Not fleeting but lasting: Limited influence of aging on implicit adaptative motor learning and its short-term retention.

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Running Head: No influence of aging on spontaneous recovery of adaptation

Summary

1   In motor adaptation, learning is thought to rely on a combination of several processes. Two of these

2   are implicit learning (incidental updating of the movement due to sensory prediction error) and

3   explicit learning (intentional adjustment to reduce target error). The explicit component is thought to

4   be fast adapting, while the implicit one is slow. The dynamic integration of such a fast and a slow

5   components can lead to spontaneous recovery. That is, after prolonged adaptation of movement to a

6   given perturbation, the learning is extinguished by presenting a perturbation in the opposite

7   direction for a few trials. After such extinction, the learned adaptation can reappear in the absence

8   of any further training, a phenomenon called spontaneous recovery. Trewartha et al. (2014) found

9   that older adults show less spontaneous recovery than their younger controls, indicating

10 impairments in short-term retention of force-field adaptation. This disagrees with evidence

11 suggesting that the implicit component and its retention do not decline with aging.

12 To clarify this discrepancy, we performed a conceptual replication of that result. Twenty-eight

13 healthy young and 20 healthy older adults learned to adapt to a forcefield perturbation in a paradigm

14 known to elicit spontaneous recovery. Both groups adapted equally well to the perturbation. Implicit

15 adaptation of the older subjects was indistinguishable from that of their younger counterparts. In

16 addition, our conceptual replication failed to reproduce the result of Trewartha et al. (2014) and

17 found that the spontaneous recovery was also similar across groups. Our results reconcile previous

18 studies by showing that both spontaneous recovery and implicit adaptation are unaffected by aging.

19 New and Noteworthy:

20 In this study, we tested whether aging influences the ability to learn to counteract a perturbation
21 during reaching movements and to recall previously learned motor memories. In contrast to a
22 previously published paper, we found that the ability of older participants to adapt to a perturbation
23 and to recall motor memories remains unimpaired.

Introduction

Young healthy adults can adapt to a change in the environment and adapt their reaching performance (1, 2). Such an adaptation process of upper limb movements is studied in the laboratory via perturbation of the visual feedback about the moving direction of the hand (3, 4), by shifting the visual field via prism goggles (5) or by applying a force on the moving arm (6, 7). For any of these perturbations, young participants can readily decrease the effect of the perturbation on their reaching performance through a combination of explicit strategies and implicit adaptation (8–11). Implicit adaptation is the incidental updating of the movement driven by sensory prediction error and occurs gradually (9, 12, 13). Explicit adaptation consists of the application of cognitive strategies to reduce target error and reduces errors rapidly (1). The explicit component contributes more to total adaptation for visuomotor rotation larger than 30° than for force-field adaptation. Indeed, in visuomotor rotation, implicit adaptation amounts to 15-20deg for 45° perturbations (30-50% of compensation, 8). In contrast, learning to counteract a force field is largely an implicit process with only a small explicit component (implicit adaptation around 60-80% of total adaptation 14).

Older adults show lower levels of total motor adaptation than young adults (15–29). Recent evidence suggests that this impairment in motor adaptation is specific to the explicit component of adaptation (21–23, 27, 28, 30–32) and that the implicit component of motor adaptation elicited by a visuomotor adaptation and its short-term retention (as measured by the decline in adaptation during one-minute breaks) remains unimpaired in individuals up to 60-70 years old (19, 27, 33–36).

Few studies have investigated the effect of age on force-field perturbation (37–41). Little difference in the amount of adaptation to a force-field perturbation has been found between young and older participants (38, 41). Yet, the explicit and implicit components of adaptation have never been measured in these studies. While we know that the contribution of explicit strategies to force-field adaptation is small (14), it is not null. Therefore, it remains unknown whether the implicit component of motor adaptation remains unaffected in older people during a force-field adaptation task. Measuring the explicit and implicit components of motor adaptation is essential in order to gain insight into the source of possible deficits. Interestingly, one study reported a very specific age-related impairment in force-field adaptation. That is, while initial adaptation was unimpaired with age, its short-term retention as measured by spontaneous recovery of adaptation was impaired (41). Furthermore, these authors suggested that this impairment was linked to low explicit memory resources.

Spontaneous recovery occurs when motor adaptation to some perturbation A, which is then hidden from view due to adaptation of a second perturbation B, reappear without any additional exposure

57 to perturbation A (42–47). It suggests that the motor memory of the adaptation to perturbation A is

58 not washed out by adaptation to perturbation B but is retained. Therefore, such spontaneous

59 recovery of motor memories linked to perturbation A represents a proxy for short-term retention of

60 the associated motor memory (47).

61 The presence of spontaneous recovery indicates the presence of at least two learning processes

62 working on different time scales. One process learns and forgets quickly, while the other is slow (47,

63 48). In this framework, the spontaneous recovery of motor memory of field A is attributed to the

64 memory trace of the slow learning process, (45, 47). This memory trace is masked by the fast

65 adaptation process during the deadaptation period. Interestingly, the slow process has been

66 associated with the implicit component of adaptation while the fast process has been linked to the

67 explicit component (45).

68 Three major concepts reviewed up to this point bear some contradictions: 1) implicit adaptation and

69 its short-term retention are not impaired by aging (27), 2) spontaneous recovery is impaired in older

70 people (41), and 3) the slow process of adaptation, which determines spontaneous recovery,

71 corresponds to the implicit component of adaptation (45). In other words, if implicit adaptation is

72 unimpaired in older people and if it determines spontaneous recovery, then spontaneous recovery

73 cannot be different across age groups. Yet, it is unclear where the contradiction comes from as these

74 different studies have marked differences in protocol, which could affect the results. Implicit

75 adaptation level was obtained using a visuomotor rotation of the cursor feedback (27), whereas its

76 short-term retention was measured in a force-field paradigm (41). As it is known that perturbation

77 type influences implicit adaptation level (8, 14), this difference in perturbation type could be

78 responsible for this discrepancy. There is thus a need to test these three observations within a single

79 experiment. Therefore, we set out to measure both implicit adaptation and its retention via

80 spontaneous recovery in a single force field paradigm in both healthy young and older adults in order

81 to test four different hypotheses, reflecting previous research: 1) implicit adaptation levels at the end

82 of the adaptation period are similar across age groups (27); 2) spontaneous recovery is larger in

83 young than in older participants (41), 3) implicit adaptation at the end of the adaptation period is

84 correlated with the amount of spontaneous recovery (45) and, 4), as suggested by Trewartha and

85 colleagues, spontaneous recovery is related to explicit memory processes such as working memory

86 capacity. We expect that at least one of the three first hypotheses will be violated because, as

87 mentioned above, they are contradicting each other.

88 **Methods**

89 **Participants**

4

90   After signing the informed consent, 28 young adults (19-27, 23 ± 2, 12 male) and 21 older adults (60-

91   75, 67 ± 4.70, 10 male) participated in the study. We excluded one older subject from analysis due to

92   an error in task execution (wrong block order). All participants were right-handed as indicated by the

93   Edinburgh inventory (49) and were screened with general health and consumption habits

94   questionnaires. Based on the general health questionnaire, participants with events, diseases or

95   injuries that could affect the control of movement were excluded (e.g. head trauma). Based on the

96   consumption habits, participants using recreational drugs or having hazardous alcohol consumption

97   (more than 21 drinks per week for men or more than 14 for women) were excluded from the study.

98   No participants were excluded for these reasons. The older adults were assessed using the Mini-

99   Mental State Examination and all scored within normal limits (score ≥ 24, (50)). Approval was

100   obtained by the Ethics Committee Research UZ / KU Leuven. Participants received financial

101   compensation (€10/h).

102   Sample size was initially planned to reproduce the 20 participants per group as in Trewartha et al.

103   2014. We first included 20 older participants (recruited 21 but one was excluded due to error in the

104   experiment) and 21 young ones. Upon data analysis, we noticed that, on average, younger people

105   moved faster than older people in this paradigm despite the speed constraints (see below). We

106   recruited an additional 7 young participants that were instructed to move slower to match hand

107   velocity across age groups (as described below in the experimental paradigm).

108   **Experimental paradigm for the adaptation task**

109   Participants made center-out, reaching movements in the horizontal plane while holding a robotic

110   handle (KINARM End-Point Lab, BKIN Technologies). Hand position was represented by a white

111   cursor on a display and vision of the hand was occluded. Movement trajectories were sampled at

112   1000 Hz. At the beginning of each trial, participants had to move their cursor to a starting point in the

113   middle of the screen, after which a target appeared on one of eight possible locations (*Figure 1*)

114   spaced ten cm away from the starting point. Participants were instructed to slice through the target

115   by making a rapid, smooth reaching movement, avoiding any corrections. Once the movement

116   amplitude exceeded ten cm, cursor position froze, providing feedback about movement accuracy and

117   movement time. Movement times within 200 to 350ms resulted in a green cursor (for 5 young

118   participants we increased the time window to 400 – 550ms and for another 2 to 300 – 400ms to keep

119   average movement times the same for both age groups). Too slow movements caused the cursor to

120   turn blue and too fast movements resulted in an orange cursor. After feedback, the starting point

121   appeared, a new trial started, and the participants had to move their hand back to the starting

122   position. On each trial, two points could be earned: one for hitting the target (hand crosses through

123 the target) and one for applying the right speed. Participants were encouraged to collect as many

124 points as possible.

125 The task started with 72 baseline trials with reaches towards eight possible targets presented in

126 pseudo-random order (9 cycles of 8 different targets) and a white cursor (Figure 1). Participants then

127 continued with a perturbation phase (trials 73 – 281), during which a viscous force field (12 Ns/m)

128 was applied perpendicular to hand velocity and the cursor had a red color (cued trials). Subjects

129 received additional instructions, which were: "Initially, your cursor was a white dot, but from now on,

130 your cursor can turn red. At that moment, something special will happen, but you still have to try to

131 do the same thing, slice through the target with your cursor. A warning sign will be shown each time

132 your cursor changes color". Interspersed with these perturbation trials were 20 trials with a white

133 cursor (uncued trials), located at one of four possible locations. While the white cursor could be

134 considered as a cue, we decided to adopt the terminology of Morehead and colleagues (2015). In

135 uncued trials, participants could move straight ahead without interference of the force field and

136 were occasionally reminded of this. Participants were thus aware that uncued trials were similar to

137 baseline trials. For these trials, they were still instructed to bring the cursor to the target. The goal of

138 these trials was to measure the implicit after-effect over a single trial by requiring participants to

139 disengage any strategies that they might be using.

140 From trial 282 to 305, the force field was reversed, washing out the adaptation to the first

141 perturbation (Deadaptation in Fig.1). Despite this change in the direction of the perturbation, the

142 instruction to the participants remained unchanged: they were instructed to bring the cursor to the

143 target.

144 Lastly, retention was tested during an error-clamp phase (trials 306 – 369). In these trials, hand

145 trajectory was constrained to a straight line from the starting point to the target, by guiding the

146 handle between two stiff virtual walls (51). Visual feedback was provided during these trials.

147 Throughout the baseline and perturbation phase, we pseudo-randomly introduced error-clamp trials

148 to measure forces participants applied on the robot (8 during baseline and 20 during the

149 perturbation phase). While all 8 targets were used during the retention phase, only 4 of them were

150 used for the error-clamp trials during the baseline and perturbation phase. The direction of the force

151 field, clockwise or counterclockwise, was counterbalanced across subjects and three one-minute

152 breaks were provided (dashed grey vertical lines on Fig.1, after trials 54, 153 and 253).

153 **Experimental paradigm for the visual working memory task**

154 Given the importance of working memory for the explicit component of motor adaptation (28, 52)

155 and its potential link with the spontaneous recovery of motor memory (41), we decided to measure

156   working memory capacity in all participants. It was quantified with a computer-based task (27, 28,

157   52, 53). Sixteen white lined squares were presented in a circular array with, in the middle, a white

158   fixation cross. Three to six red circles were presented for two seconds randomly each in one of the

159   squares. The array disappeared leaving only the fixation cross for three seconds, where after the

160   squares returned with a question mark placed in one of them. Subjects had to indicate whether the

161   probed location had contained a red circle. After three seconds of response time, a new trial began.

162   Participants completed 48 trials (12 trials/condition) after eight practice trials. Two participants did

163   not perform this task.

Data processing and analysis

165   The x and y positions of the handle and x and y forces exerted on the handle were recorded at 1000

166   Hz. To combine the data from subjects who started with a clockwise force field with those who

167   started with a counterclockwise force field, all the signs of position and force data in de x-direction

168   for the clockwise condition were flipped.

169   For each baseline or perturbation trial, lateral deviation from the optimal trajectory from starting

170   point to target was calculated at peak velocity. Total adaptation level was quantified as the lateral

171   deviation of the last 80 cued trials during the perturbation phase. Implicit learning was quantified as

172   the average of the lateral deviation over the last 12 uncued trials during that phase.

173   In the error-clamp trials, the force subjects exerted on the channel walls (perpendicular to the

174   heading direction) at peak velocity was used as a measure of adaptation. A second method we used

175   to quantify learning in error-clamp trials was to compute the slope of the relationship between ideal

176   force during reaching and the exerted lateral force (41, 47). All trials from the perturbation phase

177   onward were corrected for baseline error per target location. Retention of implicit learning,

178   spontaneous recovery, was calculated as the average of the last 48 trials during the error-clamp

179   phase. These outcome measures were controlled for peak hand velocity, because movement speed

180   influences adaptation level (7). In addition, the slope of the relationship between ideal force and

181   actual generated force was used as a control measure for the level of spontaneous recovery

182   (adaptation index, 41).

183   Working memory capacity is calculated using the following formula: $K = S * (H - F)$. K is the memory

184   capacity, S is the size of the array, H is the observed hit rate and F is the false alarm rate (54). To

185   estimate K, we used the decision tree used by Vandevoorde et al. (28) and published as

186   supplementary   material   by   Saenen   et   al.   (53)   and   available   at

187   https://doi.org/10.6084/m9.figshare.23535396.v1 .

188 For statistical testing, we used t-tests with unequal variance in all tests. All statistical tests were also

189 reproduced with non-parametric tests but the results between the parametric and non-parametric

190 tests never differed in their conclusion. Effect sizes (Robust Cohen's d) and their confidence interval

191 (computed with bootstrap with 5000 iterations) were obtained from the meanEffectSize function in

192 Matlab. ANCOVA's were performed with the aoctool function in matlab (with the model 'parallel

193 lines'), fitting a separate line to each group, but constraining these lines to be parallel as we did not

194 expect a different relationship between the covariates and the dependent variables as a function of

195 age. For all the analyses, the α-level was set at 0.05.

196 To test for the absence of age-related difference in adaptation (hypothesis 1), we compared the

197 average lateral deviation at the end of the adaptation period over the last 80 cued field trials

198 (analysis 1), the average exerted force (measured at peak velocity) during the last 12 cued clamped

199 trials of the adaptation phase (analysis 2) and the implicit adaptation level measured as the average

200 lateral deviation over the last 12 uncued trials (analysis 3) between young and older participants with

201 an independent t-test with unequal variance. Additionally, an ANCOVA was used to check for any

202 influence of hand velocity on these outcomes. The outcome was set as dependent factor and hand

203 velocity for these specific trials were used as covariate. For each of the analyses, we also performed a

204 Bayesian independent T-test with a Cauchy distribution as prior (width of 0.707).

205 In analysis 4, we tested age-related differences in spontaneous recovery level measured either as the

206 average force exerted at peak velocity or as the average adaptation index computed over the last 48

207 clamped trials of the error-clamp period. These two outcomes were submitted to the same statistical

208 tests as in analysis 1. The force data was also submitted to a Bayesian independent Samples T-test in

209 JASP to test how compatible this data was with the hypothesis that spontaneous recovery was larger

210 in young than in older participants (one-sided t-test). The selected prior for this analysis was the

211 default Cauchy prior (Scale=0.707). The Bayesian analysis was performed in JASP (55).

212 To test possible correlation between adaptation levels at the end of the perturbation phase and

213 during the error-clamp period (hypothesis 3), implicit adaptation levels at the end of the

214 perturbation period (from analysis 3) and spontaneous recovery levels (from analysis 4) were

215 correlated via multilevel correlation (Analysis 5) from the correlation package in R (56). The different

216 levels corresponded to the different age groups.

217 In analysis 6, an additional ANCOVA was used with spontaneous recovery level (from analysis 4) as

218 dependent factor and implicit adaptation level at the end of learning (from analysis 3) as covariates.

219 In analysis 7, we conducted a Bayesian independent t-test in JASP (55). The prior was centered on the

220 effect size reported in the original study by Trewartha et al (d=0.8) and followed a Cauchy

221   distribution. We used three different scales for the prior in order to test the sensitivity of our results

222   to the width of the prior distribution. In this analysis, we test the hypothesis that the difference in

223   spontaneous recovery level between age groups is equal to d=0.8.

224   In analysis 8, working memory capacity was compared between young and older participants with an

225   independent t-test with unequal variance.

226   In analysis 9, we investigate the possible association (hypothesis 4) between working memory

227   capacity (from analysis 8) and spontaneous recovery levels (from analysis 4) via multilevel correlation

228   from the correlation package in R (56). The different levels corresponded to the different age groups.

229   All data can be found on the RDR repository of the KU Leuven: https://doi.org/10.48804/KMGKLH All

230   analysis scripts can be found at: 10.5281/zenodo.8284036

Results

Force-field adaptation does not decline with aging

The aim of this experiment was to measure the impact of aging on implicit adaptation and its short-term retention through spontaneous recovery. Participants made center-out reaching movements towards targets, while adapting to a force field that pushed their hand away perpendicular to the heading direction (cued trials with red cursor). With practice, subjects gradually decreased their error over the course of learning (*Figure 2A*). Total adaptation level at the end of the perturbation phase was similar across age groups (*Figure 2C*, mean ± SD, young: 2.23±1.43mm, older: 2.29±1.87mm, Analysis 1: $t(34.07)$= -0.13, p=0.89, Cohen's d = -0.011 CI=[-0.64,0.62]) and at the end of the deadaptation period (trials 298 to 305, $t(45.25)$=0.75, p=0.46, Cohen's d=0.378 CI=[-0.19, 1.02]).

Given the importance of hand speed in force-field adaptation, we checked that the hand speed was comparable across the two groups. At the end of the adaptation period, hand velocity was comparable (Fig.2C, young: 0.55±0.15 m/s, older: 0.56±0.12 m/s, $t(45.35)$= -0.156, p=0.87, d = 0.053, CI=[-0.46,0.76]). Controlling movement speed did not change the outcome of the analysis of the lateral deviation at the end of the adaptation period (ANCOVA, $F(1,45)$=0.0161, p=0.899). The corresponding Bayesian analysis suggested that there was moderate evidence of an absence of difference (BF = 0.293).

The force that participants exerted against the perturbation built up as participants learned to counteract the perturbation (*Figure 2B*). In error-clamp trials, the exerted force reached similar levels at the end of the perturbation phase for both groups (*Figure 2E*, mean ± SD, young: 3.6±1.2N, older: 3.4±1N, Analysis 2: $t(44.15)$= 0.46, p=0.65, Cohen's d = 0.16, CI=[-0.42,0.79]). For those trials, we also did not find any evidence that the velocity varied across age groups ($t(44.34)$= -0.89, p=0.38, Cohen's d = -0.104, CI=[-0.60,0.52]). Therefore, controlling for hand speed did not change the results (Analysis 2, ANCOVA: $F(1,45)$=1.84, p=0.18). The corresponding Bayesian analysis suggested that there was moderate evidence of an absence of difference (BF = 0.315).

In some trials (uncued trials), we warned the participants that the force field would be turned off in order to force participants to stop using any strategy to compensate for the perturbation and to measure implicit adaptation (8). In these trials, perpendicular error increased with continued learning (*Figure 2A*). Participants made reaching movements to four different target locations (ordinal directions, see figure 1). These trials were randomly presented throughout the perturbation phase, but in a fixed sequence. For some reason, participants from both groups exhibited different amounts of lateral deviation in function of target direction (Figure 2A). However, this effect of target direction was identical between the two age groups. We averaged the responses of the last 12 uncued trials

264   and compared these between our age groups (*Figure 2D, Analysis 3*). We could not find evidence for

265   a difference in implicit adaptation between young and older adults (mean±sd, young: -

266   11.96±3.70mm, older: -10.91±3.09mm, Analysis 3: t(44.76)= -1.07, p=0.29, Cohen's d = -0.24, CI=[-

267   0.83,0.33]). In those trials, we did not find any evidence that hand speed differed across groups

268   (young: 0.573±0.162 m/s, older: 0.609±0.149 m/s, t(43.00)= -0.785, p=0.4368, Cohen's d = -0.076,

269   CI=[-0.56,0.61]). This result remained the same after the implicit adaptation level was controlled for

270   movement speed (Analysis 3: ANCOVA: F(1,45)=2.18, p=0.146). The corresponding Bayesian analysis

271   suggested that there was anecdotal evidence of an absence of difference (BF =0.45).

272   **No evidence that spontaneous recovery declines with aging**

273   At the end of the experiment, lateral deviation of each movement was clamped to zero, ensuring

274   participants would always hit the target. This enabled us to measure the retention of implicit

275   adaptation without interference of trial-by-trial learning. Exerted force increased over time in the

276   same direction as during the perturbation phase, characteristic of spontaneous recovery (*Figure 3A*).

277   The average response of the last 48 clamp trials was compared between age groups (*Figure 3B*) and

278   we did not find any evidence for a difference between young and older adults (median, young:

279   0.88±0.73N, older: 1.01±1.5N, Analysis 4: t(25.46)= -0.35, p=0.73, Cohen's d = 0.036, CI=[-0.54,0.67]).

280   Note that this result is independent of which trials are analyzed. Performing a trial-by-trial analysis as

281   in Trewartha et al, no between-group differences remained significant after correction for multiple

282   comparisons (p<0.05/64). Similarly, analyzing all 64 trials from the spontaneous recovery period

283   provided the same statistical results (t(25.44)= -0.367, p=0.72, Cohen's d = 0.003 CI=[-0.58,0.71]).

284   We did not find any evidence that hand speed differed across groups (young: 0.53±0.14 m/s, older:

285   0.55±0.09 m/s, t(45.99)= -0.4, p=0.69, Cohen's d= 0.034, CI=[-0.46,0.78]), indicating we succeeded in

286   this aim.

287   Controlling movement speed did not change the result (Analysis 4: F(1,45)=0.138, p=0.71). In

288   addition, the adaptation index (Figure 3C), which was used in Trewartha et al. (41) , did not differ

289   between age groups either (young: 0.15 ± 0.1, older: 0.17 ± 0.23, Analysis 4: t(24.20)= -0.335,

290   p=0.7402, Cohen's d = 0.014, CI=[-0.56,0.65]).

291   To confirm these results, we performed a Bayesian analysis on the force data in order to test how

292   compatible our data was with the idea that the spontaneous recovery level was larger in young than

293   in older participants. There was moderate support (BF=4.44) for the idea that the spontaneous

294   recovery level was not larger in young than in older participants.

295   If the level of spontaneous recovery is linked to the level of adaptation at the end of the learning

296   period, the absence of age-related difference in spontaneous recovery is consistent with the absence

297   of age-related difference in implicit adaptation in this study (Fig.2). Indeed, we expect that people

298   with more implicit adaptation at the end of learning would exhibit more spontaneous recovery,

299   resulting in a positive correlation between the two. Therefore, we pooled the data for all participants

300   and correlated both measures while taking the two different groups into account (*Figure 4, Analysis*

301   *5*). A significant positive correlation was found between the level of implicit adaptation and the level

302   of spontaneous recovery (N = 48, r = 0.55, t(46)=4.42, p < 0.001).

303   Given this correlation, it might be that small differences in implicit adaptation level at the end of the

304   learning period can mask age-related effects in spontaneous recovery. That is, if older participants

305   had slightly larger implicit adaptation levels, it could compensate for a decrease in spontaneous

306   recovery. Therefore, we compared spontaneous recovery across age groups while controlling for

307   implicit adaptation levels (Analysis 6). Yet, this additional analysis further confirmed our previous

308   result and did not provide any evidence that spontaneous recovery level was smaller in older

309   participants (F(1,45)=1.317, p=0.2571). If anything, marginal means obtained in the ANCOVA tended

310   to indicate that, when controlling for implicit adaptation levels, older adults tended to exhibit more

311   spontaneous recovery than younger adults (young: 0.88N±0.73; older: 1.009±1.5, mean±SD).

312   **Combining the data of the original study and of the present conceptual replication favor the null**

313   **hypothesis.**

314   The effect size for the difference in force used between young and older subjects during spontaneous

315   recovery in the study of Trewartha was d=0.8 (personal communication from Trewartha). We use this

316   effect size as a prior with Cauchy distribution. In this case, a Bayes Factor (BF_{10}) larger than 1 would

317   favor the effect size found in the original study (favoring the hypothesis that the difference in

318   spontaneous recovery between young and old participants is as big as claimed by Trewartha et al.

319   (d=0.8)). A Bayes Factor smaller than 1 would indicate that the effect is smaller than in the original

320   study (favoring H0). As a sensitivity analysis, we tested different widths for the prior distribution

321   (narrow 0.5, medium: 0.707, wide: 1). In all cases, the posterior was closer to 0 than the prior, with

322   Bayes Factor (BF_{10}) yielding substantial evidence (BF10>3, 57) that the difference in spontaneous

323   recovery levels should be smaller than d=0.8 (BF_{01} = 6.89 for a default prior width = 0.707, BF_{01} =

324   7.33, narrow prior with SD = 0.5; BF_{01} = 7.3, wide prior with SD = 1.414). Overall, the hypothesis that

325   the effect of age on spontaneous recovery level is smaller than 0.8 was 6 to 7 times more likely than

326   an effect size of 0.8. In other words, the Bayesian analysis favored the hypothesis that the actual

327   effect of aging on spontaneous recovery was smaller than that of the original study with a median

328   effect size of 0 and a confidence interval of [-0.58, 0.56].

No correlation between explicit adaptation level and working memory capacity score

In the study of Trewartha et al. (2014), sponanteous recovery level were linked to cognitive processes such as explicit memory (their Fig.7). Therefore, we checked whether we could link any aspects of spontaneous recovery to explicit memory processes such as working memory capacity. In our sample, we tested working memory capacity in all our participants except two young adults. Older adults exhibited lower working memory capacity than younger adults (Analysis 8, t(42.26)= 3.5, p=0.0011, Cohen's d = 1.16, CI=[0.48,2]). Yet, this does not seem to affect the amount of spontaneous recovery as this was similar across age groups (Fig.3). In addition, we did not find any evidence that the amount of spontaneous recovery was correlated with the working memory capacity score (Analysis 9, Fig. 6, N = 46, r = -0.05, t(44)=-0.36, p = 0.72). This questions the link between memory processes and spontaneous recovery of motor adaptation.

Discussion

In this study, we tested whether aging influenced the ability to adapt reaching movements accordingly when movements were perturbed. Participants reached to targets while a force field perturbed their movements in an adaptation period. In some catch trials, participants were cued that the force field would be turned off in the subsequent trial (8). Any error in reaching direction in these trials was attributed to implicit adaptation. After a short de-adaptation period with a reversed force field, spontaneous recovery of motor memories of the adaptation period was tested by guiding the hand directly towards the targets in error clamp trials (47). Across age groups, we observed little difference in performance in this task. Both total adaptation and implicit adaptation were not impaired in older adults compared to their younger controls. In addition, we failed to replicate the observation of Trewartha and colleagues (41) and found that spontaneous recovery remained also unaffected by aging. Yet, implicit adaptation and spontaneous recovery levels were correlated independently of age groups, suggesting that spontaneous recovery is linked to the memory of implicit adaptation (45). In contrast to Trewartha et al. (41), we could not find any evidence that spontaneous recovery of motor memories were linked to memory processes.

Our results potentially resolve the contradiction that spontaneous recovery, but not implicit adaptation, was impaired with aging (27, 41). Indeed, the slow process of adaptation is believed to reflect the implicit process (12, 13) and the spontaneous recovery is linked to this slow process (45). It was therefore surprising that some studies found that the implicit component of adaptation was not affected by aging (22, 27, 33) but that the spontaneous recovery was (41), given that they come from the same process (45, 47).

362   The absence of age-related impairment in spontaneous recovery implies that as we age, we do not

363   get more forgetful of movements in the short-term. Indeed, spontaneous recovery is a measure of

364   short-term retention of the slow implicit process. Following the two-state model (47), the

365   spontaneous recovery results from the rapid decay of the fast state to zero in the error-clamp phase,

366   while the slow process still contains a memory trace of the motor memory acquired during the first

367   adaptation phase. This is consistent with the correlation between the amount of implicit adaptation

368   during learning and the amount of spontaneous recovery (Fig. 5). This is also consistent with the

369   findings of McDougle et al (45). Therefore, a decrease in spontaneous recovery could be due either

370   to worse implicit adaptation during learning (which we did not find) or smaller retention rate (58).

371   The absence of age-related difference in spontaneous recovery suggests that there is no evidence for

372   age-related deficits in either implicit adaptation or retention rate. This finding is in contrast to the

373   results reported by Trewartha et al (41) who found lower spontaneous recovery in older people.

374   Previous studies that quantified short-term retention in old and young adults gave mixed results. No

375   deficit in short-term retention measured after a one-minute break was reported in a visuomotor

376   rotation task (27). These authors investigated retention of visuomotor adaptation in two different

377   adaptation paradigms. First, one-minute breaks were inserted during regular visuomotor rotation

378   paradigm. In this case, there was no evidence of a difference in retention level of total adaptation

379   between young and old participants. Second, they used one-minute breaks during task-irrelevant

380   clamped feedback paradigm that is known to elicit pure implicit adaptation (1, 13, 59, 60). In this

381   case again, there was no evidence for a deficit in short-term retention of implicit adaptation.

382   However, one other study that measured the explicit component of visuomotor rotation by asking

383   participants to report their aiming direction found that older participants exhibited worse retention

384   of implicit adaptation (58). Yet, it is unclear why people would change the explicit report of their

385   aiming direction in a one-target task after a one-minute break if nothing happened during the break.

386   Similarly, an age-related deficit in the retention did occur in a gait adaptation paradigm (24) . These

387   authors suggested that the implicit, and not the explicit component of adaptation was impaired,

388   because larger forgetting was observed in older adults independently of whether a cognitive

389   distraction was presented during the gait adaptation period or not. Such a cognitive distractor would

390   have the ability to reduce the contribution of the explicit component. For this reason, the observed

391   effect was indirectly attributed to the implicit component of adaptation.

392   **Possible sources of discrepancy with the study of Trewartha.**

393   The fact that our results differ from the study of Trewartha et al. (41) might stem from one of the

394   small differences in protocol between our studies even though we tried to use a very similar protocol

395   to theirs. Yet, they differed in several aspects.

396   The experimental design of the forcefield task here used 8 radial targets from a central start position.

397   In contrast, the Trewartha study used alternating movements between two targets, with forces only

398   applied to movements in one direction. The impact of target number on age-related differences in

399   implicit motor adaptation (or absence thereof) remains unknown.   Our protocol had a more

400   extensive adaptation period (209 trials vs. 118 in Trewartha et al.), deadaptation phase (24 vs. 15)

401   and retention phase (63 vs. 22), while the baseline and de-adaptation phases were similar (baseline

402   73 vs. 52 trials and de-adaptation 24 vs 20). The longer adaptation period might have resulted in

403   more opportunity for the participants to learn the force field implicitly, which might have concealed

404   a learning deficit in the older adults that is then later reflected in the spontaneous recovery period.

405   However, Trewartha et al. did not observe any difference in adaptation level during learning.

406   The type of movement and allowed movement speed also differed across the studies. While our

407   participants had to slice through the target, those from Trewartha et al. had to stop on the target.

408   We allowed for a greater variability in hand velocity, allowing faster movements (0.3 – 0.5 m/s vs 0.3-

409   0.4 m/s in the Trewartha et al.). Yet, the hand velocity was matched between our group of young and

410   old participants. Because older adults tended to move slower, we asked a few young participants to

411   perform the experiment while adapting the accepted speed range. On average, our age groups

412   moved with the exact same velocity.

413   One additional difference lies in our sample. Trewartha et al. showed that, within their sample,

414   participants who scored high on an explicit memory task had better spontaneous recovery. So

415   maybe, our sample of older people all had very good cognitive memories. Yet, our sample of older

416   participants had worse working memory capacity than younger participants.

417   Finally, Trewartha measured explicit and implicit components in explicit and implicit memory tasks

418   and compared the results between age groups. Older adults scored less in both the explicit and

419   implicit memory tasks. We measure implicit adaptation within our adaptation paradigm during

420   learning and working memory in a separate task. This test of implicit adaptation could also have

421   influenced the outcomes of the study. We found no difference in implicit level even though older

422   adults had worse working memory capacity.

423   For all these reasons, our study represents a conceptual replication of the study by Trewartha et al.

424   2014 and not a direct/exact replication. If any of the factors identified as differences between our

425   study and that of Trewartha is responsible for the difference in outcomes, it means that the age-

426   related effect on spontaneous recovery, if it exists, is highly sensitive to the experimental conditions.

427   By employing multiple methodologies, conceptual replications provide a robustness test of the

428   findings. Our study suggests that the generalizability and robustness of the original results should be

429   considered with caution. The age-related difference in spontaneous recovery found by Trewartha

430   and colleagues might be true, but is likely dependent on the experimental conditions.

431   **Do explicit/cognition or implicit adaptation relate to spontaneous recovery**

432   Beyond the technical differences, there are also differences in the theoretical approaches between

433   the two studies. While Trewartha focused on the role of cognition on the spontaneous recovery, we

434   believe that implicit motor adaptation modulates spontaneous recovery. Indeed, Trewartha and

435   colleagues found that people who had "good" explicit memory had higher levels of spontaneous

436   recovery. Our attempt at a conceptual replication of this correlation failed as we did not find any

437   evidence that working memory capacity was linked to spontaneous recovery. The result of

438   Trewartha and colleagues is at odds with the study of Keisler and colleagues (61) who showed that a

439   secondary cognitive task disrupted the fast process but not the slow process responsible for

440   spontaneous recovery (45). They are also incompatible with the finding that patients with early-stage

441   Alzheimer's Disease exhibit a deficit in the fast process of motor adaptation but not in spontaneous

442   recovery or in the slow process (62). Our results rather agree with the results of Keisler than with

443   those of Trewartha. Indeed, we found that the amount of implicit adaptation measured during

444   learning correlated with the level of spontaneous recovery across participants. Future studies could

445   sample older participants based on their cognitive profiles (e.g., selecting older adults with more

446   prominent age-related impairments in working memory or set shifting in order to isolate how specific

447   cognitive attributes affect specific aspects of motor adaptation.

448   **Statistical view on this absence of replication**

449   Our study and the study of Trewartha provide conflicting results. Our Bayesian analyses aimed at

450   reconciling those conflicting results. The Bayesian analysis suggests that, given our data, the

451   influence of age on the spontaneous recovery of motor memories is very likely much smaller than

452   what was reported by Trewartha and colleagues (41). Yet, the Bayesian analysis does not prove that

453   there is no effect. It estimates that the effect size lies somewhere in an interval between -0.6

454   (medium effect size of larger spontaneous recovery for older people) and 0.55 (medium effect size

455   for a larger spontaneous recovery for younger people.

456   Yet, beyond such statistical arguments, our results are well aligned with the observation that the

457   spontaneous recovery of motor memories depends on the slow implicit component of motor

458   adaptation (45, 47, 61) and that this component is not affected by aging (20–22, 27, 29, 31, 34, 38,

459   39). The results of Trewartha and colleagues are at odds with this theory, which motivated our

460   conceptual replication attempt.

461 **Limitations of the study**

462 In this study, we measured the amount of implicit adaptation by asking people to disengage from

463 learning as instructed by a color cue and a warning sign. While other studies have used a similar

464 approach (8, 27), this method assumes that participants can effectively disengage explicit strategies,

465 which we cannot check. In addition, the implicit component of motor adaptation is quantified as the

466 distance participants deviated from the straight trajectory. However, short-term retention was

467 measured by the force that was exerted perpendicular to the heading direction. This difference in

468 units makes direct comparison between the two measures difficult. Another way of separating

469 implicit from explicit learning is described by Schween et al. (14). Implicit adaptation level was

470 determined with 'No Push'- trials, where participants were instructed to ignore the force field and to

471 not push against it. Total adaptation, including the explicit component, was measured in 'Push'-trials,

472 which had an extra reminder to push against the force field. The difference in exerted force is

473 attributed to the explicit component of motor adaptation. The results indicate that in a 'Push'-trial,

474 participants apply more force and in a 'NoPush'-trial less force, as compared to a regular trial.

475 Therefore, our study could have benefited from such an assessment.

476 Our Bayesian analysis suggests that the maximum effect size should be much smaller than

477 anticipated based on the study of Trewartha. This means that we only have 60% power to detect an

478 effect if there is one of d=0.6. This should motivate future studies to include more participants as we

479 now have a better estimate of the possible effect size range.

480 Finally, the group of older participants exhibited much more inter-subject variability than the group

481 of younger participants. This is typical in aging studies but would need to be tackled to get a better

482 estimate of the spontaneous recovery of these older participants.

483 **Conclusion**

484 We attempted a conceptual replication of the effect of age on spontaneous recovery as

485 demonstrated by Trewartha and colleagues but could not replicate their results as we failed to find

486 evidence for a difference in spontaneous recovery between young and old participants. The current

487 results are more in line with the idea that spontaneous recovery depends on the retention of implicit

488 adaptation and that implicit adaptation is not affected by aging.

489

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636

637   Legends

638   *Figure 1: Paradigm. A change in cursor color indicated presence (cued) or absence (uncued) of a force field. Interspersed*
639   *throughout the baseline and perturbation phase, were error clamp trials. Eight targets (open circles) were displayed, of*
640   *which only four (filled black circles) were used for the uncued trials during the perturbation phase and error clamp trials*
641   *during baseline and perturbation phase.*

642   *Figure 2: Total adaptation level did not decline with aging. **A** Lateral deviation from the optimal trajectory at peak velocity*
643   *for young (blue) and older adults (orange) over the course of baseline and perturbation phase. Interspersed with these*
644   *perturbation trials were uncued baseline trials (filled circles) where no perturbation was applied. **B** Exerted force*
645   *perpendicular to heading direction at peak velocity during baseline and perturbation phase for young (blue) and older adults*
646   *(orange). **C** Lateral deviation during the last 80 field trials from the perturbation phase and the corresponding hand velocity.*
647   ***D** Lateral deviation during the last 12 uncued trials from the perturbation phase and the corresponding hand velocity. **E.***
648   *Exerted force during the last 12 error clamp trials from the perturbation phase and the corresponding hand velocity. For*
649   *panels C, D and E, each dot represents the mean data from one individual. Error bar represents mean and standard error.*
650   *For all panels, data from 28 young and 20 older participants are presented.*

651   *Figure 3: Spontaneous recovery did not decline with aging. **A** Exerted force at peak velocity during the error-clamp phase for*
652   *young (blue) and older adults (orange). Each dot represents the average force exerted by the individuals from an age group*
653   *for a single trial. **B** Exerted force during the last 48 trials of the error-clamp phase. **C** Adaptation index for the last 48 trials of*
654   *the error-clamp phase. For panels B and C, each dot represents the mean data from one individual. Error bar represents*
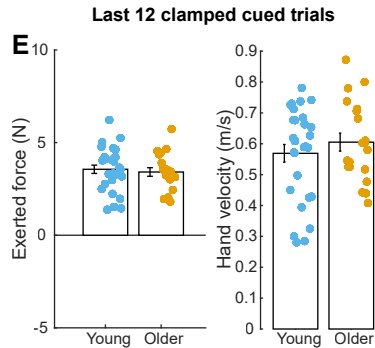655   *mean and standard error. For all panels, data from 28 young and 20 older participants are presented.*
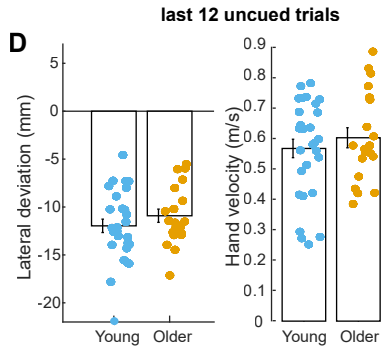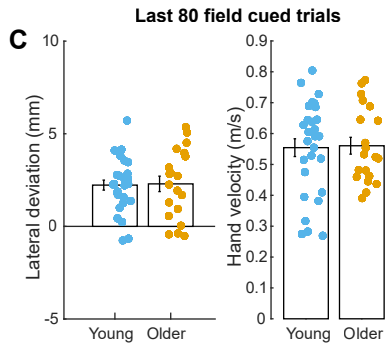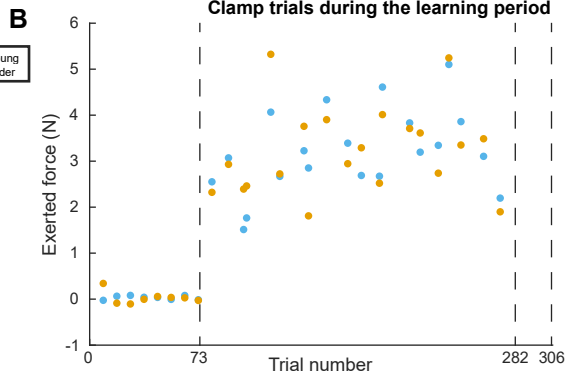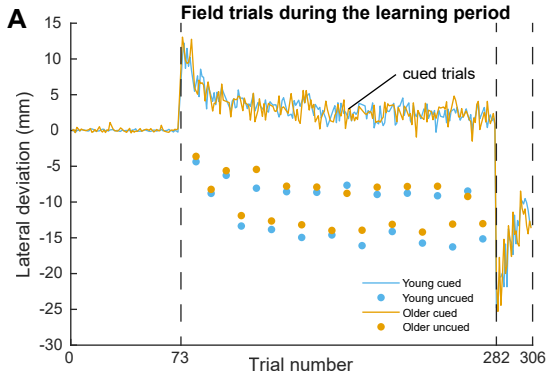
656   *Figure 4: Implicit adaptation (data from figure 2.D) and spontaneous recovery (data from figure 3.B) are correlated (N = 48).*
657   *To facilitate interpretation, implicit level was converted to positive values, such that participants with a higher implicit*
658   *adaptation level have a larger lateral deviation. Each dot represents the data from one individual. Data from both groups*
659   *were combined thanks to multilevel correlation. Regression line was obtained with robustfit method in Matlab.*
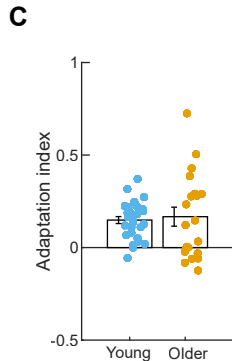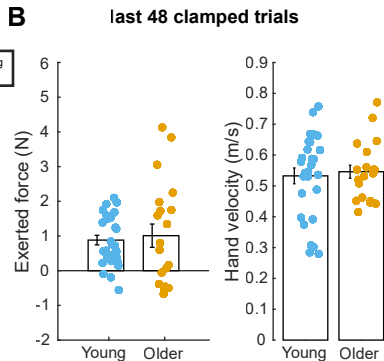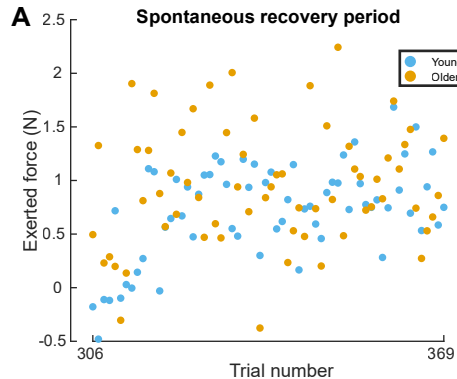
660   *Figure 5: Output of the Bayesian analysis. The Bayesian analysis takes the previous data as the prior (centered on d=0.8,*
661   *Trewartha et al. 2014) and computes the posterior based on the data of the present study.*
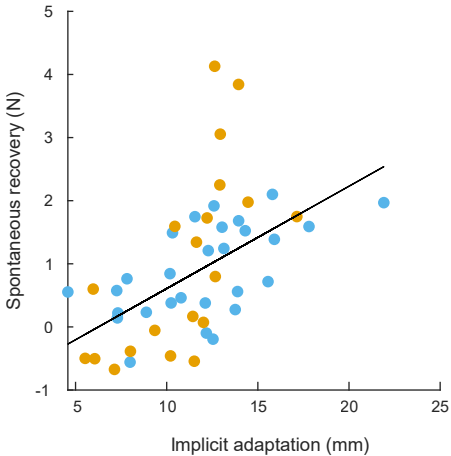
662   *Figure 6: Spontaneous recovery level was not correlated with spatial working memory capacity score (N = 46). Each dot*
663   *represents the data from one individual. Data from both groups were combined thanks to multilevel correlation. Regression*
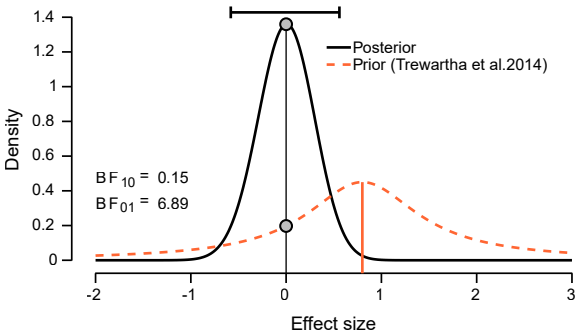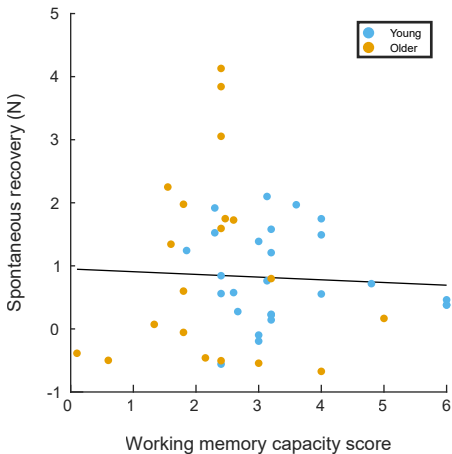664   *line was obtained with robustfit method in Matlab.*

665

A Field trials during the learning period

B Clamp trials during the learning period

C Last 80 field cued trials

D last 12 uncued trials

E Last 12 clamped cued trials

A Spontaneous recovery period

B last 48 clamped trials

C

Median: 0
95% CI: [-0.581, 0.559]

$BF_{10} = 0.15$
$BF_{01} = 6.89$

Limited influence of aging on implicit adaptation and its short-term retention.

Adaptation

Spontaneous Recovery

De-adaptation