

Age-dependent Pavlovian biases influence motor decision-making

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27 Healthy ageing is associated with decreased risk taking in motor¹ and economic²⁻⁴ decision-making.
28 However, it is unknown whether a single underlying mechanism explains these changes. Age-related
29 changes in economic risk taking are explained by reduced Pavlovian biases that promote action toward
30 reward^{2, 5, 6}. Although Pavlovian biases also promote inaction in the face of punishment, the role such
31 Pavlovian biases play in motor decision-making, which additionally depends on estimating the probability of
32 successfully executing an action⁷⁻¹⁰, is unknown. To address this, we developed a novel app-based motor
33 decision-making task to measure sensitivity to reward and punishment when subjects (n=26,532) made a
34 'go/no-go' motor gamble based on the perceived ability to execute a complex action. Using a newly
35 established approach-avoidance computational model^{2, 6}, we show motor decision-making is also subject to
36 Pavlovian influences, and that healthy ageing is mainly associated with a reduction in Pavlovian bias toward
37 reward. In a subset of participants playing an independent economic decision-making task (n=17,220), we
38 demonstrate similar decision-making tendencies across motor and economic domains. Computational models
39 that incorporate Pavlovian biases thus provide unifying accounts for motor and economic decision-making.

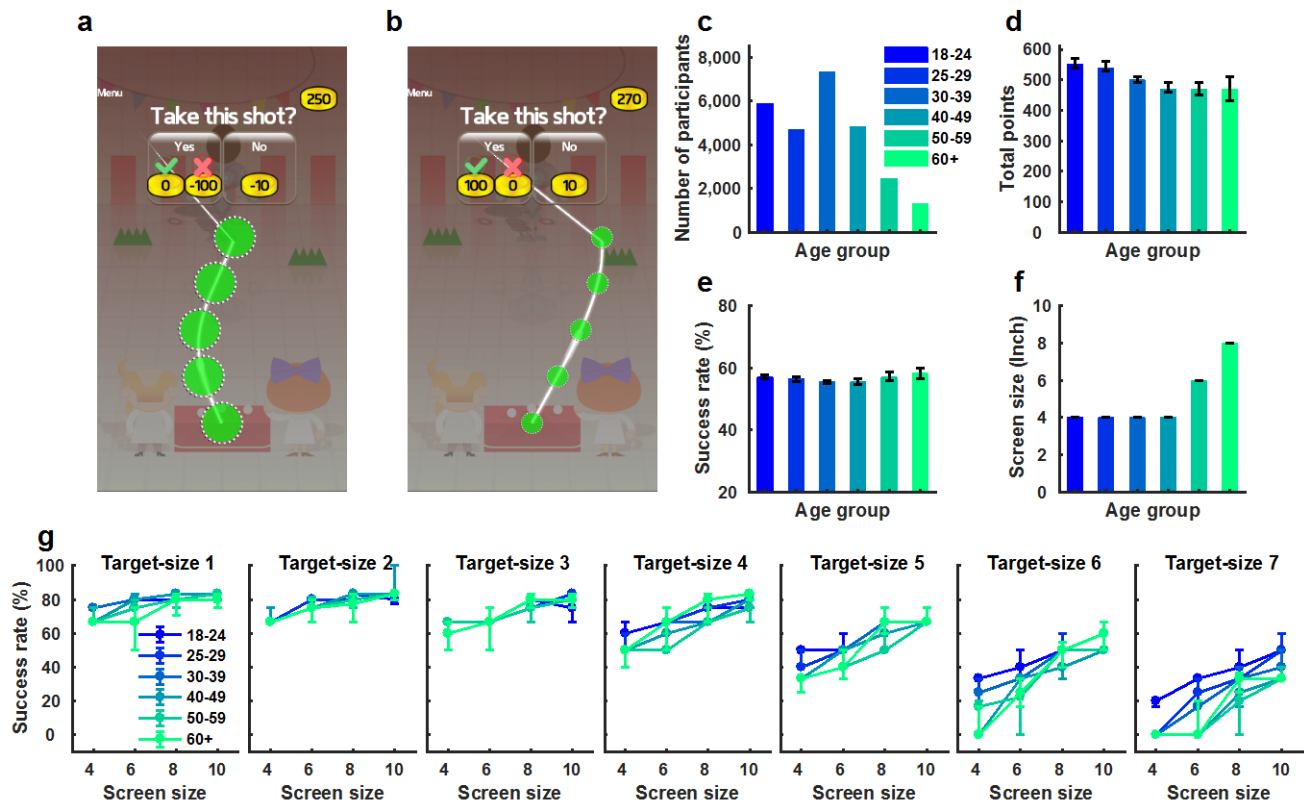
40
41 Optimal decision-making requires choices that maximise reward and minimise punishment¹¹. To achieve
42 this, humans rely on two key mechanisms; a flexible, instrumental, value-dependent process, and a hard-
43 wired, Pavlovian, value-independent process¹¹⁻¹³. Economic decision-making is often described using
44 parametric decision models based on prospect theory that operationalise instrumental (value-dependent)
45 concepts such as risk and loss aversion¹⁴⁻¹⁷. However, it has recently been shown that Pavlovian biases,
46 which promote action towards reward and inaction in the face of punishment irrespective of option value^{5, 11},
47 ¹⁸, help to explain aberrant choice behaviour. For instance, the best explanation for the diminished economic
48 risk-taking observed in older adults is a reduction in dopamine-dependent Pavlovian attraction to potential
49 reward^{2, 5}, suggesting that Pavlovian processes play a key role in explaining age-related changes in economic
50 decision-making.

51
52 In contrast to economic decision-making, motor decision-making requires weighting potential rewards and
53 punishments against the probability of successfully executing an action^{7, 19-21}. Motor decision-making has
54 primarily been explained in the context of instrumental-based processes^{1, 7-10, 22}. Within this framework, older
55 adults display reduced risk-seeking behaviour¹. However, given recent findings in economic decision-
56 making², we asked whether Pavlovian biases might provide a more parsimonious explanation of age-related
57 changes in motor decision-making. Although there is strong evidence that Pavlovian biases shape motor
58 performance²³⁻²⁶, and that healthy ageing leads to a reduction in Pavlovian biases on motor performance^{27, 28},
59 it is currently unknown whether Pavlovian biases influence motor decision-making. Sampling a large
60 population through an app-based motor-decision game, we provide a novel demonstration that Pavlovian
61 biases have a substantial impact on motor decisions, and are able to explain age-related changes in risk
62 taking during motor decision-making.

63

64 We developed a novel app-based motor decision-making task that examined participant sensitivity to reward
 65 (gaining points) and punishment (losing points) when making a ‘go/no-go’ decision based on their perceived
 66 ability to successfully execute a motor action (Figure 1a, b). Using an app-based platform (‘How do you deal
 67 with pressure?’ The Great Brain Experiment: www.thegreatbrainexperiment.com)^{18, 29, 30}, we obtained data
 68 from a large cohort (n=26,532; 15,911 males) in which six age groups were considered: 18-24yrs: n=5889;
 69 25-29yrs: n=4705; 30-39yrs: n=7333; 40-49yrs: n=4834; 50-59yrs: n=2452; and 60+yrs: n=1319 (Figure 1c;
 70 see Supplementary Methods/ Figure S1)^{18, 29, 30}.

71



72

73 **Figure 1: Motor gamble task and overall performance.** (a) Game interface: an example of a punishment trial for
 74 target-size 1 (1: largest target size; 7: smallest target size); Participants decided whether to skip the tapping task and
 75 stick with a small punishment (-10 points) or gamble on successfully executing the action. If successful then they avoid
 76 the punishment (lose 0 points); otherwise, they received a greater punishment (-100 points); (b) A reward trial for
 77 target-size 7; (c) The number of participants in each age group; (d) Final points achieved across age groups; (e) The
 78 overall success rate (%) for executing the tapping action across age groups; (f) The screen size (inches) of the devices
 79 used across age groups; (g) Success rate (%) for executing the tapping action given the age, the screen size, and target-
 80 size (1: largest target size; 7: smallest target size). Bars/Dots and error bars represent medians and bootstrapped
 81 95% CIs.

82

83 The game required participants to sequentially tap 5 targets distributed along a pre-defined path that could
 84 vary in both curvature and direction (Figure 1a, b; see Methods). If a participant accurately tapped all 5
 85 targets successfully within 1.2 seconds, then the action was considered a success. There were 7 different
 86 target sizes, with the task becoming progressively more difficult as target size decreased (Figure 1a, b; see
 87 Methods). At the beginning of each trial, participants saw the required action and were asked whether they
 88 wanted to take the motor gamble. There were two types of trials: reward and punishment. For reward trials,
 89 participants had to decide whether to skip the trial and stick with a small reward (10 points) or gamble on

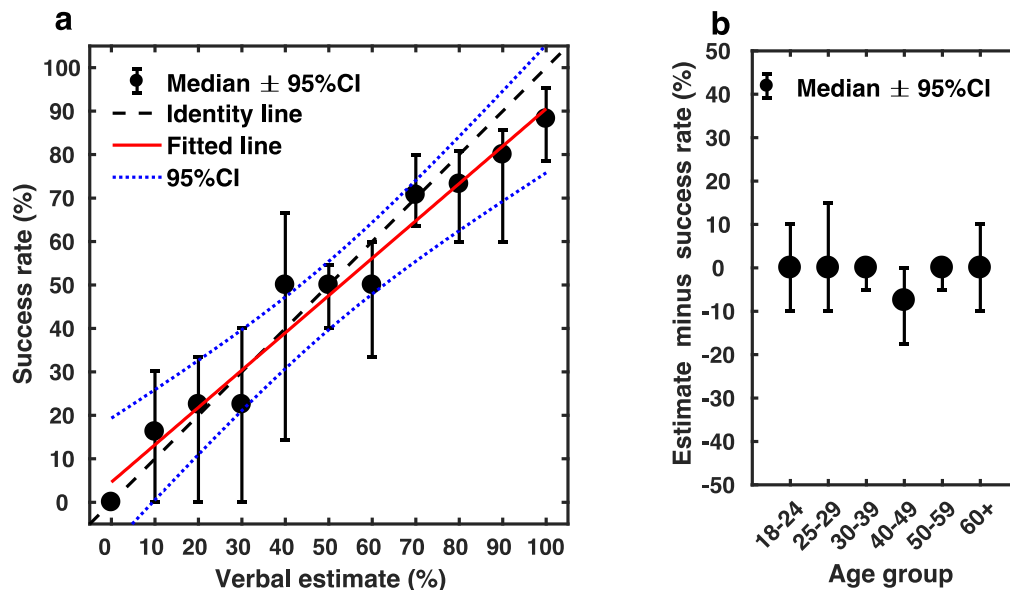
90 successfully executing the tapping action (Figure 1b). If successful they received a greater reward (20, 60 or
91 100 points) or 0 points if they failed. For punishment trials, participants had to decide whether to skip the
92 trial and stick with a small punishment (-10 points), or gamble on successfully executing the tapping action
93 (Figure 1a). If successful, they lost nothing (lose 0 points) but failure resulted in a greater punishment (-20, -
94 60 or -100 points). Participants began with 250 points and the overall goal was to accumulate as many points
95 as possible. All trial-by-trial data (including tasks parameters, behavioural results, modelling results and
96 accompanying code) are available on our open-access data depository (<https://osf.io/fu9be/>).

97
98 We found that older adults won fewer total points than younger adults (Figure 1d; $r=-0.047$, $p<0.001$; all r
99 values represent a partial correlation between the measurement of interest and age, whilst controlling for the
100 effects of gender and education; p values were computed by permutation test; see Methods). The final points
101 accumulated during this task were dependent on (1) the decisions made (to gamble or not) and (2) the motor
102 performance (success rate of executing the tapping action). Therefore, prior to examining participant choice
103 behaviour it was crucial to determine whether motor performance differed across age groups.

104
105 Although success on the motor task was similar across age groups (Figure 1e, $r=0.006$, $p=0.329$), older
106 adults used devices with larger screen sizes than younger age groups (Figure 1f, $r=0.279$, $p<0.001$). As target
107 size was scaled to device screen size (see Methods), we assessed how the relationship between age, target
108 size and screen size affected motor performance. We found that decreased success rate was linked to a
109 combination of smaller target sizes, smaller screen sizes and older age (Figure 1g, stepwise regression
110 winning model: $\text{success rate} = 1 - 0.003 * \text{age} * \text{target size} + 0.002 * \text{age} * \text{screen size} + 0.005 * \text{target size} * \text{screen}$
111 size ; all $p<0.001$; Adjusted $R^2=0.213$). Therefore, we next assessed choice behaviour in the context of how
112 these factors influenced motor performance on a trial-by-trial basis.

113
114 Participants were asked to make decisions between a gamble option and a certain option. Each option can be
115 characterised by its potential outcomes, weighted by the probability of each outcome (i.e. Expected Value³¹).
116 For the gamble option, the expected value is given by: $EV_{\text{gamble}} = P_{\text{success}} V_{\text{success}} + (1 - P_{\text{success}}) V_{\text{failed}}$, where P_{success}
117 is the probability of successfully executing the tapping action; V_{success} is the points received if successful;
118 V_{failed} is the points received on failure. The expected value of the certain option (EV_{certain}) is V_{certain} and the
119 probability of receiving this value is 1. We calculated P_{success} by estimating the probability of motor success
120 based on a participant's age, screen size of the device used and target-size level (Figure 1g; see Methods). By
121 comparing choice behaviour given the difference between these two options ($EV_{\text{gamble}} - EV_{\text{certain}}$), we were
122 then able to examine the influence of ageing on motor decisions while controlling for differences in motor
123 performance due to age, screen size and target size. However, this formulation relied on an assumption that
124 participants had a good estimate of their probability of success. To test whether this was true, we recruited an
125 additional 60 participants (10 in each age group) who were asked to estimate their probability of success
126 (from 0% to 100% in steps of 10%; see Methods) after being shown the target size and trajectory. After this
127 estimate, they were then asked to perform the tapping action (whilst ignoring the decision-making part of the

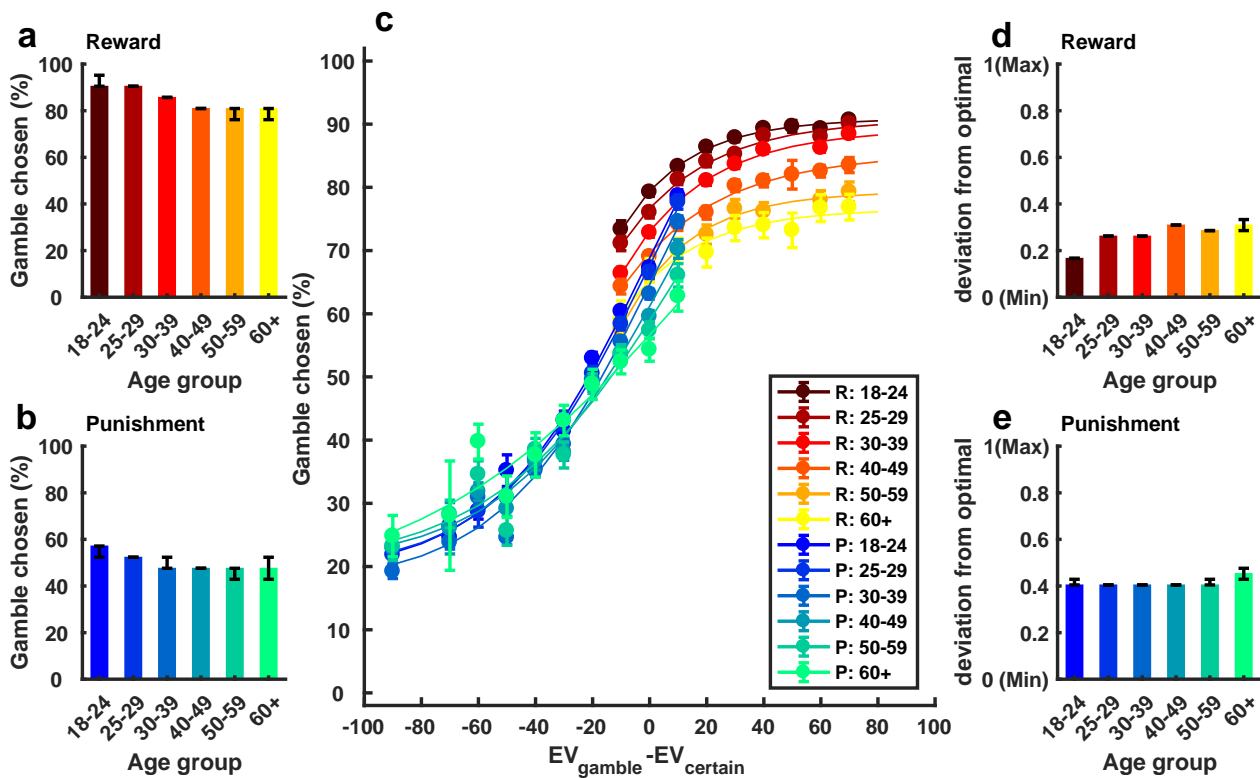
128 game). Similar to previous work^{1, 7, 20}, we found participants were able to reliably estimate the probability of
129 motor success (Figure 2a), and this estimate did not differ across age groups (Figure 2b; one-way ANOVA:
130 $F_{(5,54)}=0.859$, $p=0.515$).
131



132
133 **Figure 2: Participant ability to estimate motor performance success.** (a) For each participant ($n=60$; 10 in each
134 group), we calculated an average success rate for each available verbal estimate value (0% to 100% with 10%
135 increment). Each black dot represents the median success rate (y-axis) across participants who gave that certain verbal
136 estimate value (x-axis), and error bars represent bootstrapped 95% CI across participants; (b) The estimation error for
137 each age group. For each participant, estimation error was calculated as the median error (on each trial: estimate % -
138 100% if successful, 0% if failed) across all trials. Black dots and error bars represent the medians and bootstrapped
139 95% CIs.
140

141 We found a significant decrease in the proportion of trials in which participants chose to gamble across the
142 lifespan in reward trials (Figure 3a; $r=-0.190$; $p<0.001$), and to a lesser extent in punishment trials (Figure
143 3b; $r=-0.052$; $p<0.001$). To understand these results, age-related changes in choice behaviour had to be
144 examined given the difference between these two value options ($EV_{\text{gamble}}-EV_{\text{certain}}$). Interestingly, in reward
145 trials, there was a gradual and monotonic decrease in gamble rate across the lifespan which appeared
146 independent of the $EV_{\text{gamble}}-EV_{\text{certain}}$ value (right side of Figure 3c). In contrast, for punishment trials, older
147 adults displayed a higher gamble rate during high risk gambles (e.g., $EV_{\text{gamble}}-EV_{\text{certain}}=-90$), but conversely a
148 reduced gamble rate during low risk gambles (e.g., Figure 3c; $EV_{\text{gamble}}-EV_{\text{certain}}=0$).

149



150

151 **Figure 3: The proportion (%) of trials in which participants chose to gamble.** (a) Gamble rate in the reward and (b)
 152 punishment domain; (c) Propensity to choose the gamble option as a function of $EV_{\text{gamble}} - EV_{\text{certain}}$ (data was grouped
 153 into bin sizes of 10). As indicated in the legend, each of the warm colours represents one age group in the reward (R)
 154 condition, and each of the cool colours represents one age group in the punishment (P) condition. The lines are fitted
 155 lines to $y=a*\exp(-b*x)+c$; $R^2=0.979 \pm 0.022$; (d) Discrepancy between choice behaviour and optimal decisions in the
 156 reward domain. Specifically, using $EV_{\text{gamble}} - EV_{\text{certain}}$ we calculated whether the optimal decision on each trial was to
 157 gamble (1) or skip (0). We then subtracted this value from the observed behaviour of the participant (gamble=1, skip
 158 =0). If the average absolute difference between these values across trials was 0, then a participant was deemed as an
 159 optimal decision-maker; (e) Discrepancy between choice behaviour and optimal decisions in the punishment domain.
 160 Bars and error bars represent medians across the participants and bootstrap 95% CIs.
 161

162 Given these results, do older adults make less optimal motor decisions? An ideal (optimal) decision-maker
 163 chooses the option that has the higher expected value, and we therefore compared participant's choice
 164 behaviour with the optimal behaviour. Specifically, using $EV_{\text{gamble}} - EV_{\text{certain}}$ we calculated whether the
 165 optimal decision on each trial was to gamble or decline (coded 1 and 0 respectively). We then subtracted this
 166 value from the observed behaviour of the participant (also coded gamble = 1, decline = 0). If the average
 167 absolute difference between these values across trials was 0, then a participant was deemed an optimal
 168 decision-maker. In reward trials, there was progressive deviation from optimality across the lifespan (Figure
 169 3d; $r=0.232$; $p<0.001$). In contrast, for punishment trials, all age groups showed a similar level of sub-
 170 optimality (Figure 3e; $r=0$; $p=0.999$). Therefore, the most pronounced effect of ageing on motor decision-
 171 making was a value-independent decrease in gamble rate during reward trials which led to a significant
 172 decrease in optimality.
 173

173

174 While these data portray many similarities with decision-making under risk^{14, 15}, there are also clear
 175 differences. For example, decision-making models based on prospect theory are not able to explain the
 176 gradual, monotonic and value independent decrease in gamble rate across the life span observed during the

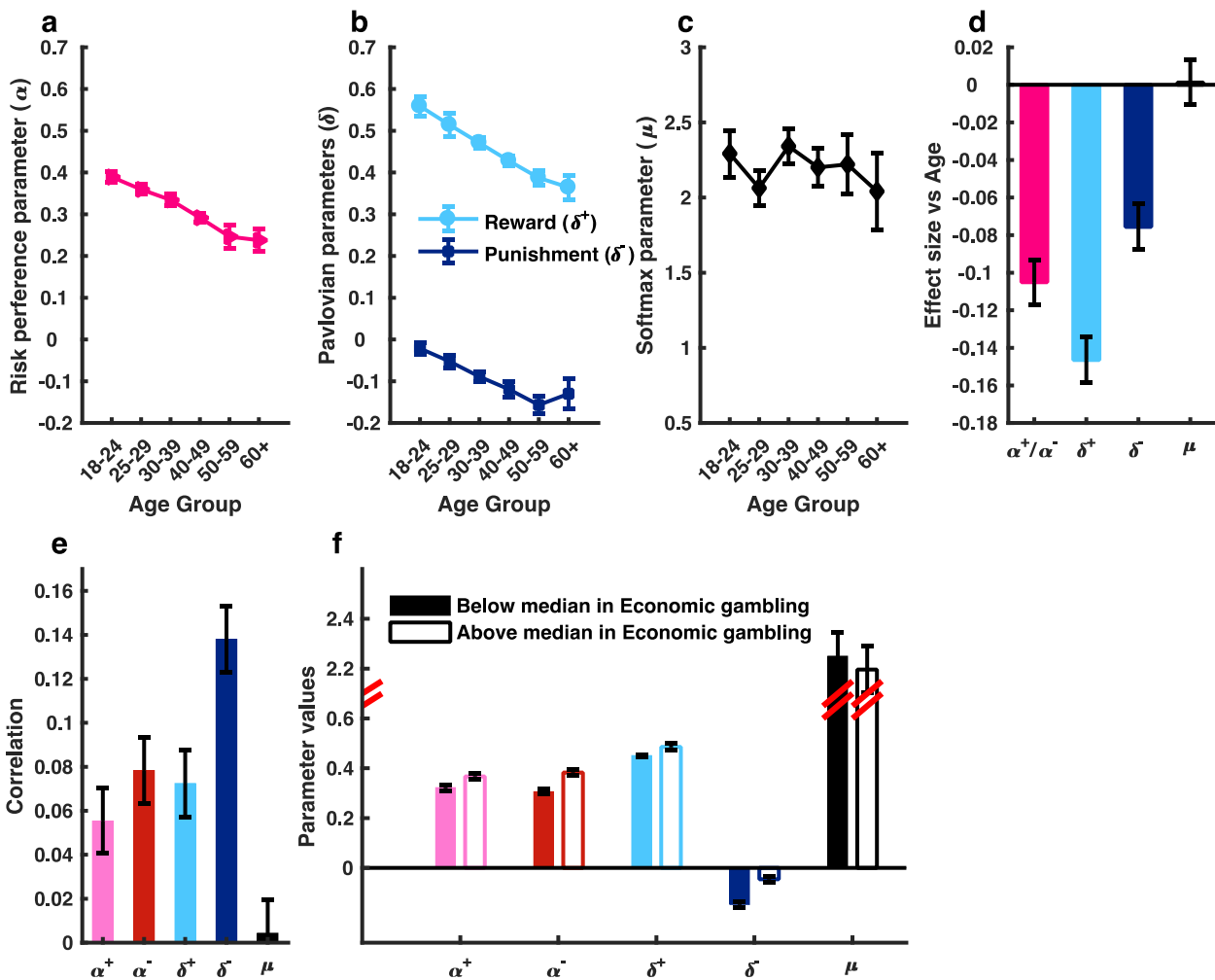
177 reward trials⁵ (Figure S1). We predicted that such dichotomies represented the contribution of value-
178 independent Pavlovian approach-avoidance biases to motor decision-making behaviour. To test this
179 prediction, we modelled the choice behaviour using an established decision-making model based on prospect
180 theory, and a newly introduced model which included Pavlovian approach-avoidance parameters^{2, 5} (see
181 Methods). The prospect theory model included three components: (1) loss aversion parameter (λ) (2) risk
182 preference parameter (α) and (3) stochasticity of decision-making captured by an inverse temperature
183 parameter (μ). The loss aversion coefficient (λ) represents the relative (multiplicative) weighting of losses
184 relative to gains, which was set to 1 as there were no gambles with both positive and negative outcomes in
185 our task. The risk preference parameter (α) represents the diminishing sensitivity to change in value with an
186 increase in absolute value (value-dependent). The logit parameter μ is the sensitivity of the choice
187 probability to an option value difference. In addition to these parameters, the Pavlovian approach-avoidance
188 model included value-independent parameters exclusively for reward (δ^+) and punishment (δ^-) trials.
189 Positive or negative values of these parameters correspond, respectively, to an increased or decreased
190 probability of gambling without regard to the value of gamble (see Methods; Eq 3). We found an approach-
191 avoidance decision model with 4 parameters (a single risk preference parameter: α , the inverse temperature
192 parameter: μ , value-independent parameters exclusively for reward δ^+ and punishment δ^- trials) fitted the
193 motor gamble (choice) data better than any decision model based on prospect theory (Table S1, Figure S2 &
194 S3; see Methods for model comparison).

195
196 Using this preferred model, we observed age-related changes across the reward and punishment domains for
197 both value-dependent and independent parameters. However, the most striking effect was a large decrease in
198 Pavlovian attraction which facilitates action in pursuit of reward. Specifically, we found that healthy ageing
199 did not affect the stochasticity parameter, μ ($r=-0.001$, $p=0.871$), but was associated with a decrease in the
200 risk preference parameter, α (Figure 4a,d; $r=-0.105$, $p<0.001$). The winning model included a single α
201 parameter, which represented different value-dependent biases in reward and punishment ($\alpha<1$ indicated risk
202 aversion in reward domain and $\alpha<1$ represented risk-seeking in punishment domain; $\alpha=1$ represented risk-
203 neutral; see Supplementary Methods). Therefore, older adults displayed a similar increase in value-
204 dependent biases across the reward and punishment domain. The greater risk-seeking effect in the
205 punishment domain was offset by the fact that ageing was also linked with greater Pavlovian avoidance
206 (Figure 4b, d; δ^- ; $r=-0.076$, $p<0.001$), an effect not previously observed in economic decision-making². Such
207 opponent effects between value-dependent and value-independent parameters help to explain the complex
208 changes observed with ageing during punishment trials (Figure 3c). Nevertheless, the largest effect of ageing
209 was a substantial decrease in Pavlovian attraction (Figure 4b, d; δ^+ ; $r=-0.146$, $p<0.001$). We found a similar
210 decline for both sexes (Figure S4; male: $n=15911$, $r=-0.140$, $p<0.001$; female: $n=10621$, $r=-0.143$, $p<0.001$),
211 and across all education levels (Figure S5; school: $n=9171$, $r=-0.152$, $p<0.001$; university: $n=11281$, $r=-$
212 0.142 , $p<0.001$; advanced: $n=6080$, $r=-0.136$, $p<0.001$). Importantly, we did not observe this age-related
213 effect for the temperature parameter (μ), indicating the changes observed in the risk and Pavlovian
214 parameters were not simply a result of large participant numbers (Figure 4d).

215

216 Finally, through this app-based platform a subset of participants (n=17,220) also performed an economic
 217 decision-making gambling task in which a similar approach-avoidance model was used to explain choice
 218 behaviour². Through correlation and median-split analysis we found a significant positive relationship for all
 219 main model parameters between the tasks (Figure 4e, f), consistent with participants manifesting similar
 220 decision-making tendencies across motor and economic domains. This relationship was relatively consistent
 221 across the lifespan whereby a positive correlation existed between these parameters within each age group
 222 (Figure S6, S7). Once again, we did not observe this correlation for the temperature parameter (μ).

223



224

225 **Figure 4: The change in approach-avoidance model parameters across the life span, and the relationship**
 226 **between approach-avoidance model parameters across a motor and economic gambling task. (a)** α across age
 227 groups; **(b)** δ^- and δ^+ across age groups; **(c)** μ across age groups; **(d)** Age-related decline across the reward and
 228 punishment domain. The largest effect size was observed for the Pavlovian approach parameter (δ^+). This age-related
 229 effect was not observed for the temperature parameter, μ ; **(e)** Positive correlation across independent motor and
 230 economic decision tasks for the main approach-avoidance model parameters. Note, the single α parameter of the motor
 231 decision-making model was correlated with both the α^- and α^+ parameters of the decision-making model. This positive
 232 correlation was not observed for the temperature parameter, μ ; **(f)** Motor decision-making approach-avoidance
 233 parameter values median split by economic parameter values. Filled bars denote participants with below-median values
 234 in the economic gambling task; Hollow bars for above-median. The participants with above-median risk parameters and
 235 Pavlovian parameters in the economic decision task had higher risk parameters and Pavlovian parameters in the motor
 236 gambling task. This median split effect was not observed for the temperature parameter, μ ; Bars/error bars reflect
 237 medians/bootstrapped 95% CIs.

238

239 Making decisions under uncertainty is crucial in everyday life, whether it is managing retirement funds,
240 choosing a career, or deciding between pulling out or not on to a busy road whilst driving. The latter example
241 describes motor decision-making, a unique kind of decision which requires weighting potential rewards and
242 punishments against the probability of successfully executing an action^{7, 19-21}, and often with immediate
243 outcomes. Although healthy ageing has been associated with decreased risk taking across both motor¹ and
244 economic²⁻⁴ decision-making, it is heretofore unknown whether a single underlying mechanism might
245 explain these changes. We addressed this question using a novel motor gambling task that exploited an app-
246 based platform which enabled us to collect a large cohort of data. Unlike previous work on motor decision-
247 making^{7, 19-21}, we considered choice behaviour in relation to both value-dependent instrumental and value-
248 independent Pavlovian processes^{5, 11, 18}. We found age-related changes across the punishment and reward
249 domain for both value-dependent and independent parameters. However, the most striking effect of ageing
250 was a decrease in Pavlovian attraction which facilitates action in pursuit of reward. Through this app-based
251 platform, we compared a subset of participant's choice behaviour during motor and economic decision-
252 making² and found similar decision-making tendencies across motor and economic domains.

253

254 Our large cohort and use of a newly established approach-avoidance computational model^{2, 6} enabled us to
255 detect subtle age-related changes in choice behaviour and surprising interactions between value-independent
256 and value-dependent processes. For instance, the risk aversion parameter (α : instrumental value-dependent
257 process) was on average less than 1 across all age groups, indicating risk aversion in reward, and risk seeking
258 in punishment. This choice behaviour was best explained using a single parameter, signifying a similar
259 degree of risk aversion in reward and risk-seeking in punishment. Importantly, this value progressively
260 decreased with age suggesting that older adults showed similar increased risk-aversion for reward and risk-
261 seeking for punishment. This is in line with previous economic decision-making work which revealed older
262 adults weigh certainty (achieving the small reward or avoiding the small punishment) more heavily than
263 younger adults³². Interestingly, the greater risk-seeking in the punishment domain was offset by the fact that
264 ageing also led to greater Pavlovian avoidance, an effect not observed in economic decision-making². It is
265 the interaction between value-dependent and independent parameters that help explain not only the complex
266 changes observed with ageing during punishment trials but also the lack of difference across age groups for
267 punishment-based optimality. Crucially, previous work in motor decision-making using only instrumental-
268 based processes would not have detected such complex behavioural interactions^{1, 7, 21}. The underlying
269 mechanism behind age-dependent increases in Pavlovian avoidance is unknown. It has been suggested that
270 the neurobiology behind Pavlovian avoidance may involve opponency between the dopaminergic and
271 serotonergic systems³³. Despite there being evidence of age-related decline in serotonin receptor
272 availability³⁴, it remains an open question as to the link between serotonin and Pavlovian avoidance during
273 either motor or economic decision-making.

274

275 The strongest effect of ageing was a decrease in Pavlovian attraction to reward. As all age groups displayed
276 risk aversion during reward trials, this decrease in Pavlovian attraction led to greater sub-optimality in older

277 adults. These results are strikingly similar to the ones observed in economic decision-making², suggesting
278 Pavlovian attraction plays a pivotal role in explaining age-related changes to reward across both motor and
279 economic decision-making. During economic decision-making, it has recently been shown that boosting
280 dopamine with L-DOPA increases the influence of Pavlovian attraction on choice behaviour⁵. In addition,
281 healthy ageing is associated with a gradual decline in dopamine availability^{35, 36} and neural responses to
282 reward³⁷. Therefore, it is possible that the decrease in Pavlovian attraction during motor decision-making in
283 older adults is a result of an age-dependent decrease in dopamine availability.

284

285 More broadly, the current work shows the importance of both instrumental value-dependent and Pavlovian
286 value-independent processes on motor decision-making. However, task design may play an important role in
287 determining the size of Pavlovian influences. Here we used a ‘go/no-go’ decision-making task as previous
288 literature has shown the ‘go/no-go’ component induces strong Pavlovian biases^{11, 25, 38}. It remains to be seen
289 whether computational models including Pavlovian biases provide a better description of choice behaviour
290 during other motor decision-making tasks which do not involve a ‘go/no-go’ component^{1, 7-10, 22}.

291

292 Finally, participants showed similar decision-making tendencies for both instrumental (value-dependent) and
293 Pavlovian (value-independent) parameters across motor and economic domains. This extends previous work
294 that revealed a similar relationship with parameters derived from parametric decision models based on
295 prospect theory^{7, 10}, and reinforces the view that the mechanisms which control cognitive (economic) and
296 motor decision-making are integrated³⁹. However, the correlation between the tasks was small, around $r=0.1$,
297 suggesting that while participants showed similar behavioural trends across the two tasks, their performance
298 in motor and economic domains was also distinct. Interestingly, the approach-avoidance model not only
299 fitted choice data substantially better for the motor decision-making task, relative to the economic task, but
300 the effect size relating to age was also nearly double in size for all parameters². This indicates that while
301 there are clear similarities between cognitive and motor decision-making, computational models including
302 Pavlovian biases appear to be particularly important for explaining motor decision-making.

303

304 In conclusion, Pavlovian biases play an important role in not only explaining motor decision-making
305 behaviour but also the changes which occur through normal ageing. This provides a greater understanding of
306 the processes which shape motor decision-making across the lifespan, and may afford essential information
307 for developing population wide translational interventions such as promoting activity in older adults.

308

309 **Methods**

310 *Participants*

311 We tested 26,532 participants (15,911 males, aged 18-70+) who completed the task between November 20,
312 2013 and August 15, 2015. Data were only included if users fully completed the game and it was their first
313 attempt. We also recruited an additional 60 participants (29 males, aged 18-70+) who were asked to estimate

314 their success rate (motor performance). All participants gave informed consent and the Research Ethics
315 Committee of University College London approved the study.

316

317 ***Materials and apparatus***

318 Using an app-based platform (The Great Brain Experiment: www.thegreatbrainexperiment.com) we
319 developed a motor decision-making task ('How do I deal with pressure?') which is freely available for Apple
320 iOS and Google Android systems. The game runs in a 640x960 (3:4 ratio) pixel area, which is then scaled to
321 fit the screen whilst maintaining this ratio. The game required participants to 'throw' a ball at a coconut in an
322 attempt to knock it off its perch. This was achieved by tapping 5 sequential targets along a pre-defined path.
323 The path was characterised by an angle parameter that represented a section of a sine curve, in degrees. The
324 curves were drawn from the bottom (the starting point) to top of the game window (Figure 1a, b). For
325 example, if the angle parameter was 360, then one complete cycle of the sine curve was used to draw the
326 curve. During the task, the angle was randomly chosen between 0 and 360. The 5 targets were evenly spaced
327 along the curves. If the participant tapped all 5 targets sequentially (from bottom to top) within 1.2 seconds,
328 then the action was considered a success and the coconut was hit. If the participant failed to tap all 5 targets
329 accurately or within the allotted time then the action was considered a failure and the ball sailed past the
330 coconut. In addition, the action was deemed a failure if participants did not start the tapping action within 7
331 seconds after they chosen to do the tapping. There were 7 different target sizes across trials with the tapping
332 action becoming more difficult as the target size was reduced. However, as mentioned above, the game
333 interface was scaled to screen size. Therefore, motor performance (success rate) was examined relative to the
334 interaction between target size and screen size (Figure 1g). All trial-by-trial data (including tasks parameters,
335 behavioural results, modelling results and accompanying code) are available on our open-access data
336 depository (<https://osf.io/fu9be/>).

337

338 ***Motor gambling task***

339 At the beginning of each trial, participants were shown the action required (i.e. the position and size of the 5
340 targets) and were asked to make a motor gamble. There were two types of trials: reward trials and
341 punishment trials (Figure 1a, b). For reward trials, participants had to decide whether to skip the trial and
342 stick with a small reward (10 points) or gamble on successfully executing the 'throw'. If successful they
343 received a greater reward (20, 60 or 100 points) but 0 points if they failed. For punishment trials, participants
344 had to decide whether to skip the trial and stick with a small punishment (-10 points) or gamble on
345 successfully executing the 'throw'. If successful they lost nothing (0 points) but failure resulted in a greater
346 punishment (-20, -60 or -100 points). Hence, there were 6 value combinations. Each combination was
347 repeated for each of the 7 different target sizes (6 values x 7 target sizes = 42 trials). Although there were 7
348 blocks of the game this did not directly relate to the 7 target sizes. In order to maintain a level of
349 unpredictability, the first 3 blocks included random presentation of the 3 largest (easiest) target sizes, the
350 next 3 blocks included target sizes 4-6 and the final block included the smallest (most difficult) target size.
351 Participants began with 250 points and the overall goal was to accumulate as many points as possible.

352

353 For the control study (Figure 2) which examined participant's ability to estimate their probability of success,
354 individuals were asked to estimate their probability of motor success (0% to 100% in steps of 10%) after
355 being shown the target size and trajectory. After this estimate, they were then asked to perform the tapping
356 action, whilst ignoring the decision-making part of the game.

357

358 *Data analysis*

359 Matlab (Mathworks, USA) was used for all data analysis. We reported partial correlation coefficients (r) for
360 the relationships between task measures and age, whilst controlling for the effects of gender and education.
361 All p values were computed based on permutation tests using 100,000 random shuffles of age labels to
362 determine null distributions². Bootstrapped 95% confidence intervals were computed based on 100,000
363 resamples with replacement in each age group².

364

365 *Parametric models*

366 On each trial participants faced a gamble that contained a certain option (CO) involving a payoff of certain
367 points (+10 in reward trials and -10 in punishment trials), and a gambling option (GO) in which the outcome
368 depended on a probability of successfully executing the tapping action. The probability was estimated given
369 a participant's age, screen size of the device used and target-size level (Figure 1g). Specifically, the
370 probability of success for a participant within a certain age group, using a certain screen size and facing a
371 certain target size on each trial was estimated using the average success rate across all the participants with
372 the same age, same screen size, and facing the same target size. Given the small amount of trials we had for
373 each participant at each target size to estimate their probability of success, we believed this group average
374 approach was the most valid estimate of success probability. However, we also conducted the analysis when
375 success probability was estimated based on each individual's own data (i.e. the probability of success for a
376 participant facing a certain target size was estimated using their own success rate over the same target size).
377 Importantly, our findings still hold (Figure S8). We modelled participant motor gamble choices using an
378 established decision-making model based on prospect theory¹⁵ and a newly introduced model which included
379 an extra Pavlovian approach-avoidance^{2, 5, 6} component. In the following, we first describe the prospect
380 theory models, followed by the approach-avoidance models.

381

382 *Parametric decision-making model based on prospect theory:* There are three key components in
383 prospect theory models. The first component is the value function. According to prospect theory, the
384 subjective desirability of outcomes is modelled as transformations of objective task quantities. The
385 subjective desirability of the outcomes, O (the points in this case) was modelled by a value function (2-part
386 power function) of the form:

387

$$388 \quad u(O) = \begin{cases} O^{\alpha^+} & \text{if } O \geq 0 \\ -\lambda \cdot (-O)^{\alpha^-} & \text{if } O < 0 \end{cases} \quad \text{Equation 1}$$

389 where, the risk preference parameter (α) represents the diminishing sensitivity to changes in values as the
 390 absolute value increases (if $\alpha < 1$). The loss aversion coefficient (λ) represents the weighting of losses
 391 relative to gains, which was set to 1 as we did not have gambles with both positive and negative outcomes.
 392 The second component of a prospect theory model is the probability weighting function. Most prospect
 393 theory models assume that probabilities are weighted non-linearly. However, we found that the probability
 394 weighting parameter (γ) did not significantly improve the model fit (Table S1, we used a 1-parameter
 395 probability weighting function⁴⁰: $w(p) = \exp(-(-\ln(p))^\gamma)$). Hence, probabilities and utilities were
 396 combined linearly in the form: $U(p, O) = p * v(O)$. The third component of a prospect theory model is the
 397 choice function. The probability of choosing to gamble is given by the logit or soft-max function:

$$398$$

$$399 \quad F(p, O_1, O_2, O_c) = (1 + \exp[-\mu(U(p, O_1, O_2) - U(O_c))])^{-1} \quad \text{Equation 2}$$

$$400$$

401 where O_1 and O_2 are the outcomes in the gamble option [$p \rightarrow O_1; (1-p) \rightarrow O_2$], and O_c is the outcome of the
 402 certain option. The logit parameter μ is the sensitivity of the choice probability to the utility difference. In
 403 summary, our prospect theory models included the following free parameters: risk preference parameter (α)
 404 and stochasticity of decision-making according to the inverse temperature parameter (μ).

405

406 *Parametric approach-avoidance decision model:* Approach-avoidance models were based on the
 407 prospect theory models, but with an additional component that allows for value-independent influences to
 408 choose or not choose gambles. Specifically, Pavlovian parameter (δ) were added to the probability of
 409 choosing to gamble (Equation 2) as follows:

$$410$$

$$411 \quad F(p, O_1, O_2, O_c) = (1 + \exp[-\mu(U(p, O_1, O_2) - U(O_c))])^{-1} + \delta$$

$$412 \quad F(p, O_1, O_2, O_c) = \max(0, \min(F(p, O_1, O_2, O_c), 1)) \quad \text{Equation 3}$$

$$413$$

414 Positive or negative values of the parameter (δ) correspond respectively to an increased or decreased
 415 probability of gambling without regard to the value of gamble. Other parts of the models were identical to
 416 the prospect theory models. In summary, the approach-avoidance model included the following free
 417 parameters: risk preference parameter (α), stochasticity of decision-making according to the inverse
 418 temperature parameter (μ) and Pavlovian parameter (δ).

419

420 ***Parameter optimisation and model selection procedures***

421 The models were fit to individual choice data. The method of maximum likelihood was used to estimate
 422 (fminsearch in Matlab) the parameter vector Θ given the participant choice (y) on each trial (p, O_1, O_2, O_c):

$$423$$

$$424 \quad L(\Theta|y, p, O_1, O_2, O_c) \quad \text{Equation 4}$$

$$425 \quad = \sum_{i=1}^N y_i \log(F(p(i), O_1(i), O_2(i), O_c(i), \Theta)) + (1 - y_i) \log(1 - F(p(i), O_1(i), O_2(i), O_c(i), \Theta)))$$

426

427 Where, i indexes the trial number; N is the number of trials; y_i indicates participant choice on trial i ;
428 Θ indicates the parameter vector to be estimated; (p, O_1, O_2, O_c) represent the gamble options on each trial.
429 Parameters were constrained to the following ranges: $\alpha: 0 \rightarrow 1$; $\mu: 0 \rightarrow 10$; $\delta: -1 \rightarrow 1$. The model was fit
430 to each participant's data, and the fitting was repeated at 200 random seed locations to avoid local minima.

431

432 For each key parameter of prospect theory and approach-avoidance models, we explored the possibility of
433 using separate and single parameters for reward and punishment domains as well as a weighted or linear
434 probability function. Therefore, we fitted each participant's choice data with 24 models (Table S1). We used
435 Akaike's information criterion (AIC)⁴¹ and Bayesian information criterion (BIC)⁴² to compare model fits.
436 Both of these represent a trade-off between the goodness of fit and complexity of the model and thus can
437 guide optimal model selection. *Pseudo* r^2 was calculated with the null model in which α, μ and δ were
438 restricted to 0 (*pseudo* $r^2 = 1 - \frac{\ln(\hat{L}(\text{model}))}{\ln(\hat{L}(\text{null model}))}$, where \hat{L} =Estimated likelihood).

439

440 **Competing interests**

441 The authors declare no competing interests.

442

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451

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542

Supplementary material: Age-dependent Pavlovian biases influence motor decision-making

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SUPPLEMENTARY METHODS

PARTICIPANTS	1
PARAMETRIC DECISION-MAKING MODEL BASED ON PROSPECT THEORY	2
PARAMETRIC APPROACH-AVOIDANCE DECISION MODEL	2
SUPPLEMENTARY RESULTS	
MODEL PARAMETER OPTIMIZATION AND MODEL SELECTION	2-4
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Supplementary Methods

Participants

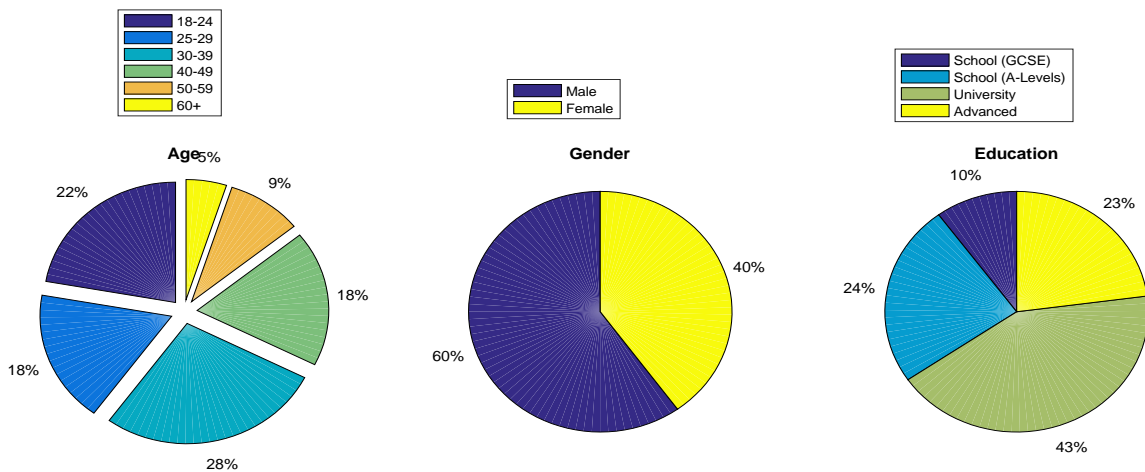
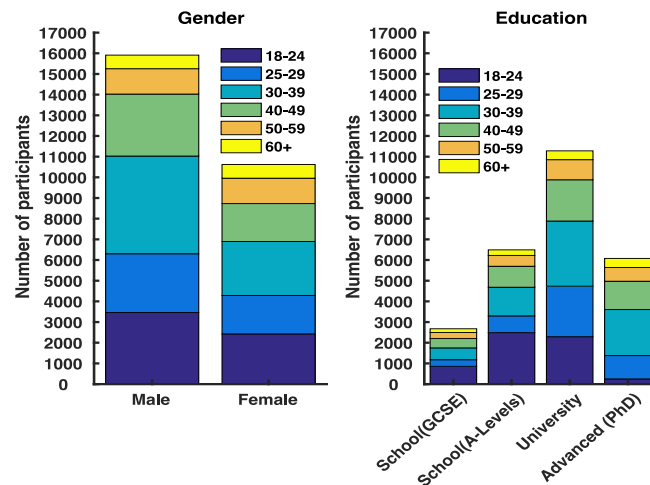


Figure S1: Additional participant demographics

29 ***Parametric decision-making model based on prospect theory***

30 As mentioned in the Methods, the subjective desirability of outcomes was modelled as transformations of
31 objective task quantities. The subjective desirability of the outcomes O (the points in this case) was modelled
32 by a value function (2-part power function) of the form as in Equation 1. The risk preference parameter (α)
33 represents the diminishing sensitivity to changes in values as the absolute value increases (if $\alpha < 1$). The
34 risk preference parameter ($\alpha < 1$) is equivalent to risk aversion in the reward domain and risk seeking in the
35 punishment domain, as demonstrated by the following examples. Imagine a gamble between a probabilistic
36 reward: 50% of £20; 50% of £0 and a sure reward of £10. The objective expected value of the gamble is £10,
37 similar to the certain option. Hence a risk neutral person would be indifferent between these two options. If
38 $\alpha = 0.8$, the gamble would have a subjective value of 5.49, and the certain option would have a subjective
39 value of 6.31, which results in participants being more likely to choose the certain option (i.e., risk aversion).
40 Now imagine a gamble between a probabilistic punishment 50% of -£20; 50% of £0 and a sure punishment
41 of -£10. The objective expected value of gamble is -£10, similar to the certain punishment option. If $\alpha = 0.8$,
42 the gamble would have a subjective value of -5.49, and the certain option would have a subjective value of
43 -6.31, which results in participants being more likely to choose the gamble option (i.e., risk seeking).
44

45 ***Parametric approach-avoidance decision model***

46 Approach-avoidance Models were based on the prospect theory models, but with an additional
47 component that allows for value-independent influences to choose or not choose gambles i.e., Pavlovian
48 parameters (δ). Positive or negative values of the parameter (δ) correspond respectively to an increased or
49 decreased probability of gambling without regard to the value of gamble. Other parts of the models were
50 identical to the prospect theory models.
51

52 **Supplementary Results**

53
54 ***Model parameter optimization and model selection***

55 For each key parameter of prospect theory and approach-avoidance models, we explored the possibility of
56 using separate and single parameters for gain and loss domains as well as a weighted or fixed probability
57 function. Therefore, we fitted each participant's choice data with 24 models (Table S1). We used Akaike's
58 information criterion (AIC) and Bayesian information criterion (BIC) to compare model fits (see main paper
59 for relevant references). Both of these represent a trade-off between the goodness of fit and complexity of the
60 model and thus can guide optimal model selection. *Pseudo* r^2 was calculated with the null model in which
61 α, μ and δ were restricted to 0 ($pseudo\ r^2 = 1 - \frac{\ln(\hat{L}(model))}{\ln(\hat{L}(null\ model))}$, where \hat{L} =Estimated likelihood). The
62 preferred model's behavioural predictions among both the prospect theory models ($[\alpha^+, \alpha^-, \mu^+, \mu^-]$; ID=4
63 Table S1) and the approach-avoidance models ($[\alpha, \mu, \delta^+, \delta^-]$; ID=10 Table S1) are plotted in
64 Figure S2 and Figure S3, respectively.
65

66

		ID	Parameters	pseudo r^2 (mean± sd)	pseudo r^2 (median)	BIC (lower value preferred)	AIC (lower value preferred)
PT model	Linear prob	1	α, μ	0.20±0.18	0.17	1426604	1334397
		2	α, μ^+, μ^-	0.30±0.15	0.30	1371245	1232934
		3	α^+, α^-, μ	0.29±0.18	0.27	1392398	1254087
		4	$\alpha^+, \alpha^-, \mu^+, \mu^-$	0.36±0.19	0.35	1382608	1198193
	Weighted prob γ	5	α, μ, γ	0.23±0.19	0.19	1494553	1356242
		6	$\alpha, \mu^+, \mu^-, \gamma$	0.31±0.15	0.30	1462708	1278293
		7	$\alpha^+, \alpha^-, \mu, \gamma$	0.30±0.18	0.28	1484189	1299773
		8	$\alpha^+, \alpha^-, \mu^+, \mu^-, \gamma$	0.35±0.19	0.32	1497729	1267210
AA model	Linear prob	9	α, μ, δ	0.44±0.24	0.43	1156367	1018056
		10	$\alpha, \mu, \delta^+, \delta^-$	0.52±0.25	0.53	1134654	950238
		11	$\alpha, \mu^+, \mu^-, \delta$	0.41±0.26	0.39	1315334	1130919
		12	$\alpha, \mu^+, \mu^-, \delta^+, \delta^-$	0.53±0.25	0.54	1223419	992900
		13	$\alpha^+, \alpha^-, \mu, \delta$	0.44±0.24	0.42	1255799	1071384
		14	$\alpha^+, \alpha^-, \mu, \delta^+, \delta^-$	0.54±0.25	0.55	1211776	981257
		15	$\alpha^+, \alpha^-, \mu^+, \mu^-, \delta$	0.46±0.24	0.43	1332344	1101825
		16	$\alpha^+, \alpha^-, \mu^+, \mu^-, \delta^+, \delta^-$	0.53±0.25	0.54	1321843	1045220
	Weighted prob γ	17	$\alpha, \mu, \delta, \gamma$	0.44±0.25	0.42	1260226	1075810
		18	$\alpha, \mu, \delta^+, \delta^-, \gamma$	0.53±0.26	0.55	1215174	984655
		19	$\alpha, \mu^+, \mu^-, \delta, \gamma$	0.42±0.27	0.41	1397167	1166647
		20	$\alpha, \mu^+, \mu^-, \delta^+, \delta^-, \gamma$	0.54±0.25	0.55	1306339	1029716
		21	$\alpha^+, \alpha^-, \mu, \delta, \gamma$	0.43±0.25	0.42	1382322	1151803
		22	$\alpha^+, \alpha^-, \mu, \delta^+, \delta^-, \gamma$	0.54±0.25	0.55	1323605	1046982
		23	$\alpha^+, \alpha^-, \mu^+, \mu^-, \delta, \gamma$	0.47±0.24	0.44	1469428	1192805
		24	$\alpha^+, \alpha^-, \mu^+, \mu^-, \delta^+, \delta^-, \gamma$	0.53±0.25	0.54	1433450	1110723

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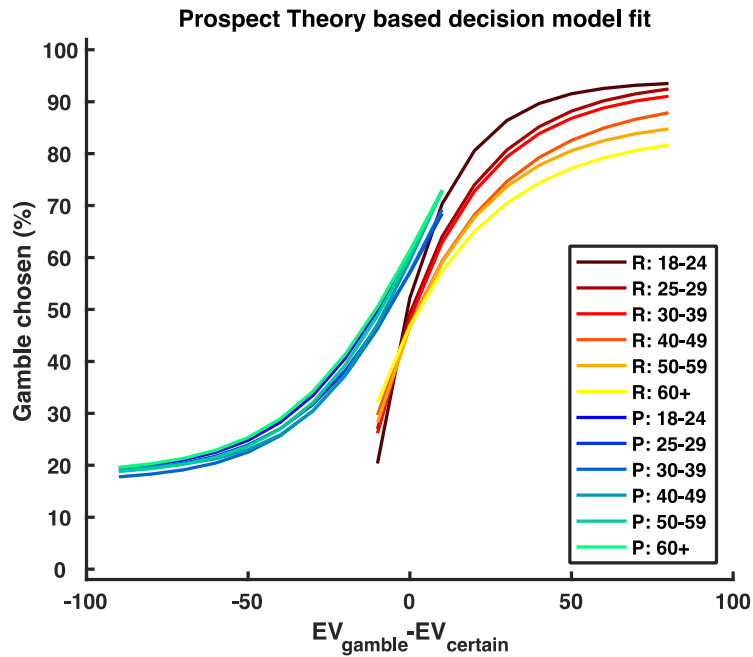
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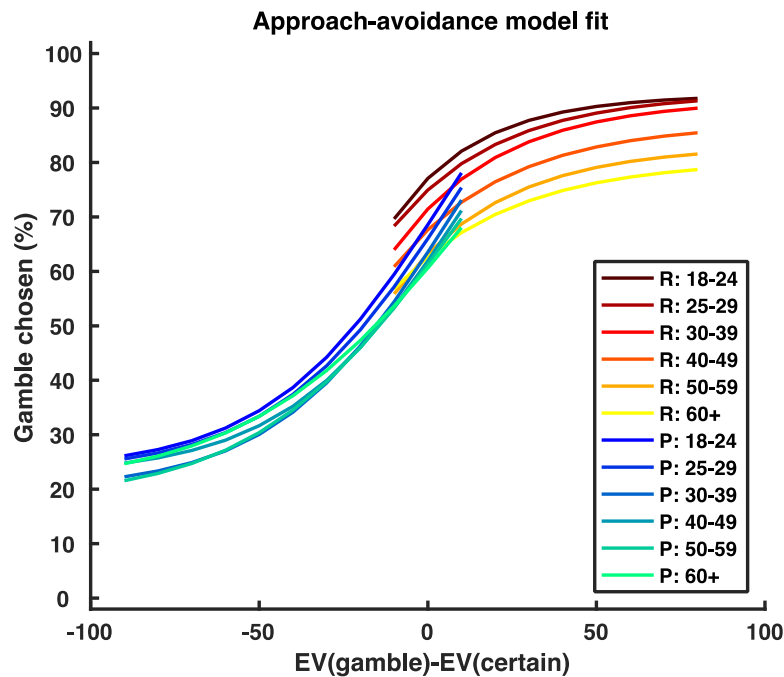
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Table S1: Comparison of decision-making models. The main parameters were (1) value function parameter (α); (2) the probability weighting parameter (γ); the Softmax temperature parameter (μ); the Pavlovian parameter (δ). For each key parameter of the prospect theory (PT) and approach-avoidance (AA) models, we explored the possibility of using separate and single parameters for reward and punishment domains as well as a weighted or fixed probability function (see Methods). According to AIC and BIC model comparison an approach-avoidance decision model (red; ID=10) fitted the choice (gamble) data better than established decision models based on prospect theory.



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Figure S2: Average model fit across participants for the winning prospect theory model (ID=4 Table S1 [α^+ , α^- , μ^+ , μ^-]). The model cannot account for the observed differences in choice behaviour during the motor decision-making task across the lifespan, including (1) the value-independent differences across age groups in the reward domain (Figure 3); (2) the changes in gamble propensity observed in the punishment domain across age groups (the model fit shows almost no difference across the age groups in the punishment domain); (3) the higher gamble rate in the reward domain relative to the punishment domain when the difference between expected values [$EV_{\text{gamble}} - EV_{\text{certain}}$] is close to 0 (the model fit shows the opposite).

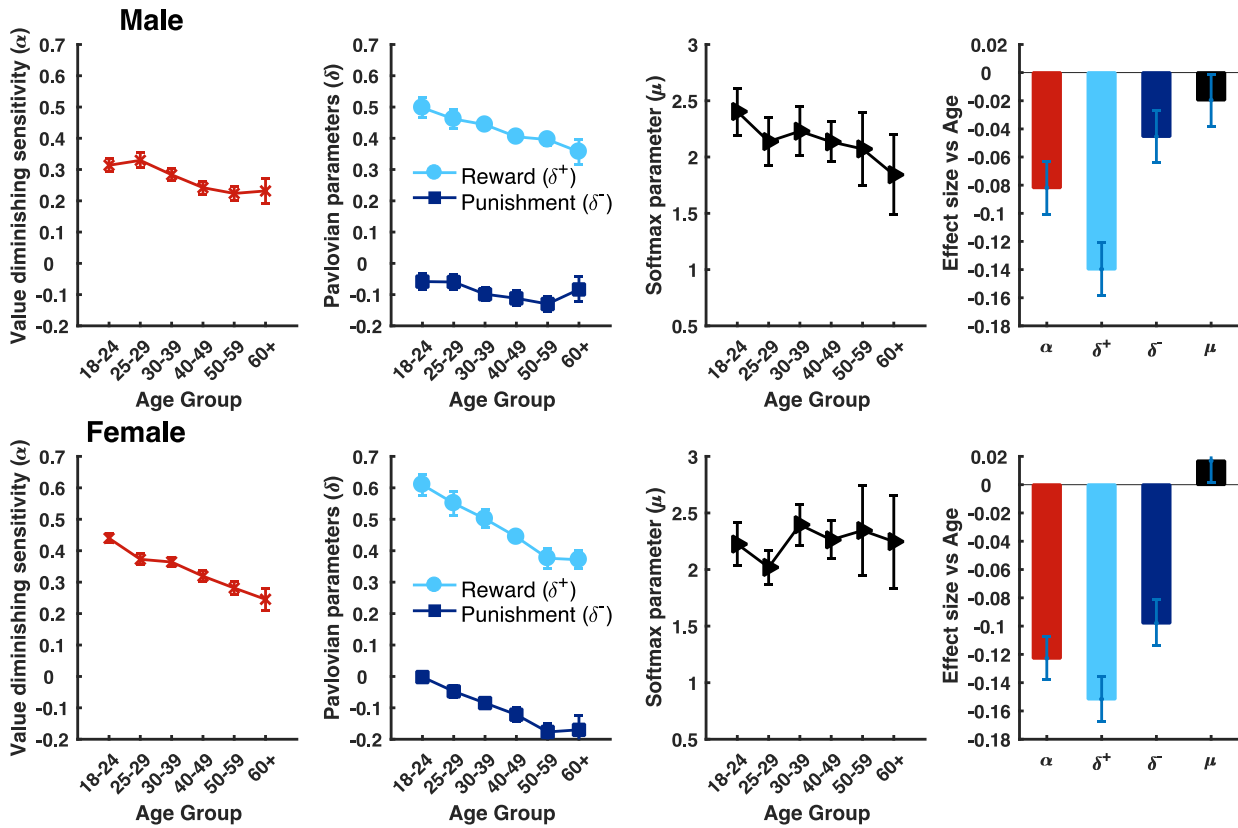


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Figure S3: Average model fit across participants for the winning approach-avoidance model (ID=10 Table S1, [α , μ , δ^+ , δ^-]). The model does a far superior job of fitting choice behaviour during the motor decision-making task across the lifespan (Figure 2).

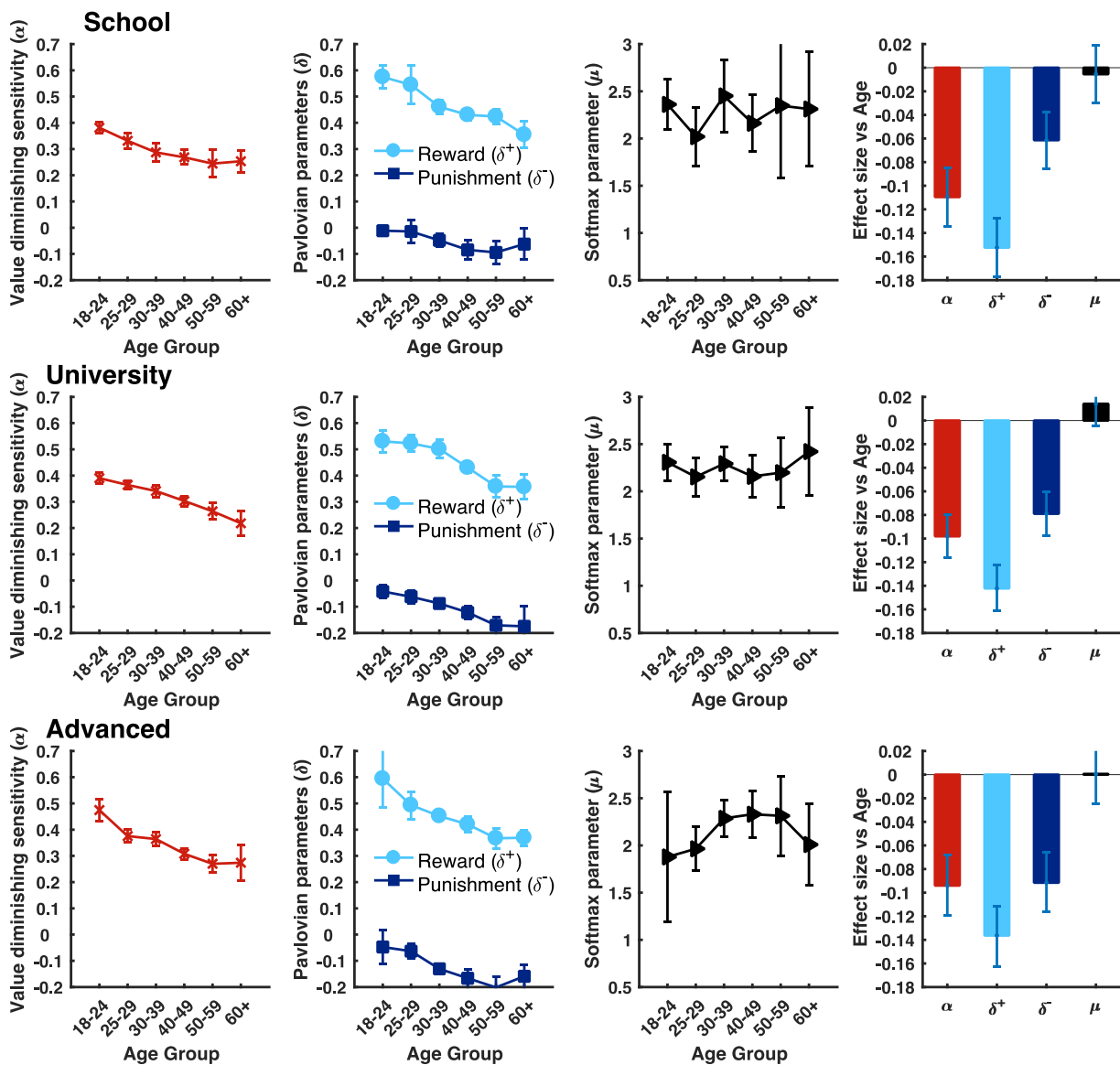
91 **The aging effect for each gender and education level**

92 We found similar aging effects in both males (n=15911, r=-0.140, p<0.001, Figure S) and females (n=10621,
 93 r=-0.143, p<0.001, Figure S), and across all education levels (school: n=9171, r=-0.152, p<0.001; university:
 94 n=11281, r=-0.142, p<0.001; advanced: n=6080, r=-0.136, p<0.001).
 95



96
 97

98 **Figure S4: The change in approach-avoidance model parameters across the life span for each gender**
 99 **(top: male; bottom: female).** Column 1 from left: α across age groups; Column 2: δ^- and δ^+ across age
 100 groups; Column 3: μ across age groups; Column 4: age-related decline across the punishment and reward
 101 domain. The largest effect size was observed for the Pavlovian approach parameter (δ^+); Bars and error bars
 102 represent medians and bootstrapped 95% CIs.



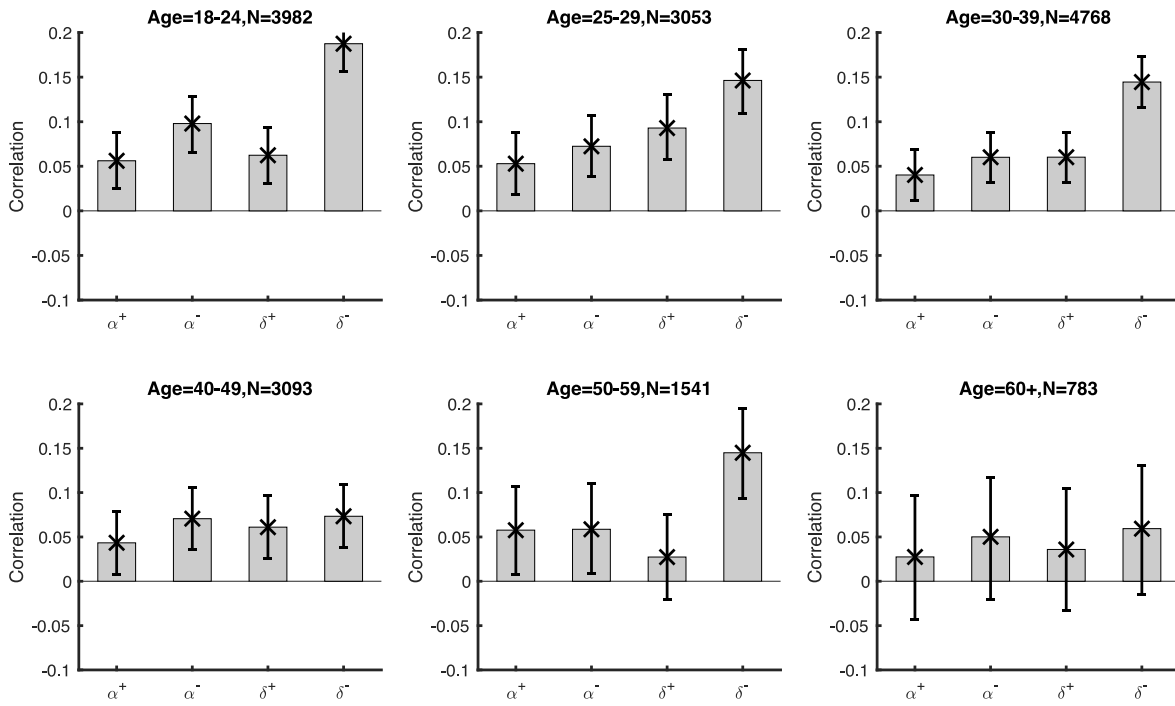
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Figure S5: The change in approach-avoidance model parameters across the life span for each education level (top: school leavers; middle: university leavers; bottom: advanced (Masters, PhD)). Column 1 from left: α across age groups; Column 2: δ^- and δ^+ across age groups; Column 3: μ across age groups; Column 4: age-related decline across the punishment and reward domain. The largest effect size was observed for the Pavlovian approach parameter (δ^+); Bars and error bars represent medians and bootstrapped 95% CIs.

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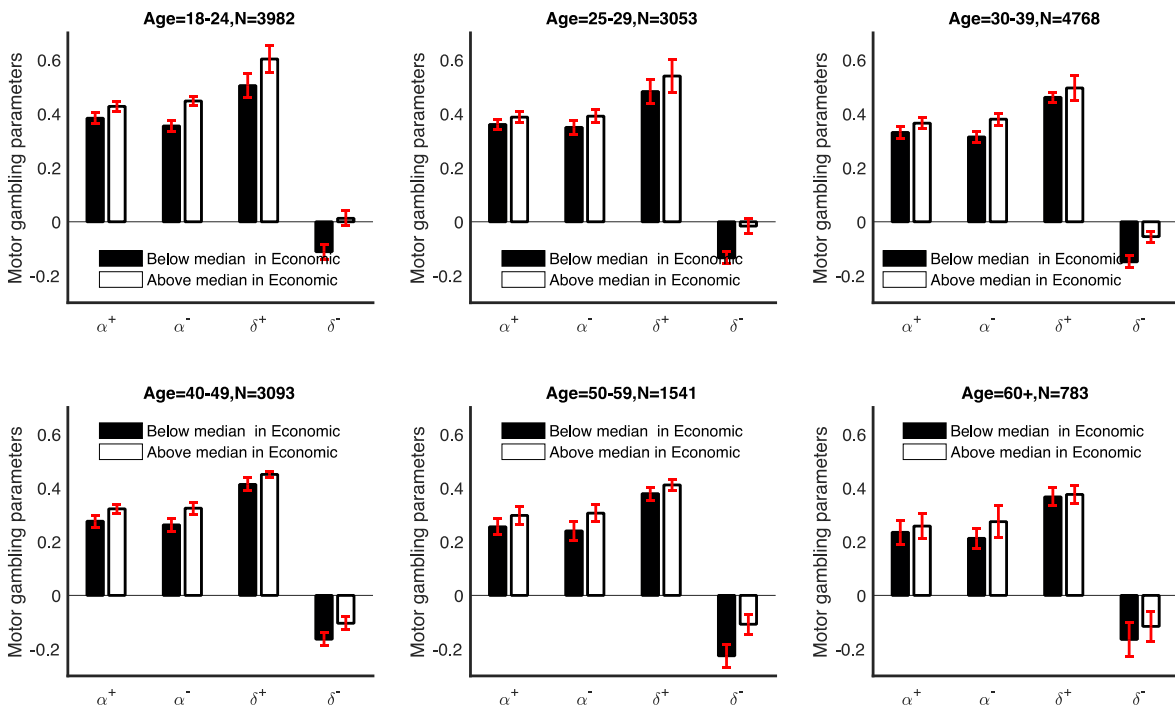
Correlation across the economic and motor decision-making tasks within each age group

Through the app-based platform a subset of participants (n=17,220) also performed an economic decision-making gambling task in which a similar approach-avoidance model was used to explain choice behaviour (see main text for relevant reference). Through correlation and median-split analysis we found a small but significant positive relationship for all main model parameters between the tasks. This relationship was relatively consistent across the lifespan whereby we found a positive correlation between these parameters within each age group (Figure S6 & S7). However, although the oldest age group (60+) showed a similar trend, we did not have enough power (participant numbers) to reliably detect effect sizes of 0.05 within this group. Specifically, whilst the 60+ age group (n=783) had 0.28 power to detect 0.05 effect sizes, the next oldest group (50-59, n=1541) had near double the amount of power of 0.5.



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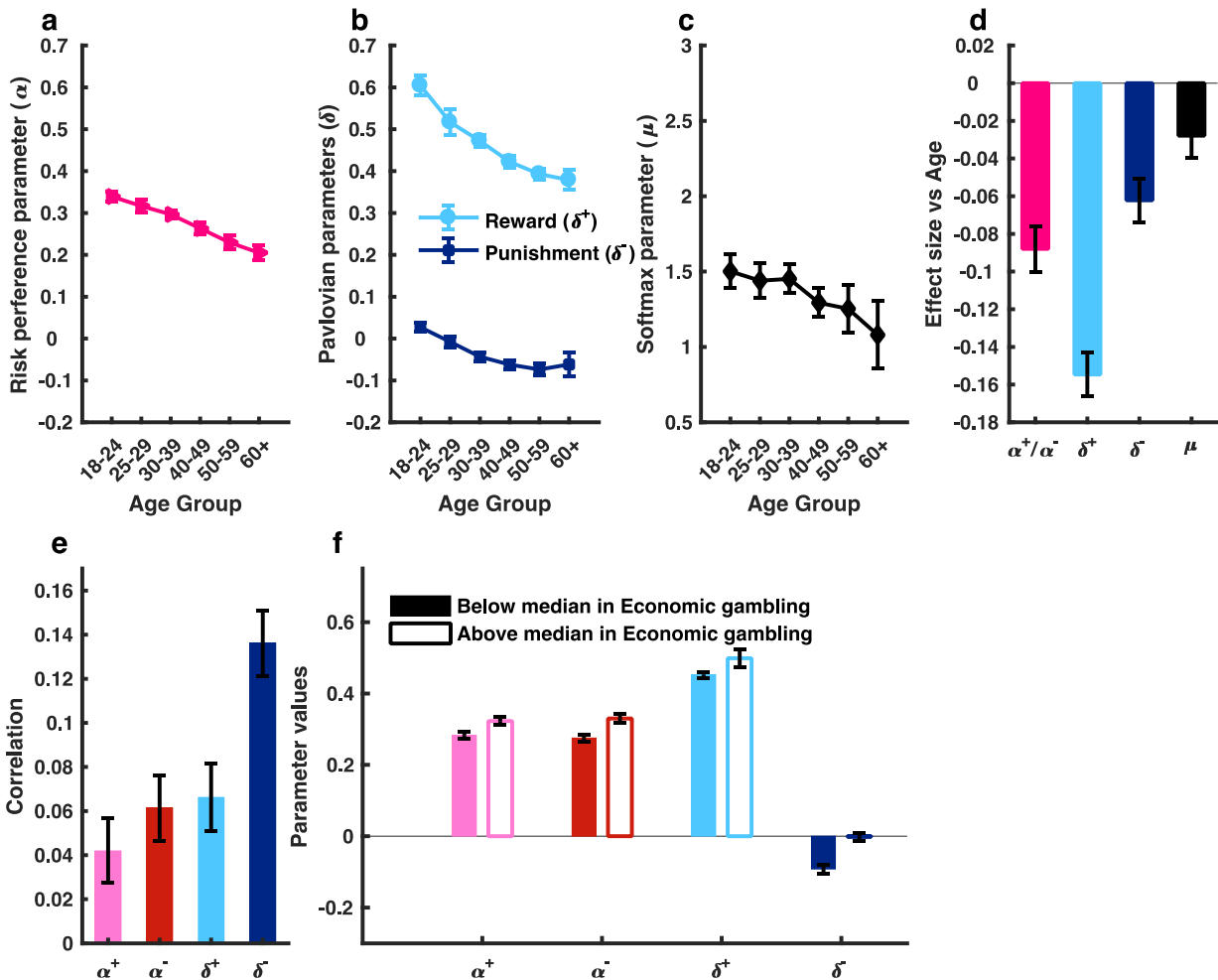
Figure S6: Correlation between motor and economic decision-making tasks for the main approach-avoidance model parameters within each age group. This relationship was relatively consistent across the lifespan whereby we found a positive correlation between these parameters within each age group. Note, the single α parameter of the motor decision-making model was correlated with both the α^- and α^+ parameters of the decision-making model. Error bars reflect bootstrapped 95% CIs.



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Figure S7: Motor decision-making approach-avoidance parameter values median split by economic parameter values within each age group. Filled bars denote participants with below-median values in the economic gambling task; Hollow bars for above-median. The participants with above-median risk parameters and Pavlovian parameters in the economic decision task had generally higher risk parameters and Pavlovian parameters in the motor gambling task. Bars/error bars reflect medians/bootstrapped 95% CIs.

137 **Model results when probability of success was based on each individual's own performance**
 138 In the main results, the probability of success for a participant within a certain age group, using a certain
 139 screen size and facing a certain target size on each trial was estimated using the average success rate across
 140 all the participants with the same age, same screen size, and facing the same target size. Given the small
 141 amount of trials we had for each participant at each target size to estimate their probability of success, we
 142 believed this group average approach was the most valid estimate of success probability. However, Figure
 143 S8 shows that similar results are observed when probability of success is estimated based on each
 144 individual's own data (i.e. the probability of success for a participant facing a certain target size was
 145 estimated using their own success rate over the same target size).
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 150 **Figure S8: Model results when probability of success was based on each individual's own performance**
 151 **(rather than group average).** Similar results are observed when the probability of success was estimated
 152 based on each individual's own data. (a) α across age groups; (b) δ^- and δ^+ across age groups; (c) μ across
 153 age groups; (d) age-related decline across the loss and gain domain. The largest effect size was observed for
 154 the Pavlovian approach parameter (δ^+); (e) positive correlation across motor and economic decision tasks for
 155 the main approach-avoidance model parameters; (f) median split. Filled bars denote participants with below-
 156 median values in the economic gambling task; Hollow bars for above-median. The participants with above-
 157 median risk parameters and Pavlovian parameters in the economic decision task had higher risk parameters
 158 and Pavlovian parameters in the motor gambling task. Bars/error bars reflect medians/bootstrapped 95% CIs.
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