

Research Articles: Behavioral/Cognitive

A neurocomputational model for intrinsic reward

<https://doi.org/10.1523/JNEUROSCI.0858-20.2021>

Cite as: J. Neurosci 2021; 10.1523/JNEUROSCI.0858-20.2021

Received: 13 April 2020

Revised: 29 July 2021

Accepted: 2 August 2021

This Early Release article has been peer-reviewed and accepted, but has not been through the composition and copyediting processes. The final version may differ slightly in style or formatting and will contain links to any extended data.

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1 **A neurocomputational model for intrinsic reward**

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Number of figures: 5

Number of tables: 3

Number of words for:

Abstract - 202

Introduction - 534

Discussion – 1104

No conflicts of interest

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49 **A neurocomputational model for intrinsic reward**50 Benjamin Chew^{1,2,*}, Bastien Blain^{1,2,4,*}, Raymond J Dolan^{1,2}, Robb B Rutledge^{1,2,3,4}51 ¹ Max Planck University College London Centre for Computational Psychiatry and Ageing
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59 **SUMMARY**

60 Standard economic indicators provide an incomplete picture of what we value both as individuals and
61 as a society. Furthermore, canonical macroeconomic measures, such as GDP, do not account for
62 non-market activities (e.g., cooking, childcare) that nevertheless impact well-being. Here, we introduce
63 a computational tool that measures the affective value of experiences (e.g., playing a musical
64 instrument without errors). We go on to validate this tool with neural data, using fMRI to measure
65 neural activity in male and female human subjects performing a reinforcement learning task that
66 incorporated periodic ratings of subjective affective state. Learning performance determined level of
67 payment (i.e., extrinsic reward). Crucially, the task also incorporated a skilled performance component
68 (i.e., intrinsic reward) which did not influence payment. Both extrinsic and intrinsic rewards influenced
69 affective dynamics, and their relative influence could be captured in our computational model.
70 Individuals for whom intrinsic rewards had a greater influence on affective state than extrinsic rewards
71 had greater ventromedial prefrontal cortex (vmPFC) activity for intrinsic than extrinsic rewards. Thus,
72 we show that computational modelling of affective dynamics can index the subjective value of intrinsic
73 relative to extrinsic rewards, a 'computational hedonometer' that reflects both behavior and neural
74 activity that quantifies the affective value of experience.

75

76 **SIGNIFICANCE STATEMENT**

77 Traditional economic indicators are increasingly recognized to provide an incomplete picture of what
78 we value as a society. Standard economic approaches struggle to accurately assign values to non-

79 market activities that nevertheless may be intrinsically rewarding, prompting a need for new tools to
80 measure what really matters to individuals. Using a combination of neuroimaging and computational
81 modeling, we show that despite their lack of instrumental value, intrinsic rewards influence subjective
82 affective state and ventromedial prefrontal cortex activity. The relative degree to which extrinsic and
83 intrinsic rewards influence affective state is predictive of their relative impacts on neural activity,
84 confirming the utility of our approach for measuring the affective value of experiences and other non-
85 market activities in individuals.

86 INTRODUCTION

87 A key index of quality of life is subjective well-being which reflects “how people experience and
88 evaluate their lives and specific domains and activities in their lives” (Oswald and Wu, 2010).
89 Individuals with higher subjective well-being display lower mortality rates (Chida and Steptoe, 2008;
90 Steptoe et al., 2015) and have a lower risk of disease (Davidson et al., 2010). In the workplace,
91 employees who report higher subjective well-being have higher productivity without loss of output
92 quality (Oswald et al., 2015), reduced rates of absenteeism (Pelled and Xin, 1999), and are rated
93 more positively by their supervisors (Peterson et al., 2011). On this basis, maximizing subjective well-
94 being should be of prime interest not only to individuals but also to companies and governments, as
95 well as a target for health and economic policies (Dolan and White, 2007).

96 A problem arises when it comes to designing effective measures likely to increase well-being. When
97 contemplating the future, people exhibit biases in *affective forecasting* when making predictions about
98 what it would feel like to experience specific events, consistently misjudging how future events will
99 impact their affective state and leading them to perform actions that may be detrimental to
100 maximization of their subjective well-being (Wilson and Gilbert, 2005; Meyvis et al., 2010). In particular,
101 people overestimate both the intensities and durations of their hedonic responses to future events,
102 and this is referred to as an impact bias (Gilbert and Wilson, 2007; Morewedge and Buechel, 2013).
103 Furthermore, the value of tangible goods can be quantified by prices or willingness-to-pay (Plassmann
104 et al., 2007), but the value of intangible goods and experiences that are intrinsically rewarding (e.g.,
105 hobbies, recreational sports) are often more difficult to define or elicit accurately due to biases (Van de
106 Mortel, 2008; Nisbet and Zelenski, 2011), while the predictive validity of implicit measures is unclear
107 (Levesque et al., 2008; Keatley et al., 2013).

108 Neuroscience-informed methods can provide a means to evaluate the subjective value of an intrinsic
109 reward (e.g., the experience of mastering a musical composition for its own sake), allowing extrinsic
110 and intrinsic rewards to be compared using a common scale of objectively measured neural activity
111 (FitzGerald et al., 2009). We hypothesized that extrinsic and intrinsic rewards would both influence
112 affective states, and the extent of their relative influences should be reflected in regional brain activity.
113 Recent studies (Rutledge et al., 2014, 2015; Vinckier et al., 2018) demonstrate that experience
114 sampling during reward-based tasks can link affective and motivational responses to extrinsic reward.
115 Here we extend this approach to investigate how affective state is influenced by the history of intrinsic
116 rewards.

117 We developed a reinforcement learning task incorporating both an explicit reward component and a
118 skilled performance component, where the latter did not affect payment (Figure 1A). On each trial,
119 subjects selected one of two options, one of which was on average more rewarding than the other,
120 and then navigated a cursor past a series of barriers (see Experimental Procedures). We
121 hypothesized that the experience of successful skilled performance, a source of intrinsic reward,
122 would influence the momentary happiness of subjects in a manner that is quantitatively akin to the
123 impacts of extrinsic rewards and that this would also be evident at the level of neural activity.

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125

126 INSERT FIGURE 1

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129 **EXPERIMENTAL PROCEDURES**

130 **Participants**

131 37 healthy young adults (age: 25.8 ± 4.7 , mean \pm SD; 8 males, 29 females) were recruited through the
132 University College London (UCL) Psychology Subject Database. Subjects were screened to ensure no
133 history of neurological or psychiatric disorders. Four subjects were excluded due to excessive head
134 movement during scanning, leaving a total of 33 subjects (age: 26.1 ± 4.9 ; 8 males, 25 females). The

135 study was approved by the UCL research ethics committee, and all subjects gave written informed
136 consent.

137 **Study Design**

138 Subjects completed the experiment at the Wellcome Centre for Human Neuroimaging at UCL in an
139 appointment that lasted approximately 90 minutes. Stimuli were presented in MATLAB (MathWorks,
140 Inc.) using Cogent 2000. The layout of each trial resembled a T-Maze (Howe et al., 2013). On each
141 trial, subjects selected a blue or magenta box, one of which resulted in 50 points on average and the
142 other which resulted in 25 points on average. The standard deviation of points received for each box
143 was 10. Points assigned based on draws from Gaussian distributions. Every 19-23 trials, a reversal
144 occurred where the box that previously contained the higher number of points on average now
145 contained a lower number of points and vice versa. On half of the trials, subjects were afforded a free
146 choice. For the remaining half, subjects were only presented with a single option. After a choice was
147 made, the chosen option was indicated and four barriers appeared on the screen along with a small
148 cursor at the bottom of the screen. Following a 1s delay, the cursor automatically advanced along the
149 path to the outcome. Subjects were able to control the horizontal position of the cursor to avoid
150 colliding with barriers. If they passed a barrier without colliding with it, the barrier turned green.
151 Contact with a barrier turned it red and provided immediate feedback about performance. Subjects
152 then had to press the appropriate directional key to navigate around the barrier for the cursor to
153 continue advancing on its course. Crucially, the subjects' final payment depended only on the number
154 of points accumulated across the experiment and not their ability to quickly navigate past barriers.
155 After the cursor had entered the chosen box, the outcome was displayed for 800ms after a 1.5s delay.
156 Total cumulative points were displayed on the top right of the screen throughout the experiment.
157 Subjects were presented with the question, "How happy are you at this moment?" after every 2-3 trials.
158 After a 1s delay period, a rating line appeared with a cursor at the midpoint and subjects had 4s to
159 move a cursor along the scale with button presses. The left end of the line was labelled "very unhappy"
160 and the right end of the line was labelled "very happy".

161 **Staircase Procedure**

162 To ensure that differences in affective responses were not due to skill-related differences in how often
163 each subject collided with barriers, we used a standard staircase procedure called the Parametric

164 Estimation by Sequential Testing (PEST) (Taylor and Creelman, 1967). This procedure calibrated the
165 speed at which the cursor moved for every subject such that they did not contact the barriers on
166 approximately 70% of trials. This calibration was carried out over 60 trials prior to the start of the task
167 in the scanner. Continuation of the procedure during the task allowed small adjustments (e.g., to
168 compensate for any fatigue) to maintain consistent successful skill performance.

169 **Questionnaire Measures**

170 Subjects were administered the Beck Depression Inventory (BDI-II) (Beck et al., 1996), Apathy
171 Evaluation Scale (AES) (Marin et al., 1991) and Apathy Motivation Index (AMI) (Ang et al., 2017).

172 **Image Acquisition**

173 MRI scanning took place at the Wellcome Centre for Human Neuroimaging at UCL using a Siemens
174 Prisma 3-Tesla scanner equipped with a 64-channel head coil. Functional images were acquired with
175 a gradient echo T2*-weighted echo-planar sequence with whole-brain coverage. Each volume
176 consisted of 48 slices with 3mm isotropic voxels [repetition time (TR): 3.36s; echo time (TE): 30ms;
177 slice tilt: 0°] in ascending order. A field map [double-echo FLASH, TE1 = 10ms, TE2 = 12.46ms] with
178 3mm isotropic voxels (whole-brain coverage) was also acquired for each subject to correct the
179 functional images for any inhomogeneity in magnetic field strength. Subsequently, the first 6 volumes
180 of each run were discarded to allow for T1 saturation effects. Structural images were T1-weighted (1 x
181 1 x 1 mm resolution) images acquired using a MPRAGE sequence.

182 **Model-based Analyses**

183 Models were fit to happiness ratings in individual subjects by minimizing the residual sum of squares
184 between actual and predicted happiness ratings, and this also served as the objective function for the
185 optimizer. Model fitting was performed using the *fmincon* optimizer in MATLAB (MathWorks, Inc). The
186 significance for individual parameters was determined using likelihood ratio tests comparing the full
187 model with a model that had only a reward or performance parameter but not both. The significance of
188 those tests is indicated by filled circles in Figure 4. Note that models were first fit to the raw happiness
189 ratings in order to test the relationship between the happiness baseline mood parameter (denoted w_0
190 in the equations below) and questionnaire measures to replicate findings in the literature. Models were
191 then fit to standardized ratings. Normalizing ratings prevents individuals with greater variance in their

192 ratings from having a disproportionate effect on model comparisons. The standard deviation of ratings
193 differs widely across participants although rating variance is known to be stable in time (Rutledge et al.,
194 2015) and across tasks (Blain and Rutledge, 2020).

195 **Recovery Analysis**

196 To ensure that the model parameters were recoverable, we performed model recovery and parameter
197 recovery analyses following established procedures (Wilson and Collins, 2019). To test for parameter
198 recovery, we first estimated the parameters for each participant. Then, we simulated data with each of
199 the four generative models using parameters estimated for each participant. To account for noise in
200 the simulation, we computed the standard deviation of the residuals from the model at the individual
201 level and then generated Gaussian noise with the same standard deviation using the MATLAB randn
202 function and added that noise to generated ratings. We then estimated parameters from the generated
203 data using the same procedure as applied to the actual mood dynamics data ($n = 33$). The standard
204 deviations of residuals in the recovery analysis were highly correlated with the noise parameter in the
205 generative process (e.g., for Reward and Performance, the correlation is Spearman $\rho(31) = 0.98$, $p <$
206 10^{-18}).

207 **RESULTS**

208 Subjects completed two trial blocks while in the MRI scanner. We first asked whether subjects could
209 learn the reward contingencies (Figure 1B) and found that they could, making $85.8 \pm 1.0\%$ (mean \pm
210 SEM, $z = 5.0$, $p < 10^{-6}$) of choices to the current high-reward option. Subjects were not penalized for
211 contact with barriers, and thus actual performance was non-instrumental to the receipt of eventual
212 monetary reward. We observed no correlation between earnings and how often subjects successfully
213 avoided barriers ($\rho(31) = 0.21$, $p = 0.24$). During debriefing, all 33 subjects reported that they believed
214 there was no association between successful skilled performance and earnings.

215 Reports of affective state for example subjects are included in Figure 1C. On average, subjects
216 reported being happier after receiving outcomes from the high- compared to low-reward option (high-
217 reward: 63.8 ± 1.9 , low-reward: 59.5 ± 2.1 , $z = 4.7$, $p < 10^{-5}$), consistent with previous research
218 (Rutledge et al., 2014, 2015). On average, subjects reported also being happier when they navigated
219 through the barriers without collisions compared to when they contacted at least one barrier (without

220 collisions: 63.5 ± 1.9 ; collision: 60.0 ± 2.1 , $z = 4.6$, $p < 10^{-5}$), suggesting that intrinsic rewards related
 221 to performance influence subjective affective state.

222 Because participants vary in how they use the scale, we next z-scored happiness ratings. Consistent
 223 with analyses using non-normalized ratings, subjects reported greater average happiness after
 224 receiving high compared to low rewards (high-reward: 0.08 ± 0.01 , low-reward: -0.18 ± 0.02 , $z = 4.8$, p
 225 $< 10^{-5}$, Figure 2A). Subjects also reported being happier after navigating through the maze without
 226 contacting any barriers compared to when they collided with at least one barrier (without collisions:
 227 0.08 ± 0.01 ; collision: -0.17 ± 0.03 , $z = 4.7$, $p < 10^{-5}$, Figure 2A), consistent with an impact of intrinsic
 228 rewards. There was considerable variation across subjects in terms of how much extrinsic rewards
 229 and skilled performance contributed to momentary happiness (Figure 2B), but there was no
 230 relationship between happiness for reward outcomes and happiness for skilled performance ($\rho(31) = -$
 231 0.20 , $p = 0.26$).

232

233 INSERT FIGURE 2

234 INSERT TABLE 1

235

236 **Computational model of affective dynamics**

237 We next employed a previously established methodology (Rutledge et al., 2014, 2015; Blain and
 238 Rutledge, 2020) to quantify the extent to which rewards impacted on the affective state of our
 239 participants. In particular, we aim to replicate that (1) the recent history of reward influences happiness
 240 and (2) that the baseline happiness parameter correlates with depressive symptoms. To that end, we
 241 fit the raw happiness ratings. We considered influences that decay exponentially in time:

$$242 \text{Happiness}(t) = w_0 + w_{\text{reward}} \sum_{j=1}^t \gamma^{t-j} \text{Reward}_j + \epsilon \quad (1)$$

243 where t and j are trial numbers, w_0 is a baseline mood parameter, w_{reward} captures the influence of
 244 reward which is the z-scored reward outcome of the selected option on each trial, and $0 \leq \gamma \leq 1$
 245 represents a forgetting factor that reduces the impact of distal relative to recent events. If this
 246 parameter is equal to 0, only the most recent reward outcome influences happiness. The model

247 includes a Gaussian noise term, $\epsilon \sim N(0, \sigma)$. The parameters of this model are recoverable (see Figure
248 3A and Table 1 for details about parameter recovery). Parameters were first fit to non-normalized
249 happiness ratings in each individual subject. The mean r^2 was 0.26 ± 0.03 and the mean forgetting
250 factor was 0.40 ± 0.06 (mean \pm SEM, Figure 1C for example subjects). Consistent with previous
251 findings (Rutledge et al., 2014, 2015), happiness was significantly associated with the history of reward
252 ($w_{\text{reward}} = 0.06 \pm 0.01$; Wilcoxon signed rank test: $z = 4.7$, $p < 10^{-5}$). Sigma was estimated to be on
253 average 0.13 ± 0.01 .

254 Likewise, consistent with previous findings during risky decision making (Rutledge et al., 2017), we
255 found that baseline mood parameters, estimated using raw happiness ratings while accounting for
256 mood dynamics due to reward history, were negatively correlated with symptom severity assessed
257 using the Beck Depression Inventory (BDI-II; Beck et al., 1996; Spearman $\rho(31) = -0.35$, $p = 0.046$).
258 This result shows that depressive symptoms relate to happiness ratings during a novel task including
259 a performance component consistent with previous findings during risky decision making (Rutledge et
260 al., 2017) and learning in volatile environments (Blain and Rutledge, 2020). This relationship is
261 consistent with an affective set point, which happiness returns to over time, that is lower in individuals
262 with a greater symptom load.

263 We also found baseline mood parameters tended to be negatively related apathy as measured by
264 Apathy Evaluation Scale (AES) (Marin et al., 1991) ($\rho(31) = -0.32$, $p = 0.07$) and behavioral apathy as
265 assessed by the Apathy Motivation Index (AMI) (27) ($\rho(31) = -0.33$, $p = 0.06$; see Table 2). The first
266 happiness rating before the start of the first trial was positively correlated with baseline mood
267 parameter ($\rho(31) = 0.46$, $p = 0.007$). In contrast to baseline mood parameters, first happiness ratings
268 were not significantly correlated with BDI-II ($\rho(31) = -0.21$, $p = 0.25$) or AES ($\rho(31) = -0.17$, $p = 0.35$),
269 but was correlated with behavioral AMI ($\rho(31) = -0.39$, $p = 0.027$). We found no correlation between
270 baseline mood parameter and the average staircased cursor speed ($\rho(31) = -0.01$, $p = 0.95$),
271 suggesting that the speed of the cursor was not associated with persistent affective state.

272 We next z-scored happiness ratings to better evaluate the relative contributions of extrinsic and
273 intrinsic reward to affective state. To that end, we z-scored the happiness ratings, thereby preventing
274 individuals with greater rating variance from disproportionately affecting analyses. With happiness
275 ratings centered on zero, as well as Rewards and Performance vectors, any constant term would be

276 expected to be near zero and we omitted the w_0 from analyses with z-scored ratings. We expanded
 277 the model to include an additional term that accounts also for influences pertaining to skilled
 278 performance:

$$279 \quad \text{Happiness}(t) = w_{\text{reward}} \sum_{j=1}^t \gamma^{t-j} \text{Reward}_j + w_{\text{performance}} \sum_{j=1}^t \gamma^{t-j} \text{Performance}_j + \epsilon \quad (2)$$

280 where t and j are trial numbers, w_{reward} and $w_{\text{performance}}$ capture the influence of task events related to
 281 reward and performance, respectively, and $0 \leq \gamma \leq 1$ represents a forgetting factor that reduces the
 282 impact of distal relative to recent events. The model includes a Gaussian noise term, $\epsilon \sim N(0, \sigma)$. The
 283 model parameters were indeed recoverable (see Figure 2C and table 2 and methods for details).
 284 Reward is the z-scored outcome of the selected option on each trial, and performance is the z-scored
 285 result of whether a barrier was contacted on each trial, assigning a 1 when no barriers were contacted
 286 and 0 if at least one barrier was contacted. This simple model explained a substantial amount of
 287 variance in happiness with $r^2 = 0.26 \pm 0.03$ (mean \pm SEM, Figure 2C). Weights for both performance
 288 ($w_{\text{performance}} = 0.18 \pm 0.03$; $z = 4.4$, $p < 10^{-4}$, Figure 2D) and reward ($w_{\text{reward}} = 0.39 \pm 0.04$, $z = 4.9$, $p <$
 289 10^{-5} , Figure 2D) were positive on average. The forgetting factor γ was 0.48 ± 0.05 (mean \pm SEM),
 290 indicating that happiness depended on the past 4-5 trials on average. Sigma was estimated to be on
 291 average 0.85 ± 0.02 .

292 In previous studies we found expectations of reward exerted a substantial influence on happiness
 293 (Rutledge et al., 2014, 2015; Blain and Rutledge, 2020). In the current study, we used high- and low-
 294 reward distributions with minimal overlap to maximize learning accuracy. We also employed a
 295 staircase to keep skilled performance stable and at a similar level across individuals. These features
 296 render the current design unsuitable for quantifying the impact of expectations on happiness. We
 297 chose a design that maximized our power for quantifying individual differences in the relative
 298 subjective values of extrinsic and intrinsic rewards.

299

300

INSERT FIGURE 3

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302 Model comparison (Table 2) shows that a model with parameters for past rewards and performance
 303 (mean $r^2 = 0.26$) outperformed models containing individual terms for reward (mean $r^2 = 0.19$) or

304 performance (mean $r^2 = 0.09$) alone. These results show that the happiness of subjects in this task is,
305 on average, dependent on both receipt of explicit rewards (e.g., money) and the non-instrumental
306 experience of skilled performance.

307

308

INSERT TABLE 2

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310 We found considerable variation across individuals in how much reward outcomes contributed to
311 affective dynamics, even though subjects on average learned reward contingencies to a similar
312 degree (Figure 4A). Despite performance being held constant due to staircasing of cursor speed
313 (successful performance: $69.1 \pm 2.4\%$, mean \pm SD, Figure 4B), there was considerable variation also
314 across individuals in how much non-instrumental performance influenced affective state. Many
315 subjects showed a negligible impact of successful performance on affective state, despite a similar
316 level of successful performance. Furthermore, learning choice accuracy was not correlated with either
317 happiness reward parameters ($\rho(31) = 0.12$, $p = 0.49$) or successful skilled performance ($\rho(31) = -0.05$,
318 $p = 0.78$).

319 Intrinsic rewards can be associated with an increased motivation or metacognitive strategy to improve
320 performance over time (Son and Metcalfe, 2005). Prior to scanning, participants completed 60 practice
321 trials to determine an appropriate starting speed for the experiment. $W_{\text{performance}}$ was positively
322 correlated with the starting cursor speed ($\rho(31) = 0.38$, $p = 0.03$). There was no correlation between
323 percent successful skilled performance and $w_{\text{performance}}$ derived from the happiness model ($\rho(31) =$
324 0.056 , $p = 0.76$). Intrinsic rewards are often thought as resulting from uncertainty reduction, or from
325 learning progress (Gottlieb and Oudeyer, 2018). However, we did not find any significant difference in
326 the median cursor speed between blocks ($z = 0.63$, $p = 0.53$), suggesting that participants were at a
327 stable level of performance from the start that did not improve over time. Similarly, $w_{\text{performance}}$ was not
328 significantly different between blocks ($z = 1.47$, $p = 0.14$). These results together suggest that
329 performing this task accurately was intrinsically rewarding with a stable relationship between
330 performance and happiness despite no signs of learning progress during the experiment.

331

332 We then checked whether we can extend the link between the baseline mood parameter from the
333 reward model (see above) and apathy and depression scores to the baseline mood parameter of
334 models including a performance term. Results indicate a trend towards the same relationship as for the
335 reward model (see Table 3).

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339 INSERT FIGURE 4

340

341 INSERT TABLE 3

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343

344 **Neural correlates of extrinsic and intrinsic rewards**

345 Having established inter-individual variability in the impact of outcomes and performance on reported
346 happiness, we next asked whether this variability was also predictive of neural responses to both
347 rewards and performance. The experiment was separated into two scans and we first evaluated
348 whether happiness model parameters were stable across scans. We found that both extrinsic ($p(33) =$
349 0.35 , $p = 0.044$) and intrinsic ($p(33) = 0.35$, $p = 0.044$) reward computational parameters were
350 positively correlated across the two scans.

351 We regressed event-related activity on parametrically modulated task events to assess brain activity
352 related to receipt of extrinsic and intrinsic rewards. We found an effect of reward magnitude at time of
353 outcome in vmPFC (Figure 4A, top: $-3, 38, -1$; $t_{32} = 5.92$, $p < 0.05$ Family-Wise-Error (FWE) cluster-
354 corrected at the whole brain level), as well as an effect of successful skilled performance in an
355 overlapping region of the vmPFC (Figure 4A, bottom: $-3, 50, -1$; $t_{32} = 4.24$, $p < 0.05$ FWE cluster-
356 corrected).

357 The vmPFC is widely implicated in representation of subjective reward value. On this basis, we used
358 an independent vmPFC mask from a meta-analysis of subjective value studies of extrinsic reward for
359 further analysis (Bartra et al., 2013). Within this region-of-interest (ROI), we extracted weights for

360 reward magnitude and skilled performance from each individual subject. We found that within this
361 independent ROI, BOLD activity was significantly associated with both reward magnitude (0.26 ± 0.08 ,
362 $Z = 3.0$, $p = 0.0029$) and skilled performance (0.38 ± 0.13 , $Z = 2.8$, $p = 0.0052$, Figure 5B).

363 Having established that neural responses in vmPFC are associated with both extrinsic and intrinsic
364 rewards, we next examined whether neural responses were predicted by computational parameters
365 estimated from individual affective dynamics. Across subjects, we found a positive relationship ($\rho(31)$
366 $= 0.50$, $p = 0.003$, Figure 5D) between the relative weights for extrinsic and intrinsic rewards in our
367 happiness computational model and the relative effect sizes for neural responses in the vmPFC. Initial
368 happiness ratings deviate from model predictions on average (Figure 2C). The relationship between
369 relative happiness weights and relative neural effect sizes was still present after removing the initial 10%
370 of ratings ($\rho(31) = 0.54$, $p = 0.0015$). The relationship was also present after removing the initial 10%
371 and detrending the remaining ratings before estimating model parameters ($\rho(31) = 0.49$, $p = 0.0038$).

372 We also subdivided subjects into two groups comprising a group with higher $W_{\text{performance}}$ than reward
373 parameters and a group with the opposite pattern. The group with higher performance than reward
374 parameters showed greater vmPFC responses for skilled performance compared to the group with
375 larger reward than performance parameters ($Z = 2.8$, $p = 0.0047$, Figure 5C). These findings suggest
376 that the pattern of momentary affective dynamics reflects the impact of both extrinsic and intrinsic
377 rewards and is mirrored at the level of vmPFC activity.

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INSERT FIGURE 5

381

382 **DISCUSSION**

383 Using experience sampling (Reis and Gable, 2000; Kahneman et al., 2004) combined with functional
384 neuroimaging, we show that extrinsic and intrinsic rewards contribute to affective dynamics (i.e.,
385 happiness). Recent studies demonstrate that computational approaches can quantify consistent
386 relationships between subjective feelings and value-based decision making (Rutledge et al., 2014;
387 Eldar et al., 2016, 2018; Vinckier et al., 2018; Blain and Rutledge, 2020), including in relation to

388 individual social preferences (Rutledge et al., 2016). Here, using the same computational approach
389 applied during reinforcement learning, we show that momentary happiness is influenced by both
390 extrinsic and intrinsic rewards. The computational parameters we extract from affective dynamics
391 enabled us to quantify, within a common value scale, the relative affective value of intrinsic relative to
392 extrinsic rewards. Our key finding here is that the relative weight of intrinsic and extrinsic reward
393 extracted from affective dynamics predicts neural activity in the vmPFC, a region proposed to
394 represent rewards in a common neural currency (Chib et al., 2009; Levy and Glimcher, 2011, 2012),
395 validating our computational approach.

396 While improvements in skilled performance can be enhanced by rewarding individuals for
397 performance (Sugawara et al., 2012), holding performance constant across subjects allowed us to
398 investigate how happiness varied independently of the level of skill individuals manifest in the task.
399 We show that individuals, whose happiness was substantially influenced by intrinsic rewards, had
400 increased vmPFC BOLD responses for successful versus unsuccessful skilled performance, relative
401 to individuals whose happiness was influenced more by extrinsic rewards.

402 The vmPFC is known to represent the value of different types of goods, including food and juice
403 (Padoa-Schioppa, 2007; Hare et al., 2011), money (De Martino et al., 2006), aesthetic judgments
404 (Kawabata and Zeki, 2004; Jacobsen et al., 2006), and even perceived pleasantness (Plassmann et
405 al., 2008). This suggests that vmPFC plays a central role in representing qualitatively different types of
406 goods on a common scale, an operation that can facilitate making decisions between otherwise
407 incommensurable goods (Chib et al., 2009; Levy and Glimcher, 2011, 2012). Our study builds on
408 these prior results by now identifying an association between vmPFC BOLD activity and intrinsic
409 rewards, here the experience of performing a skilled task without error. Whole-brain analysis showed
410 that the representation of subjective intrinsic reward values involved an adjacent region in the vmPFC,
411 anterior to the representation for extrinsic rewards but still residing within a central vmPFC cluster
412 (Clithero and Rangel, 2014), a finding that parallels a distinction between experienced and decision
413 values previously mapped to anterior and posterior vmPFC, respectively (Smith et al., 2010).

414 The vmPFC has been demonstrated to play a role in affect with subjective emotional experiences
415 elicited by images and pleasurable music leading to changes in both vmPFC BOLD activity and
416 regional cerebral blood flow (Blood and Zatorre, 2001; Zald et al., 2002; Winecoff et al., 2013).

417 Damage to the vmPFC can lead to aberrant emotional responses (Koenigs et al., 2007; Zald and
418 Andreotti, 2010; Hiser and Koenigs, 2018) and maladaptive decision making in environments where
419 emotional regulation may be useful (Grossman et al., 2010; Spaniol et al., 2019). Numerous studies
420 suggest that subjective reward values are represented by vmPFC neural activity. Unfortunately, the
421 constraints and expense of neuroimaging makes it impractical as an every-day tool for assessing
422 individual values for non-market activities. The strong association between neural responses for
423 intrinsic and extrinsic rewards and computational parameters extracted from affective dynamics
424 suggests that computational models combined with experience sampling can provide a valid measure
425 for the subjective reward value of experience.

426 A limitation of the current study is that the staircase procedure we used does not allow us to address
427 questions related to the intrinsic motivation for learning of our subjects. The staircase procedure can
428 be useful for study of interindividual variation either by keeping performance constant across
429 individuals despite differences in abilities (Fleming et al., 2010) or for tailoring choice options to
430 individuals (Klein-Flügge et al., 2015). Using the staircase procedure meant that subjects quickly
431 reached the limit by which they could improve performance. Our design is thus unsuitable for studying
432 intrinsic motivation pertaining to learning. However, such a framework for measuring affective value
433 could be valuable for other features related to intrinsic rewards (Blain and Sharot, 2021), like
434 metacognitive control and learning (Son and Sethi, 2006), resource allocation under external
435 pressures (Son and Metcalfe, 2005), as well as curiosity-driven exploration of the environment where
436 rewards may be more dependent on the learning progress of an individual (Gottlieb and Oudeyer,
437 2018).

438 Humans exhibit biases when it comes to predicting how future events are likely to impact on their
439 affective states, and are prone to making sub-optimal decisions by misjudging the hedonic
440 consequences of options (Wilson and Gilbert, 2005; Meyvis et al., 2010; Nisbet and Zelenski, 2011).
441 Increasing subjective well-being is widely believed to be an appropriate societal goal (OECD, 2020),
442 but these biases pose a difficulty for enacting policies that are likely to be successful. Additional
443 factors such as social desirability bias (Van de Mortel, 2008) can decrease the reliability of self-
444 reported values when an individual's assessment of a hypothetical experience or good, such as the
445 availability of public parks, differs from prevailing social norms. An advantage of our method (i.e.,
446 repeated mood sampling combined with computational modelling) is that it can be in principle applied

447 not only to any cognitive task but also to any repeatable experience (e.g., commuting, walking in a
448 park, exercising, doing yoga, etc.) without a need to probe people explicitly about the content of those
449 experiences (e.g., how do you feel after having done yoga?). Mood measurements make no reference
450 to recent events but allow the relative influence of multiple factors to be simultaneously estimated,
451 reducing biases associated with social desirability (e.g., following social norms about how one should
452 feel after doing yoga). For example, affective dynamics reflect depressive symptoms (Rutledge et al.,
453 2017; Blain and Rutledge, 2020), show consistent relationships to reward in the lab and outside the
454 lab in anonymous participants who did not interact with an experimenter (Rutledge et al., 2014), and
455 allow quantification of the extent of guilt and envy in response to social inequality (Rutledge et al.,
456 2016). A potential application of our approach, yet to be tested, would be to combine our
457 computational approach with experience sampling in different naturalistic settings such as a corporate
458 workplace, in order to identify factors important for employee well-being. Thus, the approach we use in
459 this study demonstrates a novel tool for understanding preferences and well-being.

460

461 Over a century ago, Francis Edgeworth described an idealized instrument, which he called a
462 hedonometer, for ‘continually registering the height of pleasure experienced by an individual’
463 (Edgeworth, 1881). Here, we introduce a ‘computational hedonometer’ that has a distinct advantage
464 over Edgeworth’s hypothetical hedonometer in that it mathematically quantifies the relative
465 contributions of different factors to an affective state, including the relative values of intrinsic and
466 extrinsic rewards. We validate our computational tool using objective neural measurements,
467 suggesting that computational parameters can capture the affective values for abstract goods and
468 experiences that may be otherwise challenging to accurately quantify.

469

470

471

472 **ACKNOWLEDGMENTS**

473

474 We thank Tobias Hauser, Matilde Vaghi, and Rachel Bedder for helpful comments. B.C. is a
475 predoctoral fellow of the International Max Planck Research School on Computational Methods in
476 Psychiatry and Ageing Research. The participating institutions are the Max Planck Institute for Human

477 Development and the University College London (UCL). B.C. is also supported by a scholarship from
478 the Singapore Institute of Management. R.J.D. holds a Wellcome Trust Investigator Award
479 (098362/Z/12/Z). R.B.R. is supported by a Medical Research Council Career Development Award
480 (MR/N02401X/1), a 2018 NARSAD Young Investigator Grant (27674) from the Brain and Behavior
481 Research Foundation, P&S Fund, and by the National Institute of Mental Health (1R01MH124110).
482 The Max Planck UCL Centre is a joint initiative supported by UCL and the Max Planck Society. The
483 Wellcome Centre for Human Neuroimaging is supported by core funding from the Wellcome Trust
484 (203147/Z/16/Z).

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- 642
- 643

644 **Figure 1. Extrinsic and intrinsic reward paradigm**

645 (A) Subjects ($n = 33$) experienced both extrinsic and intrinsic rewards on each trial. A trial starts with
646 subjects selecting from one or two available options each associated with an implicit extrinsic reward.
647 One option on average leads to the larger reward (mean 50, SD 10) whereas the other leads to a
648 lower reward (mean 25, SD 10) with a reversal every 19-23 trials. Four barriers then appear along the
649 path to the outcome and a cursor appears at the bottom of the screen which automatically advances
650 after a 1s delay. Subjects press left and right keys to navigate around barriers, constituting a form of
651 skilled performance that can be intrinsically rewarding. Successfully avoiding a barrier turns it green
652 whereas contact with a barrier turns it red. There is no financial penalty for contact with barriers nor
653 financial benefit for avoiding them. Earnings depend only on the outcome delivered at the end of the
654 trial. After every 2-3 trials, subjects report their current happiness by moving a cursor on a rating line.

655 (B) Probability of choice to the initial high-reward option averaged across subjects ($n = 33$) in black.
656 Shaded areas correspond to SEM. Grey vertical bands represent intervals where probability reversals
657 could occur.

658 (C, D) Happiness trajectories and model fits for a computational model with both reward and
659 performance parameters are displayed for two example subjects (C: $r^2 = 0.45$, D: $r^2 = 0.42$). Also see
660 Figure 2, Figure 3, Table 1 and Table 2.

661

662 **Figure 2. Computational modelling of affective dynamics**

663 (A) Subjects were happier when they received a reward from high- compared to low-reward
664 options ($Z = 4.7$, $p < 10^{-5}$, in blue). Subjects were happier on average when they navigated through
665 the barriers without contacting them, compared to when they contacted at least one barrier ($Z = 4.6$, p
666 $< 10^{-5}$, in orange). *** $p < 0.001$.

667 (B) The majority of subjects (29 of 33) were happier after receiving a reward from a high-
668 compared to low-reward option. The majority of subjects (29 of 33) were happier after successful
669 compared to unsuccessful performance. There was no relationship between happiness for reward
670 outcomes and happiness for skilled performance ($\rho(31) = -0.20$, $p = 0.26$).

671 (C) Average happiness across all subjects and model fit is displayed for the computational model
672 ($n = 33$, mean $r^2 = 0.26$).

673 (D) According to the computational model, happiness was significantly related to the history of
674 extrinsic rewards in the form of points converted to money ($Z = 4.9$, $p < 10^{-5}$) and also to the history of
675 skilled performance, a proxy for intrinsic rewards ($Z = 4.4$, $p < 10^{-4}$).

676 *** $p < 0.001$.

677

678 **Figure 3. Parameter recovery analysis for reward model (A), performance model (B), and**
679 **reward and performance model (C)**, plotting the parameter values used to generate the data
680 against the estimated parameters for z-scored happiness ratings. The model parameters were
681 recoverable with no bias. See Experimental Procedures for details. *** $P < 10^{-7}$

682 **Figure 4. Computational model parameters and task behavior**

683 (A, B) The contribution of reward to happiness varied across subjects despite a similar high choice
684 accuracy across subjects. Despite titrating difficulty at the individual level to match performance
685 across subjects at 70%, subjects displayed considerable variation in the degree to which performance
686 impacted affective state as captured by the computational model. Filled circles indicate betas that are
687 significant at the individual level.

688

689 **Figure 5. Relative affective impacts of reward and performance predict vmPFC activity**

690 (A) *Top.* BOLD activity in vmPFC was parametrically modulated by reward magnitude (Peak: -3,
691 38, -1). *Bottom.* Bold activity in an overlapping region of vmPFC was modulated by trial-by-trial
692 successful skilled performance (Peak: -3, 50, -1).

693 (B) An independent vmPFC ROI shows modulation by both reward magnitude and skilled
694 performance (both $p < 0.01$).

695 (C) In the independent vmPFC ROI, subjects with higher performance than reward weights in the
696 computational analysis of affective dynamics displayed stronger neural responses in the vmPFC for
697 performance than subjects with higher reward than performance weights ($p = 0.003$).

698 (D) The difference between performance and reward weights in the happiness computational
699 model predicted the difference in vmPFC neural responses for successful skilled performance relative
700 to reward magnitude ($\rho(31) = 0.50$, $p = 0.003$).

701 * $p < 0.05$, ** $p < 0.01$.

702

703 **Table 1. Model parameter recovery results**

704 **The values correspond to the Spearman correlation between the generated parameters and the**
705 **estimated** parameters of 33 agents using z-score happiness ratings. See Experimental Procedures
706 for details. *** $p < 0.001$

707 **Table 2. Model comparison results**

708 Bayesian Information Criterion (BIC) scores are summed across 33 subjects. The winning model
709 (lowest BIC) was the model with both reward and performance having the same forgetting factor γ
710 rather than a model where the influence of past reward and performance differs in their forgetting
711 factor. Δ BIC refers to the difference in BIC between each model and the winning model. Ratings are z-
712 scored to prevent individuals with greater rating variance from disproportionately influencing model
713 comparison.

714

715 **Table 3. Correlation between baseline mood parameter and questionnaire score.** Values
716 correspond to the Spearman coefficient ρ . * $p < 0.05$, † < 0.1

717

Model	Spearman ρ between generated and estimated parameters			
	W_{reward}	$W_{performance}$	Y_1	Y_2
Reward	0.91 ***	-	0.82***	-
Performance	-	0.70***	0.61***	-
Reward and performance	0.89 ***	0.73***	0.76***	-
Reward and performance (separate γ)	0.86***	0.90***	0.81**	0.81***

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719

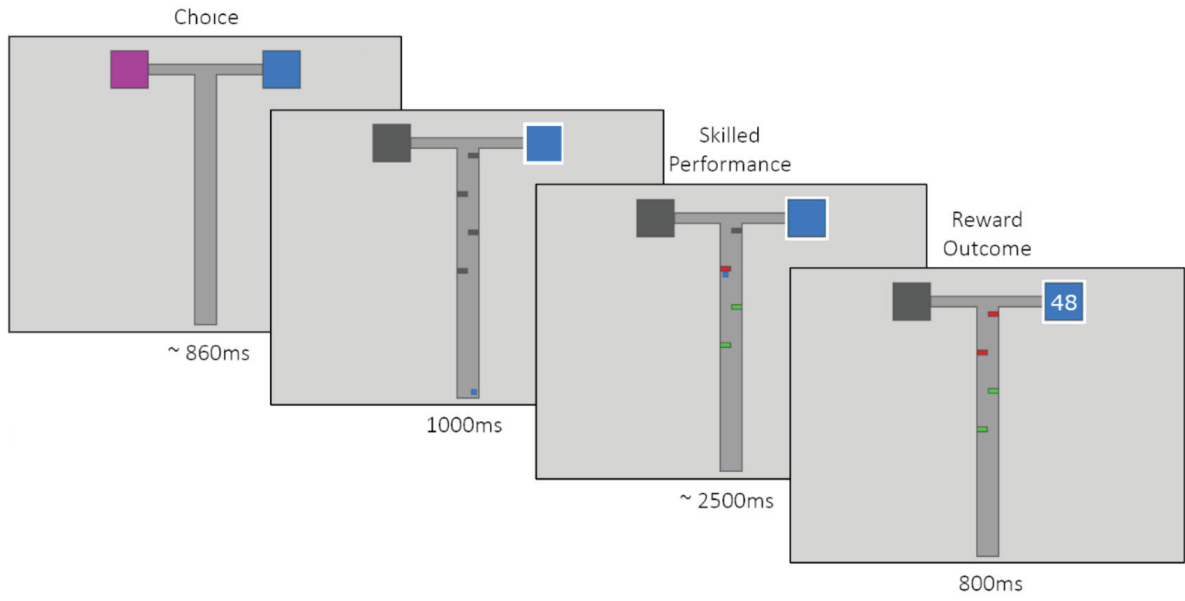
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Model	Parameters	Mean r^2	BIC	Δ BIC
Reward	2	0.19	-326	145
Performance	2	0.09	-26	445
Reward and Performance	3	0.26	-471	0
Reward and Performance (separate γ)	4	0.27	-351	120

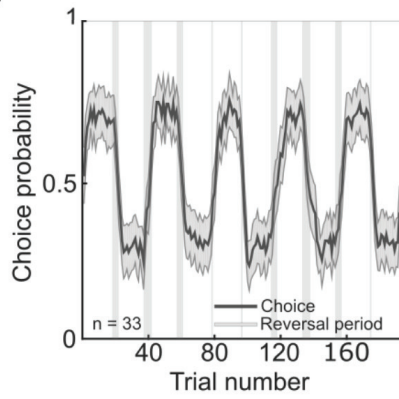
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	W_0 reward	W_0 performance	W_0 reward & performance
<i>BDI</i>	-0.35*	-0.31 †	-0.34†
<i>AES</i>	-0.32 †	-0.32 †	-0.30 †
<i>bAMI</i>	-0.33 †	-0.32 †	-0.29 †

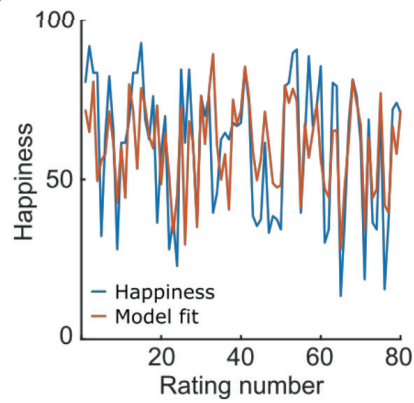
A



B



C



D

