

## RESEARCH ARTICLE | *Control of Movement*

# Why is the explicit component of motor adaptation limited in elderly adults?

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**Vandevoorde K, Orban de Xivry JJ.** Why is the explicit component of motor adaptation limited in elderly adults? *J Neurophysiol* 124: 152–167, 2020. First published May 27, 2020; doi:10.1152/jn.00659.2019.—The cognitive component of motor adaptation declines with aging. Yet, in other motor tasks, older adults appear to rely on cognition to improve their motor performance. It is unknown why older adults are not able to do so in motor adaptation. To solve this apparent contradiction, we tested the possibility that older adults require more cognitive resources in unperturbed reaching compared with younger adults, which leaves fewer resources available for the cognitive aspect of motor adaptation. Two cognitive-motor dual-task experiments were designed to test this. The cognitive load of unperturbed reaching was assessed via dual-task costs during the baseline period of visuomotor rotation experiments, which provided us with an estimation of the amount of cognitive resources used during unperturbed reaching. However, we did not observe a link between dual-task costs and explicit adaptation in both experiments and, therefore, failed to confirm this hypothesis. Instead, we observed that explicit adaptation was mainly associated with visuospatial working memory capacity. This suggests that visuospatial working memory of an individual might be linked to the extent of explicit adaptation for young and older adults.

**NEW & NOTEWORTHY** Our work addresses the contradiction between the age-related increase in the contribution of cognition for the execution of motor tasks and the age-related decrease in the cognitive component of motor adaptation. We predicted that elderly adults would need more cognitive resources for reaches and would, therefore, not have enough cognitive resources available for adaptation. Rather, we observed that visuospatial abilities could better explain the amount of cognition used by our participants for motor adaptation.

## INTRODUCTION

Age-related movement deficits are observed during simple point-to-point reaching movements, in which spatial and temporal movement variability increased with aging, and movements slow down (Darling et al. 1989; Ketcham et al. 2002; Van Halewyck et al. 2015; Yan et al. 1998). Apart from these age-related changes in movement parameters, controlling movement might impose increased cognitive demand on older adults compared with younger adults. Increased cognitive demand is associated with increased neural recruitment with aging during motor tasks (Heuninckx et al. 2005, 2008). This age-related overactivation is compensatory and linked to better task performance (Reuter-Lorenz and Cappell 2008). In motor

tasks, older adults are thought to rely more on cognition to improve their motor performance [motor coordination: Heuninckx et al. (2008); balance: Boisgontier et al. (2013)].

Motor learning in general and motor adaptation in particular are also affected by aging. Motor adaptation is the adjustment of movement to perturbations (Shadmehr et al. 2010). It can be divided into an explicit and an implicit component (Benson et al. 2011; Mazzoni and Krakauer 2006; McDougale et al. 2015; Taylor et al. 2014). The explicit component is under cognitive control, while the implicit component is the part of adaptation that cannot be controlled consciously by the participant. The explicit component has been quantified by asking participants to report their aiming (Taylor et al. 2014) or by asking them to switch their explicit strategy on or off in response to color cues (Morehead et al. 2015; Werner et al. 2015). Explicit strategies are useful to speed up the learning process, since the explicit learning rate is higher than the implicit learning rate (McDougale et al. 2015). A higher capacity of working memory is linked to a larger explicit component of motor adaptation, while differences in working memory capacity are not linked to the implicit component (Christou et al. 2016).

Motor adaptation declines with aging, and this decline can be attributed to the decline of the explicit component of motor adaptation (Heuer and Hegele 2008; Vandevoorde and Orban de Xivry 2019). But why are elderly people relying more on cognition in motor tasks (Boisgontier et al. 2013; Heuninckx et al. 2008), but are they unable to do so in motor adaptation (Heuer and Hegele 2008; Vandevoorde and Orban de Xivry 2019)? One possible explanation is that the increased reliance on cognition for simple reaching movements in elderly people would leave fewer cognitive resources available for concurrent tasks (here, motor adaptation) as cognitive resources are limited (Heuninckx et al. 2005, 2008; Li and Lindenberger 2002; Seidler et al. 2010). To investigate this, we propose the “cognitive resources hypothesis” (Fig. 1), which suggests that older adults already require most of their available cognitive resources for simple reaching movements. The increased cognitive demand in “simple” reaching movements might, in turn, result in an age-related decline of explicit adaptation because of a lack of remaining cognitive resources. This hypothesis is in line with the compensation-related utilization of neural circuits hypothesis (CRUNCH) that describes over-recruitment and under-recruitment of neural resources depending on the cognitive load in elderly. During a task with low levels of cognitive load, older adults tend to recruit more cognitive resources compared with younger adults to maintain task

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## Cognitive resources hypothesis

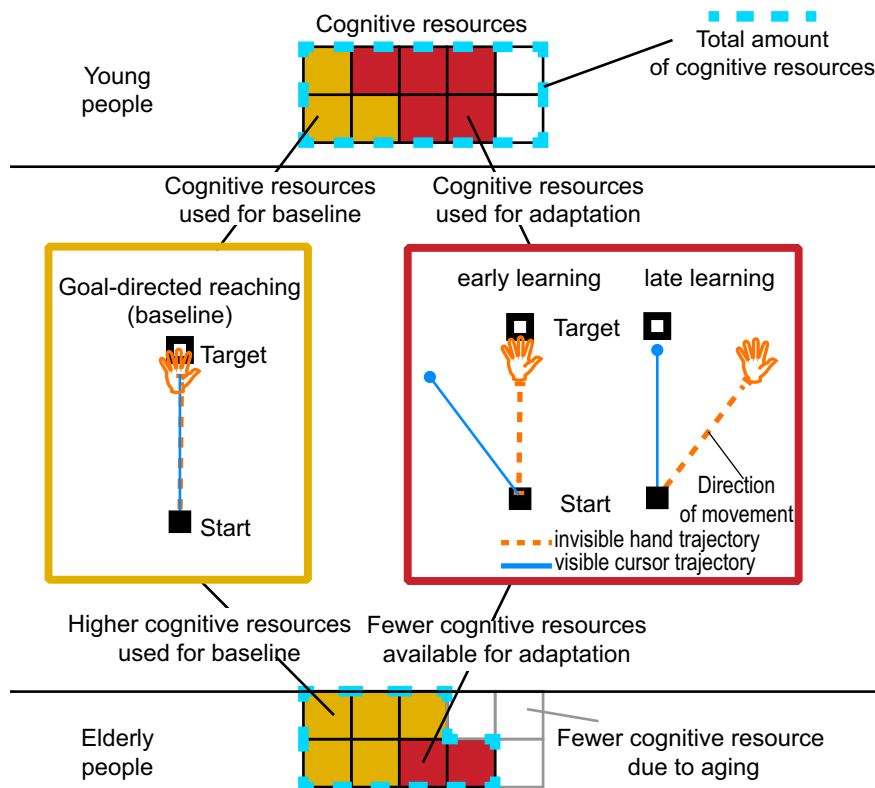


Fig. 1. Cognitive resources hypothesis. Elderly adults require more cognitive resources to perform goal-directed reaching compared with younger adults (orange blocks). The total amount of resources is reduced with aging (blue dashed area). As a result, fewer resources are available for explicit adaptation in the elderly. The elderly have a saturation of their resources when adjusting their movement (two red blocks). Young adults, instead, do not reach their total amount of available resources (five red blocks, still two additional blocks remain available).

performance (Reuter-Lorenz and Cappell 2008). Instead, during tasks with higher levels of loads, older adults cannot compensate their performance anymore, and they recruit similar cognitive resources or fewer cognitive resources than younger adults (Grady 2012).

The amount of cognitive resources applied during a motor task can be assessed with cognitive-motor dual-task experiments (Boisgontier et al. 2013). In dual-task experiments, a cognitive task is performed during a motor task, which reduces motor and/or cognitive performance. The reduction of performance can be quantified as a dual-task cost (Boisgontier et al. 2013; Li and Lindenberger 2002). Dual-task costs show that cognition is involved in natural motor tasks, such as standing (Boisgontier et al. 2013). A link between cognitive resources in baseline movement and explicit adaptation would show that the deficit of explicit adaptation with aging could be defined as a resource competition problem (Fig. 1): Resources that are necessary for the adaptation process are already used for allowing simple reaching movement.

To investigate this hypothesis, we designed two cognitive-motor, dual-task experiments that allowed us to quantify the amount of cognitive resources used during simple reaching movements with a dual task in the baseline of a motor adaptation experiment. A response inhibition task was selected as a cognitive task during the first dual-task experiment (Fig. 2A), and a working memory task was selected as a cognitive task during the second dual-task experiment (Fig. 2B). Both cognitive tasks would interfere with resources that are required for motor adaptation, such as selective attention and working memory.

## MATERIAL AND METHODS

### Participants

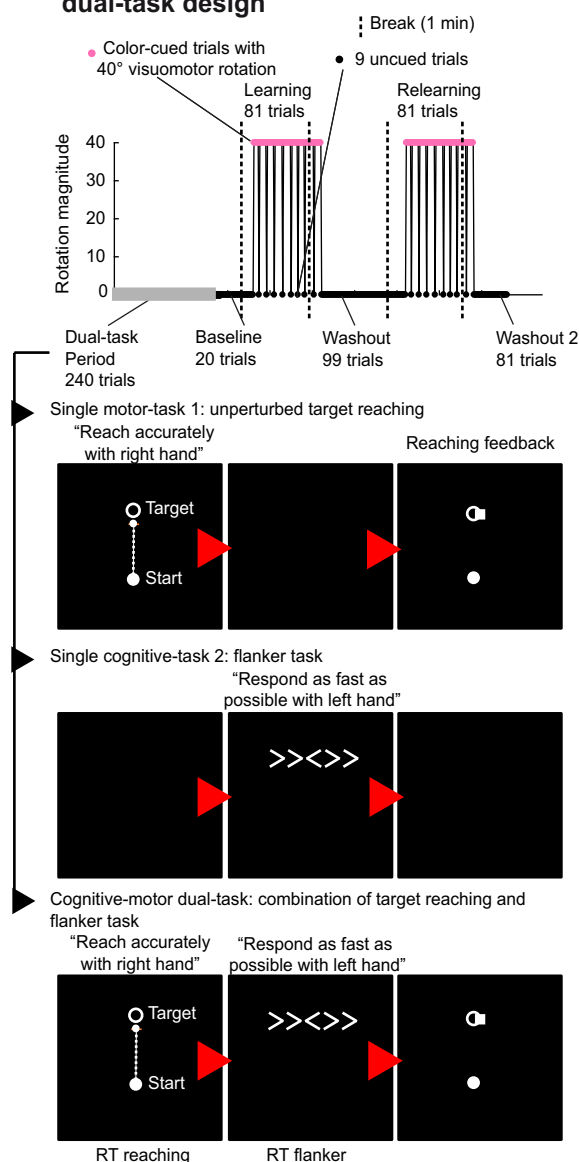
A total of 143 healthy adults were recruited and participated after providing written informed consent. Eighty-one participated in *experiment E1*, and 62 participated in *experiment E2*.

All 81 participants were included in the final analyses for *experiment E1*. These 81 participants consisted of 41 young adults (between 20 and 35 yr old, age:  $23.1 \pm 3.5$  yr; means  $\pm$  SD; 25 females) and 40 older adults (between 60 and 75 yr old, age:  $67.5 \pm 4.5$  yr; 23 females). Sixty-two of the 81 participants were already included in our previous article (Vandevorode and Orban de Xivry 2019). In the 2019 article, we report the adaptation capabilities of these participants in the cued visuomotor rotation task (labeled E1 in the current article). Here, we analyzed an aspect of the data that was not reported in our previous manuscript (Vandevorode and Orban de Xivry 2019), and we included more participants (11 young and 10 older participants).

For *experiment E2*, we recruited a new group of 62 participants. These 62 additional participants consisted of 30 young adults (between 20 and 32 yr old, age:  $22.9 \pm 2.7$  yr, mean  $\pm$  SD; 15 females) and 32 older adults (between 61 and 75 yr old, age:  $67.6 \pm 4.5$  yr; 13 females).

The Edinburgh handedness questionnaire (Oldfield 1971) was used to confirm that all participants were right-handed. All participants were screened with a general health and consumption habits questionnaire. None of them reported a history of neurological disease or were taking psychoactive medication. In older adults general cognitive functions were assessed using the Mini-Mental State Examination (MMSE) (Folstein et al. 1975). All elderly scored within normal limits (MMSE-score  $\geq 26$ ). The protocol was approved by the local ethical committee of KU Leuven, Belgium (project number: S58084). Participants were financially compensated for participation (10 €/h).

### A Experiment 1 (E1): Flanker dual-task design



### B Experiment 2 (E2): Working memory dual-task design

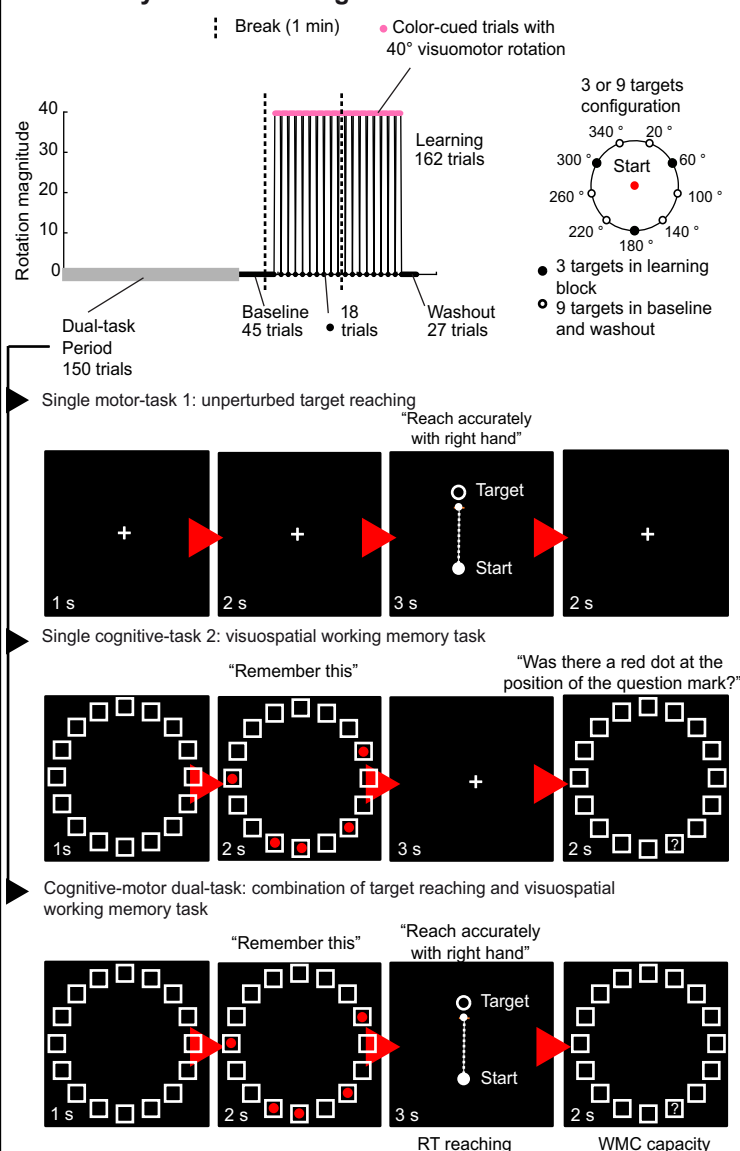


Fig. 2. Cognitive-motor dual-task paradigms. Explicit adaptation level was assessed with cued motor adaptation. A change in cursor color indicated the presence or absence of a 40° visuomotor rotation. In the baseline of the cued motor adaptation experiment, a dual-task period was introduced to quantify the amount of cognitive resources applied during unperturbed reaching. Each dual task was a combination of a single motor task (first row), a single cognitive task (second row), and a dual-task (third row). Two designs of the dual task were used: A: flanker dual-task design (*experiment 1*, E1). The single motor task was a reaching task. During the single cognitive task, the flanker task, participants had to indicate the direction of the middle arrow among several arrows as fast as possible. The dual-task consisted of a combination of an unperturbed reaching task and a flanker task. B: working memory dual-task design (*experiment 2*, E2). The single motor task was a reaching task. In the single cognitive task, the visuospatial working memory task, participants had to remember positions of red dots, which were presented in a circular array. Afterward, they had to indicate whether a probed position contained a red dot. The dual-task consisted of a combination of unperturbed reaching and a visual working memory task. (1 s = 1 second).

#### Experimental Setup

Participants were seated in front of a table. With their right hand, participants performed a reaching task on a digitizing tablet (Intuos pro 4; Wacom) with a digitizing pen. A wooden cover above the tablet prevented participants from receiving visual feedback of their moving arm. Movement trajectories were recorded at 144 Hz. The only visual feedback was displayed on a 27-inch, 2,560 × 1,440 optimal pixel resolution LCD monitor with 144-Hz refresh rate (S2716DG, Dell), vertically mounted in front of the participant.

#### Assessment of Dual-Task Cost

**Overall dual-task design.** In the first experiment (E1; Fig. 2A), the first part (260 trials) was used to assess the dual-task cost during baseline of the cued motor adaptation task. Participants first performed 20 reaches to a target for familiarization purpose (not represented in Fig. 2A). Then, each participant performed 30 familiarization trials for the dual-task period to make sure that they understood the instructions and that they performed the cognitive task (10 flanker trials, executed with the left hand), the reaching task (10 reaching trials, executed with the right hand), and the dual task (10 dual motor-cognitive

trials) correctly. This was followed by 240 trials divided in blocks of 60 trials (20 single reaching trials + 20 single flanker trials + 20 dual motor-cognitive trials, Fig. 2A). A break of 60 s was applied before trial 141 of the dual task.

Similarly, the first part (150 trials) of the second experiment (E2; Fig. 2B) was used to assess the dual-task cost during baseline of the cued motor adaptation task. However, in E2, the flanker task was replaced by a working memory task. In E1, we grouped our individual tasks (single motor, single cognitive, and dual motor-cognitive) in three groups of 20 trials, while in E2 we did not group individual tasks. The dual-task period of E2 consisted of a single reaching motor task, a single working memory task, and the two tasks combined. The dual-task period of E2 consisted of 150 trials, which was divided in 50 blocks of three trials (one reaching trial, one working memory trial, and one dual motor-cognitive trial). At the start of the experiment, participants could familiarize themselves with the three tasks ( $5 \times 3$  trials). This was important to get familiarized with every aspect: e.g., timing of task, answering for working memory capacity, and reaching speed. Breaks of 30 s were introduced before trials 51 and 102 of the dual-task experiment.

**Reaching task (single motor task).** In the reaching task (Fig. 2, first row), participants were instructed to slide through a target with a white cursor representing the invisible hand position with fast and straight arm movements. The participants held a digitizing pen in their right hand as if they were writing. They were instructed to always touch the surface of the tablet with the tip of this pen and to move their right arm, and not only their wrist. During the dual-task period, the target was presented at 9 possible locations in E1 and 10 locations in E2. The locations of the target were evenly distributed on a circle 10 cm away from the starting position.

The reaching target was always a single white circular target. The diameters of the starting point and the target were both 10 mm, and the feedback cursor had a diameter of 5 mm. The feedback cursor, which represented hand position was visible until movement amplitude exceeded 10 cm. At this point, a white square marked the position where movement amplitude reached 10 cm, providing visual feedback about the end point accuracy of the reach. The white square had sides of 5 mm and remained visible for 1.5 s. The zone for receiving 25 points was an additional 6 mm at both sides of the target. In the flanker dual task (E1), while returning to the central starting position, the cursor disappeared, and only a white arc (i.e., half circle) was visible. The radius of the return arc depended on the position of the pen on the tablet, i.e., the radius of the arc was equal to the radial distance between the position of the hand and the starting point. The center of the return arc was the central starting position. The reach area was divided in three different zones of  $120^\circ$ . The arc was in the same  $120^\circ$  zone as where the participant's (invisible) hand was. Participants had to move their hand in the opposite direction of the arc to return to the starting location. The arc allowed participants to return to the starting position and at the same time prevented the participants from using the visual feedback during the return movement to learn about the perturbation. In the working memory dual task (E2), no return arc, but normal cursor feedback was used. To receive points, participants were required to reach the target between 175 and 375 ms after movement onset. On the one hand, we wanted participants to move fast enough to prevent within-trial correction for error. On the other hand, we did not want the two age groups to move with different reaching speeds. Since older participants tend to move slower than younger participants (Yan et al. 1998), it was recommended to have an upper and lower limit for movement time. If the reaching movement was too slow, a low-pitched sound was played, and the target color switched from white to purple. If the reaching was too fast, a high-pitched sound was played, and the target color switched from white to red.

The only differences between the reaching tasks for *experiment E1* and *E2* were the number of targets, the score system, and the timing of the trials. In the reaching task of E2, 10 targets were used instead of 9 in E1. In E2, 50 single reaching trials were used, such that each

target could be repeated five times. When hitting the target with the correct speed (i.e., between 125 and 375 ms), participants received 50 points. In E1, they could receive bonus points: When hitting targets for several trials in a row, participants received 10 extra bonus points for each extra target hit. In E2, they could not obtain bonus points. When reaching in close proximity of the target, they received 25 points and no bonus points. The cumulative score of all previous trials was displayed throughout the experiment. In *experiment E1*, the feedback cursor froze for 1.5 s at the end of the reach to provide information about reaching accuracy. The participant had then to move the tip of the pen back to center of the tablet and wait there between 350 ms and 850 ms (in steps of 50 ms) to initiate the next trial. If participants were slower than 5 s, the next trial would automatically initiate. Therefore, in E1, trial duration varied from trial-to-trial and between the participants because it depended on how fast participants moved to the target and back to the start position (Fig. 2A, first row). In contrast, in E2, the timing of each reaching trial was strictly controlled, such that each trial took exactly 8 s, the same length as a cognitive-motor, dual-task trial. To obtain a reaching trial of 8 s, a fixation cross was first displayed for 3 s (Fig. 2B, first row). Then the participants reached before having to wait for an extra 2 s. Depending on how fast participants reached, additional waiting time was added to obtain a fixed time duration of 8 s per trial. If they exceeded the 8 s per trial, the next trial would be initiated automatically.

**Cognitive task (single cognitive task).** In *experiment E1*, the cognitive task was a flanker task, adapted from Eriksen and Eriksen (1974). In this task, an uneven number of left or right pointing arrows were presented to the participant (Fig. 2A, second row). Participants needed to answer with a left or right key press whether the middle arrow was pointing to the left or right direction. The arrows surrounding the middle arrow could either have congruent directions ( $>>>>>$ ) or incongruent directions ( $>><<>>$ ) with respect to the middle arrow. Reaction times are reported to be lower with incongruent flanker arrows (Kopp et al. 1994). This task was executed with the left hand. The goal for the participant was to indicate the direction of the middle arrow as fast as possible. The next trial was initiated immediately after pressing the left or right key. All blocks consisted of 20 flanker trials with the middle arrow randomly presented to the left or the right side. In addition, each of these blocks contained 10 congruent and 10 incongruent trials. We repeated the same order (number of arrows and congruency) of 20 flanker trials for the single-task block and the subsequent dual-task block. The flanker task was modulated from the beginning toward the end of the dual-task period by gradually increasing the number of flanker arrows from block to block from two (first repetition) to eight [last repetition (fourth one)].

In *experiment E2*, the cognitive task was a working memory task (McNab and Klingberg 2008; Christou et al. 2016). Sixteen (empty) white squares ( $1.9 \text{ cm} \times 1.9 \text{ cm}$ ) were presented in a circular array (11.2 cm diameter) for 1 s (Fig. 2B, second row) on a monitor. Two, three, four, five, or six red circles (0.8-cm diameter) were visualized for 2 s in the 16 white squares with each red circle presented randomly in one of the 16 squares. Participants were instructed to remember the positions of the red circles. After these 2 s, the circles and the squares disappeared, and the participants fixated on a white cross ( $0.6 \text{ cm} \times 0.6 \text{ cm}$ ) for 3 s. Afterward, they were asked whether a cued location corresponded to one of the squares that contained a red circle before. They had two seconds to give their answer by moving the cursor to a target on the right side (to answer yes) or on the left side (to answer no). The cursor was controlled by moving the pencil on the tablet. Each trial lasted precisely for 8 s. The five conditions (two, three, four, five, or six red circles, 10 trials per condition) were randomly presented. For each condition, five trials were "no answers" and five trials were "yes answers".

**Cognitive-motor, dual-task design.** In *experiment E1*, a dual-task trial was a combination of the above-described reaching (motor) and



flanker (cognitive) task in one trial. The trial started as a reaching trial. However, at the end of the reach, arrows were presented at the position of the target, instead of the feedback on the reaching accuracy (Fig. 2A, third row). This feedback was presented after the participants had indicated the direction of the middle arrow. After the feedback, participants returned to the start position at a self-selected pace. Participants were instructed to first reach to the target as accurately as possible by moving the right hand, and immediately afterward, perform the correct left/right key press as fast as possible with the left hand. The dual task was expected to have a negative effect on both motor and cognitive performance compared with single-task performance: a decreased accuracy or increased reaction time for the reaching task, and a decreased accuracy or an increased reaction time for the flanker task. The reward-feedback (score system) was the same as in the single-task conditions. Since reward was implemented for the reaching trials but not for the flanker task, task priority might be expected in favor of the reaching task. The instructions did not specify task priority, but we asked participants to do their best for both tasks.

In *experiment E2*, a dual-task trial was a combination of the above-described reaching (motor) and working memory (cognitive) task in one trial (Fig. 2B, third row). A dual-task trial started with the presentation of 16 white squares for 1 s. Next, the red dots (between 2 and 6) were displayed for two seconds. Immediately after this, participants performed a reaching movement, after which, extra time was added to obtain 3 s in total for the reaching part. Finally, they gave their answer to the working memory task by moving the cursor to the “yes” or “no” location. They had two seconds to execute this last part. Again, every trial had a strictly controlled time duration of 8 s. We matched trial duration for the single- and dual-task condition to avoid that a difference in trial duration would cause a difference in performance between single- and dual-task trials. Participants performed 50 dual-task trials in total, such that every condition (2–6 red dots) of the working memory capacity trial could be repeated 10 times, and each of the 10 targets could be reached five times. All conditions were pseudo-randomly mixed. The scoring system was the same as in the single-task conditions. In other words, the points obtained for one successful working memory trial was twice that for the points for one successful reaching trial. However, bonus points could also be obtained in the reaching trials. The instructions did not specify task priority. Participants were instructed to obtain as many points as possible by doing their best for both tasks.

*Assessment of explicit and implicit component of adaptation with cued adaptation experiment.* In both *experiments E1* and *E2*, we used a cued motor adaptation to assess implicit and explicit components of motor adaptation. The methods of this cued motor adaptation experiment were already described in Vandewoerde and Orban de Xivry (2019) as *experiment E1b*. It is a visuomotor rotation experiment, adapted from *experiment 4* of Morehead et al. (2015), with a perturbation magnitude of 40°. The direction of the perturbation (clockwise or counter-clockwise) was counter-balanced across participants.

In *experiment E1*, explicit adaptation level was assessed with cued motor adaptation. A change in cursor color indicated the presence or absence of a 40° visuomotor rotation. The cued motor adaptation paradigm consisted of a baseline block of 20 trials, a learning block of 81 trials (nine cycles), a first washout of 99 trials (11 cycles), a relearning block of 81 trials (nine cycles) and a second washout of 81 trials (nine cycles) (Fig. 2A). In *experiment E2*, participants performed 45 unperturbed reaching trials (baseline, five cycles). A learning block of 162 trials (18 cycles) and a short washout of 27 trials (three cycles) followed the baseline (Fig. 2B).

During baseline and washout blocks of the cued adaptation task of *experiment E1*, we used the same nine targets as in the reaching task (from 20° to 340°, spaced 40° apart). A single start point location (solid red circle in Fig. 2B) was used. Targets were presented pseudo-randomly in cycles during baseline and washout with each of the nine targets presented once per cycle. During learning blocks, only three

targets were used, spaced 120° (60°, 180°, and 300°) (solid black targets in Fig. 2B). Therefore, in the learning blocks, nine-trial cycles consisted of three subcycles of three trials each. In each subcycle, each of the three targets was presented once. Both learning blocks consisted of nine cycles (or 27 subcycles or 81 trials). The cursor dot remained white during the baseline and washout blocks. In contrast, during the two adaptation blocks, the cursor was a pink square (i.e., cued trial) instead of a white cursor dot. This cue indicated the presence of a 40° rotation. In each adaptation block, the cursor became white again (i.e., uncued trials) for a few trials, indicating the absence of the perturbation. The instructions were as follows: “First, the cursor will be a white dot, but at some point, the cursor will change to a pink square. At that moment, something special will happen but you still have to try to do the same thing, reach to the target with the cursor. The cursor will sometimes change back to a white dot. These trials with a white dot are normal reaching trials like in baseline.” The change in behavior induced by the cue was, thus, a measure of the explicit component of adaptation, as participants could use the cue to switch off any conscious strategies they were applying to counteract the perturbation (Morehead et al. 2015). We reinforced the awareness of cue switches (signaling a cued trial among uncued ones or an uncued trial among cued ones) with a warning sound played for each cue switch and with a text that indicated the cue switch, displayed for 5 s: “Attention! The color of the cursor has changed.” Nine uncued trials were presented per adaptation block (trials 7, 16, 25, 35, 45, 53, 61, 72, and 81). These uncued trials were equally distributed among the three targets (three uncued trials per target). In *E1*, breaks of 60 s were introduced in the cued adaptation experiment before trial 15, 95, 175, and 275. These breaks occurred in 5 trials before the onset of the first perturbation block, in 6 trials before onset of the first washout block, in 25 trials before the onset of the second perturbation, and in 6 trials before the onset of the second washout.

The cued motor adaptation task that was used in *experiment 2* was similar to that of *E1*. The main differences were the number of learning blocks and the timing of the trials. In *E2*, we used only one learning block (162 trials) instead of two (2 times 81 trials for *E1*).

Each trial of the cued adaptation task in *E2* took exactly 4.5 s. First, participants performed a target reach. Immediately after the reaching, extra time was added to obtain exactly 4.5 s per trial. After 4.5 s, the next trial started automatically. If participants exceeded 3 s before coming back to the central target, a warning sign was shown and a high-pitched tone was played to instruct participants to speed up. The instructed reaching time was between 175 and 375 ms. Feedback about the reaching duration was indicated by the color of the target at the end of the reach. If reaching time was above 375 ms, the target became purple. If reaching time was below 175 ms, the target became red. It stayed white otherwise. Two breaks of 1 min were given to participants, one before the 4th cycle (trial 36) of the baseline and one before the 9th cycle (trial 81) of the learning block.

### Preregistration

*Experiment E1* was preregistered online: <https://aspredicted.org/sv5d6.pdf>. This preregistration included the main hypotheses, the key dependent variables, the number of participants, the main analyses, and some of the secondary analyses investigated. In the preregistration, we mentioned that we would include 30 participants per group. However, in the end, we included 21 additional subjects (11 young, 10 older adults) for this preregistered study (*E1*) in the context of a master student project, but these additional participants did not change the outcome of our study. The main preregistered analysis tested for a significant negative correlation between explicit adaptation and dual-task cost.

### Cognitive Assessment

**Visuospatial working memory capacity.** Participants from *experiment E1* also performed a working memory task. The task is the same as described by Christou et al. (2016), but it is slightly different from the working memory dual-task experiment (E2), described above. The main differences with the working memory task of E2 were 1) only three, four, five, or six red circles (0.8-cm diameter) were used (the two target conditions were not used); 2) the timing of the events was the same in both tasks, except that participants had 3 s to indicate the right answer instead of 2 s; 3) indicating the right answer was performed by making a button press, instead of moving the cursor to a “yes answer” location or a “no answer” location; 4) after the 3 s for responding, they had to fixate on a small blue cross (0.2 cm × 0.2 cm) for 1 s; 5) in total, one trial had a fixed time duration of 9 s, instead of 8 s. All participants had a first practice session of eight trials. After this, each participant had to complete 40 trials instead of 50 trials, as in *experiment E2*. The 40 trials contained three, four, five, or six red circles (10 trials/condition) with all conditions randomly mixed.

### Data Availability

All data, analysis scripts, and supplemental materials are available on Open Science Framework: [https://osf.io/ks2j8/?view\\_only=c135f485872649c1a30e85a1e4fd8518](https://osf.io/ks2j8/?view_only=c135f485872649c1a30e85a1e4fd8518).

### Data Analysis

Analyses of E1 were preregistered, while analyses of E2 were performed without preregistration.

### Preprocessing

All analyses and statistical calculations were performed in MATLAB 2018b (The MathWorks). For each reaching movement, the hand angle (relative to target angle) was calculated from the first data point exceeding 4-cm distance from the middle of the starting point. The time for reaching 4 cm was on average 172 ms in E1 and 144 ms in E2. The hand angle was the primary dependent variable in cued adaptation experiments. The angular error is the angle the cursor deviated from the target. Angular errors above 60° were due to inattentive reaches to previous target directions and were considered as outliers. These outliers were removed before processing the data. The number of outliers that we removed, constituted 0.81% of all trials for E2. For E1, this procedure was not implemented, but this would not change the outcome of the study. The statistically significant threshold was set at  $P < 0.05$  for the ANOVAs. We reported effect sizes (eta squared:  $\eta^2$ ), as well as  $F$  and  $P$  values.

### Analysis 1: Final Adaptation Level for E1 and E2

We applied the same analysis as described by Vandevorode and Orban de Xivry (2019) for E1 and E2. To assess the final adaptation level of each participant, we averaged the hand angles of the last 18 trials of the learning block (the first one for E1). These hand angles were first corrected with the average hand angles of the last 18 baseline trials before each learning block. Statistical comparison was performed with a two-way ANOVA with two between-subject factors: age group and rotation direction.

### Analysis 2: Implicit Adaptation for E1 and E2

We applied the same analysis, as described by Vandevorode and Orban de Xivry (2019) for E1 and E2. The learning block was first corrected for baseline errors by subtracting the average error of the last 18 trials of baseline. For E1, the second adaptation block was corrected by subtracting the average error of the last 18 trials of

washout. We analyzed the data in all of the uncued trials that were preceded by a cued trial (nine uncued trials per learning block). The amount of implicit learning was calculated per learning block, as the average hand angle in the uncued trials (Morehead et al. 2015). For each learning block separately, we performed a two-way ANOVA with the implicit adaptation level as the dependent variable and with age and rotation direction as the between-subject factors.

### Analysis 3: Explicit Adaptation for E1 and E2

We applied the same analysis as described by Vandevorode and Orban de Xivry (2019). The amount of explicit learning was calculated by subtracting hand angle in the uncued trials (*Analysis 2*) from the hand angles in the cued trials immediately preceding those (Morehead et al. 2015). Two separate two-way ANOVA's were used to analyze the first and second learning block with the explicit adaptation level as the dependent variable and with the between-subject factors, age and rotation. The two-way ANOVA to analyze the first learning block of *experiment E1* was preregistered as a primary analysis. We followed this procedure for E1 and E2.

### Analysis 4: Dual-Task Cost Measures

For the data from *experiment E1*, the dual-task cost (DTC) was calculated for each subject for the motor and cognitive tasks separately. These dual-task costs were based on difference in median reaction time (RT) between the single and dual-task conditions for the reaching task and for the flanker task. This first dual-task cost was preregistered:

$$\begin{aligned} \text{motor DTC E1 (\%)} \\ &= \frac{\text{Dual task median RT (of reaching)} - \text{Single task median RT (of reaching)}}{\text{Dual task median RT (of reaching)}} \cdot 100 \end{aligned} \quad (1)$$

$$\begin{aligned} \text{cognitive DTC E1 (\%)} \\ &= \frac{\text{Dual task median RT (of flanker - task)} - \text{Single task median RT (of flanker - task)}}{\text{Dual task median RT (of flanker - task)}} \cdot 100 \end{aligned} \quad (2)$$

For *experiment E2*, the dual-task cost was calculated for each subject and for each task separately. For the motor task, it was based on the difference in reaction time between single and dual-task conditions. For the cognitive tasks, it was based on the difference in working memory capacity (WMC) between the two conditions:

$$\begin{aligned} \text{motor DTC E2 (\%)} \\ &= \frac{\text{Dual task median RT (of reaching)} - \text{Single task median RT (of reaching)}}{\text{Dual task median RT (of reaching)}} \cdot 100 \end{aligned} \quad (3)$$

$$\text{cognitive DTC E2 (\%)} = \frac{\text{Single task WMC} - \text{Dual task WMC}}{\text{Single task WMC}} \cdot 100 \quad (4)$$

We used two different formulas for calculating dual-task costs, derived from single-task (ST) and dual-task (DT) performance:  $\text{DTC} = [(\text{DT} - \text{ST})/\text{DT}] \cdot 100$  if an increase in the metric were related to a performance decline (e.g., higher reaction time) and  $\text{DTC} = [(\text{ST} - \text{DT})/\text{ST}] \cdot 100$  if an increase in the metric were related to a performance increase (e.g., higher working-memory capacity). Positive and negative DTC values, therefore, always corresponded to decreased and increased performance from single- to dual-task condition, respectively (Boisgonnier et al. 2013; Dumas et al. 2008).

Two-sample two-tailed  $t$ -tests were applied to test whether these dual-task costs were different for young and old participants. We also tested these dual-task costs against zero via one-sample  $t$ -tests. We reported effect sizes (Cohen's  $d$ ) as well as  $t$  and  $P$  values for all  $t$ -tests.

### Analysis 5: Correlation Between Dual-Task Cost and Explicit Adaptation

Robust linear regression (robustfit in MATLAB) was performed between the measure of explicit adaptation and dual-task cost. Robust linear regression was chosen to make sure that correlations were not influenced by between-group differences in these variables. Explicit adaptation ( $Y$ ) was estimated using a linear combination of dual-task cost ( $X$ ), a binary age vector ( $G$ ), and the interaction of  $X$  and  $G$  in the regression equation with intercept  $A$  and regression coefficients ( $B$ ,  $C$ ,  $D$ ):

$$Y = A + B \cdot X + C \cdot G + D \cdot X \cdot G \quad (5)$$

Standardized  $\beta$ -coefficients ( $B$ ,  $C$ ,  $D$ ) were obtained by first converting variables  $X$  and  $Y$  to  $z$ -scores.

Our main prediction was that, especially in elderly people, the two variables (explicit adaptation and dual-task cost) will be negatively correlated. This robust linear regression was preregistered for *experiment E1*. In addition, we performed the robust linear regression for the two age groups separately. Explicit adaptation ( $Y$ ) was estimated using a linear regression with the independent variable, the dual-task cost ( $X$ ):

$$Y = A + B \cdot X \quad (6)$$

With this regression, standardized  $\beta$ -coefficients ( $\beta_{\text{DTC}}$ ) were obtained for young and old age groups separately.

### Analysis 6: Working Memory Capacity

The working memory task allows the determination of working memory capacity (WMC) with the  $K$  value, estimating the number of items that can be stored in working memory (WM) (Vogel et al. 2005), calculated as  $K = S(H - F)$  using two (in E2) or three (in E1) to six items. This is similar to the original experiment (Vogel et al. 2005) but differs from what previous adaptation studies (Christou et al. 2016) have used where the  $K$  value (i.e., K56) was obtained from the trials with five and six items only. We chose to measure WMC with all items because it allowed us to better estimate the  $K$  value for elderly than with the  $K$  value with only five and six items. This correlation with working memory capacity measured with all items and overall adaptation was also significant in the study of Christou et al. (2016) (personal communication from J. M. Galea). Two-sample two-tailed  $t$ -tests were applied to verify whether the working memory capacity was different for young and old (preregistered as a secondary analysis for E1). To test whether working memory capacity was related to the level of explicit adaptation, a robust linear regression (robustfit in MATLAB) was performed to partial out the effect of age group on the correlations, as explained in *Analysis 5*. In addition, we performed the robust linear regression for the two age groups separately, as described in *Analysis 5*, resulting in standardized  $\beta$ -coefficients ( $\beta_{\text{WMC}}$ ) for both young and old age groups separately.

## RESULTS

It is well established that explicit adaptation is reduced in older adults (Heuer and Hegele 2008; Vandevorode and Orban de Xivry 2019). One hypothesis to explain this reduction is the “cognitive resources hypothesis,” which states that older adults require more cognitive resources compared with younger adults for unperturbed reaches, which leaves then fewer cognitive resources available for the adaptation process (Fig. 1). To assess the amount of cognitive resources used for simple reaching movements, we measured the dual-task cost during unperturbed reaching trials via a cognitive-motor dual task.

### Experiment E1: Decrease in the Explicit Component of Adaptation with Age

In *experiment E1*, we observed a decrease of final adaptation level for older adults in the cued visuomotor rotation experiment [Fig. 3, *A* and *B*; *Analysis 1*; learning:  $F(1,77) = 8.5$ ,  $P = 0.005$ ,  $\eta^2 = 0.1$ ; relearning:  $F(1,77) = 11.1$ ,  $P = 0.001$ ,  $\eta^2 = 0.1$ ]. We did not observe any difference between younger adults and older adults for implicit adaptation [Fig. 3C: *Analysis 2*; learning:  $F(1,77) = 3.1$ ,  $P = 0.08$ ,  $\eta^2 = 0.03$ ; relearning:  $F(1,77) = 0.3$ ,  $P = 0.60$ ,  $\eta^2 = 0.003$ ]. One outlier data point was present in the young adult's group in the first learning block for implicit adaptation (Fig. 3C). However, removing this outlier did not change the result for implicit adaptation during the first learning block. Explicit adaptation was decreased for older adults in both learning blocks [Fig. 3D; *Analysis 3*; learning:  $F(1,77) = 4.4$ ,  $P = 0.04$ ,  $\eta^2 = 0.05$ ; relearning:  $F(1,77) = 9.5$ ,  $P = 0.003$ ,  $\eta^2 = 0.10$ ].

### Experiment E1: No Difference in Dual-Task Cost During Baseline

In a first preregistered study, the flanker task was introduced as the cognitive task during the baseline period to assess dual-task costs. According to the cognitive resources hypothesis, we expected a larger dual-task cost in elderly people and a negative correlation between explicit adaptation and the dual-task costs.

The motor dual-task cost was not different between young and older adults (Fig. 4A; *Analysis 4*;  $t(79) = -1.6$ ;  $P = 0.12$ ,  $d = 0.35$ ), which could indicate that the amount of cognitive resources required for unperturbed reaching was not higher for older adults. In addition, we did not observe any difference in cognitive dual-task cost between young and older adults [Fig. 4B; *Analysis 4*;  $t(79) = 0.4$ ;  $P = 0.66$ ,  $d = 0.10$ ]. These two dual-task cost measures (Eqs. 1 and 2) were positive, for both age groups [Fig. 4, *A* and *B*; Motor DTC: Young:  $t(40) = 6.1$ ,  $P = 4 \times 10^{-7}$ ,  $d = 0.95$ , Old:  $t(39) = 7.5$ ,  $P = 5 \times 10^{-9}$ ,  $d = 1.18$ ; Cognitive DTC: Young:  $t(40) = 7.7$ ,  $P = 2 \times 10^{-9}$ ,  $d = 1.21$ , Old:  $t(39) = 4.9$ ,  $P = 2 \times 10^{-5}$ ,  $d = 0.78$ ], which shows that the dual-task manipulation worked as the performance of the motor and cognitive tasks was reduced in dual-task condition compared with single-task condition.

We did not find any evidence in favor of the cognitive resource hypothesis as there was no correlation between the motor dual-task cost and explicit adaptation (Fig. 4C, *Analysis 5*;  $\beta = 0.04$ ;  $P = 0.76$ ,  $R = -0.04$ ). In addition, no relation was observed between the cognitive dual-task cost and the amount of explicit adaptation (Fig. 4D; *Analysis 5*;  $\beta = -0.07$ ;  $P = 0.56$ ;  $R = 0.02$ ). As such, we failed to find any evidence for the cognitive resources hypothesis in *experiment E1*.

### Experiment E1: There Is a Link Between Working Memory Capacity and Explicit Adaptation

It has been previously shown that a high working memory capacity was linked to an individual's capacity to use an explicit strategy (Christou et al. 2016). In this experiment, working memory capacity was lower for older adults compared with younger adults [Fig. 5A; *Analysis 6*;  $t(76) = 4.46$ ;  $P = 2.8 \times 10^{-5}$ ,  $d = 1.01$ ]. Furthermore, there was a positive link between explicit adaptation and working memory capacity (Fig. 5B; *Analysis 6*;  $\beta_{\text{WMC}} = 0.39$ ;  $P = 0.002$ ,  $R = 0.14$ ). This link was also observed



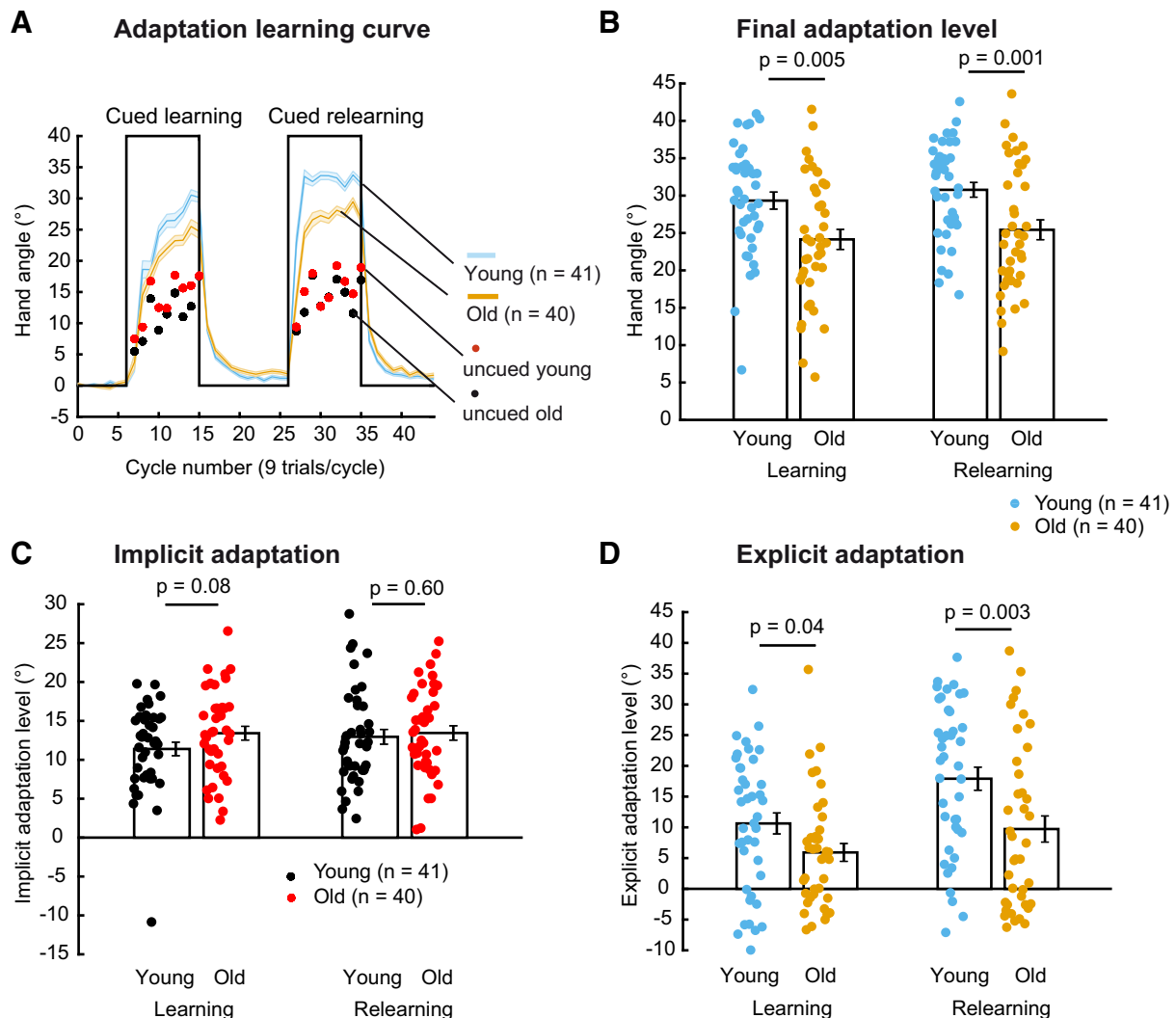


Fig. 3. Differences in motor adaptation between young and older adults. *A*: decreased overall cue-evoked adaptation in older adults compared with younger adults in learning and relearning block. During the uncued trials, the level of implicit adaptation was measured and the cued trials preceding the uncued trials allowed us to calculate explicit adaptation. *B*: final adaptation level at the end of the learning and relearning block was lower in older adults. *C*: implicit adaptation was not different for younger adults and older adults in learning and relearning. *D*: explicit adaptation was reduced in the learning and the relearning block for older adults compared with younger adults.

for the amount of explicit adaptation in the relearning block (*Analysis 6*;  $\beta_{WMC} = 0.39$ ;  $P = 0.004$ ,  $R = 0.19$ ).

One disadvantage of the flanker dual-task experiment was the serial design of the reaching and cognitive tasks. Since the same cognitive resources could be used for the sequential tasks, the dual-task costs might not be the best estimate of the amount of cognitive resources used for simple reaching movements (despite the fact that there was a significant dual-task cost). Therefore, we used a second dual-task design where a working memory task was performed in parallel with the reaching task. The working memory task appeared suitable, as we had just shown that it is linked to the explicit component of adaptation.

#### Experiment E2: Decrease in the Explicit Component of Adaptation with Age

In terms of adaptation, the results were largely similar to the results obtained in *experiment E1*. We observed a decrease of final adaptation level for older compared with younger adults in the cued visuomotor rotation experiment with a single learning block [Fig. 6, *A* and *B*; *Analysis 1*;  $F(1,58) = 9.7$ ,  $P =$

0.003,  $\eta^2 = 0.14$ ]. Implicit adaptation was slightly larger in old compared with young participants [Fig. 6*C*; *Analysis 2*; implicit adaptation:  $F(1,58) = 1.6$ ,  $P = 0.22$ ,  $\eta^2 = 0.02$ ], while explicit adaptation was decreased for older adults [Fig. 6*D*; *Analysis 3*; explicit adaptation:  $F(1,58) = 10.3$ ,  $P = 0.002$ ,  $\eta^2 = 0.14$ ]. Individual trials were strictly constrained in timing in *experiment E2*. This time constraint might have resulted in a more pronounced age difference for explicit adaptation in the second paradigm, as suggested by the higher effect size [*E1*:  $\eta^2 = 0.05$  (Fig. 3*D*), *E2*:  $\eta^2 = 0.14$  (Fig. 6*D*)].

#### Experiment E2: the Motor Dual-Task Cost Did Not Differ Between Young and Old Participants

In *experiment E2*, the working memory task was implemented as a cognitive task during the baseline period (Fig. 2*B*) to assess dual-task costs during unperturbed reaching movements. The hypothesis remained unchanged from the first preregistered study: we expected a larger dual-task cost for elderly adults and a negative link between two dual-task costs and explicit adaptation according to the cognitive resources hypothesis.



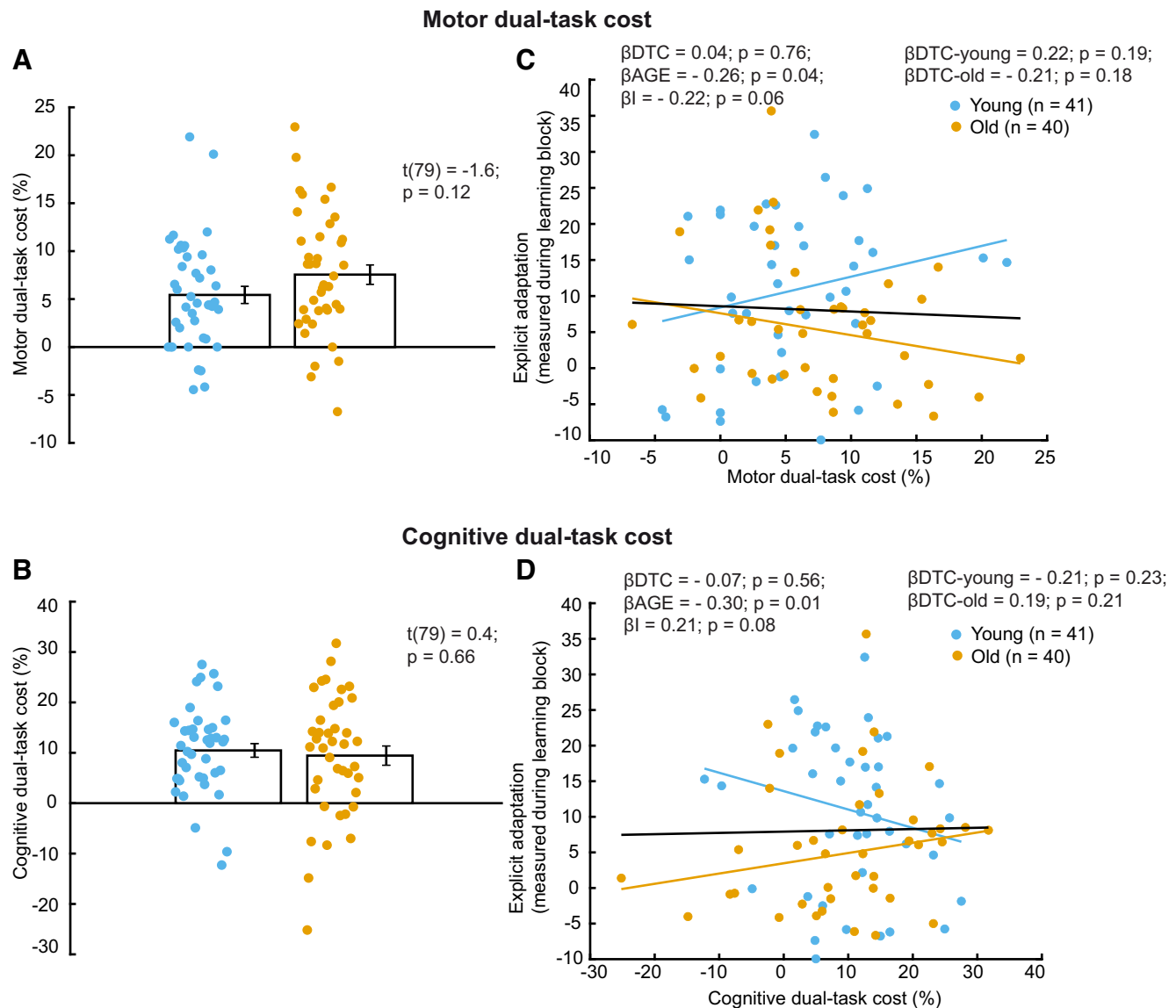


Fig. 4. Motor and cognitive dual-task costs. *A* and *B*: dual-task costs were not different for young and older adults. However, the two dual-task costs were bigger than zero for both age groups. *C* and *D*: no link was observed between explicit adaptation and dual-task costs. AGE, age effect; DTC, dual-task cost; I, interaction.

The motor dual-task cost was not different between young and older adults [Fig. 7A: Analysis 4:  $t(60) = 1.4$ ,  $P = 0.18$ ,  $d = 0.35$ ]. In addition, the cognitive dual-task cost was not different either between the two age groups [Fig. 7B: Analysis 4:  $t(60) = -0.78$ ,  $P = 0.44$ ,  $d = 0.20$ ]. The motor dual-task cost based on reaction time was not different from zero [Fig. 7A: Young:  $t(29) = 1.2$ ,  $P = 0.25$ ,  $d = 0.21$ ; Old:  $t(31) = -0.65$ ,  $P = 0.52$ ,  $d = -0.11$ ] but other motor dual-task costs were (see Supplemental Materials S1, <https://doi.org/10.17605/OSF.IO/KS2J8>; all supplemental materials may be found at this website). Furthermore, the cognitive dual-task cost was positive, both for young and old [Fig. 7B: Young:  $t(29) = 4.2$ ,  $P = 0.0002$ ,  $d = 0.76$ ; Old:  $t(31) = 4.1$ ;  $P = 0.0003$ ,  $d = 0.72$ ]. This positive dual-task cost indicates that unperturbed reaching partially depends on working memory capacity resources for both young and older adults. In addition, it showed that the dual-task manipulation worked. However, contrary to our hypothesis, older adults did not require more of these resources than younger adults did.

Finally, there was neither a link between motor dual-task cost and explicit adaptation (Fig. 7C: Analysis 5;  $\beta = -0.21$ ;  $P = 0.14$ ,  $R = -0.15$ ) nor a link between cognitive dual-task cost and explicit adaptation (Fig. 7D: Analysis 5;  $\beta = -0.05$ ;  $P = 0.74$ ,  $R = -0.05$ ). Therefore, we did not find any evidence in favor of the cognitive resources hypothesis. The absence of any robust link between other dual-task cost measures and explicit adaptation in the flanker dual-task cost (Fig. 4; Supplemental Table S1) and in the working memory dual-task cost (Fig. 7; Supplemental Table S2) shows that it is unlikely that a link exists between the cognitive resources required for unperturbed reaching in baseline and the level of explicit adaptation.

#### Experiment E2: the Link Between Working Memory Capacity and Explicit Adaptation Is Confirmed

In this experiment, working memory capacity, which was quantified in the single- and dual-task condition, was lower in older than in younger adults [Fig. 8, *A* and *B*: Analysis 6:

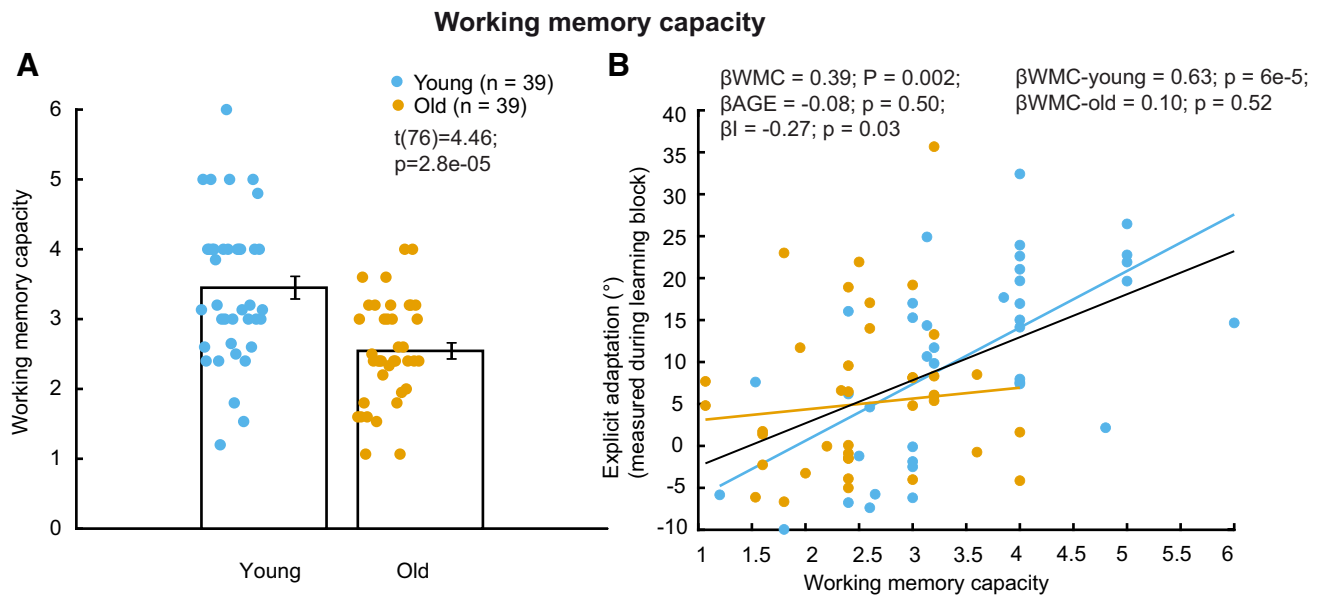


Fig. 5. Link between working memory capacity (WMC) and explicit adaptation. *A*: working memory capacity was lower for older adults compared with younger adults. For three (of 81) subjects, no working memory capacity data were obtained. *B*: a positive correlation existed between explicit adaptation during the learning block and working memory capacity. AGE, age-effect; I, interaction; WMC, working memory capacity.

$t(60) = 2.6$ ,  $P = 0.01$ ,  $d = 0.67$ ;  $t(60) = 2.6$ ,  $P = 0.01$ ,  $d = 0.67$ ]. As a confirmation of our earlier finding from *experiment E1*, we found a link between explicit adaptation and working memory capacity in the single-task condition (Fig. 8C: *Analysis 6*:  $\beta = 0.29$ ;  $P = 0.03$ ,  $R = 0.39$ ). This link did not reach significance in the dual-task condition (Fig. 8D: *Analysis 6*:  $\beta = 0.18$ ;  $P = 0.18$ ,  $R = 0.28$ ).

To conclude, we found no evidence for the cognitive resources hypothesis as none of the cognitive or motor dual-task cost measurements in baseline were related to explicit adaptation for both dual-task designs. In addition, cognitive and motor dual-task costs were not different for young and older adults. However, in both experiments, working memory capacity was consistently linked with explicit adaptation, and working memory capacity was smaller in older adults.

#### Link Between Cognitive Status and Explicit Adaptation: Exploratory Analyses

Finally, several other variables were affected by the dual-task condition, as indicated by positive cognitive and motor dual-task costs (Supplemental Table S1 and Table S2).

In the flanker dual task, other dual-task costs were observed for the motor and the cognitive task (see Supplemental Table S1). In *experiment E2*, dual-task costs were only observed for the cognitive task (Fig. 7, *A* and *B*), which might indicate that priority was given to the motor task. However, dual-task cost outcomes based on reaching speed and reaching error suggest that it was not the case (Supplemental Table S2). Indeed, reaching was slower and more reaching errors occurred during the dual-task condition compared with the single task. Therefore, the reaching was also affected by the working memory task in *experiment E2*.

In addition, we tested the link between these additional parameters and the amount of explicit adaptation. For *E1*, we found a negative link between the reaction time in the flanker task and the amount of explicit adaptation (Supplemental Table S1, single-task condition:  $\beta = -0.50$ ;  $P = 0.01$ ;  $R = -0.30$ ;

dual-task condition:  $\beta = -0.49$ ;  $P = 0.003$ ;  $R = -0.33$ ). Finally, there was a positive correlation between the figure recall score and the explicit component of adaptation (Supplemental Table S4,  $\beta = 0.44$ ;  $P = 0.0004$ ;  $R = 0.46$ ). This is in line with the correlation between working memory capacity and the amount of explicit adaptation, as the figure recall score is a proxy for visuospatial abilities and visuospatial memory.

#### DISCUSSION

In this study, we did not find any evidence that the amount of explicit adaptation was negatively linked to the amount of cognitive resources used during unperturbed reaching (i.e., baseline). In both dual-task experiments, cognitive and motor dual-task costs measured during the baseline period were similar for young and older adults, indicating that there is no evidence that the amount of cognitive resources used during unperturbed reaching differ between age groups. Altogether, we found no evidence for the cognitive resources hypothesis (Fig. 1). However, the association between the level of explicit adaptation and visuospatial working memory points toward the importance of cognitive abilities for the achieved level of explicit adaptation. In other words, it is the reduced working memory abilities of older adults and not the use of cognitive resources for reaching that might account for the reduced explicit adaptation in older adults.

#### Working Memory as Underlying Mechanism Contributing to Decline in Explicit Strategy

However, this does not resolve the contradiction that existed between previous studies where improved motor performance relied on increased cognitive control in older participants (Heuninckx et al. 2008) and the age-related decline of the cognitive component in motor adaptation (Heuer and Hegele 2008; Vandevorode and Orban de Xivry 2019). One possible explanation is that the increased cognitive control was only present at task level requiring low cognitive control (easier

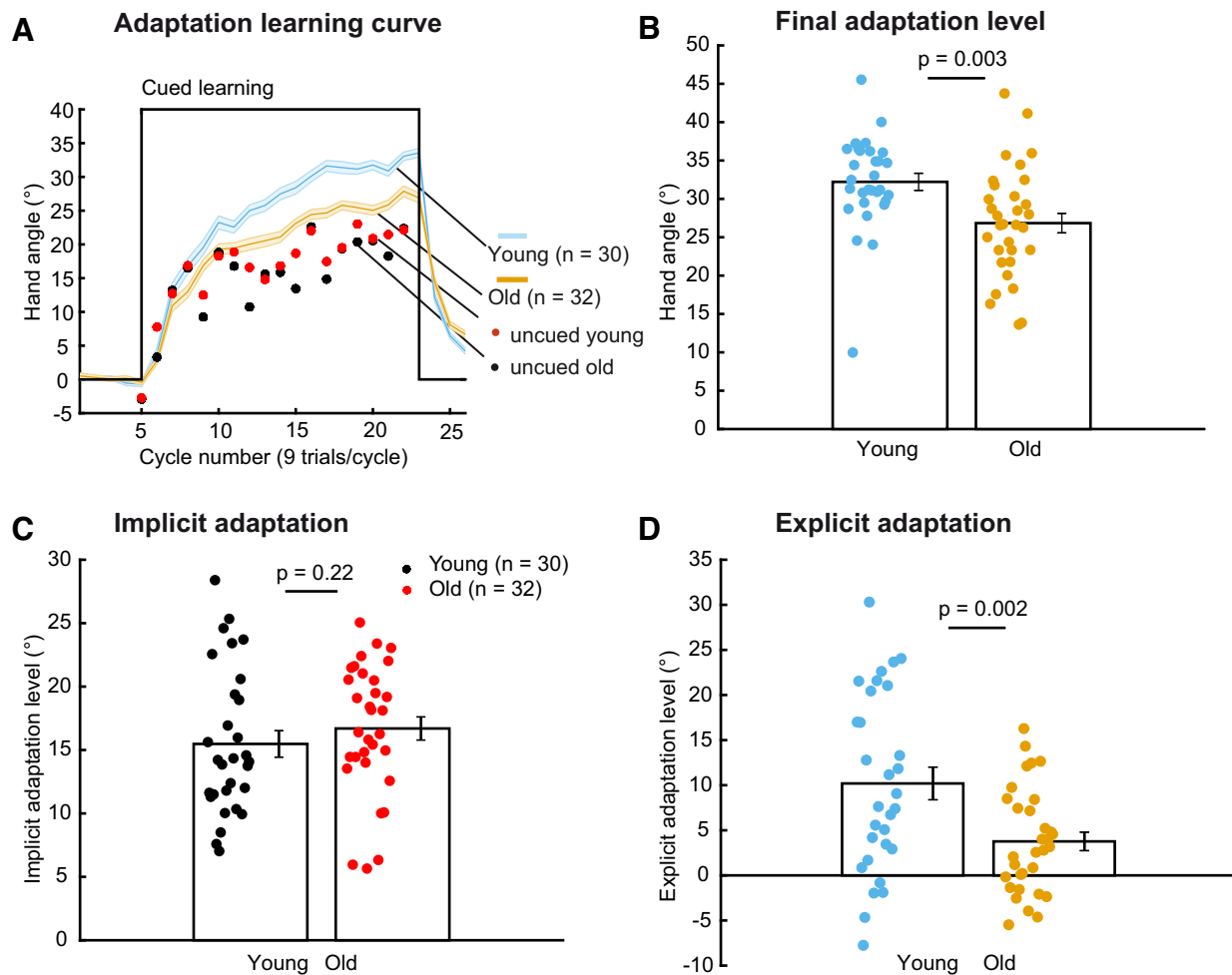


Fig. 6. Differences in adaptation between young and older adults. *A*: decreased overall cue-evoked adaptation in older adults. During the uncued trials, the level of implicit adaptation was measured, and the cued trials preceding the uncued trials allowed us to calculate explicit adaptation. *B*: final adaptation level at the end of the learning block was lower in older adults. *C*: implicit adaptation was not different for younger and older adults. *D*: explicit adaptation was reduced for older adults compared with younger adults.

motor task), while it was useless for more difficult tasks where higher cognitive load was observed. Indeed, increased prefrontal cortex activation in older compared with younger adults was limited to easy tasks. While at higher task level, working memory performance was lower in older adults and the increased brain activity disappeared (Cappell et al. 2010; Mattay et al. 2006; Schneider-Garces et al. 2010).

The idea of reduced working memory contributing to the decline of motor adaptation is in line with Anguera et al. (2011). They suggested that spatial working memory contributes to the age-related deficits in visuomotor adaptation. They observed a reduced spatial working memory for old compared with younger adults. In addition, they found a link between their measure of visuospatial working memory and early rate of learning for younger adults. We expanded their work by dissociating overall adaptation in an implicit and an explicit component of adaptation, of which only the explicit component is known to be affected with aging (Vandevorde and Orban de Xivry 2019). In addition, we quantified working memory capacity using a visuo-spatial task (Christou et al. 2016) instead of a mental rotation task (Anguera et al. 2011). By these adjustments together with bigger sample sizes, a robust link between working memory capacity and the explicit com-

ponent could be identified in two experiments, while accounting for the effect of age (Figs. 5*B* and 8*C*). In addition, older adults' working memory capacity was lower than younger adults' capacity in both experiments (Figs. 5*A* and 8, *A* and *B*). In addition, recently Rajeshkumar and Trewartha (2019) showed that, when reducing working memory demands during motor adaptation by repeating a specific order of target locations, the difference between young and older adults' adaptation rates disappeared. Together, this allows us to confirm that working memory abilities have an important contribution to the age-related deficits of motor adaptation.

Since working memory appears to be robustly linked with explicit strategy, cognitive training might resolve the age-related decline of motor adaptation. It would be interesting to verify whether specifically training visuospatial working memory has an impact on the level of explicit strategy. This approach has been attempted by Anguera et al. (2012) in younger adults, however, without success. They even mention an opposite effect after extensive training of visuospatial working memory: The training might have resulted in depletion of spatial working memory resources, which negatively affected subsequent visuomotor adaptation. Nevertheless, for older adults the outcome might still be beneficial since working



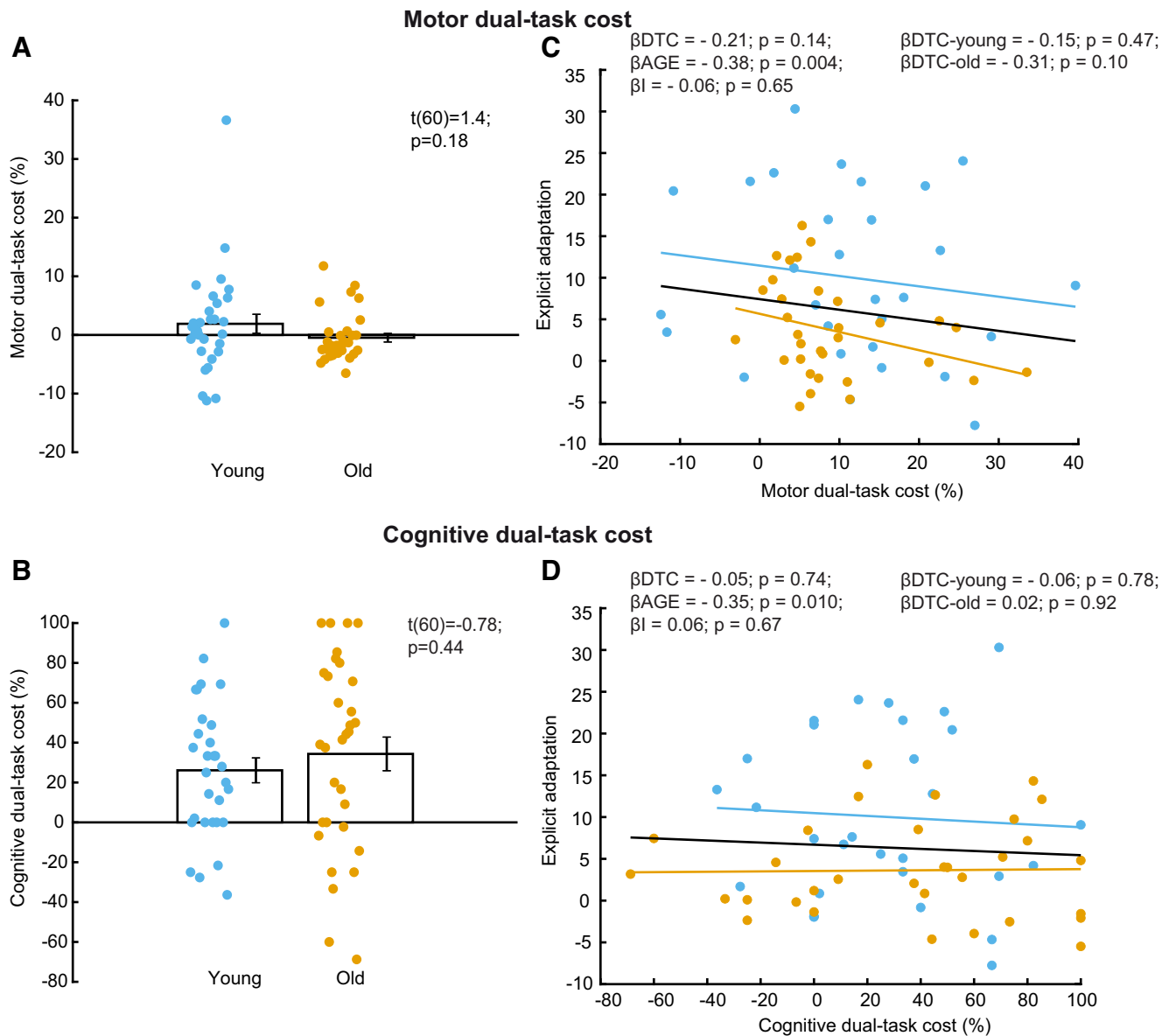


Fig. 7. Motor and cognitive dual-task cost. *A*: motor dual-task cost was calculated as the relative change in median reaction time of reaching and was not different between young and older adults. *B*: cognitive dual-task cost for working memory capacity was not different between young and older adults. *C*: no link was observed between explicit adaptation and motor dual-task cost. *D*: no link between explicit adaptation and cognitive dual-task cost was found. The outlier in *A* was removed for the correlation analyses (*C* and *D*). AGE, age effect; DTC, dual-task cost; I, interaction.

memory training is effective in elderly and might be a useful tool for cognitive intervention (Karch and Verhaeghen 2014; Klingberg 2010). However, such training study should be carefully designed given the limitations in working memory training literature such as lack of consistency in experimental methods and findings (Morrison and Chein 2011).

#### Components of Working Memory

Recently, McDougall and Taylor (2019) showed that two different representations of working memory are involved in generation of explicit strategy: one is parametric mental rotation and the other is discrete response caching. With a lower number of targets (2), response caching is the main working memory process involved. With a higher number of targets (12), both working memory processes seem to be involved; early adaptation relies on mental rotation, whereas late adap-

tation depends on response caching (McDougall and Taylor 2019). Only three targets were used in our learning blocks, which suggests that response caching might be involved in our measure of explicit strategy. Our working memory task was assessing response caching as well since participants had to remember a discrete number of items (Spellman et al. 2015). The link that we observed between working memory capacity and explicit strategy, therefore, likely originates from the involvement of response caching. In contrast, it is possible that the link that Anguera et al. (2011) observed between working memory and visuo-spatial working memory originates from parametric mental rotation as they used a mental rotation task. Therefore, together, our studies show that both aspects of working memory, response caching, and mental rotation, might be contributing to the age-related declines of motor adaptation. It would be interesting to further explore this idea with the recent

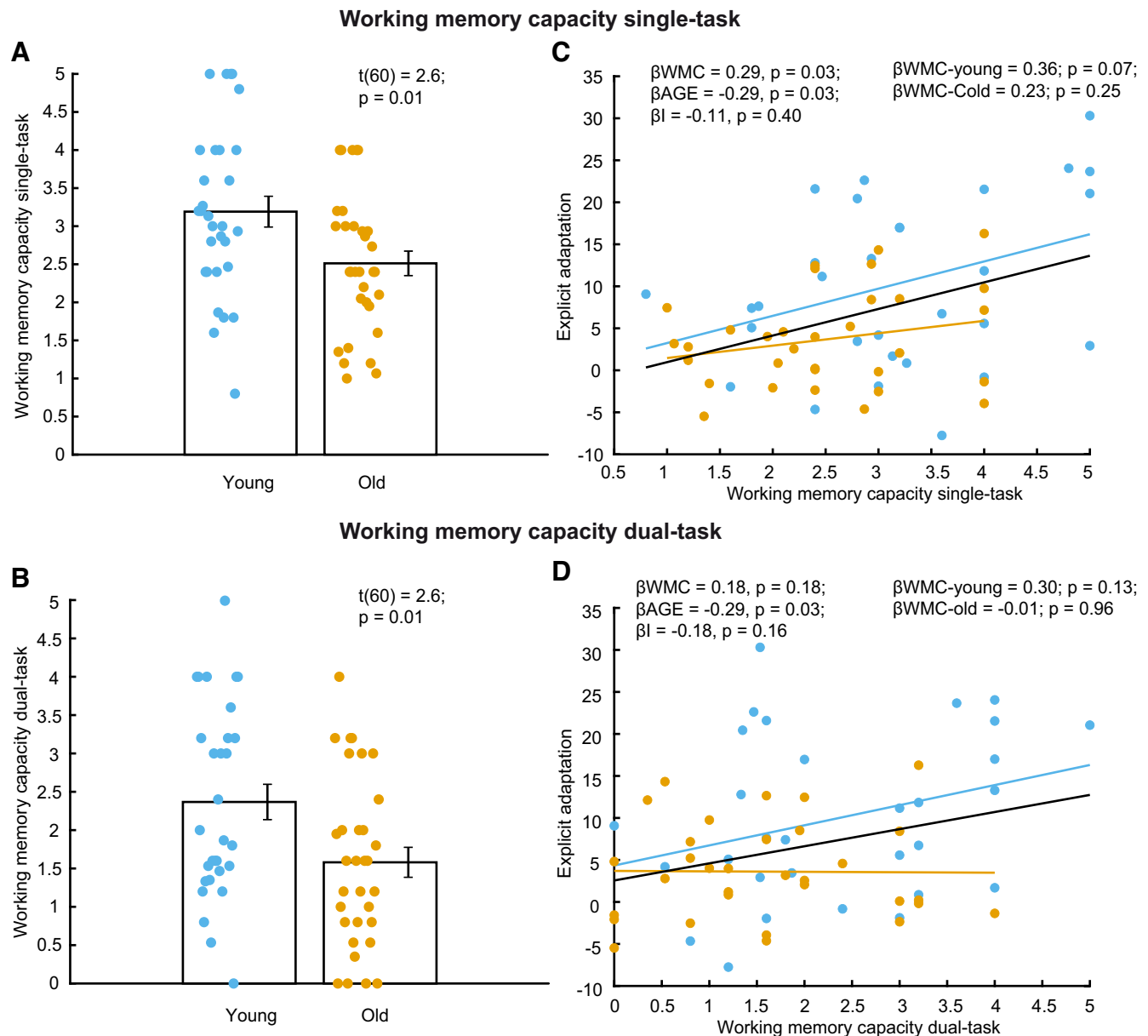


Fig. 8. Link between working memory capacity and explicit adaptation. *A*: single-task working memory capacity was lower for older adults. *B*: dual-task working memory capacity was lower for older adults. *C*: positive link between explicit adaptation and single-task working memory capacity. *D*: no link observed between explicit adaptation and dual-task working memory capacity. AGE, age effect; I, interaction; WMC, working memory capacity.

approaches taken by McDougle and Taylor (2019) by constraining reaction time and applying small versus large set sizes.

#### *Cognitive Resources in Unperturbed Reaching*

The goal of both our dual-task designs was to quantify the amount of cognitive resources applied during unperturbed reaching movement. This is a common procedure in gait (Ebersbach et al. 1995) and balance studies (Melzer et al. 2001; Huxhold et al. 2006); however, for reaching movements, it has been reported for only a few studies (Bekkering et al. 1994; Ma et al. 2009; Pratt and Neggers 2008). The presence of motor and cognitive dual-task costs shows that performance of both tasks was negatively affected by performing them simultaneously. This negative impact might indicate that the same cognitive resources were required for both tasks and that the

dual-task design succeeded in its goal of measuring cognitive resources during reaching. For instance, a reduction of working memory capacity with more than 20% was observed when combining reaching with the working memory capacity task; working memory capacity resources appear involved in unperturbed reaching. We did not observe differences in dual-task cost between young and older adults. However, increasing the complexity of the dual task (Fig. 2) might result in different dual-task cost for young and old participants. This would be in line with studies that reported a more pronounced effect of aging, when the cognitive load of the dual task was higher (Boisgontier et al. 2013). Nevertheless, a relation between dual-task cost and explicit adaptation seems unlikely given the absence of any relation so far (Figs. 4, *C* and *D*, and 7, *C* and *D*).

### *Alternative Approaches and Limitations*

A limitation of the flanker dual task was the serial design of the cognitive and motor task. Therefore, it resembled more a switching task instead of a dual task (Monsell 2003). This shows that older participants have more difficulty switching between motor and cognitive tasks, which is in line with research that shows switching between cognitive tasks is more difficult for the elderly (Kray and Lindenberger 2000). However, since the flanker dual task is executed with both hands, it might also reflect a reduced performance in bimanual control with aging (Maes et al. 2017). Nevertheless, a link between task-switching performance and explicit adaptation was not observed. The deficit in task-switching or bimanual control appears not to be the explanation for the reduced explicit adaptation with aging.

Despite the serial dual-task design, we observed an impact of the flanker task on the reaching movement that is hard to explain as a switching task cost. Participants were asked to divide their attention to two tasks simultaneously as they should already prepare for the flanker task while reaching (Fig. 2A). This was visible in the difference in movement parameters between single and dual trials (Fig. 4A). This effect can be interpreted as a dual-task cost and not as a switching-task cost, since there was no time pressure for switching from the flanker task to the reaching task, but there was pressure to switch from reaching to the flanker task.

To tackle the limitations of the first experiment, we introduced the second dual task with true parallel features (Fig. 2B). However, even for the parallel design, no relation was observed between explicit adaptation and dual-task costs (Fig. 7, C and D). The cognitive tasks introduced in the baseline were different, but single-task performance for both cognitive tasks appeared to be linked to explicit adaptation (Figs. 5B and 8, C and D).

Besides shared cognitive resources for working memory among the cognitive and motor tasks, studies often link dual-task performance to other components of the executive system, such as planning, shifting, inhibition, or coordination (Meyer and Kieras 1997; Sigman and Dehaene 2008; Watanabe and Funahashi 2018). Consequently, interpretation of reduced dual-task performance is rather difficult, which represents an important limitation of this study.

### *Neural Mechanisms of Explicit Strategy*

The increased (compensatory) brain activity observed in elderly during motor tasks is often located in frontal brain regions, such as prefrontal cortex (Cappell et al. 2010; Mattay et al. 2006; Schneider-Garces et al. 2010), which is a region that is highly affected by aging as evidenced by structural (Raz and Rodrigue 2006) and connectivity deficits (Madden et al. 2010; Nagel et al. 2011). At the same time, brain regions responsible for the explicit component of adaptation are most likely frontal lobe regions, including lateral and medial aspects of prefrontal cortex, as well as premotor cortex (Krakauer et al. 2004; McDougale and Taylor 2019; Shadmehr and Holcomb 1997). Together, prefrontal cortex appears to be the region where both age-related compensatory brain activity takes place, and the region that might be responsible for the explicit component of adaptation. This might indicate that the same

(prefrontal) cognitive resources are required for compensation with aging and are responsible for motor adaptation decline.

Since age-related changes in dorsolateral prefrontal cortex activity were observed during information retrieval from working memory (Rypma and D'Esposito 2000), we would expect to see different neural activation in prefrontal cortex depending on the level of explicit strategy acquired. A relationship between neural activity in dorsolateral prefrontal cortex and early learning rate was, indeed, observed in Anguera et al. (2011). In addition, this study observed a relationship between early learning rate and spatial working memory performance for young, but not for older adults (Anguera et al. 2011). However, replication of this relation would be useful to verify its robustness. In addition, it would be interesting to further refine the region of interest, quantify explicit strategy directly, and disturb activity of this brain region to investigate causality.

However, it appears that dorsolateral prefrontal cortex, a brain region responsible for higher-level task execution might be the key, as it is: 1) structurally degraded with aging (Raz and Rodrigue 2006), 2) likely responsible for reduced explicit adaptation (Anguera et al. 2011), and 3) important for working memory capacity (Rypma and D'Esposito 2000). This brain region appears to be an interesting target when designing future studies that investigate the cause for explicit strategy decline with aging.

### *Conclusion and Outlook*

In this study, we found that older adults did not have higher motor or cognitive dual-task costs during unperturbed reaching movements and that the observed dual-task costs could not explain the age-related decline in the explicit component of motor adaptation (Heuer and Hegele 2008; Vandevorde and Orban de Xivry 2019). Rather, we observed that the explicit component of motor adaptation was reliably associated with working memory capacity. This suggests that the amount of memory resources of an individual correlates with the magnitude of the explicit component during a visuomotor rotation task. Our study leaves several questions unanswered: 1) While cognition has been shown to be used by older people to maintain good motor performance in some motor learning tasks (Heuninckx et al. 2005), we found that the cognitive component of motor adaptation was responsible for the impaired total adaptation in older participants (Vandevorde and Orban de Xivry 2019). This suggests that cognition is used differently in different motor (learning) tasks. Why and how this occurs remains unknown? 2) How can we train people to overcome a decline of explicit strategy? One possibility is to reduce working memory demands in older adults during motor learning (Rajeshkumar and Trewartha 2019). Another possibility is to train working memory capacity in older adults (Anguera et al. 2012). 3) Are the same underlying mechanisms leading to a decline in the explicit component and in working memory, or is there a direct causal link between the decline in working memory and the decline in the explicit component of adaptation?

Working memory can be approached as a multicomponent (Baddeley and Hitch 1974) or as a state-based model (D'Esposito and Postle 2015). Therefore, to further explore the nature of the explicit strategy decline in older adults, it might be useful to relate it to different states or components of



working memory. This approach would require the design of novel paradigms that can dissociate working memory components with respect to explicit strategy development, an approach recently initiated by McDougale and Taylor (2019). This seems a promising approach to gain further insights in the decline of explicit strategy with aging.

To overcome the decline of explicit strategy with aging, it needs to be tested whether targeted cognitive training might resolve some of the deficits. Another possibility is the application of noninvasive brain stimulation, which is a technique that appears to be suited to restore some of the age-related deficits (Grimaldi et al. 2016; Hardwick and Celnik 2014; Orban de Xivry and Shadmehr 2014). A twofold approach is possible to restore the decline of explicit strategy in elderly: either directly, by stimulation of a region such as dorsolateral prefrontal cortex, which might temporarily boost some working memory resources (Seidler et al. 2017), or indirectly, by stimulation of the cerebellum, which might boost the already intact implicit component of motor adaptation (Galea et al. 2011). Finally, we expect that the observed age-related decline of explicit strategy is having widespread consequences on other features and components of motor adaptation, such as reduced generalization, increased interference of motor memories, reduced savings, and reduced reinforcement learning.

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## DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

## AUTHOR CONTRIBUTIONS

K.V. and J.-J.O.d.X. conceived and designed research; K.V. performed experiments; K.V. analyzed data; K.V. and J.-J.O.d.X. interpreted results of experiments; K.V. prepared figures; K.V. drafted manuscript; K.V. and J.-J.O.d.X. edited and revised manuscript; K.V. and J.-J.O.d.X. approved final version of manuscript.

## ENDNOTE

At the request of the authors, readers are herein alerted to the fact that additional materials related to this manuscript may be found at the Open Source Framework: [https://osf.io/ks2j8/?view\_only=c135f485872649c1a30e85a1e4fd8518]. These materials are not a part of this manuscript and have not undergone peer review by the American Physiological Society (APS). APS and the journal editors take no responsibility for these materials, for the website address, or for any links to or from it.

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