of the 12 angular rotations) experimental trials. The order of the concurrent and sequential conditions was counterbalanced across participants. When a participant made a gross error, such as initiating the movement before the go-signal or making too short a movement, that trial was redone during a given block or set. A total of 120 experimental trials were recorded and analyzed for each condition.

## 2.4. Data analysis

Data were analyzed with respect to the discrimination of seen (the cursor) and felt (the hand) movement directions and to the influence of the seen direction on the felt direction (visual capture). The present study was designed to test the hypothesis that the discrimination performance was poorer and visual capture was stronger in the older adults compared to the young adults. The sequential condition served as a control of the concurrent condition to examine whether age-related changes of discrimination were specific to concurrent processing of bimodal information. It also served as a control for our novel indirect procedure to assess visual capture: in the sequential condition, visual capture should be zero, because the visual feedback was presented after the third stroke.

Although the procedures of the concurrent and sequential conditions were basically similar aside from the main timing manipulation of visual feedback, there were some subtle, but inevitable differences. For example, the target of the second movement was experimenter selected, defined for the cursor, and clearly indicated in the concurrent condition, whereas the target position was self-selected, defined for the hand, and not explicitly indicated in the sequential condition. The T2 target area of the sequential condition was also wider than the maximum T2 eccentricity of the concurrent condition as described above. Because we cannot exclude potential confounding effects of these differences that add to the main difference in the timing of visual feedback, no direct comparison between the 2 conditions will be made.

### 2.4.1. *Discrimination of seen direction of the cursor and felt direction of the hand*

For each rotation angle, each condition (concurrent, sequential), and each participant, the relative frequency of “right” judgments out of 10 trials was calculated and plotted against rotation angles to obtain psychometric functions. A logistic function was fitted to the relative frequencies by a least-squares criterion:

$$y = 1/[1 + \exp(-(x - k_1)/k_2)], \tag{1}$$

where $y$ is the estimated probability of “right” judgments, $x$ is the rotation angle, and $k_1$ and $k_2$ are mean and spread parameters, respectively. The spread (inverse steepness) parameters indicating the discrimination performance were estimated individually for all participants and used for comparisons between groups. The larger the spread parameter is, the poorer is the discrimination of the seen direction of the cursor and the felt direction of the hand movement.

To identify outliers among the spread parameters, the following screening was performed for each condition. First, the mean and standard deviation across all participants of both groups were calculated. Second, spread parameters greater than mean $\pm$ 3 SD were defined as outliers. These steps were repeated until no further outliers were found. The participants with outliers were excluded from all analyses including the indirect measure of the felt position of the hand (discussed below).

In addition to the parametric analysis of the psychometric functions, we counted the number of judgment errors across all rotation angles. The error frequency, which is positively related to the spread of the psychometric function, has the advantage that it does not depend on assumptions on the shape of the psychometric function. This measurement, however, lacks a detailed description of the discrimination performance relative to rotation angles. The spread parameters and the error frequencies were subjected to 1-tailed *t*-tests of the directed hypothesis that discrimination is poorer in the older than in the young participants.

The mean parameter ($k_1$) of the psychometric function serves to assess the point of subjective equality, that is, the difference between visual and proprioceptive directions at which they appear equal. The mean parameters for all participants were subjected to 1-sample *t*-tests against 0 as well as to t-tests to compare the means of the 2 age groups.

### 2.4.2. *Indirect measure of the felt direction of the hand*

The influence of the seen cursor direction on the felt hand direction (visual capture) was investigated by means of an indirect measure with the following 3 steps. First, the angle ($\alpha$ in Fig. 2) between the line connecting T1 with the end of the second stroke (i.e., line A) and the line connecting the end of the second stroke with the end of the third stroke (i.e., line B) was measured. Second, line B was shifted in parallel to the axes of the coordinate system until its end (i.e., the end of the third stroke, solid white circle in Fig. 2) was in T1. Third, the location of the other end of the shifted line (line B′) served as an estimate of the felt hand position at the end of the second stroke (dotted white circle in Fig. 2). As estimate of the rotation of the felt hand position relative to the actual position, we used the angle between the line A and the line B′ ($\alpha'$ in Fig. 2). When line B′ (i.e., third stroke) was rotated into the CCW or CW direction compared to line A (i.e., second stroke), $\alpha'$ had a positive or negative sign, respectively.

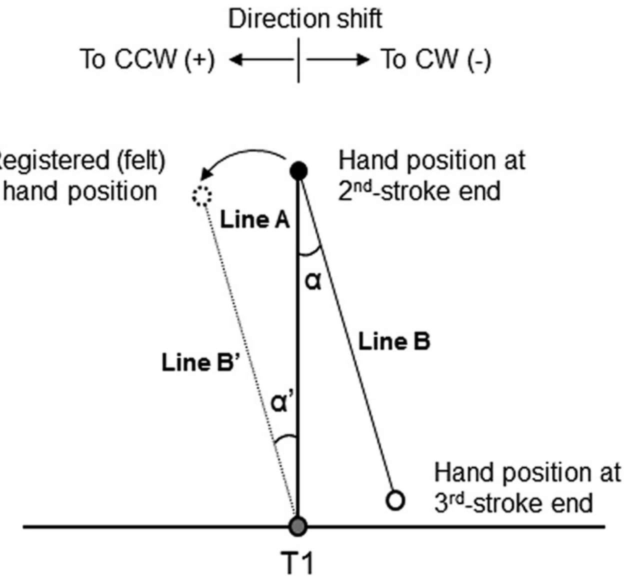


**Fig. 2.** The relationship between the actual hand position (filled [black] circle) at the end of the second-stroke and its felt hand position (dotted open [white] circle).

To examine the influence of the rotation of the cursor motion on the felt hand position relative to the physical one, $\alpha'$ values across all trials for each condition and each participant were subjected to a linear regression where $\alpha'$ was a dependent variable and rotation angle was an independent variable. The resulting slope parameter is an estimate of the rotation of the felt hand position per degree of the rotation of the visual feedback. We shall refer to it as the visual-capture parameter. As mentioned before, there should be no influence of the feedback rotation on $\alpha'$ in the sequential condition. Hence, slopes unequal to zero observed in the sequential condition would indicate influences other than that of the rotated visual feedback, and accordingly would serve as a control for the concurrent condition. The individual slopes (capture parameters) were subjected to a 1-tailed *t*-test of the directed hypotheses that visual capture is stronger in the older than in the young participants.

## 3. Results

### 3.1. *Discrimination of seen direction of the cursor and felt direction of the hand*

In a first step, we examined the individual relative frequencies of “right” judgments across the range of rotation angles (Fig. 3). Some participants in both groups produced highly precise discriminations in both the concurrent and sequential conditions (Y20 and O16 in Fig. 3). They rarely made discrimination errors for large

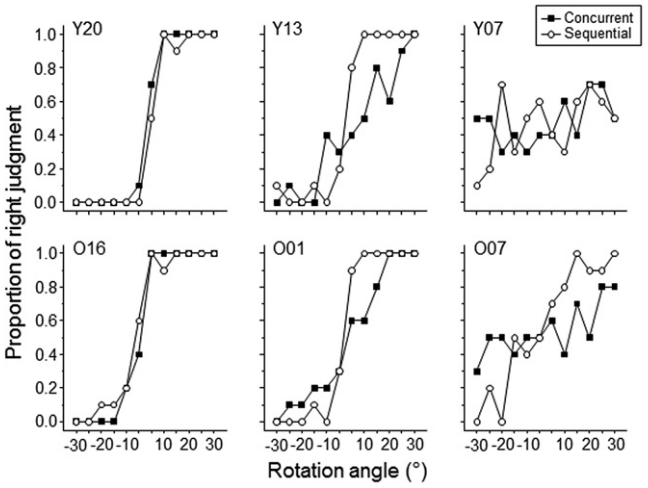


**Fig. 3.** Individual examples of the proportions of right judgment for the concurrent (filled squares) and sequential (open circles) conditions. The abscissa is the rotation angles of visual feedback. Examples are shown for high (young adult, Y20; older adult, O16), modest (Y13, O01), and low (Y07, O07) precision of discrimination.

rotation angles, and the range of rotations for which errors were observed was only small. Hence, the spread of the psychometric functions was very small in these participants. Some other participants made more judgment errors, resulting in less steep psychometric functions (Y13, O01). Finally, there were participants with very poor discrimination. The examples of Fig. 3 (Y07, O07) show that these participants could hardly discriminate the seen and felt directions in 1 or both conditions.

Next, logistic functions were fitted to the individual relative frequencies of "right" judgments as a function of the rotation of the visual feedback. Fig. 4 shows histograms of the spread parameters for the young (A, B) and older (C, D) groups. Based on the criterion for the identification of outliers (detailed in Methods), spread parameters greater than 16.52 were identified as outliers for the concurrent condition, and spread parameters greater than 11.76 for the sequential condition. Accordingly, outliers were found in 2 young and in 3 older participants in the concurrent condition (A, C). In the sequential condition, only 1 young adult with an outlier was identified (B) who also had an outlier in the concurrent condition. The spread parameters across participants excluding those with outliers (young, n = 18; older, n = 17) were greater in the older group (C, D) than in the young group (A, B).

To test whether the observed interindividual differences in discrimination performance were related to those in the results of the Digit Symbol Test and the Vocabulary Test, we correlated the spread parameters with the scores of each test by using Pearson's correlation. No significant correlation was found for both tests for both groups for the concurrent condition (Digit Symbol Test, $r = -0.143$ [young, n = 18], $r = -0.296$ [older, n = 17]; Vocabulary Test, $r = 0.018$ [young], $r = 0.281$ [older], $p > 0.1$ for all correlations). Similarly, there was no significant correlation in the sequential condition (Digit Symbol Test: $r = -0.278$ [young], $r = -0.017$ [older]; Vocabulary Test: $r = -0.093$ [young], $r = -0.035$ [older], $p > 0.1$ for all correlations). Thus, individual differences in perceptuo-motor processing speed (tested by the Digit Symbol Test) and in culturally mediated knowledge (tested by the Vocabulary Test) did not account for the individual differences in discrimination performance.

To illustrate the group differences in discrimination, logistic functions were fitted to the mean relative frequencies of "right" judgments across all participants (excluding those with outliers) as a function of the rotation of the visual feedback (Fig. 4E and F). The

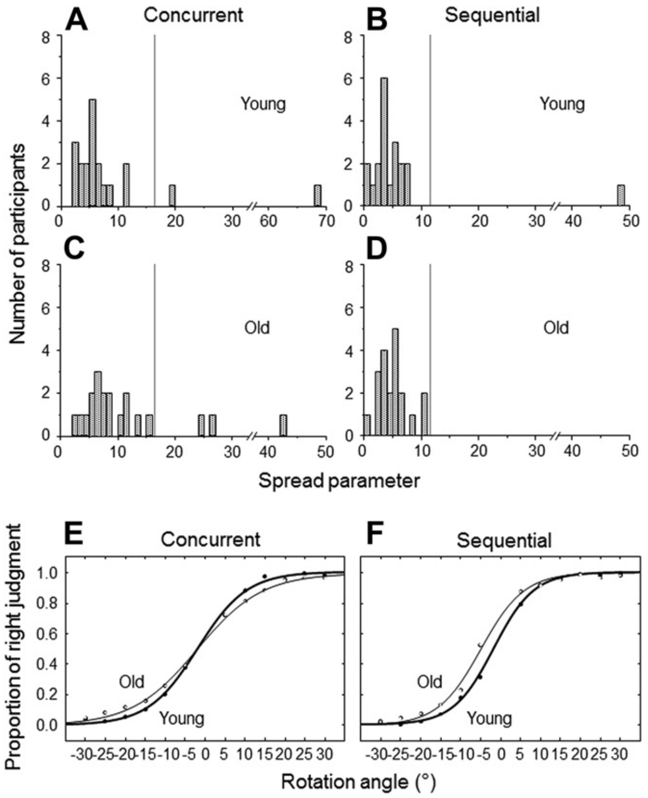


**Fig. 4.** Plots A through D show histograms of the spread parameter for the young and older groups in the concurrent (A and C) and sequential (B and D) conditions. Dotted lines mark the threshold of separating outliers from the main population. Plots E and F show the average proportions of right judgment across all participants (excluding outliers) and the logistic fit curves for the concurrent (E) and sequential (F) conditions. The abscissa is the rotation angles of visual feedback. Filled circles and thick lines refer to the young group, whereas open circles and thin lines refer to the older group.

psychometric function of the young group was steeper than that of the older group for the concurrent condition (Fig. 4E), indicating that the young adults were more precise in their discriminations. For the sequential condition (Fig. 4F), the slope of the young group was only slightly steeper than that of the older adults. Finally, in the concurrent condition, the psychometric functions were less steep overall than in the sequential condition, indicating that discrimination was less precise when the visual feedback was presented concurrently with the hand movements compared to when it was presented after the movements.

The observed group differences were statistically verified by the analysis of the individual spread parameters (young, n = 18; old, n = 17). The mean (±SE) values were 7.939 ± 0.865 vs. 5.797 ± 0.598 (older vs. young) in the concurrent condition. The comparable values in the sequential condition were 4.814 ± 0.604 vs. 3.860 ± 0.478. Whereas the older group had a significantly greater mean spread parameter than the young group in the concurrent condition [$t(33) = 2.05$, $p < 0.05$, 1-tailed], the somewhat larger spread parameter of the older adults did not reach statistical significance in the sequential condition [$t(33) = 1.24$, $p = 0.11$].

The findings obtained with the analysis of the spread parameters of individually fitted psychometric functions were confirmed by the analysis of the individual frequencies of discrimination errors. The mean number of errors (±SE) across participants was 12.9 ± 1.5 in the young group (n = 18) and 17.6 ± 2.0 in the older group (n = 17) in the concurrent condition [$t(33) = 1.85$, $p < 0.05$, 1-tailed], and 9.8 ± 1.1 and 13.6 ± 1.4, respectively, in the sequential condition [$t(33) = 2.14$, $p < 0.05$, 1-tailed]. Thus, in this analysis, the

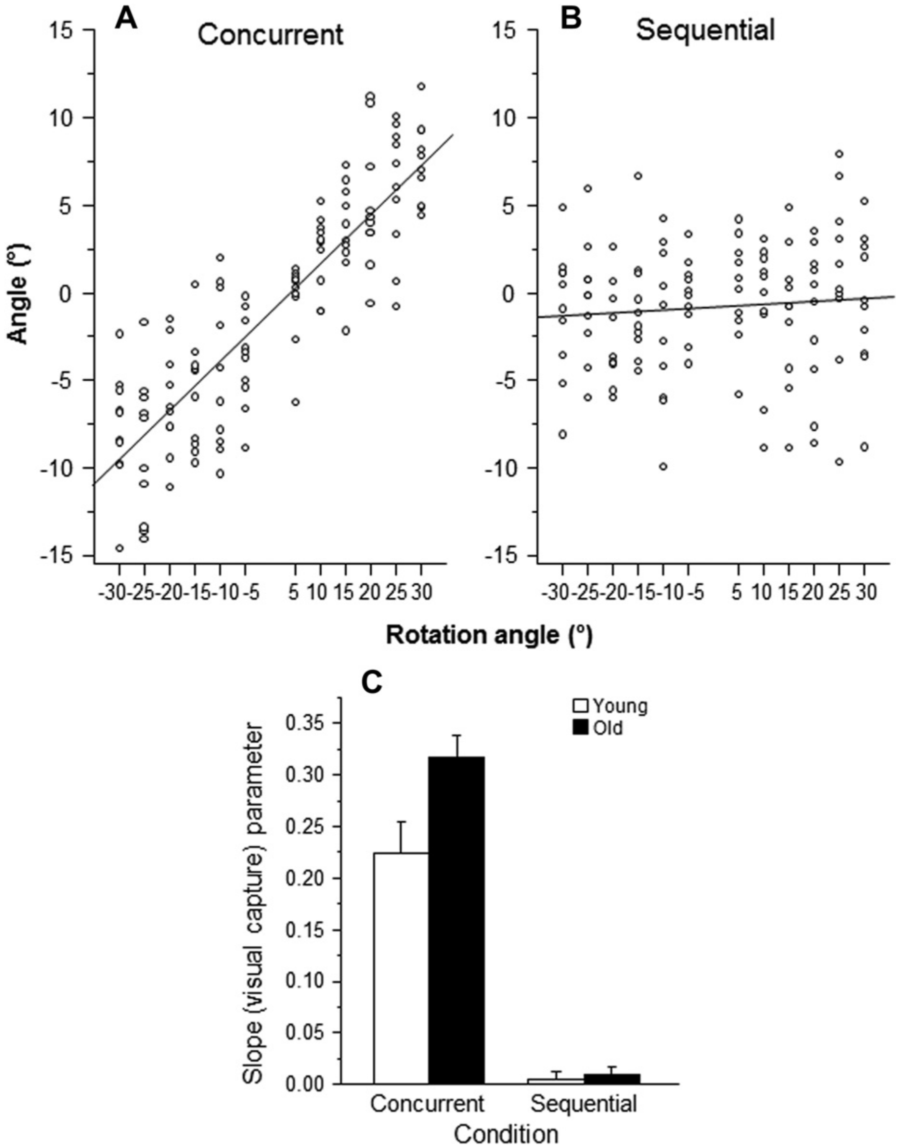


**Fig. 5.** Typical individual examples of the angle $\alpha'$ that characterizes the shift of registered hand position at the end of second stroke (Fig. 2) are shown for the concurrent (A) and sequence (B) conditions. The mean slopes (visual capture parameters) across all participants (excluding outliers) for both conditions are shown in (C). Open and filled columns refer to the young (n = 18) and older (n = 17) groups, respectively. Error bars represent the standard errors (SE).

difference between the 2 age groups reached statistical significance also in the sequential condition.

The points of subjective equality were assessed by way of the means ($k_1$) of the individually fitted psychometric functions. The group means (±SE) were −1.75 ± 1.07 in the young group (n = 18) and −2.15 ± 1.06 in the older group (n = 17) in the concurrent condition. In the sequential condition, the comparable group means were −1.62 ± 1.10 and −5.26 ± 0.74, respectively. One-sample *t*-tests revealed that the means of the young group did not significantly differ from zero ($p > 0.1$ in both conditions). However, the means of the older group almost significantly differed from zero in the concurrent condition [$t(16) = 2.03$, $p < 0.1$], and in the sequential condition the difference from zero was significant ($t(16) = 7.11$, $p < 0.001$). Between-group t-tests further showed that there was no difference between the 2 age groups in the mean parameters in the concurrent condition [$t(33) = 0.26$, $p > 0.1$], but in the sequential condition [$t(33) = 2.71$, $p < 0.05$]. Thus, the older adults, especially in the sequential condition, tended to judge the felt direction of the hand and of the cursor as identical when the direction of the cursor was slightly counterclockwise to the direction of the hand. The reason for this bias is unknown.

### 3.2. Indirect measure of the felt direction of the hand

If the felt direction of the hand at the end of the second stroke were attracted by the seen direction of the cursor under the concurrent presentation of rotated visual feedback (visual capture), it should be shifted away from the actual hand position. We estimated this shift from the end positions of the hand in the third stroke. Any deviation of the actual hand position from the felt position at the end of the second stroke should be propagated to the end of the third stroke, resulting in a systematic shift of the end point of the third stroke compared to the T1 location (Fig. 2). Based on the shifted end positions of the third stroke, the shift of the felt hand direction at the end of the second stroke was estimated by the angle $\alpha'$ (Fig. 2), which was measured for each trial (detailed in Methods).

A typical individual example of $\alpha'$ as a function of the feedback rotation in the concurrent condition is shown in Fig. 5A. The angle $\alpha'$ was negative at $-30°$, that is, CW feedback rotation, indicating that the felt hand direction was shifted clockwise. At the 30° CCW rotation, the angle $\alpha'$ was positive, indicating that the felt hand direction was shifted counter clockwise. A linear regression analysis revealed a significant increase of $\alpha'$ across visual feedback rotation angles ($r = 0.864$, slope $= 0.281$, $p < 0.001$, Fig. 5A). Thus, per degree of the rotation of the visual feedback (cursor motion), the felt direction of the hand was rotated by 0.28° in the same direction. In contrast, a typical example of the sequential condition from the same participant did not show any trend of the angle $\alpha'$ across visual feedback rotation angles ($r = 0.087$, slope $= 0.017$, $p > 0.1$; Fig. 5B). This result was expected because the visual feedback of the second stroke was displayed after the execution of the third stroke in this condition, thereby having no influence on the felt hand position. The result shows that the systematic changes of $\alpha'$ are indeed due to the rotation of the visual feedback.

The linear regression, illustrated in Fig. 5A and B for a single participant, was run for all participants. The mean slopes (visual-capture parameters) across all participants (excluding those with outliers) are shown in Fig. 5C. In the concurrent condition, both groups shifted their felt hand direction toward the rotated visual feedback. However, the mean capture parameter of the older group was greater than that of the young group [$t(33) = 2.4$, $p < 0.05$, 1-tailed], indicating that the felt hand directions of the older adults were more influenced by the visual feedback. In the sequential condition, the slopes were close to zero for both groups, and no group difference was observed [$t(33) = 0.5$, $p > 0.1$, 1-tailed], which was in line with our expectation.

## 4. Discussion

### *4.1. Age-related decline of inter-modal discrimination in tool-use actions*

Integration of multimodal sensory information has received considerable attention in recent years (Cheng et al., 2007; Ernst and Bülthoff, 2004). Typically the information refers to a certain characteristic of one and the same object, such as its size or curvature of a surface. This justifies integration. In the current study, however, tool-use actions justified discrimination rather than integration of bimodal spatial information as vision and proprioception referred to different objects, the cursor and the hand. Furthermore, the vertical plane of cursor motion and the horizontal plane of hand movement were clearly distinct, with no direct link between them. Both the spatial separation and the absence of a visible link reduce bimodal integration even with object identity (Gepshtein et al., 2005; Takahashi et al., 2009), and they should facilitate bimodal discrimination in tool use where it is a prerequisite of the conscious experience of the input–output relation of the tool.

We hypothesized that inter-modal discrimination declines at older adult age. This hypothesis is suggested by 2 sets of previous results. First, there is evidence of reduced sensitivity of both visual perception and proprioception at older age (Betts et al., 2007; Goble et al., 2009). With an age-related decline of intra-modal sensitivity, inter-modal discrimination capability should decline as well. Second, there is evidence of neural dedifferentiation in aging individuals, both from single-cell recordings in monkeys (e.g., Liang et al., 2010) and from neuroimaging in humans (e.g., Carp et al., 2011). In addition, computational models of neural dedifferentiation have been proposed (e.g., Li and Sikström, 2002). The poorer neural differentiation of cortical activity associated with different sources of stimulation could result in assimilation of the respective (spatial) information, which again should impede discrimination.

Our present findings confirmed that aging reduces individuals' capability to discriminate visually perceived cursor directions and proprioceptively perceived hand directions. That is, we found an age-related decline in the capability to discriminate the input and the output of a visuo-motor transformation. This finding is in line with a tentative result of our recent study (Wang et al., 2012) as well as with a rather incidental observation in a recent adaptation study in which rotated visual feedback was displayed in the plane of the hand movements rather than on a monitor placed in front of the workspace of the hand (Cressman et al., 2010). The age-related decline of inter-modal discrimination can account for the poorer adaptation of older adults to visuo-motor rotation, in particular with respect to explicit knowledge (Bock, 2005; Heuer and Hegele, 2008; Heuer et al., in press). The current study revealed that the threshold of conscious detection of the discrepancy between the seen direction of cursor motion and the felt direction of hand movement is higher for older adults than for young adults. Independent of the underlying cause, the higher threshold should result in poorer explicit knowledge of visuo-motor rotations.

### *4.2. Two factors in the age-related decline of inter-modal discrimination*

A change in inter-modal discrimination capability can result from changes of both intra-modal sensitivity and inter-modal assimilation of sensory representations. As discussed above, the neural dedifferentiation should result in inter-modal assimilation, which is manifested as visual capture (Hay et al., 1965) with our particular task. We assessed the age-related change in visual capture by using a novel procedure that was based on the observation of error propagation in aiming movements (Bock and Eckmiller, 1986; Heuer and Sangals, 1998; Heuer and Sülzenbrück, 2012).

In movements to a target without vision of the hand, the felt position of the hand at the end of the movement corresponds to the target location, and the actual position of the hand deviates from the felt position. This deviation is measured as the error, and it is propagated to the error of a subsequent movement. In applying error propagation to the estimation of visual capture, we presuppose that the deviation of the actual hand position at the end of the second stroke from the felt hand position is propagated to the third stroke. Whereas random errors of the second and third stroke are cancelled by averaging, systematical errors due to the rotated visual feedback should remain. Our result of the absence of such constant errors in the sequential condition confirmed that the constant errors found in the concurrent condition were not errors of the third stroke but, rather, propagated deviations of actual and felt hand positions at the end of the second stroke related to the rotated visual feedback.

The visual capture of the perceived hand movement in the concurrent condition amounted to about 25% to 30% of the angular discrepancy between the directions of the hand movements and the cursor motions. This appears as a rather strong visual capture, given that the bimodal direction information referred to different objects (the cursor and the hand), which moved in different planes (and different fames of reference). Furthermore, visual capture turned out to be significantly stronger for the older adults than for the young adults, which indicates that stronger visual capture is indeed one of the factors that underlie the age-related decline of inter-modal discrimination.

Even though we did not assess intra-modal changes of sensitivity directly, the analysis of the spread parameters and visual-capture parameters in the concurrent condition provides some evidence of a second factor for the declined discrimination. The spread parameter $k_2$ of the psychometric function formally represents a compression ($k_2 < 1$) or expansion ($k_2 > 1$) of the abscissa. The capture parameter $b$ can be transformed into a parameter s = 1/(1-b) that also characterizes compression or expansion of the abscissa of the psychometric function. Thus, the spread parameter can be expressed as $k_2 = cs$, with $c$ as the basic spread of the psychometric function for $s = 1$ (or $b = 0$), that is, without a compression due to visual capture, and s as the effect of visual capture. For each participant we estimated $c = k_2/s$, that is, the basic spread of the psychometric function without visual capture. The means (±SE) were 4.49 (±0.490) in the young and 5.29 (±0.518) in the older participants. Thus, the older adults had a larger basic spread parameter than the young adults. Even though the difference between the 2 age groups was no longer statistically significant after eliminating the effect of visual capture on discrimination performance, it provides at least tentative evidence of a second factor (i.e., the reduced intra-modal sensitivity) in the age-related decline of inter-modal discrimination.

This conjecture is supported by the observed age-related decline of discrimination in the sequential condition. We used this condition as a control and did not assess the shift of the felt hand position. Nevertheless, it is likely that it was smaller than in the concurrent condition or even absent, because visual capture is known to decrease rapidly when a temporal offset is introduced between visual and proprioceptive inputs (Botvinick and Cohen, 1998; Graziano et al., 2000). If so, the age-related decline of discrimination mainly stemmed from larger basic spread parameters, again suggesting the age-related decline of intra-modal sensitivity. The declined intra-modal sensitivity could be in part a consequence of the age-related decline of signal-to-noise ratios, a widely accepted consequence of aging (Li et al., 2001, 2004; Welford, 1981). If signal-to-noise ratios decline, noisier perceived directions (or other spatial dimensions) have to be compared for discrimination, which leads to more discrimination errors.

The present results of stronger visual capture in the older adults compared with the young adults under the concurrent condition may be related to the age-related differences in sensory weighing and reweighing between vision and proprioception. There is evidence suggesting that older adults have higher sensory weighing toward vision compared with young adults. For example, older adults make more directional errors of saccades to the visually presented stimulus in anti-saccade tasks (Bojko et al., 2004; Nieuwenhuis et al., 2000). Older adults also increase force variability with a greater extent than young adults when the display gain of visual feedback of constant force production is increased on the monitor (Kennedy and Christou, 2011; Sosnoff and Newell, 2006), and in upright standing they rely more on vision (Simoneau et al., 1999). Thus, older adults seem to have higher coherence between what they do and what they see.

From a related perspective, according to the current understanding of multimodal integration, the weighing of different modalities depends critically on their predicted variabilities (Bays and Wolpert, 2007; Van Beers et al., 2002). Older adults are known to have a higher variability in aiming movements (Ketcham et al., 2002) and force productions especially under concurrent complex visual feedback (Kennedy and Christou, 2011; Ofori et al., 2010). If this is taken as an indicator of a particularly strong age-related increase in variability of the proprioceptive modality, older adults should have greater weighing on vision compared to proprioception when concurrent bimodal information is present. Such an effect may partly account for the current visual capture results in the older adults.

### *4.3. Discrimination of concurrent and sequential bimodal information*

We avoided direct comparisons between the concurrent and sequential conditions because we cannot exclude confounding effects of inevitable differences between these conditions in addition to the timing of visual feedback. Nevertheless, it seems noteworthy that both age groups showed poorer discrimination with concurrent visual feedback than in the sequential condition, in which visual feedback was provided after the movement of the hand. This finding is quite astonishing, because simultaneously presented stimuli had to be discriminated in the concurrent condition, whereas in the sequential condition the remembered direction of hand movement had to be discriminated from the visible direction of cursor motion. It is known that memory of proprioceptively sensed hand positions decays within seconds (Adams and Dijkstra, 1966; Paillard and Brouchon, 1968). Thus, one would expect that discrimination of a fading memory trace and a stimulus in the sequential condition is worse than discrimination of 2 stimuli in the concurrent condition.

The fact that discrimination in the concurrent condition was actually poorer than in the sequential condition suggests the presence of factors that specifically degrade discrimination of concurrent visual and proprioceptive direction information. One such factor, of course, is visual capture that might be stronger in the concurrent than in the sequential condition. Another factor is likely a functional neglect of proprioceptive information. In the monitoring of tool-use actions, only the visual information refers to the effective part of the tool, and attention tends to be focused on it (Collins et al., 2008; Reed et al., 2010). Conversely, conscious awareness of the position of the hand, based on proprioceptive information, becomes severely limited under these circumstances (Knoblich and Kircher, 2004; Müsseler and Sutter, 2009). This functional neglect is likely to facilitate performance, as is suggested by the observation of superior mirror drawing in a deafferented patient (Lajoie et al., 1992) or after repetitive transcranial magnetic stimulation (rTMS) over the contralateral somatosensory cortex (Balslev et al., 2004).

In summary, the present results support 2 firm conclusions and 1 tentative conclusion: (1) older adults are poor in discrimination of concurrent bimodal information under a visuo-motor rotation as compared to young adults; (2) an enhanced visual capture contributes to the poor discrimination; and (3) most likely there is an additional contributing factor, namely, a reduced sensitivity of visual perception and proprioception.

## Disclosure statement

The authors declare no conflicts of interest.

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