# Ageing disrupts reinforcement learning whilst learning to help others is preserved

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#### 1 Abstract

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3 Reinforcement learning is a fundamental mechanism displayed by many species from 4 mice to humans. However, adaptive behaviour depends not only on learning 5 associations between actions and outcomes that affect ourselves, but critically, also 6 outcomes that affect other people. Existing studies suggest reinforcement learning 7 ability declines across the lifespan and self-relevant learning can be computationally 8 separated from learning about rewards for others, yet how older adults learn what 9 rewards others is unknown. Here, using computational modelling of a probabilistic 10 reinforcement learning task, we tested whether young (age 18-36) and older (age 60-11 80, total n=152) adults can learn to gain rewards for themselves, another person 12 (prosocial), or neither individual (control). Detailed model comparison showed that a 13 computational model with separate learning rates best explained how people learn 14 associations for different recipients. Young adults were faster to learn when their 15 actions benefitted themselves, compared to when they helped others. Strikingly 16 however, older adults showed reduced self-bias, with a relative increase in the rate at 17 which they learnt about actions that helped others, compared to themselves. 18 Moreover, we find evidence that these group differences are associated with changes 19 in psychopathic traits over the lifespan. In older adults, psychopathic traits were 20 significantly reduced and negatively correlated with prosocial learning rates. 21 Importantly, older people with the lowest levels of psychopathy had the highest 22 prosocial learning rates. These findings suggest learning how our actions help others 23 is preserved across the lifespan with implications for our understanding of 24 reinforcement learning mechanisms and theoretical accounts of healthy ageing.

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26 Keywords: Prosocial behaviour, ageing, reinforcement learning, computational27 modelling

28 Learning associations between actions and their outcomes is fundamental for adaptive 29 behaviour. To date, the majority of studies examining reinforcement learning have 30 tested how we learn associations between actions and outcomes that affect ourselves. 31 and largely focused on these processes in young age, both in humans and other 32 species<sup>1–5</sup>. However, such self-relevant learning may be computationally separable from learning about actions that help other people. Studies suggest slower learning of 33 34 associations between actions and outcomes when they are about<sup>6</sup> or affect others<sup>7</sup>, 35 henceforth referred to as 'prosocial learning'.

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37 Senescence is associated with a multitude of changes including declines in cognitive 38 functioning and perception, but perhaps preservation of affective processing<sup>8</sup>. It is largely unknown how ageing affects social functioning, despite the critical importance 39 40 of this question. Social isolation has been found to be as damaging to physical health 41 as smoking or excessive drinking<sup>9</sup>. Prosocial behaviours, or actions intended to benefit others, have a key role in maintaining vital social interactions and relationships<sup>10</sup> 42 43 across the lifespan. In addition to the benefits for others, prosociality has been linked to improved life satisfaction<sup>11</sup>, mental wellbeing<sup>12</sup>, and physical health<sup>13</sup> for the person 44 45 being prosocial, all of which could contribute to healthy ageing. A key aspect of 46 prosocial behaviour is the ability to learn associations between our own actions and 47 outcomes for other people<sup>7</sup>. Here, we use computational models of reinforcement 48 learning in young and older participants to examine the mechanisms that underpin 49 self-relevant and prosocial learning and associations with healthy individual 50 differences in socio-cognitive ability.

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52 Reinforcement Learning Theory (RLT) provides a powerful framework for 53 understanding and precisely modelling learning<sup>14</sup>. In RLT, prediction errors signal the 54 unexpectedness of outcomes and affect the choices we make in the future. The influence that prediction errors have on choices can be modelled individually through 55 56 the learning rate, which quantifies the effect of past outcomes on subsequent 57 behaviour. The plausibility of reinforcement learning as a core biological mechanism for action-outcome associations is bolstered by our understanding of neurobiology, 58 with prediction errors encoded by single neurons in the ventral tegmental area<sup>15</sup>. 59

Although essential for successful adaptive behaviour, some studies have found that
our propensity for reinforcement learning declines in later life<sup>8</sup>. For example, Mell et

62 al. (2005) showed that older adults are impaired at learning and reversing action-63 outcome associations, compared to younger adults. This decline could be due to the 64 significant age-related decrease in dopamine transmission<sup>17–19</sup>, which has been suggested to code prediction errors<sup>2,20,21</sup>. Indeed, one study showed that 65 administering L-DOPA, a dopamine precursor, to older adults increased their learning 66 rate<sup>22</sup>. Therefore, if reinforcement learning in general declines in older age, we would 67 hypothesise lower learning rates for both self-relevant and prosocial learning in older, 68 69 compared to younger, adults.

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71 Alternatively, prosocial learning may depend not only on our learning ability, but also 72 our motivation to help others. Results from experiments using economic games to 73 measure prosociality have found that older adults tend to be more generous<sup>23,24</sup>. There 74 is also evidence of an age-related increase in charitable donations to individuals in 75 need<sup>25</sup>. At work, older adults engage in more prosocial behaviours than younger adults, according to both self-report data and colleagues' ratings<sup>26</sup>. Finally, self-76 77 reported altruism and decisions to donate to others have been shown to increase with 78 age<sup>27</sup>. However, one limitation of these studies is that the paradigms often place self 79 and other reward preferences in conflict. Money for the other person depends on less 80 money for oneself. Moreover, older adults generally have higher accumulated wealth, 81 which would be an important confound in studies of monetary exchange<sup>28</sup>. 82 Nevertheless, if older adults are indeed more prosocial, we might expect that whilst 83 self-relevant learning declines with ageing, prosocial learning could be preserved.

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85 While studies point to potential group differences between young and older adults, 86 there is also substantial variability in self and other reward sensitivity. For example, 87 psychopathy is a key trait associated with decreased prosocial behaviour and altered 88 self and other reward processing<sup>29,30</sup>. Psychopathy has dysfunctional affectiveinterpersonal features at its core<sup>31,32</sup> but is also characterised by lifestyle and antisocial 89 traits<sup>33</sup>. At the extreme, psychopathy is a severe personality condition linked to poor 90 life outcomes, violence, and criminality<sup>34–36</sup>. However, several studies suggest similar 91 behavioural and neural profiles between community samples with high levels of 92 psychopathic traits<sup>37</sup> and those with clinical diagnoses of psychopathy, consistent with 93 94 the Research Domains of Criteria (RDoC) conceptualisation of a dimensional approach to psychiatry<sup>38</sup>. 95

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97 Intriguingly, ageing is also associated with changes in psychopathic traits. Criminal 98 activity increases during adolescence then declines in older adulthood<sup>39</sup>. Antisocial 99 and aggressive behaviours also significantly decrease in older age, with young adults 100 (age 16-24 years) having the highest rates of homicide<sup>40</sup>. Even within violent male 101 offenders, psychopathic traits linked to an antisocial lifestyle are negatively correlated 102 with age<sup>41</sup>. In community samples, ageing is associated with a decrease in both the 103 antisocial lifestyle and affective interpersonal elements of psychopathic traits<sup>42</sup>.

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105 Taken together, previous research supports opposing hypotheses for how ageing is 106 associated with self-relevant and prosocial reinforcement learning. On the one hand, 107 evidence suggests that older adults should be impaired at learning, regardless of the 108 recipient, consistent with ageing-related declines in learning ability and dopamine 109 availability. On the other hand, potential increases in valuing outcomes for others in 110 older, compared to younger, adults would predict preserved prosocial learning ability 111 but reduced self-relevant learning ability. Finally, we expected variation in 112 psychopathic traits to be associated with learning for others but not self in both age 113 groups.

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To distinguish between these competing hypotheses, we tested 75 young (aged 18-36, mean=23.07, 44 females) and 77 older (aged 60-80, mean=69.84, 40 females) adults carefully matched on gender, years of education, and IQ. Participants completed a probabilistic reinforcement-learning task (Figure 1) designed to separate self-relevant (rewards for self) from prosocial learning (rewards for another person), as well as controlling for the general valence of receiving positive outcomes (rewards for neither self or other).

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Detailed model comparison showed that a computational model with separate learning rates best explained how people learn associations for different recipients (Figure 2). Young adults were faster to learn when their actions benefitted themselves, compared to when they helped others. Strikingly however, older adults showed a reduced selfbias, with a relative increase in the rate at which they learnt about actions that helped others, compared to themselves (Figure 3a & b). These group differences were associated with changes in psychopathic traits over the lifespan. In older adults,

- 130 psychopathic traits were significantly reduced and correlated with prosocial learning
- rates (Figure 4a & b). These effects were not explained by individual differences in IQ,
- 132 memory or attention abilities. Overall, we show that older adults are less self-biased
- 133 in reinforcement learning than young adults, and this change is associated with a
- 134 decline in psychopathic traits. These findings suggest learning how our actions help
- 135 others is preserved across the lifespan.



#### 136

137 Figure 1. Prosocial learning task and social role assignment. (a) The role assignment 138 procedure involved the participant (dark blue), confederate (light blue) and two experimenters 139 (green). Top: from above showing the positioning of the participant and two experimenters 140 inside the testing room, and the confederate the other side of the door. Bottom: the participant 141 and confederate wore a glove to disguise their identity and waved to each other from either 142 side of the door. Participants were instructed that they would be assigned to roles of 'Player 143 1' and 'Player 2'. After this procedure they were informed that they would play a game where 144 they could gain rewards for themselves, the other participant (Player 2) or neither participant. 145 They were told that Player 2 would not play the same game for them and that Player 2 would 146 not know that they may receive an additional bonus based on the choices the participants. 147 This meant that participants' choices were made anonymously and should not be affected by 148 reputational concerns. (b) Participants performed a reinforcement learning task ('prosocial 149 learning task') in which they had to learn the probability that abstract symbols were rewarded 150 to gain points. At the beginning of each block, participants were told who they were playing 151 for, either themselves, for the other participant, or in a condition where no one received the 152 outcome. Points from the 'self' condition were converted into additional payment for the 153 participant themselves, points from the 'other' condition were converted into money for Player 154 2 and points from the 'no one' condition were displayed but not converted into any money for 155 anyone.

#### 156 Results

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158 We analysed the behaviour of 75 younger adults and 77 older adults who completed 159 the probabilistic reinforcement learning task (Figure 1b), neuropsychological tests, and 160 trait psychopathy measure (see Methods). To ensure comparability, older adults with 161 dementia, as diagnosed by the Addenbrooke's Cognitive Examination (ACE)<sup>43</sup>, were 162 not included in the study. The two age groups were matched on gender  $(\chi^2(1)=0.45)$ , 163 p=0.5) and did not differ in years of education or IQ (Supplementary Table 1). IQ was 164 guantified using age-standardised scores on the Wechsler Test of Adult Reading 165 (WTAR)<sup>44</sup>. We conducted additional analyses controlling for IQ (standardised WTAR) 166 score, measured for young and older adults), and memory and attention (memory and 167 attention subscales of the ACE, older adults only). These control analyses showed 168 that our results are not accounted for by general intelligence or executive function (see 169 Methods and Supplementary Information).

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### Learning occurs for all recipients for both age groups

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173 We first examined whether participants were able to learn for all three recipients to 174 validate their ability to complete the task. We quantified performance as selecting the 175 option associated with a high chance of receiving reward. Participants in both age 176 groups were able to learn to obtain rewards for themselves, another person, and no 177 one. This was demonstrated through average performance above chance level (50%; 178 all ts>15, all ps<0.001) and a significant effect of trial number in predicting trial-by-trial 179 performance (all zs>4.48, ps<0.001) for each separate recipient and age group 180 combination.

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#### 182 Learning rate depends on who receives reward

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184 Next, to quantify learning, we used computational models of reinforcement learning to 185 estimate learning rates ( $\alpha$ ) and temperature parameters ( $\beta$ ), key indices for the speed 186 by which people update their estimates of reward, and the precision with which they 187 make choices, respectively. Models were fitted using a hierarchical approach and 188 compared using Bayesian model selection as used previously by Huys et al.<sup>45</sup> and 189 Wittmann et al.<sup>46</sup> (see Methods). We tested multiple models that varied with respect

190 to whether learning could be explained by shared or separate free parameters across

191 recipient (self, other, no one). Based on our previous results<sup>7</sup>, we examined whether

shared or separate learning rates in particular resulted in a better model fit. We used

193 four candidate models:

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195 (i)  $1\alpha 1\beta$ : one  $\alpha$  for all three recipients & one  $\beta$  for all three recipients;

196 (ii)  $3\alpha 1\beta$ :  $\alpha_{self}$ ,  $\alpha_{other} \& \alpha_{no one}$ , one  $\beta$ ;

197 (iii)  $2\alpha 1\beta$ :  $\alpha$  self &  $\alpha$  not-self [other + no one], ONE  $\beta$ ;

198 (iv)  $3\alpha 3\beta$ :  $\alpha_{self}$ ,  $\alpha_{other}$ ,  $\alpha_{no one}$ ,  $\beta_{self}$ ,  $\beta_{other}$  &  $\beta_{no one}$  (see Supplementary Table 2).

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Initially, we aimed to establish that both our experimental schedule and our models 200 201 were constructed in a way that allowed us to disentangle recipient-specific learning 202 rates. To this end, we created synthetic choices using simulations based on each of 203 our four models (see Methods). We fitted the models to the data and assured that the 204 best fitting model was the one that had been used to create the data. In such a way, 205 we established model identifiability, both when considering the exceedance probability 206 (Figure 2a and see Methods) and the number of times a model was identified as the 207 best one (Figure 2b). As a second prerequisite for testing for agent-specific learning 208 rates, we performed parameter recovery using our key model of interest, the  $3\alpha 1\beta$ 209 model. Over a wide parameter space, we were able to recover the parameters 210 underlying our choice simulation (Figure 2c).

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Having established the models were identifiable and parameters recoverable, we performed Bayesian model selection on the data from our participants. Participant's choices were best characterised by the  $3\alpha 1\beta$  model. This indicated that the learning process underlying the choices is most accurately captured by assuming separate learning rates for each recipient ( $\alpha_{self}$ ,  $\alpha_{other} \& \alpha_{no one}$ ). This model fit the data best (exceedance probability=97%;  $\Delta BIC_{int}$ =122; Figure 2d) and predicted choices well ( $R^2$ =51%; see Methods for further details).



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220 Figure 2. Model identifiability and parameter recovery. (a) Model identifiability average 221 exceedance probability confusion matrix and (b) model identifiability best model selection 222 confusion matrix. Data were simulated from 150 synthetic participants with each of our four 223 models then Bayesian model selection was applied, and this procedure was repeated 10 224 times. Identifiability is shown by strong diagonals. (c) Parameter recovery was performed on 225 data simulated by the winning  $3\alpha 1\beta$  model from 1296 synthetic participants. Confusion matrix 226 represents correlations between simulated and fitted parameters. Strong correlations on the 227 diagonal show parameters can be recovered. (d) The  $3\alpha 1\beta$  model ( $\blacktriangle$ ) is the best model on 228 both exceedance probability and integrated Bayesian Information Criterion (BIC) fit measures.



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230 Figure 3. Age-group differences in accuracy and learning rates. (a) Comparison of 231 learning rates from the computational model. Bars show group median. Between-group and 232 within-group Wilcoxon t-tests show older adult's prosocial learning was preserved: learning 233 rates in the other condition did not differ from the self condition or from young adult's prosocial 234 learning rates. Only young participants showed self-bias, n=150 (75 young, 75 older). (b) 235 Median difference between learning rates in the other and self conditions illustrates the larger 236 self-bias in young, compared to older, adults, n=150. Asterisks represent significant 237 differences (p<0.05). (c) Group-level learning curves showing choice behaviour in the three 238 recipient conditions for each age group. Trials are averaged over the three blocks (48 trials 239 total per recipient presented in three blocks of 16 trials) for the self, other, and no one 240 recipients, n=152 (75 young, 77 older).

#### 241 Older adults show a reduced self-bias in learning rates

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Next, we used this validated model to test our hypotheses as to whether there were group differences in learning rates when learning to reward self, other or no one. Two participants had learning rates for two of the three recipients more than three standard deviations (SDs) above the mean ( $\alpha_{self}$  6.68 &  $\alpha_{no one}$  9.64;  $\alpha_{self}$  7.96 &  $\alpha_{other}$  3.78 SDs above the mean) and were excluded from all analysis of learning rates.

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Across age groups, participants showed a higher learning rate when rewards were for 249 250 themselves, compared to for another person (b=-0.024, 95% confidence interval [-251 0.034, -0.014], z=-4.79, p<0.001). Importantly however, this pattern differed between 252 age groups. The difference between self and other learning rates was reduced in older 253 adults, consistent with a reduced self-bias (recipient [self vs. other] \* age group 254 interaction: b=0.016 [0.002, 0.03], z=2.29, p=0.022). To explore this interaction, we 255 ran planned between-group comparisons between the older and young group, in each 256 recipient condition. Comparing  $\alpha_{self}$  between age groups showed older adults learnt 257 significantly more slowly for themselves (W=3512, Z=-2.6,  $r_{(150)}=0.21$  [0.06, 0.73], 258 p=0.009). In contrast, prosocial learning was maintained in older adults, with a Bayes 259 factor suggesting strong evidence in favour of no difference in  $\alpha_{other}$ , compared to voung adults (W=3042, Z=-0.86,  $r_{(150)}=0.07$  [0.003, 0.23], p=0.39, BF<sub>01</sub>=4.26). As 260 261 expected, across age groups learning was slower for no one than self (recipient [self 262 vs. no one] main effect: *b*=-0.023 [-0.033, -0.013], *z*=-4.57, *p*<0.001). α<sub>no one</sub> did not 263 significantly differ between groups, although there was not strong evidence in support 264 of the null (W=3241, Z=-1.6,  $r_{(150)}=0.13$  [0.008, 0.29], p=0.11, BF<sub>01</sub>=2.04).

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We also ran planned within-subject comparisons between recipients for each age 266 267 group separately. As predicted, young adults learnt preferentially for themselves (vs. 268 αother V=659, Z=-4.0, r<sub>(75)</sub>=0.47 [0.27, 0.63], p<0.001; vs. αno one V=928, Z=-2.62, 269  $r_{(75)}=0.30$  [0.09, 0.51], p=0.009) and did not differentiate between another person and 270 no one (V=1533, Z=-0.57, r<sub>(75)</sub>=0.067 [0.003, 0.30], p=0.57, BF<sub>01</sub>=5.08). In contrast, 271 for older adults, there was no significant difference between  $\alpha_{self}$  and  $\alpha_{other}$  (V=1150, 272 Z=-1.4, r<sub>(75)</sub>=0.17 [0.01, 0.37], p=0.15, BF<sub>01</sub>=1.08) but learning rates were slower for 273 no one (vs. α<sub>self</sub> V=901, Z=-2.8, r<sub>(75)</sub>=0.32 [0.10, 0.52], *p*=0.006; vs. α<sub>other</sub> V=976, Z=-

274 2.4,  $r_{(75)}=0.27$  [0.05, 0.50], p=0.02). This demonstrates specificity of the age-related 275 change to prosocial learning. In other words, older adults showed a relative increase 276 in the willingness to learn about actions that helped others. Finally, we also observed 277 a main effect of age on both learning rates and temperature parameters. Older adults 278 showed slower learning overall compared to younger adults (*b*=-0.019 95% CI [-0.028, 279 -0.009], Z=-3.73, *p*<0.001) and higher levels of exploration of choice options (median 280  $\beta$  young: 0.05, older: 0.19, W=1511, Z=-4.9,  $r_{(150)}=0.4$  [0.25, 0.54], *p*<0.001).

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### 282 Participants perform better for themselves, compared to no one

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284 For completeness, we also tested the effects of recipient and age group on trial-by-285 trial tendency to pick the high reward stimuli (Figure 3c). In addition to the main effect 286 of trial number (b=1.71 [1.29, 2.13], z=7.97, p<0.001), showing learning, these models 287 revealed older adults chose the high reward option less frequently (mean for young: 288 80%, older: 64%, b=-1.18 [-1.65, -0.70], z=-4.84, p<0.001), and improved less during 289 the task (trial number \* age group interaction b=-0.81 [-1.34, -0.27], z=-2.95, p=0.003) 290 across recipients. When averaging across age groups, performance was better for the 291 self (75%), compared to no one (70%; b=-0.36 [-0.05, 0.16], z=-2.28, p=0.02). 292 However, there was no difference between accuracy for other (72%) and self (b=-0.22 293 [-0.49, 0.05], z=-1.63, p=0.10), or any significant interactions between age group and 294 recipient (*b*s<0.16, *z*s<0.96, *p*s>0.34).

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# Psychopathic traits are lower in older adults and explain variance in prosocial learning

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299 Finally, we examined individual variability in psychopathic traits, considering age-300 related differences and influence on prosocial learning. Several studies have 301 suggested that individual differences in psychopathic traits can be meaningfully and 302 accurately captured in community samples and often parallel findings in criminal 303 offenders<sup>37</sup>. Critically, psychopathic traits are most closely linked to alterations in 304 social behaviour and willingness to help others. Therefore, we also asked participants 305 to complete the Self-report Psychopathy Scale<sup>33</sup>, a measure of psychopathic traits that 306 robustly capture its latent structure (see Methods). One participant in each age group 307 had missing questionnaire data and are not included in these analyses. Psychopathic 308 traits are consistently divided into two components that this scale measures: core 309 affective-interpersonal traits, which capture lack of empathy and guilt; and lifestyle-310 antisocial traits, which capture impulsivity and antisocial tendencies. Comparing the 311 two age groups on these scales showed that older participants had significantly lower 312 scores than young participants on both the affective-interpersonal (W=3558, Z=-3.1, 313  $r_{(148)}=0.26$  [0.11, 0.41], p=0.002) and the lifestyle-antisocial subscales (W=3471, Z=-314 2.8, r<sub>(148)</sub>=0.23 [0.07, 0.38], *p*=0.005). These findings suggest that both components 315 of psychopathic traits were reduced in older, compared to younger, adults.

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317 Next we sought to test our hypothesis that individual differences in core psychopathic 318 traits would explain variability in learning rates, specifically for prosocial learning. We 319 observed a significant negative relationship between  $\alpha_{other}$  and core psychopathic 320 traits among older participants ( $r_{s(74)}$ =-0.33 [-0.52, -0.11], p=0.005). Intriguingly, this 321 relationship was significantly more negative (Z=3.3, p=0.001) than the equivalent 322 correlation in young adults, which had a positive sign ( $r_{s(74)}=0.21$  [-0.02, 0.42], p=0.07; 323 Figure 4a). This pattern of results was the same when correlating the relative difference between  $\alpha_{other}$  -  $\alpha_{self}$  (rather than the raw  $\alpha_{other}$ ) with core psychopathic traits 324 325 (Figure 4b). We also conducted control analyses, correlating the same pairs of 326 variables but using partial correlations controlling for B. The negative relationship 327 between prosocial learning (when quantified as  $\alpha_{other}$  or  $\alpha_{other}$  -  $\alpha_{self}$ ) and psychopathic 328 traits was still present for older adults, showing that the correlations with learning rates 329 were independent of individual choice exploration (all *p*s<0.05; see Supplementary 330 Table 3). The negative relationship between  $\alpha_{other}$  and core psychopathic traits for 331 older adults also remained significant after applying false discovery rate correction for 332 multiple comparisons across this correlation and the five other age group & recipient 333 combinations (see Supplementary Table 4). Moreover, the finding that no significant 334 correlations were apparent between psychopathy and  $\alpha_{self}$  or  $\alpha_{no one}$  (ps>0.15; 335 Supplementary Table 4) suggests a specificity in the relevance of psychopathy to 336 prosocial learning in older adults.



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338 Figure 4. Correlations between prosocial learning rates ( $\alpha_{other}$ ) and scores on 339 the affective interpersonal subscale of the Self Report Psychopathy scale. (a) 340 For older adults, trait psychopathy levels are negatively correlated with prosocial 341 learning rates ( $r_s$ =-0.33 [-0.52, -0.11], p=0.005). (b) There is no significant relationship 342 for young adults ( $r_s=0.21$  [-0.02, 0.42], p=0.07) and the correlation is significantly more 343 negative (Z=3.3, p=0.001) for older than young adults. This pattern of results is the 344 same when considering correlations between trait psychopathy and the lack of self-345 bias in learning ( $\alpha_{other}$  -  $\alpha_{self}$ ; not shown). This measure of prosocial learning is also 346 negatively correlated with trait psychopathy scores in older adults ( $r_s$ =-0.25 [-0.45, -347 0.02], p=0.03) but not younger adults ( $r_s=0.11$  [-0.12, 0.33], p=0.36; difference Z=2.1, 348 *p*=0.03).

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## 351 Discussion

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353 Reinforcement learning is a fundamental process for adaptive behaviour in many 354 species. However, existing studies have largely focused on young people and self-355 relevant learning, but the decisions we make often occur in a social context<sup>47</sup> and our 356 actions affect outcomes for others. Here, for the first time, we apply computational 357 models of reinforcement learning to the question of ageing-related changes in self-358 relevant and prosocial learning. We found a clear decrease in learning rates for self-359 relevant rewards in older, compared to younger, adults. Intriguingly, despite this 360 reduction in self-relevant learning, learning rates for outcomes that affected others did 361 not differ between older and young adults, with Bayesian analyses supporting no 362 difference. Moreover, not only did older adults have a relative increase in their prosocial learning rates, ageing was also associated with lower psychopathic traits,which were specifically linked to prosocial learning ability.

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366 Models of learning are a powerful tool for understanding prosocial behaviour. By 367 isolating the learning rate, we can precisely examine the influence of reward history 368 on learning. We robustly replicated previous findings that self-relevant learning can be 369 computationally separated from prosocial learning<sup>7</sup>, with different learning rates for 370 different recipients providing the best explanation of behaviour. Including separate 371 learning rates improved the model fit and, on average across participants, there was 372 a self-bias, learning rates were higher for self-relevant rewards, compared to when 373 someone else or no one received the reward. However, this self-bias was reduced in 374 older adults, who showed a relative increase in prosocial learning rates. As expected, 375 older adults learnt more slowly for themselves than young adults but in the prosocial 376 condition, the learning rates did not significantly differ between the age groups. 377 Bayesian analyses additionally confirmed that prosocial learning was preserved 378 between young and older adults.

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380 As with much research on age-related changes on cognitive and social tasks, our key 381 finding that self-bias in learning is reduced in older adults could be interpreted as due 382 to changes in ability, motivation, or a combination of these factors. Importantly, 383 learning rates were not associated with executive function or an age-standardised 384 measure of intelligence. We also show that our results remain the same after 385 controlling for these measures. These findings suggest that the observed decline in 386 self-relevant learning rates, but relative increase in prosocial learning rates, for older 387 adults are not explained by changes in these broad abilities. Considering learning 388 more specifically, a recent comparison of motivation and ability as explanations for 389 ageing-related reductions in model-based strategies during self-relevant learning 390 supported the limited cognitive abilities account<sup>48</sup>. Our finding that learning rates for 391 self-relevant outcomes were reduced in older adults is in line with a degeneration in 392 the neurocognitive systems required for successful learning. Research combining 393 models of learning with neuroimaging and pharmacological manipulations suggests ageing reduces the ability to generate reward prediction errors<sup>49</sup> due to declines in 394 dopamine functioning<sup>22,50</sup>. Differences in motivation could also be applicable for self-395

relevant learning as the subjective value of financial outcomes is also likely to
 decrease in older age, due to changes in wealth across the lifespan<sup>28</sup>.

398 Our findings suggest that despite declines in learning ability associated with ageing. 399 motivation could play a role in preserving learning to help others. This interpretation 400 aligns with an emerging literature showing older adults may be more prosocial and 401 less self-biased than younger adults<sup>23,24,51</sup>. The assertion that relatively preserved 402 prosocial learning is related to increased prosocial motivation is supported by our 403 observed link between learning rates and psychopathic traits. Psychopathic traits were 404 significantly reduced in our older adult sample, dovetailing with similar previous findings on this trait<sup>41,42</sup> and broader trait benevolence<sup>27</sup>. Importantly, we found 405 406 psychopathic traits in older adults negatively correlated with prosocial learning rates. 407 Self-bias in learning rates (i.e. higher learning rate for self compared to other) was 408 most reduced, and even reversed, in the older people lowest on psychopathic traits. 409 Notably, this negative correlation between psychopathy and prosocial learning was 410 only found for older adults. This suggests that age-related differences in prosocial 411 learning could be linked to basic shifts in individual traits and motivations over the 412 lifespan, not just to domain-general reductions in cognitive abilities.

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414 Moreover, our task included a control condition where no one benefitted. This was 415 important to establish that the lack of difference between self and other learning rates 416 for older adults was not simply due to an age-related reduction in the absolute dynamic 417 range as maximum learning rates decrease. Older adults had higher learning rates for 418 both others and themselves, compared to this control condition. In contrast, young 419 adults did not differentiate another person from no one (if anything they learned faster 420 for no one). Older adults therefore showed a relative increase in learning rates that 421 was specific to the prosocial condition. This is also evidence against the idea that 422 lower learning rates in older people are reflective of a general reduced sensitivity to 423 who gets the reward. It is interesting to note that the magnitude of the decrease in 424 learning rates associated with being older, compared to younger, is similar to the 425 decrease associated with a young person learning for someone else, compared to 426 themselves. The preservation of prosocial learning rates between age groups may 427 seem at odds with the decreased self-relevant learning rates in our sample of older 428 adults and existing evidence of underlying neurobiological deterioration. However, 429 learning from outcomes for self and other have been linked to distinct regions of the

brain in humans, shown though neuroimaging<sup>7,52</sup>, and causally in monkeys with focal
lesions<sup>53</sup>.

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433 Taken together, our results add to a growing body of literature suggesting age-related 434 increases in prosocial motivation. If this is the case, the next question is how and why 435 this happens, as there are many possible reasons to be prosocial. For example, 436 prosocial behaviours can be motivated by reputational concerns<sup>54</sup>, the 'warm glow' of 437 helping<sup>55–57</sup>, or vicarious reinforcement from positive outcomes for others<sup>58</sup>. In our 438 procedure, we were very careful to prevent reputational concerns influencing learning 439 to help others. Participants underwent an extensive procedure to introduce them to 440 another participant but to hide information about their age and identity. This meant we 441 could assess tendency for prosocial learning in a situation where reputational 442 motivations were excluded, and identity-based influences were controlled. Using a 443 reinforcement learning task, in which performance generates positive outcomes for 444 others also focusses on vicarious rewards from the outcome, rather than warm glow 445 associated with the action of helping. Thus, the relative increase in prosocial learning 446 rates suggests older adults are reinforced by outcomes for others and themselves 447 more similarly than younger adults. Many prosocial measures such as the dictator 448 game<sup>59</sup> are costly, requiring direct trade-offs between outcomes for oneself and 449 others. This also makes it hard to detect whether changes are in the value of outcomes 450 for oneself, or outcomes for others, or both. In contrast, separating self-relevant 451 learning, prosocial learning, and the control condition allows us to differentiate 452 increases in the value of prosocial outcomes from decreases in the value of outcomes 453 for the self. Our results are consistent with older adults having both decreased self-454 relevant learning rates (compared to young adults) and increased prosocial learning 455 rates (compared to their performance in the control condition).

456

While our procedure and task have many benefits, it is important to also recognise limitations. To test for age-related differences in prosocial learning, we recruited a group of older adults and a group of younger adults. This increases power to detect differences, but we are unable to assess at what age or how quickly changes take place. Further research with participants of all ages is required to address these outstanding questions. Moreover, future studies could manipulate the identity of the recipient as we show a preservation in tendency to help others when there are no 464 particular characteristics known about the other person, but these effects might465 additionally be modulated by factors such as perceived social distance.

466

467 To conclude, we find new evidence that despite declines in self-relevant learning in 468 older adults, the ability to learn which actions benefit others is preserved. Moreover, 469 the bias with which people favour self-relevant outcomes is reduced. Not only do older 470 adults have relatively preserved prosocial learning they also report lower levels of core 471 psychopathic traits that index lack of empathy and guilt, and this trait difference is linked to the changes in prosocial learning. These findings could have important 472 473 implications for our understanding of reinforcement learning and theoretical accounts 474 of healthy ageing.

#### 475 Materials and Methods

476

#### 477 Participants

478

We recruited 80 young participants and 80 older participants through university databases, social media and the community. This sample size gave us 88% power to detect a medium size effect (d=0.5). Exclusion criteria included previous or current neurological or psychiatric disorder, non-normal or non-corrected to normal vision and, for the older sample, scores on the Addenbrooke's Cognitive Examination that indicate potential dementia (cut-off score 82)<sup>43</sup>.

485

486 Five young and three older participants were excluded due to: diagnosis of a 487 psychiatric disorder at the time of testing (1 young participant); previous study of 488 psychology (2 young participants); and incomplete or low-quality data (2 young and 3 489 older participants). This left a final sample of 152 participants, 75 young adults (44 490 females aged 18-36, mean=23.07) and 77 older adults (40 females aged 60-80, 491 mean=69.84). Two older participants were excluded from all analyses involving 492 learning rates due to each having two learning rate estimates more than three 493 standard deviations (SDs) above the mean (for one  $\alpha_{self}$  was 6.68 SDs above the mean 494 &  $\alpha_{no}$  one 9.64 SDs above the mean; for the second  $\alpha_{self}$  was 7.96 &  $\alpha_{other}$  3.78 SDs 495 above the mean). One further participant from each age group was missing data on 496 the SRP measure so are not included in the relevant analyses.

497

Participants were paid at a rate of £10 per hour plus an additional payment of up to £5 depending on the number of points they earned for themselves during the task. They were also told the number of points that they earned in the prosocial condition would translate into an additional payment of up to £5 for the other participant (see details of the task below). All participants provided written informed consent and the study was approved by the Oxford University Medical Sciences Inter Divisional Research Ethics Committee and National Health Service Ethics.

#### 505 Prosocial learning task

506

507 The prosocial learning task is a probabilistic reinforcement learning task, with rewards 508 in one of three recipient conditions: for the participant themselves (self), for another 509 participant (other, prosocial condition), and for no one (control condition). Each trial 510 presents two symbols, one associated with a high (75%) probability of gaining points 511 and the other with a low (25%) probability of gaining points. The two symbols were 512 randomly assigned to the left or right side of the screen and selected via a 513 corresponding button press. Participants select a symbol then receive feedback on 514 whether they obtained points or not (see Figure 1b) so learn over time which symbol 515 maximises rewards. The experiment was subdivided into blocks, i.e. 16 trials pairings 516 the same two symbols for the same recipient. Participants completed three blocks, a 517 total of 48 trials, in each recipient condition, resulting in 144 trials overall (see 518 Supplementary Information for trial structure). Blocks for different recipients were 519 pseudo-randomly ordered such that the same recipient block did not occur twice in a 520 row.

521

522 On trials in the self condition, points translated into increased payment for the 523 participant themselves. These blocks started with "play for you" displayed and had the 524 word "you" at the top of each screen. Blocks in the *no one* condition had "no one" in 525 place of "you" and points were not converted into any extra payment for anyone. In 526 the prosocial 'other' condition, participants earned points that translated into additional 527 payment for a second participant, actually a confederate. Participants were told that 528 this payment would be given anonymously, they would never meet the other person, 529 and that the person was not even aware of them completing this task (see 530 Supplementary Information). The name of the confederate, gender-matched to the 531 participant, was displayed on these blocks at the start and on each screen (Figure 1b). 532 Thus, participants were explicitly aware who their decisions affected on each trial. 533 Presentation (Neurobehavioral Stimuli were presented using Systems 534 https://www.neurobs.com/).

#### 535 **Questionnaire measures**

#### 536

537 **Dementia screening and executive function.** Older adults were screened for 538 dementia using the Addenbrooke's Cognitive Examination (ACE-III)<sup>43</sup>. The ACE 539 examines five cognitive domains; attention, memory, language, fluency and 540 visuospatial abilities. The ACE-III is scored out of 100 and as a screening tool, a cut-541 off score of 82/100 denotes significant cognitive impairment. We also used scores on 542 the attention and memory domains in control analyses as proxies for executive 543 function in older adults.

544

545 General intelligence. All participants completed the Wechsler Test of Adult Reading (WTAR)<sup>44</sup> as a measure of IQ. The WTAR requires participants to pronounce 50 words 546 that have unusual grapheme-to-phoneme translation. This means the test measures 547 reading recognition or existing knowledge of the words, rather than ability to apply 548 549 rules for pronunciation. The WTAR was developed and standardised with the 550 Wechsler Memory and Adult Intelligence Scales and correlates highly with these 551 measures<sup>60</sup>. Standardisation involves adjusting for healthy age-related differences. 552 The test is suitable for participants aged 16-89, covering our full sample, and scores 553 in older age have been shown to correlate with cognitive ability earlier in life<sup>61</sup>.

554

555 Psychopathic traits. Participants completed the short form of the Self-Report Psychopathy Scale 4<sup>th</sup> Edition (SRP-IV-SF)<sup>33</sup>. This scale consists of 29 items, 7 each 556 557 measuring: interpersonal, affective, lifestyle and antisocial tendencies (plus 'I have 558 been convicted of a serious crime'). We used the two-factor grouping, summing the 559 core, affective-interpersonal items and separately, the lifestyle-antisocial items for use 560 in analysis. The robust psychometric properties of this measure have been established 561 in community<sup>62</sup> and offender populations through construct and convergent validity<sup>63</sup>, 562 internal consistency, and reliability<sup>33</sup>.

563

564

#### 565 Procedure

#### 566

567 **Role assignment.** To enhance belief that points earned in the prosocial recipient 568 benefitted another person, we conducted a role assignment procedure based on setup used in several studies of social decision-making<sup>64,65</sup>. Participants were instructed 569 570 not to speak and wore a glove to hide their identity. A second experimenter brought 571 the confederate, also wearing a glove, to the other side of the door. Participants only ever saw the gloved hand of the confederate, but they waved to each other to make it 572 573 clear there was another person there (Figure 1a). The experimenter tossed a coin to 574 determine who picked a ball from the box first and then told the participants which 575 roles they had been assigned to, based on the ball they picked. Our procedure 576 ensured that participants always ended up in the role of the person performing the 577 prosocial learning experiment. Participants were unaware of the age of the other 578 person, but the experimenter used a name for them suggesting their gender was the 579 same as the participant.

580

581 Task procedure. Participants received instructions for the learning task and how the 582 points they earned would be converted into money for themselves and for the other 583 participant. Instructions included that the two symbols were different in how likely it 584 was that choosing them lead to points but that which side they appeared on the screen 585 was irrelevant. Participants then completed one block of practice trials before the main 586 task and were aware outcomes during the practice did not affect payment for anyone. 587 After the task, participants completed measures of psychopathic traits and the 588 dementia screening

589

#### 590 Computational modelling

591

We modelled learning during the task with a reinforcement learning algorithm<sup>14</sup>, creating variations of the models through the number of parameters used to explain the learning rate and temperature parameters in the task<sup>66</sup>. The basis of the reinforcement learning algorithm is the expectation that an action (or stimulus) *a* will provide reward on the following trial. This expected value,  $Q_{t+1}(a)$  is quantified as a

597 function of current expectations  $Q_t(a)$  and the prediction error  $\delta_t$ , which is scaled by 598 the learning rate α:

599

600

$$Q_{t+1}(a) = Q_t(a) + \alpha \times \underbrace{[r_t - Q_t(a)]}_{\text{Prediction error } \delta_t}$$

601

602 Where  $\delta_t$ , the prediction error, is the difference between the actual reward experienced 603 on the current trial  $r_t$  (1 for reward and 0 for no reward) minus the expected reward on 604 the current trial  $Q_t(a)$ .

605

The learning rate  $\alpha$  therefore determines the influence of the prediction error. A low learning rate means new information affects expected value to a lesser extent. The softmax link function quantifies the relationship between the expected value of the action  $Q_t(a)$  and the probability of choosing that action on trial *t*:

610

611 
$$p_t[(a|Q_t(a))] = \frac{e^{(Q_t(a)/\beta)}}{\sum_{a'} e^{(Q_t(a')/\beta)}}$$

The temperature parameter  $\beta$  represents the noisiness of decisions – whether the participant explores or always chooses the option with the highest expected value. A high value for  $\beta$  means choices seem random as they are equally likely irrespective of the expected value of each option. A low  $\beta$  leads to choosing the option with the greatest expected value on all trials.

617

### 618 Model fitting

619

620 We used MATLAB 2019b (The MathWorks Inc) for all model fitting and comparison. 621 To fit the variations of the learning model (see below) to (real and simulated) 622 participant data we used an iterative maximum a posteriori (MAP) approach previously 623 described<sup>45,46</sup>. This method provides a better estimation than a single-step maximum 624 likelihood estimation (MLE) alone by being less susceptible to the influence of outliers. 625 It does this via implementing two levels: the lower level of the individual subjects and 626 the higher-level reflecting our full sample. For the real participant data, we fit the model 627 across groups to provide the most conservative comparison, so this full sample 628 combined young and older participants.

629 For the MAP procedure, we initialized group-level Gaussians as uninformative priors 630 with means of 0.1 (plus some added noise) and variance of 100. During the 631 expectation, we estimated the model parameters ( $\alpha$  and  $\beta$ ) for each participant using 632 an MLE approach calculating the log-likelihood of the subject's series of choices given 633 the model. We then computed the maximum posterior probability estimate, given the 634 observed choices and given the prior computed from the group-level Gaussian, and 635 recomputed the Gaussian distribution over parameters during the maximisation step. 636 We repeated expectation and maximization steps iteratively until convergence of the 637 posterior likelihood summed over the group, or a maximum of 800 steps. Convergence 638 was defined as a change in posterior likelihood <0.001 from one iteration to the next. 639 Note that bounded free parameters were transformed from the Gaussian space into 640 the native model space via appropriate link functions (e.g. a sigmoid function in the 641 case of the learning rates) to ensure accurate parameter estimation near the bounds. 642 The detailed code for the models and implementation of the fitting algorithm can be 643 found here: https://osf.io/xgw7h/.

644

#### 645 Model comparison

646

647 Our hypotheses generated four models to compare which differed in whether the 648 model parameters ( $\alpha$  and  $\beta$ ) for each participant had one value across recipient 649 conditions or depended on the recipient (self, other and no one). For model 650 comparison, we calculated the Laplace approximation of the log model evidence 651 (more positive values indicating better model fit; MacKay, 2003) and submitted these 652 to a random-effects analysis using the spm BMS routine<sup>68</sup> from SPM 8 653 (http://www.fil.ion.ucl.ac.uk/spm/software/spm8/). This generates the exceedance 654 probability: the posterior probability that each model is the most likely of the model set 655 in the population (higher is better, over .95 indicates strong evidence in favour of a 656 model). For the models of real participant data, we also calculated the integrated BIC (lower is better<sup>45,46</sup>) and R<sup>2</sup> as additional measures of model fit. To calculate the model 657 R<sup>2</sup>, we extracted the choice probabilities generated for each participant on each trial 658 659 from the winning model. We then took the squared median choice probability across 660 participants. The  $3\alpha 1\beta$  model had the best evidence on all measures (see 661 Supplementary Table 2).

#### 662 Simulation experiments

663

664 We used simulation experiments to assess that our experiment allowed us to 665 dissociate models of interest, as well as parameters of interest within the winning 666 model. We simulated data from all four models to establish that our model comparison 667 procedure (see above) could accurately identify the best model across a wide range 668 of parameter values. For this model identifiability analysis, we simulated data from 150 669 participants, drawing parameters from distributions commonly used in the reinforcement learning literature<sup>69,70</sup>. Learning rates ( $\alpha$ ) were drawn from a beta 670 671 distribution (betapdf(parameter, 1.1, 1.1)) and softmax temperature parameters ( $\beta$ ) 672 from a gamma distribution (gampdf(parameter, 1.2, 5)). We fitted the models to this 673 simulated data set using the same MAP process as applied to the experimental 674 participants' data and repeated this whole procedure 10 times. By plotting the confusion matrices of average exceedance probability (across the 10 runs; Figure 2a) 675 676 and how many times each model won (Figure 2b), we show the models are identifiable 677 using our model comparison process.

678

679 Our winning model contained 4 free parameters ( $\alpha_{self}$ ,  $\alpha_{other}$ ,  $\alpha_{no one}$ ,  $\beta$ ). To assess the 680 reliability of this model and the interpretability of the free parameters, we also 681 performed parameter recovery on simulated data (see Supplementary Information for 682 procedure) as recommended for modelling analyses that use a 'data first' 683 approach<sup>66,71</sup>. We simulated choices 1296 times using our experimental schedule and 684 fitted them using MAP. We found strong Pearson's correlations between the true 685 simulated and fitted parameter values (all rs>0.7, see Figure 2c), suggesting our 686 experiment was well suited to estimate the model's parameters.

687

#### 688 Statistical analysis

689

Analysis of group and recipient differences in the fitted model parameters and
behavioural data was run in R<sup>72</sup> with R Studio<sup>73</sup>. Correlations of learning rates with
trait psychopathy (Supplementary Table 3 & 4) and neuropsychological measures
(Supplementary Table 5) were calculated with Spearman's Rho nonparametric tests.
We used robust linear mixed-effect models (*rlmer* function; robustlmm package<sup>74</sup> to

695 predict learning rates and generalised linear mixed-effects models (*glmer* function; 696 Ime4 package<sup>75</sup>) for the trial-by-trial data (binary outcome of choosing the high vs. low 697 reward option). Each included fixed effects of age group, recipient (self, other, no one), 698 and their interaction, plus a random subject-level intercept. Analysis of trial-by-trial 699 choices also included trial number in the fixed terms, interacting with recipient and 700 group (including the three-way interaction), and in the random terms, interacting with 701 recipient. In the analysis of learning rates controlling for IQ, standardised scores on 702 the WTAR were also included as a fixed term (Supplementary Table 6). To control for 703 IQ and executive function in the associations between older adults' prosocial learning 704 rates and trait psychopathy, we ran partial correlations each controlling for one of 705 WTAR, ACE memory and ACE attention scores (Supplementary Table 7).

706

707 For simple and post hoc comparisons, we used nonparametric tests when measures 708 violated normality assumptions, which included learning rates. Effect sizes and 709 confidence intervals for paired and independent nonparametric comparisons were 710 calculated using the *cohens* d and *wilcox* effsize functions respectively from the 711 rstatix package<sup>76</sup>. Bayes factors (BF<sub>01</sub>) for non-significant results were calculated using nonparametric paired and independent t-tests in JASP<sup>77</sup> with the default prior. 712 713 BF<sub>01</sub> corresponds to how many times more likely the data are under the null hypothesis 714 of no difference than under the alternative hypothesis that there is a difference. A BF<sub>01</sub> 715 larger than 3 (equal to BF<sub>10</sub> less than 1/3) is considered substantial evidence in favour 716 of the null hypothesis whereas a  $BF_{01}$  between 1/3 and 3 indicates the data cannot 717 clearly differentiate between hypotheses<sup>78</sup>.

718	Data availability
719	
720	Data are available at: https://osf.io/xgw7h/.
721	
722	Code availability
723	
724	Code for modelling and analysis is available at: https://osf.io/xgw7h/.
725	
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727	
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733	
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737	
738	Author contributions
739	
740	PL designed the study. AA, LH, DD & PL collected the data. JC, MW & PL analysed
741	the data. JC, MW, MH & PL wrote the paper.
742	
743	Competing interests
744	
745	The authors declare no competing interests
746	

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936