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

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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 sensory prediction error) and explicit learning
3 (intentional adjustment to reduce target error). The explicit component is thought to be fast adapting,
4 while the implicit one is slow. The dynamic integration of these components can lead to an adaptation
5 rebound, called spontaneous recovery: the trace of a first, longer learned adaptation reappears after
6 it is extinguished by a shorter period of de-adaptation. The slow implicit process is still decaying from
7 the first adaptation, resulting in the before mentioned adaptation rebound. Trewartha et al. (2014)
8 found that older adults show less spontaneous recovery than their younger controls, indicating
9 impairments in implicit learning. This is in disagreement with evidence suggesting that the implicit
10 component and its retention does not decline with aging.

11 To clarify this discrepancy, we performed a conceptual replication of that result. Twenty-eight healthy
12 young and 20 healthy older adults learned to adapt to a forcefield perturbation in a paradigm known
13 to elicit spontaneous recovery. Both groups adapted equally well to the perturbation. Implicit
14 adaptation of the older subjects was indistinguishable from their younger counterparts. In addition,
15 we failed to replicate the result of Trewartha et al. (2014) and found that the spontaneous recovery
16 was also similar across groups. Our results reconcile previous studies by showing that both
17 spontaneous recovery and implicit adaptation are unaffected by aging.

Introduction

19 Young healthy adults can adapt to a change in the environment and optimize their reaching
20 performance (Morehead and Orban de Xivry 2021; Shadmehr et al. 2010). Such adaptation process of
21 upper limb movements is studied in the laboratory via perturbation of the visual feedback about the
22 moving direction of the hand (Krakauer et al. 2005; Orban de Xivry and Lefèvre 2015), by shifting the
23 visual field thanks to prism goggles (Welch 1969) or by applying a force on the moving arm (Lackner
24 and DiZio 1994; Shadmehr and Mussa-Ivaldi 1994). For any of these perturbations, young participants
25 can readily decrease the effect of the perturbation on their reaching performance thanks to a
26 combination of explicit strategies and implicit adaptation (Morehead et al. 2015; Taylor et al. 2014;
27 Taylor and Ivry 2011; Welch et al. 1974). Implicit adaptation is the incidental updating driven by
28 sensory prediction error and occurs gradually (Mazzoni and Krakauer 2006; Morehead et al. 2017;
29 Taylor et al. 2014). Explicit adaptation consists of the application of cognitive strategies to reduce
30 target error and reduces errors rapidly (Morehead and Orban de Xivry 2021). The explicit component
31 contributes more to total adaptation for visuomotor rotation than for force-field adaptation. Learning

32   to counteract a force field is largely an implicit process with only a small explicit component (Schween

33   et al. 2020).

34   Older adults show lower levels of total motor adaptation than young adults (Aucie et al. 2021; Bakkum

35   et al. 2021; Bock 2005; Cressman et al. 2010; Hegele and Heuer 2010; Malone and Bastian 2015;

36   Sombric and Torres-Oviedo 2021)(Buch et al. 2003; Heuer and Hegele 2008; Li et al. 2021; Seidler 2006,

37   2007; Vandevoorde and Orban de Xivry 2019). Recent evidence suggest that this impairment in motor

38   adaptation is specific to the explicit component of adaptation (Bock and Girgenrath 2006; Hegele and

39   Heuer 2010, 2013; Heuer and Hegele 2008; Li et al. 2021; Vandevoorde and Orban de Xivry 2019, 2020;

40   Wolpe et al. 2020) and that the implicit component of motor adaptation elicited by a visuomotor

41   adaptation and its short-term retention remains unimpaired up to 60-70 years old (Huang et al. 2017;

42   Reuter et al. 2020; Tsay et al. 2023; Vachon et al. 2020; Vandevoorde and Orban de Xivry 2019).

43   Few studies have investigated the effect of age on force-field perturbation (Cesqui et al. 2008; Huang

44   and Ahmed 2014; Kitchen and Miall 2021; Reuter et al. 2018; Trewartha et al. 2014). Little difference

45   has been found during adaptation to force-field perturbation (Huang and Ahmed 2014; Trewartha et

46   al. 2014). Yet, the explicit and implicit components of adaptation have never been measured in these

47   studies. While we know that the contribution of explicit strategies to force-field adaptation is small

48   (Schween et al. 2020), it is not null. Therefore, it remains unknown whether the implicit component of

49   motor adaptation remains unaffected in older people during a force-field adaptation task.

50   Interestingly, one study reported a very specific age-related impairment in force-field adaptation. That

51   is, while initial adaptation was unimpaired with age, its short-term retention as measured by

52   spontaneous recovery of adaptation was impaired (Trewartha et al. 2014).

53   Spontaneous recovery occurs when motor adaptation to some perturbation A, which are then hidden

54   from view due to adaptation of a second perturbation B, reappear without any additional exposure to

55   perturbation A (Coltman et al. 2019; Ethier et al. 2008; Kojima et al. 2004; McDougle et al. 2015;

56   Sarwary et al. 2018; Smith et al. 2006). It suggests that the motor memory of the adaptation to

57   perturbation A is not washed out by adaptation to perturbation B but is retained. Therefore, such

58   spontaneous recovery of motor memories linked to perturbation A represents a proxy for short-term

59   retention of the associated motor memory (Smith et al. 2006).

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

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

62   (Kording et al. 2007; Smith et al. 2006). In this framework, the spontaneous recovery of motor memory

63   of field A is attributed to the slow learning process, which is not washed out by the few deadaptation

64   trials whilst also forgetting rapidly (McDougle et al. 2015; Smith et al. 2006). Interestingly, the slow

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65   process has been associated with the implicit component of adaptation while the fast process has been

66   linked to the explicit component (McDougle et al. 2015).

67   Three major concepts reviewed up to here bear some contradictions: 1) implicit adaptation and its

68   short-term retention are not impaired by aging (Vandevoorde and Orban de Xivry 2019), 2)

69   spontaneous recovery is impaired in older people (Trewartha et al. 2014), and 3) the slow process of

70   adaptation, which determines spontaneous recovery, corresponds to the implicit component of

71   adaptation (McDougle et al. 2015). Yet, it is unclear where the contradiction comes from as these

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

73   adaptation level was obtained using a visuomotor rotation of the cursor feedback (Vandevoorde and

74   Orban de Xivry 2019), whereas its short-term retention was measured in a force-field paradigm

75   (Trewartha et al. 2014). It is known that perturbation type influences implicit adaptation level

76   (Morehead et al. 2015; Schween et al. 2020), this difference in perturbation type could be responsible

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

78   Therefore, we set out to measure both implicit adaptation and its retention via spontaneous recovery

79   in a single force field paradigm in both healthy young and older adults in order to test three different

80   hypotheses: 1) implicit adaptation levels at the end of the adaptation period are similar across age

81   groups; 2) spontaneous recovery is different across age groups, and 3) implicit adaptation at the end

82   of the adaptation period is correlated with the amount of spontaneous recovery.

Methods

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Participants

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

86   75, 67 ± 4.70, 10 male) participated in the study. We excluded one older subject from analysis due to

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

88   Edinburgh inventory (Oldfield 1971) and were screened with general health and consumption habits

89   questionnaires. The older adults were assessed using the Mini-Mental State Examination and all scored

90   within normal limits (score ≥ 24, (Folstein et al. 1975)). Approval was obtained by the Ethics Committee

91   Research UZ / KU Leuven. Participants received financial compensation (€10/h).

Experimental paradigm

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93   Participants made center-out, horizontal reaching movements while holding a robotic handle (KINARM

94   End-Point Lab, BKIN Technologies). Hand position was represented by a white cursor on a display and

95   vision of the hand was occluded. Movement trajectories were sampled at 1000 Hz. At the beginning of

96   each trial, participants had to move their cursor to a starting point in the middle of the screen, after

97   which a target appeared on one of eight possible locations (*Figure 1*) spaced ten cm away from the

98   starting point. Participants were instructed to slice through the target by making a rapid, smooth

99   reaching movement, avoiding any corrections. Once the movement amplitude exceeded ten cm,

100   cursor position froze, providing feedback about movement accuracy and movement time. Movement

101   times within 200 to 350ms resulted in a green cursor (for 5 young participants we increased the time

102   window to 400 – 550ms and for another 2 to 300 – 400ms to keep average movement times the same

103   for both age groups). Too slow movements caused the cursor to turn blue and too fast movements

104   resulted in an orange cursor. After feedback, the starting point appeared and a new trial started. On

105   each trial, two points could be earned: one for hitting the target and one for applying the right speed.

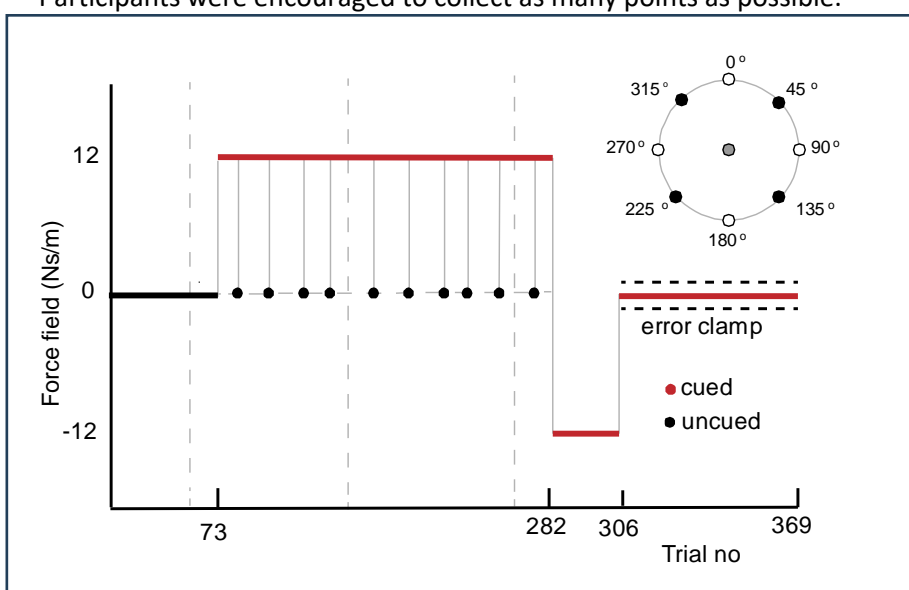106   Participants were encouraged to collect as many points as possible.

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

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

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

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

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

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

117   cursor can turn red. At that moment, something special will happen, but you still have to try to do the

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

119   cursor changes color". Interspersed with these perturbation trials were trials with a white cursor

120   (uncued trials), located on one of four possible locations. Participants could move straight ahead

121   without interference of the force field and were occasionally reminded of this. From trial 282 to 305,

122   the force field was reversed, washing out the adaptation to the first perturbation. Lastly, retention was

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123   tested during an error-clamp phase (trials 306 – 369). Hand trajectory was constrained to a straight

124   line from the starting point to the target, by guiding the handle through a channel. Throughout the

125   baseline and perturbation phase, we pseudo-randomly introduced error-clamp trials to measure

126   forces participants applied on the robot. Direction of the force field, clockwise or counterclockwise,

127   was counterbalanced across subjects and three one-minute breaks were provided (after trials 54, 153

128   and 253).

129   Given the importance of working memory for the explicit component of motor adaptation (Christou et

130   al. 2016; Vandevoorde and Orban de Xivry 2020) and its potential link with the spontaneous recovery

131   of motor memory (Trewartha et al. 2014), we decided to measure working memory capacity in all

132   participants. It was quantified with a computer-based task (Christou et al. 2016; Saenen et al. 2022;

133   Vandevoorde and Orban de Xivry 2019, 2020). Sixteen white lined squares were presented in a circular

134   array with, in the middle, a white fixation cross. Three to six red circles were presented for two seconds

135   randomly each in one of the squares. The array disappeared leaving only the fixation cross for three

136   seconds, where after the squares returned with a question mark placed in one of them. Subjects had

137   to indicate whether the probed location had contained a red circle. After three seconds of response

138   time, a new trial began. Participants completed 48 trials (12 trials/condition) after eight practice trials.

139   Two participants did not perform this task.

140   **Data analysis**

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

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

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

144   clockwise condition were flipped. For each field trial, lateral deviation from the optimal trajectory from

145   staring point to target was calculated at peak velocity. In the error-clamp trials, the force subjects

146   exerted on the channel walls (perpendicular to the heading direction) at peak velocity was used as a

147   measure of adaptation. A second method we used to quantify learning in error-clamp trials was to

148   compute the slope of the relationship between ideal force during reaching and the exerted lateral

149   force (Smith et al. 2006; Trewartha et al. 2014). All trials from the perturbation phase onward were

150   corrected for baseline error per target location.

151   Total adaptation level was quantified as the perpendicular error of the last 80 cued trials during the

152   perturbation phase. Implicit learning was quantified as the average of the last 12 uncued trials during

153   that phase. Retention of implicit learning, spontaneous recovery, was calculated as the average of the

154   last 48 trials during the error-clamp phase. These outcome measures were controlled for peak hand

155   velocity, because movement speed influences adaptation level (Shadmehr and Mussa-Ivaldi 1994). In

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156 addition, the slope of the relationship between ideal force and actual generated force was used as a

157 control measure for the level of spontaneous recovery (adaptation index, Trewartha et al. 2014).

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

159 capacity, S is the size of the array, H is the observed hit rate and F is the false alarm rate (Vogel et al.

160 2005). To estimate K, we used the decision tree used by Vandevoorde et al. (2020) and published as

161 supplementary   material   by   Saenen   et   al.   (2022)   and   available   at

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

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

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

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

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

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

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

169 a different relationship between the covariates and the dependent variables in function of age. For all

170 the analyses, the α-level was set at 0.05.

171 In analysis 1, perpendicular error at the end of the first learning period (last 80 cued field trials) was

172 compared between young and older participants with an independent t-test with unequal variance.

173 Additionally, an ANCOVA was used to check for any influence of hand velocity on these outcomes. The

174 outcome was set as dependent factor and hand velocity for these specific trials were used as covariate.

175 In analysis 2, the same statistical analyses were performed for the exerted force at the end of the

176 learning period (last 12 cued clamped trials) as in analysis 1.

177 In analysis 3, the same statistical analyses were performed for the implicit adaptation level (last 12

178 uncued trials) as in analysis 1.

179 In analysis 4, spontaneous recovery level (force exerted during the last 48 clamped trials of the

180 spontaneous recovery period) and the adaptation index (averaged ove same trials) were submitted to

181 the same statistical tests as in analysis 1. The force data was also submitted to a Bayesian independent

182 Samples T-test in JASP in order to test how compatible this data was with the hypothesis that

183 spontaneous recovery was larger in young than in older participants (one-sided t-test). The selected

184 prior for this analysis was the default Cauchy prior (Scale=0.707). The Bayesian analysis was performed

185 in JASP (JASP Team 2023).

186 In analysis 5, implicit learning and spontaneous recovery levels were correlated via multilevel

187 correlation from the correlation package in R (Makowski et al. 2020).

188   In analysis 6, an additional ANCOVA was used with spontaneous recovery level as dependent factor

189   and implicit adaptation level at the end of learning as covariates.

190   In analysis 7, we conducted a Bayesian independent t-test in JASP (JASP Team 2023). The prior was

191   centered on the effect size reported in the original study by Trewartha et al (d=0.8) and followed a

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

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

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

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

196   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 2B*, 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]). Given the importance of hand speed in force-field adaptation, we checked that the hand speed was comparable across the two groups (Fig.1C, 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 this analysis (ANCOVA, F(1,45)=0.0161, p=0.899).

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 2D*, 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).

In some trials (uncued trials), we warned the participants that the force field would be turned off in order to forced participants to stop using any strategy to compensate for the perturbation and to measure implicit adaptation (Morehead et al. 2015). 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 amount of lateral deviations 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 and compared these between our age groups (*Figure 2E, Analysis 3*). We could not find evidence for a difference in implicit adaptation between young and older adults (mean±sd, young: -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=[-0.83,0.33]). In those trials, we did not find any evidence that hand speed differed across groups (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, CI=[-

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230   0.56,0.61]). This result remained the same after the implicit adaptation level was controlled for

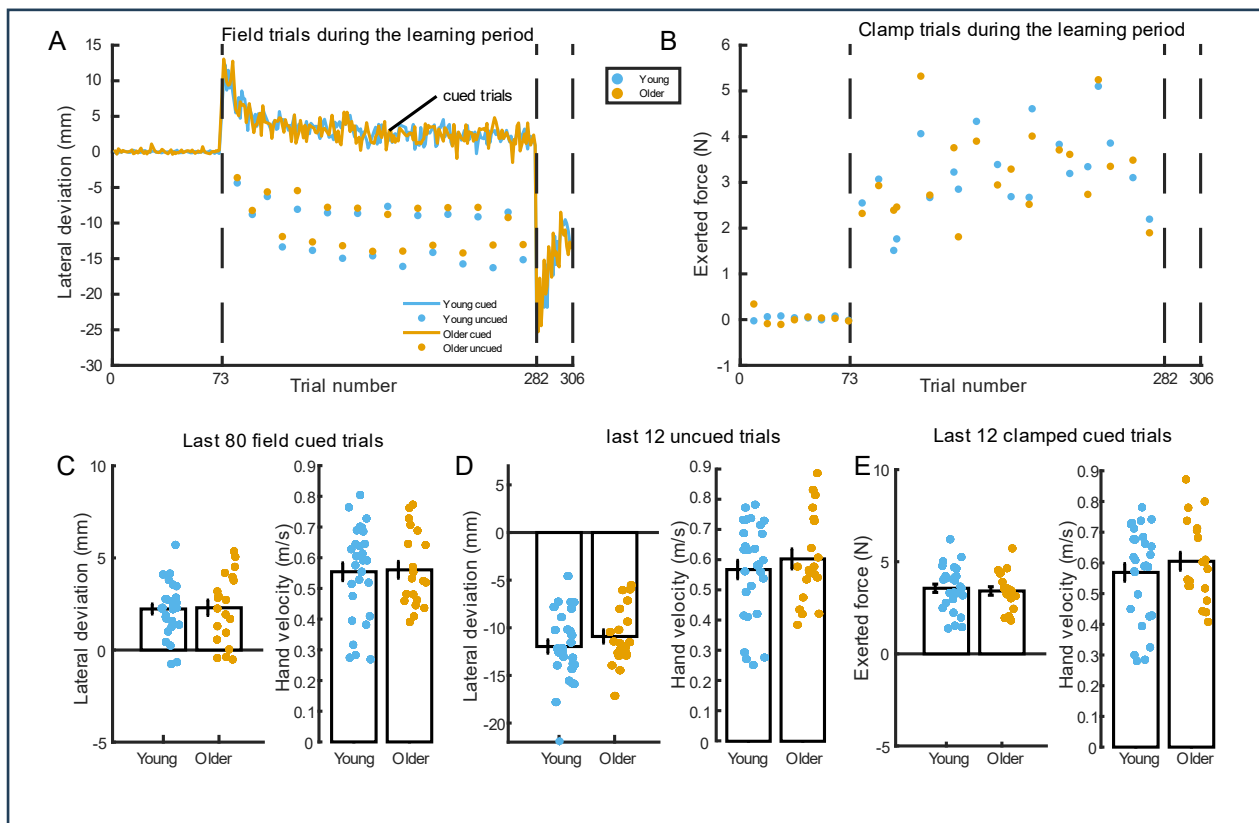231   movement speed (Analysis 3: ANCOVA: $F_{(1,45)}=2.18$, p=0.146).

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

No evidence that spontaneous recovery declines with aging

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

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

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

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

247   average response of the last 48 clamp trials were compared between age groups (*Figure 3B*) and we

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

249   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]).

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

251   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

252   this aim.

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

254   the adaptation index (Figure 3C), which was used in Trewartha et al. (2014) , did not differ between

255   age groups either (young: 0.15 ± 0.1, older: 0.17 ± 0.23, Analysis 4: t(24.20)= -0.335, p=0.7402, Cohen's

256   d = 0.014, CI=[-0.56,0.65]).

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

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

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

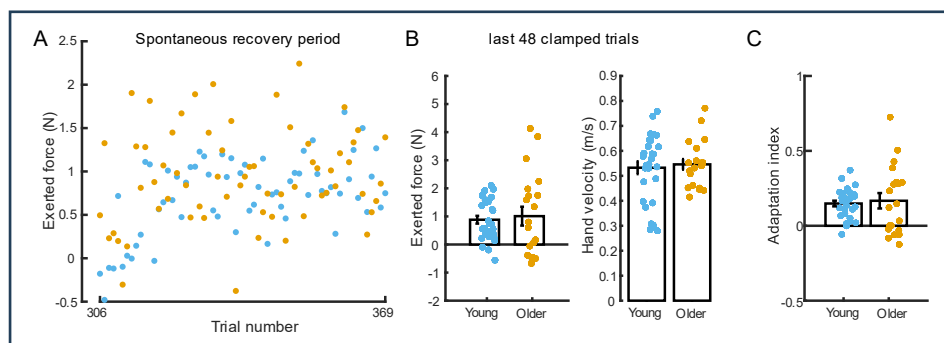260   recovery level was not larger in young than in older participants.

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262   *Figure 3: Spontaneous recovery did not decline with aging. **A** Exerted force at peak velocity during the error-clamp phase for*
263   *young (blue) and older adults (orange). Each dot represents the average force exerted by the individuals from an age group*
264   *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*
265   *the error-clamp phase. For panels B and C, each dot represents the mean data from one individual. Error bar represents mean*
266   *and standard error. For all panels, data from 28 young and 20 older participants are presented.*

267   This failure to replicate the result of Trewartha et al. is consistent with the fact that we did not find

268   any evidence for a difference in implicit adaptation between the two age groups in this study (Fig.2)

269   and in previous studies (Vandevoorde and Orban de Xivry 2019, 2021) if the level of spontaneous

270   recovery is linked to the level of adaptation at the end of the learning period. Indeed, we expect that

271   people with more implicit adaptation at the end of learning exhibit more spontaneous recovery,

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

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

274   *5*). A significant positive correlation was found between the level of implicit adaptation and the level

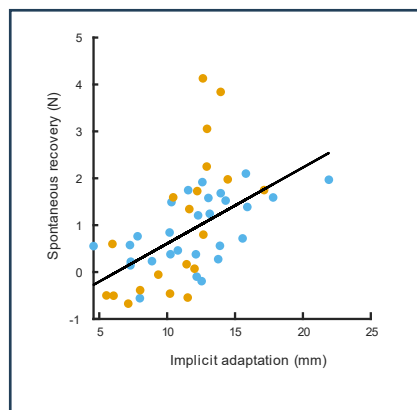275   of spontaneous recovery (N = 48, r = 0.55, t(46)=4.42, p < 0.001).

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Figure 4: Implicit adaptation (data from figure 2.D) and spontaneous recovery (data from figure 3.B) are correlated (N = 48). To facilitate interpretation, implicit level was converted to positive values, such that participants with a higher implicit adaptation level have a larger lateral deviation. Each dot represents the data from one individual. Data from both groups were combined thanks to multilevel correlation. Regression line was obtained with robustfit method in Matlab.

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

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

283   slightly larger implicit adaptation levels, it could compensate for a decrease in spontaneous recovery.

284   Therefore, we compared spontaneous recovery across age groups while controlling for implicit

285   adaptation levels (Analysis 6). Yet, this additional analysis further confirmed our previous result and

286   did not provide any evidence that spontaneous recovery level was smaller in older participants

287     $(F(1,45)=1.317, p=0.2571)$. If anything, marginal means obtained in the ANCOVA tended to indicate

288   that, when controlling for implicit adaptation levels, older adults tended to exhibit more spontaneous

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

290   **Combined data of the original study and the replication favor the null hypothesis.**

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

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

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

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

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

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

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

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

299   Bayes Factor (BF_{10}) yielding substantial evidence (BF10>3, Dienes 2014) that the difference in

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

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

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

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

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

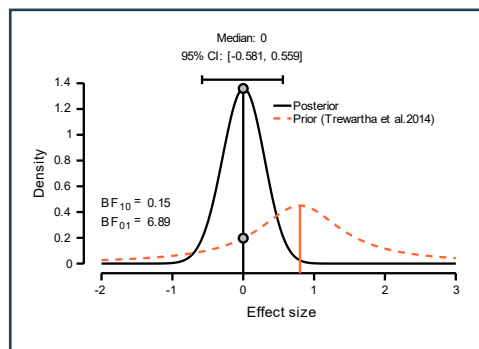305   effect size of 0 and a confidence interval of [-0.58, 0.56].

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Figure 5: Output of the Bayesian analysis. The Bayesian analysis takes the previous data as the prior (centered on d=0.8, Trewartha et al. 2014) and computes the posterior based on the data of the present study.
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309   **No correlation between explicit adaptation level and working memory capacity score**

310   In the study of Trewartha et al. (2014), sponanteous recovery level were linked to cognitive processes

311   such as explicit memory (their Fig.7). Therefore, we checked whether we could link any aspects of

312   spontaneous recovery to explicit memory processes such as working memory capacity. In our sample,

313   we tested working memory capacity in all our participants except two young adults. Older adults

314   exhibited lower working memory capacity than younger adults (t(42.26)= 3.5, p=0.0011, Cohen's d =

315   1.16, CI=[0.48,2]). Yet, this does not seem to affect the amount of spontaneous recovery as this was

316   similar across age groups (Fig.3). In addition, we did not find any evidence that the amount of

317   spontaneous recovery was correlated with the working memory capacity score (Fig. 6, N = 46, r = -0.05,

318   t(44)=-0.36, p = 0.72). This questions the link between memory processes and spontaneous recovery
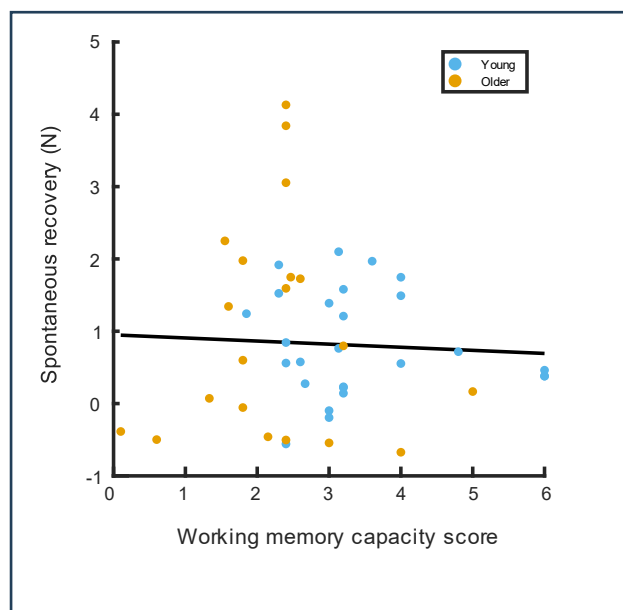
319   of motor adaptation.

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Figure 6: Spontaneous recovery level was not correlated with spatial working memory capacity score (N = 46). Each dot represents the data from one individual. Data from both groups were combined thanks to multilevel correlation. Regression line was obtained with robustfit method in Matlab.

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 (Morehead et al. 2015). 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 (Smith et al. 2006). 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 (2014) 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 (McDougle et al. 2015). In contrast to Trewartha et al. (2014), 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 (Trewartha et al. 2014; Vandevoorde and Orban de Xivry 2019). Indeed, the slow process of adaptation is believed to reflect the implicit process (Mazzoni and Krakauer 2006; Morehead et al. 2017) and the spontaneous recovery is linked to this slow process (McDougle et al. 2015). It was therefore surprising that some studies found that the implicit component of

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344 adaptation was not affected by aging (Heuer and Hegele 2008; Huang et al. 2017; Vandevoorde and

345 Orban de Xivry 2019) but that the spontaneous recovery was (Trewartha et al. 2014), given that they

346 come from the same process (McDougle et al. 2015; Smith et al. 2006).

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

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

349 term retention of the slow implicit process. Following the two-state model (Smith et al. 2006), the

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

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

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

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

354 findings of McDougle et al (2015). Therefore, a decrease in spontaneous recovery could be due either

355 to worse implicit adaptation during learning (which we did not find) or smaller retention rate (Bindra

356 et al. 2021). The absence of age-related difference in spontaneous recovery suggests that there is no

357 evidence for an age-related deficits in either implicit adaptation or retention rate. This finding is in

358 contrast to the results reported by Trewartha et al (2014) who found lower spontaneous recovery in

359 older people.

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

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

362 rotation task (Vandevoorde and Orban de Xivry 2019). These authors investigated retention of

363 visuomotor adaptation in two different adaptation paradigms. First, one-minute breaks were inserted

364 during regular visuomotor rotation paradigm. In this case, there was no evidence of a difference in

365 retention level of total adaptation between young and old participants. Second, they used one-minute

366 breaks during task-irrelevant clamped feedback paradigm that is known to elicit pure implicit

367 adaptation (Avraham et al. 2021; Kim et al. 2019; Morehead et al. 2017; Morehead and Orban de Xivry

368 2021). In this case again, there was no evidence for a deficit in short-term retention of implicit

369 adaptation. However, one other study that measured the explicit component of visuomotor rotation

370 by asking participants to report their aiming direction found that older participants exhibited worse

371 retention of implicit adaptation (Bindra et al. 2021). Yet, it is unclear why people would change the

372 explicit report of their aiming direction in a one-target task after a one-minute break if nothing

373 happened during the break. Similarly, an age-related deficit in the retention did occur in a gait

374 adaptation paradigm (Malone and Bastian 2015) . These authors suggested that the implicit, and not

375 the explicit component of adaptation was impaired, because larger forgetting was observed in older

376 adults independently of whether a cognitive distraction was presented during the gait adaptation

377 period or not. Such a cognitive distractor would have the ability to reduce the contribution of the

378   explicit component. For this reason, the observed effect was indirectly attributed to the implicit
379   component of adaptation.

Possible sources of discrepancy with the study of Trewartha.

381   The fact that our results differ from the study of Trewartha et al. (Trewartha et al. 2014) might stem
382   from one of the small differences in protocol between our studies even though we tried to use a very
383   similar protocol to theirs. Yet, they differed in several aspects.

384   Our protocol had a more extensive adaptation period (209 trials vs. 118 in Trewartha et al.) and
385   retention phase (63 vs. 22), while the baseline and de-adaptation phases were similar (baseline 73 vs.
386   52 trials and de-adaptation 24 vs 20). The longer adaptation period might have resulted in more
387   opportunity for the participants to learn the force field implicitly, which might have concealed a
388   learning deficit in the older adults that is then later reflected in the spontaneous recovery period.
389   However, Trewartha et al. did not observe any difference in adaptation level during learning. We
390   allowed for a greater variability in hand velocity, allowing faster movements (0.3 – 0.5 m/s vs 0.3-0.4
391   m/s in the Trewartha et al.). Yet, the hand velocity was matched between our group of young and old
392   participants. Because older adults tended to move slower, we asked a few young participants to
393   perform the experiment while adapting the accepted speed range. On average, our age groups moved
394   with the exact same velocity.

395   One additional difference lies in our sample. Trewartha et al. showed that, within their sample,
396   participants who scored high on an explicit memory task had better spontaneous recovery. So maybe,
397   our sample of older people all had very good cognitive memories. Yet, our sample of older participants
398   had worst working memory capacity than younger participants.

399   Finally, Trewartha measured explicit and implicit components in separate tasks and compared the
400   results between age groups. Older adults scored less in both the explicit and implicit task. We measure
401   implicit adaptation within our adaptation paradigm during learning and working memory in a separate
402   task. We found no difference in implicit level even though older adults had worse working memory
403   capacity.

Do explicit/cognition or implicit adaptation relate to spontaneous recovery

405   Beyond the technical differences, there are also differences in the theoretical approaches between the
406   two studies. While Trewartha focused on the role of cognition on the spontaneous recovery, we
407   believe that implicit motor adaptation modulates spontaneous recovery. Indeed, Trewartha and
408   colleagues found that people who had "good" explicit memory had higher levels of spontaneous
409   recovery. Our attempt at a conceptual replication of this correlation failed as we did not find any

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

411 and colleagues is at odds with the study of Keisler and colleagues (2010) who showed that a secondary

412 cognitive task disrupted the fast process but not the slow process responsible for spontaneous

413 recovery (McDougle et al. 2015). Our results rather agree with the results of Keisler than with those of

414 Trewartha. Indeed, we found that the amount of implicit adaptation measured during learning

415 correlated with the level of spontaneous recovery across participants.

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

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

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

419 of age on the spontaneous recovery of motor memories is very likely much smaller than what was

420 resported by Trewartha and colleagues (2014). Yet, the Bayesian analysis does not prove that there is

421 no effect. It estimates that the effect size lies somewhere in an interval between -0.6 (medium effect

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

423 spontaneous recovery for younger people.

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

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

426 adaptation (Keisler and Shadmehr 2010; McDougle et al. 2015; Smith et al. 2006) and that this

427 component is not affected by aging (Cressman et al. 2010; Hegele and Heuer 2010, 2013; Heuer and

428 Hegele 2008; Huang and Ahmed 2014; Kitchen and Miall 2021; Reuter et al. 2020; Vandevoorde and

429 Orban de Xivry 2019, 2021). The results of Trewartha and colleagues are at odds with this theory, which

430 motivated our replication attempt.

431 **Limitations of the study**

432 In this study, we measured the implicit component of motor adaptation by looking at the distance

433 participants deviated from the straight trajectory. However, short-term retention was measured by

434 the force that was exerted perpendicular to the heading direction. This difference in units makes direct

435 comparison between the two measures difficult. Another way of separating implicit from explicit

436 learning is described by Sween et al. (2020). Implicit adaptation level was determined with 'No Push'-

437 trials, where participants were instructed to ignore the force field and to not push against it. Total

438 adaptation, including the explicit component, was measured in 'Push'-trials, which had an extra

439 reminder to push against the force field. The difference in exerted force is attributed to the explicit

440 component of motor adaptation. The results indicate that in a 'Push'-trial, participants apply more

441 force and in a 'NoPush'-trial less force, as compared to a regular trial. Therefore, our study could have

442 benefited from such an assessment.

Our Bayesian analysis suggests that the maximum effect size should be much smaller than anticipated based on the study of Trewartha. This means that we only have 60% power to detect an effect if there is one of d=0.6. This should motivate future studies to include more participants as we now have a better estimate of the possible effect size range.

Finally, the group of older participants exhibited much more inter-subject variability than the group of younger participants. This is typical in aging studies but would need to be tackled to get a better estimate of the spontaneous recovery of these older participants.

Conclusion

We attempted to replicate the effect of age on spontaneous recovery as demonstrated by Trewartha and colleagues but could not replicate their results as we failed to find evidence for a difference in spontaneous recovery between young and old participants. The current results are more in line with the idea that spontaneous recovery depends on the retention of implicit adaptation and that implicit adaptation is not affected by aging.

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