1 **Suboptimality in foraging and its association with age and mental**
2 **health factors**

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Abstract

People constantly decide how much time to invest in more versus less rewarding activities. Foraging tasks, during which participants visit contexts with diminishing reward rates, examine this type of decision-making by measuring when individuals choose to switch contexts. It is widely known that humans and other animals perform suboptimally in these tasks. However, the precise nature of this suboptimality, and its links to other behaviourally relevant traits, remain unclear. Here, we developed a foraging task to disambiguate the impacts of initial reward rates and reward rate changes. We investigated how foraging behaviour differs with age and relates to apathy and depression, which are key factors known to influence reward-based decision-making, while controlling for cognitive factors. In addition to overstaying, we found that participants performed more suboptimally as reward decay rate increased, and that many participants expressed a heuristic preference for staying in the single best condition. Moreover, overstaying was strongly associated with higher scaling of stay durations to each condition, and this overstaying/scaling behaviour was positively associated with age but negatively associated with depressive symptoms. No associations were found between foraging behaviour and apathy. Together, our results suggest that people may counterproductively interpret staying in a patch as persistence in reward extraction, which would explain the tight link between overstaying but high sensitivity to reward conditions, and their association with depressive symptoms.

Introduction

Decision-making is a fundamental cognitive process that involves selecting an action among alternatives based on expected costs and outcomes. Yet how individuals choose to maximise their gains or reward over time, and how much time and effort they are willing to invest in a task varies significantly. There are numerous factors – both within and across individuals – that influence decision-making. Across individuals, age influences decision-making, particularly in the context of risk or outcome uncertainty (Eppinger et al., 2011; Nassar et al., 2016). Despite significant changes in reward processing (Dhingra et al., 2020; Eppinger et al., 2012, 2013), there does not seem to be a consistent change in behavioural response to reward in older adults (Chowdhury et al., 2013). Another factor influencing decision-making is apathy – that is, reduced motivation and diminished goal-directed behaviour (Husain & Roiser, 2018; Levy & Dubois, 2006). Apathy is associated with a reduced willingness to invest effort for reward, both in healthy population and in various neuropsychiatric populations (Chong et al., 2017; Jurgelis et al., 2021; Nair et al., 2021; Saleh et al., 2023; Treadway et al., 2009), although mixed findings have been reported in the literature (Valton et al., 2024).

Foraging behaviour, a concept from ecological studies, has recently gained attention as a model for studying decision-making in different neuropsychiatric populations (Barack, 2024; Barack et al., 2024; Bustamante et al., 2024). In foraging tasks, participants decide when to stay with a current resource or 'patch' and when to switch to a potentially better one. Such paradigms can dissect components of decision-making, such as tendency to perseverate and responsiveness to continuous changes in reward, possibly with a more ecological experimental set-up. In humans, foraging studies have revealed that tonic dopamine levels may play a central role in deciding when to switch (Constantino et al., 2017; Le Heron et al., 2020; Niv et al., 2007; Raio et al., 2022). Dopamine facilitates foraging or switching behaviours (Le Heron et al., 2020), possibly by enhancing the computed 'opportunity cost' (Beierholm et al., 2013; Niv et al., 2007; Wolpe et al., 2024).

Opportunity cost, or the forgone reward that is missed whilst engaging in the current course of action, is considered a key metric in the decision of whether and when to switch in foraging behaviour. In normative models, such as the Marginal Value Theorem (MVT) (Charnov, 1976), individuals are thought to switch between 'foraging' (~switch) and 'harvesting' ('stay') so as to maximise accumulated reward over time (Stephens & Krebs, 1986). According to MVT, the optimal point for switching is when the rate at which reward is acquired falls below the potential average rewards of other available options (Charnov, 1976). People's behaviour generally aligns with principles of MVT, though it is typically suboptimal (Pearson et al., 2014), as animals including humans tend to overstay in a given patch (Harhen & Bornstein, 2023; Kendall & Wikenheiser, 2022; Kolling et al., 2012; Le Heron et al., 2020; Nonacs, 2001). Several studies have investigated the sources of this suboptimality (Garrett & Daw, 2020; Harhen & Bornstein, 2023; Kendall & Wikenheiser, 2022). However, it is unknown whether and how foraging behaviour changes across the lifespan in humans, and how it relates to key cognitive and mental health variables.

91   In this study, we investigated the relationship between foraging behaviour and three principal
92   variables: age, depression, and apathy. We also measured processing speed and planning
93   ability to control for potential cognitive confounds. Young and older participants completed a
94   timed foraging task online, requiring them to collect as much reward as possible in the face
95   of changing reward accumulation rate (Fig. 1). Participants also completed self-rated
96   depression and apathy questionnaires, and two additional cognitive tasks to independently
97   measure processing speed and planning ability as control. Based on the literature reviewed
98   above, we hypothesised that older adults would show more suboptimal foraging behaviour
99   due to increased perseveration and reduced sensitivity to changes in reward; that individuals
100   with higher apathy would demonstrate reduced willingness to stay for diminishing rewards,
101   and that depression would be associated with reduced reward sensitivity and earlier
102   switching behaviour.
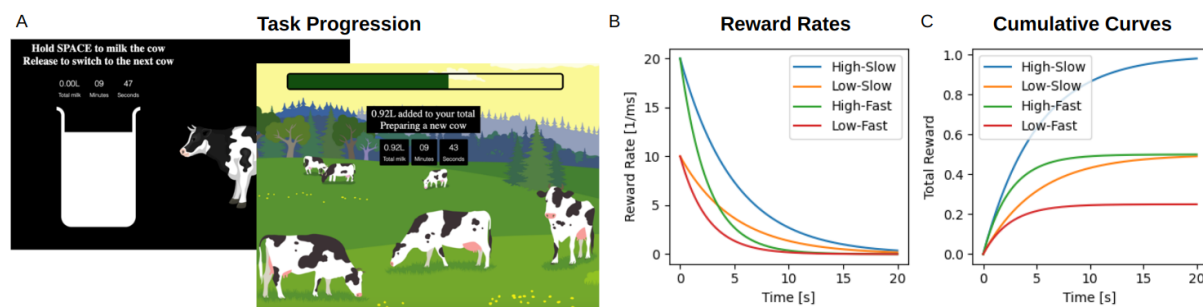
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104   **Figure 1**: Schematic of foraging in the milkman task. **(A)** In the task, participants had 10
105   minutes to maximise the amount of milk they collect. In the main milking screen, participants
106   held the spacebar key to fill a bucket with milk. Animated milk filling the bucket showed
107   participants the milk accumulation rate, and participants chose when to release the spacebar
108   key in order to switch to the next cow. Switching cows ("travel") resulted in a fixed (4 s) time
109   cost. Milk accumulation rate followed an exponential function, and there were four types of
110   cows (uncued, pseudo-random differences, observable only via reward accumulation), each
111   combining one of two initial milk accumulation (reward) rate and one of two reward decay
112   rate parameters. **(B)** Instantaneous reward-rates over time by condition. **(C)** Total reward
113   accumulation by time for each condition.

Results

Optimal policies depended on initial reward rate and speed of decay

In order to understand how people should ideally behave in the foraging task, we first computed the optimal policy using optimization methods (see Methods). We found that optimal policies depended both on the initial reward rate and the speed of decay, with the high reward rate-slow decay condition (High-Slow) prescribing the maximal stay duration 7.5 s and the low reward rate-fast decay condition (Low-Fast) prescribing the minimal stay duration of 2.5 s. The two intermediate conditions had similar optimal policies, with 4.1 s for Low-Slow and 3.8 s for High-Fast. Given these large differences between all but the intermediate conditions, we expected the optimal policy would be learned quickly by most participants.

Participants differentiated conditions and showed several forms of suboptimality

Participant behaviour differed across conditions in accordance with normative predictions (Fig. 2A). Group means differed significantly between pairs of conditions (two-tailed paired t-tests; $t_{(316)}$=22.9, 22.2, 14.8; p=3.8e-85, 2.5e-2, 5.4e-43 for the three adjacent ordered comparisons starting with High-Slow vs. Low-Slow; d'=1.8, 0.2, and 0.9, respectively). Note that the two middle conditions have optimal stay durations within ~300 milliseconds of one another, and, consistent with this, average participant responses were similar across those conditions. As a result, individual participants did not always stay longer in the Low-Slow (slightly better) condition than the High-Fast (slightly worse) condition. Importantly, compared to optimal behaviour, most participants exhibited overstaying behaviour (Fig. 2A), and this had a substantial impact on total reward in the task (Fig. 2B). Group mean stay durations were substantially longer than those of an optimal agent, with mean overstaying of 2.6 s, 1.6 s, 1.6 s, and 1.7 s for the High-Slow, Low-Slow, High-Fast and Low-Fast conditions. Overstaying compared to an optimal agent was significant for all conditions (two-tailed one sample t-tests; $t_{(316)}$=16.9, 13.0, 20.5, and 23.8; p=6.6e-46, 2.8e-31, 6.3e-60, and 2.5e-72; d'=1.0, 0.7, 1.2, and 1.4).

A second primary determinant of reward in the task was response latency (Fig. 2C), which was correlated with total reward (Pearson's r=-0.33, p=1.6e-9), but was unrelated to average stay durations (Pearson's r=-0.02, p=0.8). Moreover, similar to stay duration, participant exit thresholds (their reward rates at exit time) were roughly half to three-quarters of the optimal values (Fig. 2D) (optimal threshold: 0.44 L/s; average thresholds: 0.30, 0,35, 0.27, 0.25).

Notably, we observed that participants overstayed more in some conditions than others. Specifically, participants performed more optimally in the two slow decay-rate conditions, whereas they overstayed the most in the worst (low-fast) condition (compare red to black in figures 2D and 2E). This tendency cannot be simply explained by a fixed overstay duration pattern, as optimal stay durations were similar in the intermediate-quality (Low-Slow and High-Fast) conditions, whereas participants overstayed differently in these conditions. As a result, overstaying behaviour (measured as exit threshold differences) was distinct across task conditions (two-sided paired sample t-test, $t_{(316)}$=-9.7, 2.8, 6.4; p=8.5e-21, 1.3e-111, 3.5e-10; d'=-0.77, 2.21, 0.50, ordered as above).

159 Examining individual participant exit thresholds in more detail, we computed each
160 participant's variation around their own exit threshold baseline (Fig. 2E). This confirmed that
161 *individual* participants tended to perform most suboptimally in the fast decay rate conditions,
162 and most optimally on the Low-Slow condition. Many participants also overstayed in the
163 High-Slow (best) condition more than in the Low-Slow (second best) condition. Participant
164 suboptimality was therefore most pronounced in the fast decay rate conditions, over and
165 above the (average) exit thresholds reflecting their generalised overstaying behaviour. One
166 possible explanation for this may be that participants are less capable of approximating an
167 internally defined exit threshold in the fast decay rate conditions (because of the higher rate
168 of reward change, and perhaps an associated response lag) than in the slow decay rate
169 conditions, but this would not explain the difference between high-slow and low-slow
170 suboptimality. Notably, the differences between participants' highest and lowest exit
171 thresholds were also significantly correlated with their average exit thresholds (Pearson's
172 r=0.65, p=1.3e-38; Fig. 2F), suggesting that the magnitude of this suboptimality difference is
173 significantly related to the flattening reward rate curves at increasing stay durations. Better
174 performing (more optimal) participants therefore had *less* consistent exit thresholds than
175 poorer performing ones.
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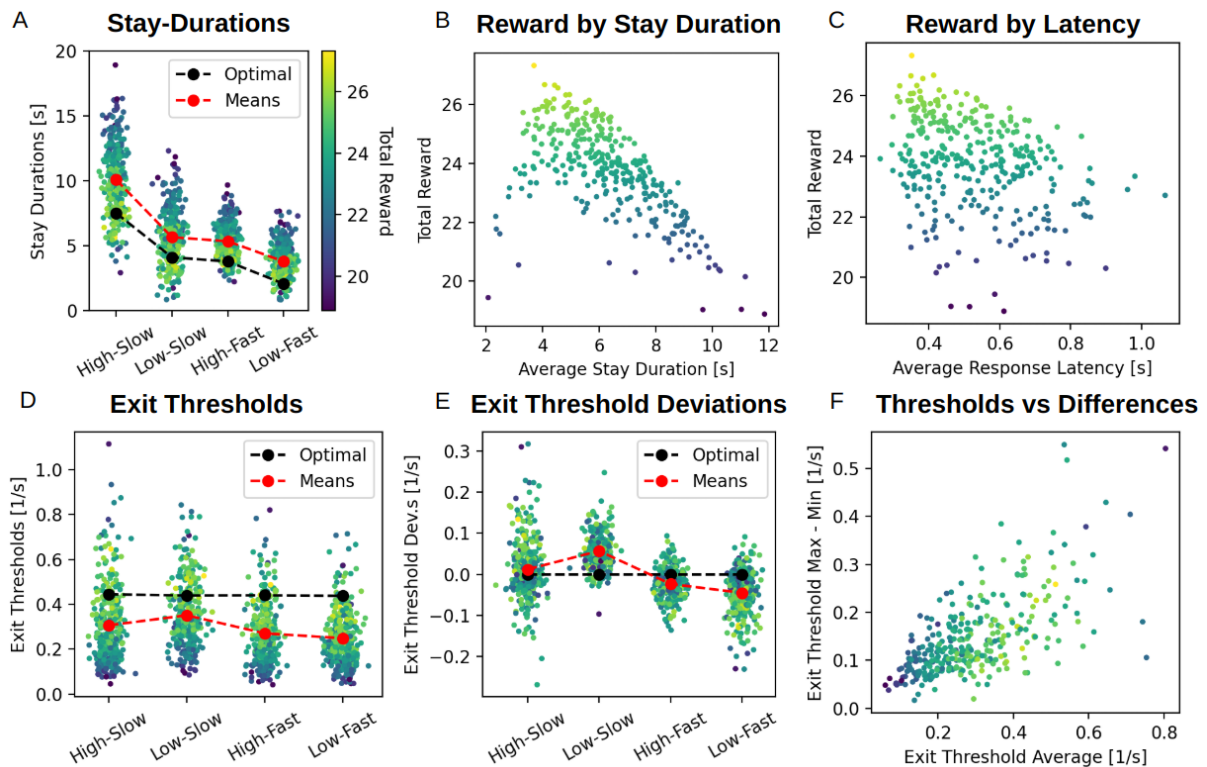
178 **Figure 2:** Summary of participant performance. **(A)** Average stay durations (over trials) for
179 each task condition are plotted in a colour scale reflecting total reward obtained over the
180 course of the experiment (lighter colours indicate higher reward, same colouring across
181 panels). Participants stayed for longer than they should in all conditions, but recovered the
182 rank ordering correctly (as a group). Participants showing better performance also tended to
183 cluster around the optimal for each condition, indicating that performing one condition
184 correctly is associated with performing others correctly, whereas worse performance tended
185 to affect all conditions. **(B)** Reward was strongly, but not entirely, determined by average

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186 stay durations. In particular, it was reduced by overstaying, which most participants
187 exhibited, but also by under-staying, making the relationship nonlinear. **(C)** Response
188 latency was a second significant determinant of total reward, and was not related (see the
189 text) to total stay durations. **(D)** Participant exit thresholds, which show differential
190 overstaying by condition, with the least overstaying in the Low-Slow condition and the most
191 in the Low-Fast. **(E)** Exit threshold deviations (from by-participant grand means) for each
192 condition. Having a higher exit threshold deviation is generally better (less suboptimal). A
193 minority of participants were in the vicinity of optimal performance, or even under-stayed,
194 and for these participants, this higher-is-better interpretation will not always be correct.
195 Participants can be seen to perform most suboptimally in the Low-Fast condition, followed by
196 the High-Fast, High-Slow, and lastly, Low-Slow condition. **(F)** Participants with larger
197 differences between their highest and lowest exit threshold, i.e., who had *less* consistent exit
198 thresholds, had higher average exit thresholds and performed better on the task.

Participants differed in overstaying behaviour

201 To further examine how participants' policies differed, we performed PCAs on stay durations
202 and exit thresholds. The first two principal components explained 90%, and 8% of the
203 variance in stay durations across participants, respectively, and we obtained similar results
204 for exit threshold PCs (Fig. 3A). The first PC (PC1) represented a combination of average
205 stay duration shifting and scaling (Fig. 3B-C). Specifically, PC1 loaded positively on all stay
206 durations, indicating baseline (or average) offsets between participants, but increased more
207 for the "better" two conditions than the "worse" ones, indicating scaling or exaggeration of
208 the between-condition stay durations. We found this to be a consequence of transforming
209 approximately uniform exit threshold variations into duration space. In particular, the exit
210 threshold variation (PC1 in figure 3C) implied greater stay duration variability in the slow-
211 decay conditions (PC1 in figure 3B) and vice versa.

213 Overstaying behaviour therefore had two components: a baseline stay duration offset
214 (relative to the optimal set of stay durations), and a condition-difference exaggeration
215 component. Examining this decomposition further, we computed participant's offset
216 components by taking mean stay durations, and computed their scale components by
217 projecting mean-subtracted stay durations onto a mean-subtracted, unit-normed transform of
218 the optimal policy. These components were highly correlated (Pearson's r=0.69, p=7.0e-47),
219 suggesting that participants that overstayed more, tended to exaggerate condition
220 differences as well (Fig. 3D).

222 In contrast to PC1, the second PCs in both stay duration and exit threshold spaces
223 measured a tendency to stay in the best (High-Slow) condition over all others (Fig. 3B-C).
224 Therefore, systematic variation between participants was dominated by differences in their
225 baseline overstaying behaviour and scaling (PC1: baseline stay or overstay and scaling) and
226 their expressed preferences for the single best patch in the task (PC2: High-Slow
227 preference). In subsequent analyses, where possible, we chose to primarily analyse
228 participant stay behaviour in stay duration space rather than exit threshold space, since the
229 two were strongly related, and exit reward-rates asymptoted to zero as stay durations
230 increased (Fig. 3E).

Differences in overstaying and scaling (PC1) were strongly related to total reward earned in the task. In line with the strong impacts of average policy stay durations across conditions, participants with lower PC1 scores tended to earn more reward (Pearson's r=-0.63, p=1.1e-35) (Fig. 3F). When breaking PC1 down to baseline overstaying and scaling, the correlation between PC1 and reward was largely driven by a strong relationship between overstaying and reward (Pearson's r=-0.63, p=4.9e-36), whereas there was no association between scaling and reward, independent of the relationship with overstaying (when scaling residualised by baseline overstaying, Pearson's r=-0.01, p=0.89). Similarly, the orthogonal aspect of preference for the best task condition (PC2) did not meaningfully impact participants' earned rewards (Pearson's r= 0.02; p=0.73). The remainder of reward variation was due in large part to response latency differences, as noted above, and consistency differences over the course of the task, to which we turn next.
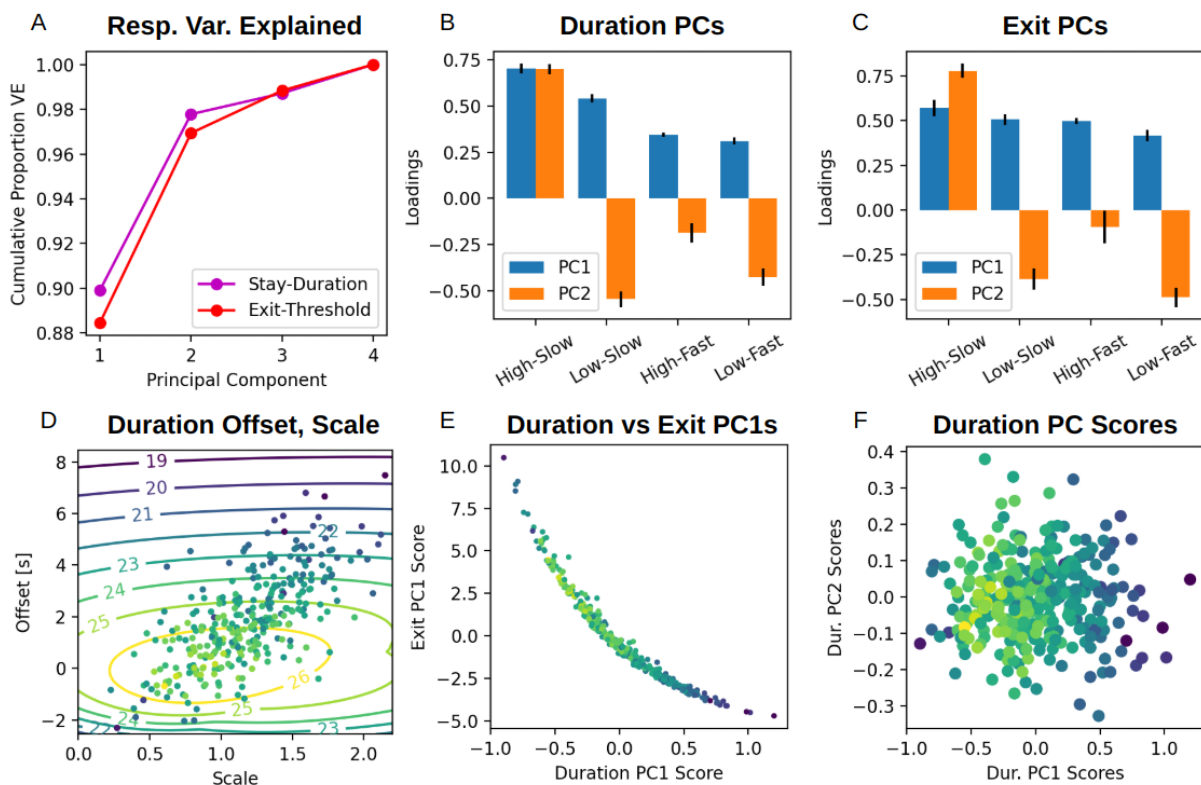

Figure 3: Participants mainly varied in their baseline stay durations, scaling of condition differences, and their preference for staying in the high-slow condition. **(A)** In both duration-space and exit threshold-space, the first PC explained roughly 90% of the variance, and the second PC explained most of the remaining variance. **(B)** PCs for participant average policies. The top PC combines baseline shifting and condition-difference scaling. The second reflects preference for the high-slow condition. Error bars show standard errors, estimated via jackknife resampling. **(C)** PCs for participant average exit thresholds by condition. Note the approximately flat structure of the first PC. Converting uniform exit threshold variation into stay durations produces the shifted and scaled variability seen in PC1 of (B). Parallel structure across (B) and (C) indicates that apparent condition preference structure in the data is robust, and is not an artefact of measuring either time-domain data or exit threshold data in particular. **(D)** Duration PC1 involves both a total stay duration offset

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259　(y-axis) and an exaggeration of condition differences (a scaling component, x-axis). The best
260　performing participants had offsets near 0 and scale factors near 1 (normalised to
261　differentiation under the optimal policy). Reward contours are plotted, showing that scaling
262　had little effect on performance, whereas offset had a strong effect. **(E)** Duration and exit
263　PCs scores are highly correlated, but exit PC1 scores saturate, showing a floor effect,
264　because they are bounded by zero as stay durations increase. **(F)** The first stay duration PC
265　was highly correlated with reward, whereas the second PC was uncorrelated with it.
266
267　**Task performance was consistent over time**
268　To assess whether our task measures were stable over the course of the experiment, we
269　examined split-halves of our data. Recomputing PCs using the initial and final data
270　segments, we observed strong agreement over the course of the task for both PC1 (Fig. 4A)
271　and PC2 (Fig. 4B) (cosine angles: 3.0 and 2.9 degrees for PC1 and PC2 initial vs. final).
272　Similarly, the profile of exit deviations (computed as above) was conserved (Fig. 4C),
273　although there was a notable increase in the relative optimality of participants' responses to
274　the Low-Slow condition over the task (start vs end bars, Low-Slow group, Fig. 4C). In
275　addition to PC stability, participants' initial and final scores were high correlated for both PC1
276　(Pearson's r=0.80, p=1.5e-72, Fig. 4D), and PC2 (Pearson's r=0.57, p=4.4e-29, Fig. 4E).
277　Exit deviations were correlated at a range of values between about 0.3 and 0.6 (Fig. 4F).
278　Taken together, these results therefore indicated that both group factor structure and
279　individual participant scores reliably reflected suboptimality over the duration of the task.
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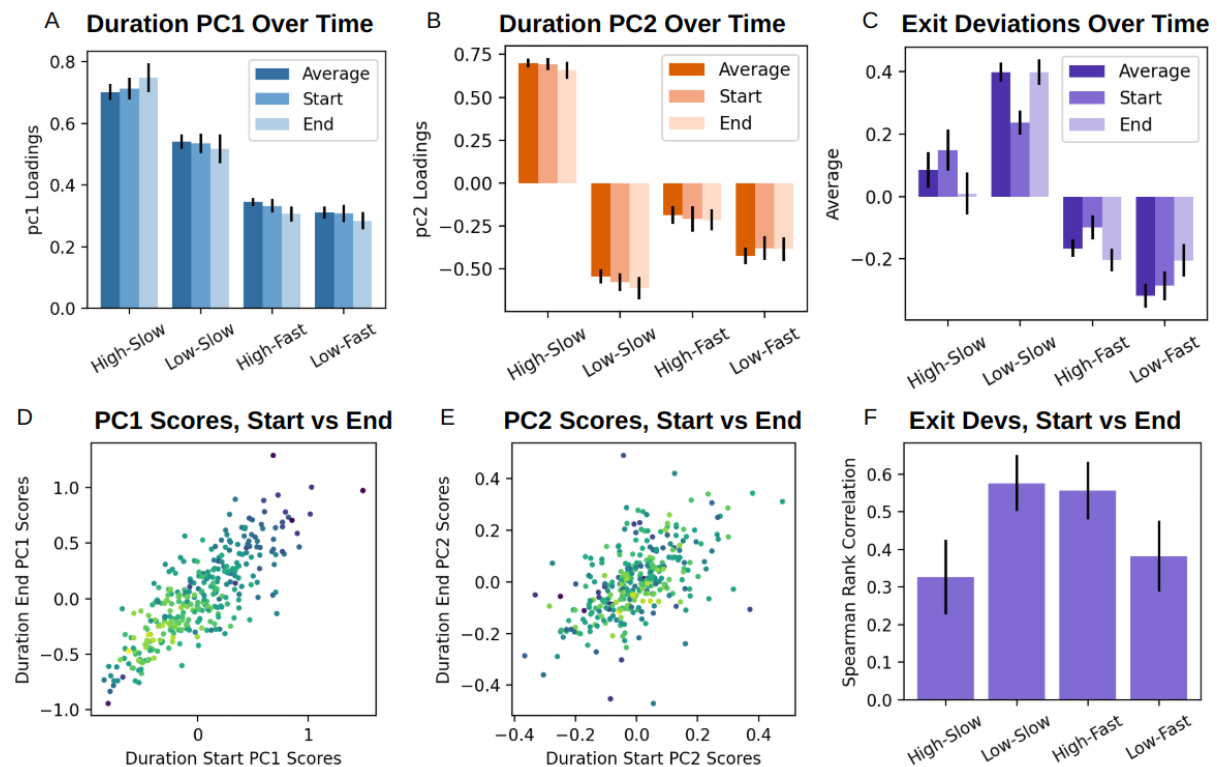
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282
283　**Figure 4:** Stability of measures over experiment duration. **(A-B)** Principal components of
284　participant stay durations, computed from the first and second halves of the task, were
285　consistent with one another, and with those computed from the whole task. Error bars for

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loadings are 2 standard errors, computed via jackknife resampling. **(C)** Exit deviations over the course of the task were largely stable as well, although there was evidence that participants become systematically more suboptimal in the Low-Slow condition. Bars are means and error bars are +/- 2 SEM. **(D-E)** Scatterplots of participant PC1 (respectively, PC2) scores on the first and second halves of the experiment. **(F)** Rank correlations of participant exit deviations on the first and second half of the experiment.

Age and depression symptoms were associated with overstaying

Lastly, we investigated the associations of task performance with age and mental health variables, while controlling for cognitive abilities. Mental health variables included apathy and depression symptoms, measured with the AES and PHQ-9. Cognitive abilities included planning ability and processing speed, measured with accuracy and response time in the Tower of London task and a simple reaction time task.

To assess the unique contributions of these variables to differences in foraging behaviour, we fit several linear regression models. First, we residualised our task-exogenous variables by age, as age was significantly associated with all variables (Fig. 5A). These variables were then entered into two regression analyses, predicting PC1 and PC2. In the first regression model (Fig. 5B), age and PHQ scores showed significant associations with PC1 (β=0.13, -0.21; SE=0.06, 0.07; $t_{(274)}$=2.3, -3.50; p=0.02, 0.003, for age and PHQ-9, respectively). By contrast, none of the variables was associated with PC2 in the second regression model (Fig. 5C).

Post hoc zero-order correlations showed there was a positive association between PC1 and age (r=0.20, p=4.3e-4, uncorrected; Fig. 5D), a negative association with PHQ (r=-0.13, p=0.025, uncorrected; Fig. 5E). For completeness, we also illustrate the positive association between PC1 and response times in the Tower of London task (Fig. 5F), which was interestingly abolished when residualising by age. Considering the high correlation between offset and scaling behaviour (see above), these analyses meant that older adults (Fig. 5D) and those with lower depression scores (Fig. 5E) showed both a greater tendency to overstay and greater scaling to each reward condition.
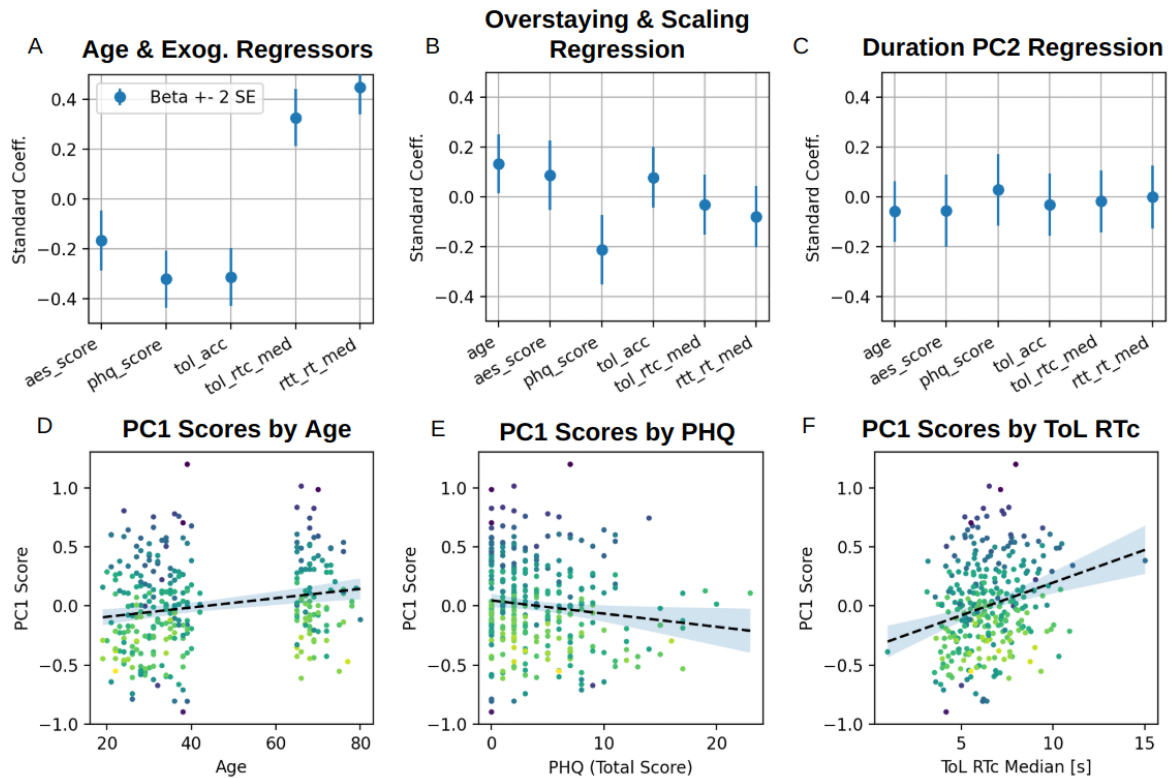
Figure 5: Relationships between foraging behaviour, age, mental health and cognitive covariates. **(A)** Regression coefficients predicting age, according to Apathy Evaluation Scale score (aes_score), Patient Health Questionnaire-9 (phq_score), Tower of London accuracy (tol_acc), median reaction time for correct responses in Tower of London (tol_rtc_med), and median reaction times in reaction time task (rtt_rt_med). Error bars indicate 2 standard errors. **(B)** Regression coefficients for linear models predicting participant overstaying/scaling (stay duration PC1). **(C)** Same as (B), bur for the association with a preference for best condition (stay duration PC2). **(D)** PC1 scores by age, with a linear regression line and 95% confidence interval. **(E)** Same as (D), but for PC1 scores by PHQ. **(F)** Same as (D), but for PC1 scores by Tower of London median correct reaction time (RTc).

Discussion

The present study investigated the structure of suboptimal behaviour in a foraging task, and the correlates of this structure with plausible task- and individual-related factors. Our results indicate that suboptimality in foraging behaviour does indeed have more structure than perhaps previously discussed. Specifically, the most significant form of task suboptimality was overstaying, which was highly correlated with condition-specific scaling or sensitivity. People who overstayed longer also adjusted their stay durations more across reward conditions. Interestingly, the simpler heuristic, namely preference for the best (High-Slow) condition further contributed to suboptimality (in the sense of deviating from the use of consistent exit thresholds). Across participants, overstaying/scaling was increased with age and decreased with depressive symptoms, while we could not isolate contributors to the preference for the single best task condition.

Suboptimality in foraging

As also reported in previous research, we found that most participants tend to consistently overstay in a patch, beyond what is predicted by normative models such as the MVT (Kendall & Wikenheiser, 2022). Cognitive and motor mechanisms have been suggested for why people overstay in a patch compared to normative models. First, temporal discounting (Kane et al., 2019) can make individuals overstay because leaving one source of reward incurs a cost in the form of a time delay before the next source of reward becomes available. This time delay spent on 'travelling' reduces the value of the future reward (Kane et al., 2019). Second, sensitivity to costs or effort in the task may contribute to overstaying, specifically in relation to costs incurred during travel to a different patch or while extracting reward within a patch (i.e., harvesting). Although we did not directly manipulate the effort involved in harvesting or travelling (Bustamante et al., 2023), individuals may perceive the effort of harvesting by holding down the button and monitoring the filling milk bucket differently. Those who are less sensitive to this effort would exhibit more overstaying behaviour. Third, foragers need to infer the structure of their environment and use the uncertainty about this inferred structure to adjust their strategies (Harhen & Bornstein, 2023). This means that future reward value is discounted by uncertainty about the environment, leading to overstaying behaviour (Harhen & Bornstein, 2023). Fourth, overstaying can be explained by perseveration – whether cognitive or motor (Sombric & Torres-Oviedo, 2021) – that is, the inappropriate, or in this case suboptimal, prolongation of behaviours (sometimes termed 'continuous perseveration' (Sandson & Albert, 1984)).

Interestingly, we found that the tendency to overstay ('offset') was highly correlated with condition-specific exaggeration of stay durations ('scale'). In other words, participants who tended to overstay for longer, were also more sensitive to changes in the reward conditions. This suggests that overstaying tendency cannot be simply explained by a reduced attention to the task or general slowness, which was indeed not associated with this behavioural pattern in our study. Instead, people who tend to stay longer may place a greater subjective value on extracting reward from each condition, which also makes them more sensitive to differences between conditions. That is, people may suboptimally perceive (over)staying as persistence in the task, and hence those who are more engaged and reward-driven may counterproductively overstay in each patch. This interpretation is consistent with the negative association between overstay/scaling and depression (see below).

375

376 Another important observation in our study is the differential effects of initial reward rate and
377 reward decay rate on stay durations. Classical theories like the Marginal Value Theorem
378 (MVT) typically focus on optimal exit thresholds as a function of current reward rates relative
379 to average environmental rewards, without considering the specific factors that contribute to
380 the instantaneous reward rate. However, we found that the initial reward rate and decay rate
381 have differential influence on suboptimality in foraging behaviour. Specifically, we found that
382 participant exit thresholds were not only consistently lower than optimal across all conditions,
383 but the extent of this deviance from suboptimally was dependent on the specific reward
384 condition: participants were more suboptimal in the fast decay-rate conditions compared to
385 the slow decay-rate conditions, while initial reward rate had no consistent effect on
386 suboptimality.

387

388 This pattern suggests that participants did not effectively adapt to conditions with rapidly
389 diminishing rewards. This may highlight a limitation in cognitive flexibility or suggest that
390 individuals favour stability in their reward-seeking behaviours, even in environments that
391 would benefit from more agile adjustments. Moreover, this finding aligns with research on
392 reinforcement learning and decision-making, which suggests that individuals may rely on
393 heuristics or learned expectations rather than constantly recalibrating their behaviour to
394 account for rapid changes in reward contingencies (Niv et al., 2007). The adoption of simple
395 heuristics is further supported by our finding that some variability of foraging behaviour in our
396 task was explained by preference for the best condition or patch.

397

398 **Age-related differences in foraging behaviour**
399 Consistent with our expectations, older adults demonstrated a greater tendency to overstay
400 in a patch compared to younger adults. This was evidenced by a reduced exit threshold and
401 an increased baseline stay tendency after accounting for sensitivity to reward. These
402 findings align with previous literature suggesting that ageing is associated with increased
403 perseveration as seen in rule-switching tasks (Daigneault et al., 1992; Haaland et al., 1987;
404 Head et al., 2009). Such perseveration may reflect a resource rational response to increased
405 computational costs associated with cognition in the ageing brain, which in other work have
406 been shown to give rise to both perseverative and anchoring biases that are amplified in
407 older adults (Bruckner et al., 2020). Alternatively, a tendency to overstay in older adults can
408 reflect age-related risk (Mata et al., 2011) or loss aversion (Guttman et al., 2021), where it is
409 perceived as 'safer' to stick to the same action. Relatedly, when learning the statistics of an
410 environment, older adults are thought to underestimate uncertainty about outcomes (Nassar
411 et al., 2016), which would, according to certain foraging models (Harhen & Bornstein, 2023),
412 lead to earlier switches rather than overstaying behaviour. Directly manipulating
413 environmental reward uncertainty in a future study would resolve these alternative
414 hypotheses.

415

416 The high correlation between overstaying and sensitivity to reward conditions in our task
417 meant that although older adults generally waited longer until they decided to switch, they
418 remained highly responsive to the declining value of a resource over time. This heightened
419 sensitivity could be an adaptive response to their overall tendency to stay in a patch,
420 allowing them to reach similar levels of reward to that of young adults over time. Moreover,

421 increased sensitivity to reward decay speaks to a large body of literature looking at reward
422 processing in ageing (Cutler et al., 2022). Previous research has shown that reward
423 processing changes in the brain across the lifespan (Dhingra et al., 2020; Eppinger et al.,
424 2012, 2013), but behaviourally, there are no clear age-related changes in reward sensitivity
425 (Chowdhury et al., 2013; Cutler et al., 2022). The lack of a consistent behavioural change
426 could be related to the inconsistent age-related changes in dopamine (Chowdhury et al.,
427 2013).
428
429 Dopamine has been suggested to control responsiveness to reward in the decision to switch
430 (Constantino et al., 2017; Le Heron et al., 2020; Niv et al., 2007; Raio et al., 2022).
431 Specifically, dopamine drives switching behaviour (Constantino et al., 2017; Raio et al.,
432 2022), particularly in low-reward or 'poor' environments (Le Heron et al., 2020), and it has
433 been suggested that tonic levels of dopamine reflect average reward rate (Niv et al., 2007).
434 Thus, a simplistic interpretation of our finding could be that overstaying behaviour in older
435 adults is related to lower tonic dopamine levels. However, this interpretation would need to
436 be reconciled with the finding of increased sensitivity to reward decay rate in older adults,
437 which is in turn thought to be more related to phasic dopamine levels (Niv et al., 2007).
438 Future studies could more specifically test these hypotheses, for example in groups of
439 patients with Parkinson's disease where tonic dopamine is primarily affected (Le Heron et
440 al., 2020).
441
442 **Relationship to apathy and depression**
443 Contrary to one of our hypotheses, we did not find a significant correlation between
444 overstaying/scaling behaviour and apathy, as measured using the AES. This is in contrast to
445 previous research linking apathy to the opportunity cost of time (Nair et al., 2021); to
446 temporal discounting and impulsivity (Fellows & Farah, 2005; Lansdall et al., 2017; Petitet et
447 al., 2021; Sinha et al., 2013); to perseveration (Kim et al., 2020; Scholl et al., 2022); and to
448 an inflated sensitivity to effort (Dalléry et al., 2023; Husain & Roiser, 2018; Jurgelis et al.,
449 2021; Le Heron et al., 2018; Müller et al., 2021) (but see (Valton et al., 2024)).
450
451 Interestingly, another recent study found no significant relationship between task parameters
452 in an effort foraging task and apathy, although measured using a different apathy scale
453 (Bustamante et al., 2023). Moreover, a second reported only a weak association between
454 AES and choice bias in an effort-reward decision-making task, but no association between
455 AES and effort or reward sensitivity (Mehrhof & Nord, 2024). Still another study reported no
456 association between AES and behavioural parameters in an effort-reward decision-making
457 task (Valton et al., 2024).These studies raise the possibility that in the general population,
458 where changes in apathy scores are more subtle than in clinical populations, and where the
459 meaning and validation of clinical scales such as the AES are less established, associations
460 with task parameters can be weak.
461
462 In contrast to the lack of association between foraging behaviour and apathy in our study, we
463 found a negative association between overstaying/scaling and depressive symptoms, as
464 measured by the PHQ-9. This association indicates that individuals with more depressive
465 symptoms tended to stay in a patch for a shorter duration. This finding is consistent with our
466 interpretation that overstaying in the task could be seen as persistence (see above). On this

14

account, more depressed individuals experience lower subjective value for extracting reward in each patch, leading them to switch earlier and have lower exit thresholds than those with less depressive symptoms. This result is also consistent with theories of lower average reward expectations in depression (Bustamante et al., 2024; Huys et al., 2015). Moreover, a reduced scaling or reward sensitivity (tightly linked to overstaying in our task) aligns with existing research showing diminished reward sensitivity in individuals with depression (Halahakoon et al., 2020).

Strengths and limitations

The strengths of our study include the use of a new time-constrained foraging task, together with cognitive tasks looking at processing speed and executive function. When measuring more complex behaviours with new tasks, and especially when testing differences between different populations, such as older adults or patient groups, it is crucial to consider new tasks in conjunction with well-established measures of robustly identified cognitive traits, as we did here. However, our study has several notable limitations. First, the study was cross-sectional, and our age-related results could not assess longitudinal changes with age. Moreover, we used a simple foraging task that could potentially be applied to clinical populations with varying degrees of cognitive impairments. However, this meant that the task was more limited in what it could measure, as for example only one environment was included, and we did not manipulate effort or background reward rate as has been elegantly done before (Bustamante et al., 2023; Le Heron et al., 2020). Lastly, this study was largely descriptive, and a more mechanistic account of task-related behavioural differences would, of course, be preferable.

Conclusion

Our principal findings indicate that suboptimal foraging behaviour arises from multiple behavioural factors, including a general tendency to overstay in a patch, difficulties adapting to rapid changes in reward rate, and the use of simple heuristics, such as a preference for a single best patch. Moreover, age and less depressive symptoms were associated with a tendency to overstay, suggesting that overstaying may reflect heightened engagement with reward extraction rather than simply suboptimal decision-making.

Methods

Participants

We recruited participants through the Prolific platform (https://www.prolific.co/). Screening criteria included age of 18-45 years for the young adult group and 65+ years for the older adult group, no chronic condition/illness, and no ongoing mental health/illness/condition. Participants also had to pass a colour-blind test. All participants were asked to read the study information pages and to confirm they are eligible to participate and their consent to participate in the experiment. Participants were paid £4.50 (approximately £9 an hour rate), which included a fixed £1 bonus (see below). The study was approved by the Tel Aviv University local ethics committee (ref: 0003132).

Power analysis showed that with a 2:1 young-to-older adult group ratio, and a sample size of 230 young adults and 115 older adults, the study would have >95% powered to detect significant associations between foraging performance and the variables of interest: age, depression and apathy in two regression analyses (see below), while controlling for the three cognitive variables (see below), with f2=0.15, α=0.05/2. We therefore recruited 235 young adult participants (96 female) with a mean age = 30.81 years and SD = 5.79 years (age range 19-42 years) and 120 older adult participants (54 female) with a mean age = 69.26 years and SD = 3.81 years (age range 65-80 years).

Experimental procedures

Participants performed three behavioural tasks and two questionnaires. The tasks examined foraging behaviour (milkman task), basic processing speed (choice reaction time task), and executive function or planning abilities (Tower of London task).

Milkman task: Inspired by (Le Heron et al., 2020), we developed a task that operationalises the decision to switch in a time constrained experiment (Fig. 1A). Participants were asked to collect as much milk as possible in a 10-minute experiment. To incentivise them, they were informed that only those ranked in the top third in terms of total amount of milk collected would receive a bonus payment of £1.

To milk a cow, participants held down the spacebar key while a bucket, representing the accumulating milk, was displayed on the screen ('milking screen'). They were informed that as milking continued, it would become increasingly difficult to obtain milk from a cow. In reality, the milk accumulation rate followed an exponential function (Fig. 1B) of the form:

$$N_{(t)} = N_0 e^{-\lambda t}$$

Where $N_{(t)}$ is milk accumulation rate at time t, and N_0 is the initial accumulation rate and λ is the milk accumulation decay rate. The total milk accumulated (Fig. 1C), as shown in the bucket, reflected the closed-form integral of this function. N_0 was taken from the set {0.01, 0.02} and λ from the set {2e^{-4}, 4e^{-4}}, creating a 2x2 design and four cows 'types' or conditions with high/low initial reward rate and fast/slow reward decay rate: High-Slow, High-Fast, Low-Slow, Low-Fast. Conditions were interleaved and pseudorandomly presented, such that each cycle of four consecutive trials contained each condition.

After releasing the spacebar, participants saw a 'travel screen', where they were told the next cow was being prepared for milking. Travel time was fixed at 4 s, and a progress bar

was displayed showing the remaining time for the travel screen. On the travel screen, participants could see how much milk was added to their total. Participants were discouraged from pressing the spacebar key during the travel screen, and if premature pressing occurred, they received a warning on the screen which appeared for 2 s. Throughout the experiment (during both milking and travel screen), time remaining was displayed as a countdown timer, as well as the total milk acquired so far. The experiment began with a 1-minute practice to familiarise participants with the task.

Mental health scale. To investigate the relationship between foraging, depression, and apathy, in addition to the foraging task, participants completed two scales: Apathy Evaluation Scale (AES) (Marin et al., 1991) was used to examine individual differences in apathy symptoms. In addition, we evaluated depressive symptoms to control for depression, which typically correlates with apathy, by using the nine-item Patient Health Questionnaire (PHQ-9) (Kroenke et al., 2001). We included two attention check items per questionnaire in the format of nonsensical or 'infrequency' items (Zorowitz et al., 2023).

Control cognitive tasks. Choice reaction time task: In the choice reaction time task, two empty circles were displayed horizontally on the screen. After a pseudorandom interval of 1-5 s (drawn from uniform distribution), one of the circles turned black, and participants were asked to press the left or right arrow key as fast as they can, if the left or right circles turned black, respectively. There were 50 trials overall, and the task took approximately 5 minutes. The measure of interest for each participant was median reaction time in ms, as overall accuracy (whether the button pressed corresponded to the circle turning black) was at ceiling (minimum 89% across individuals, with median accuracy of 100% across individuals).
Tower of London task: In the Tower of London task (Shallice et al., 1997), participants were instructed to move coloured discs, one by one, from a 'start state' depicted in one image, to match a 'goal state' depicted in another image. The discs are stacked vertically across three positions, with different configurations in each trial. During three practice trials, participants indicated the required number of moves to reach the goal state and then demonstrated these moves using a mouse. Only after correctly indicating and performing the moves did participants proceed to the experimental trials. In the 20 experimental trials, participants had 20 seconds to indicate the number of moves needed, without having to demonstrate the moves. The task was designed similarly to that in the Brief Assessment of Cognition in Schizophrenia (Keefe et al., 2008): It was terminated after five incorrect responses, and conversely, participants who were correct on all 20 trials completed two additional trials. The measure of interest was the total number of correct responses in the experimental trials.

Statistical analyses
All analyses were performed in python version 3.11.7, and code for performing them can be found at https://github.com/DanielNScott/milkman-analysis/.

We implemented several basic quality controls. Our data included some participants who did not engage with the task properly, including one that only completed several trials, waited approximately 8 minutes (out of a total of 10), then re-engaged, and a second that foraged in each patch for an average of 50-60s. After excluding these two participants, we performed

590   further exclusions by computing robust z-scores of stay durations, response latencies, stay
591   duration PCA scores, and total reward, then removing participants falling outside of 3 robust
592   SDs on these measures (a robust SD being defined as 1.48 times the median absolute
593   deviation). These exclusions are shown on rank-value plots in Supplementary Figure 1. Our
594   exclusion criterion can be considered lenient, because it translates into an average stay
595   duration threshold of over 10 seconds and an average latency threshold of over 1 second.
596   Many of the participants who failed one of these tests also failed multiple of them, as can be
597   seen in Supplementary Figure 2. Ultimately, our 3-SD outlier exclusion rule removed 31
598   participants from our foraging analyses, for a retention of 91% of the data, 317/350
599   participants for the main behavioural analyses.
600
601   For analysing the associations between task performance and age and mental health
602   variables, we further excluded participants who either failed attention check questions on the
603   AES or PHQ-9, or had implausible mean response times on the reaction time task. The
604   implausible response times were also determined according to the 3-SD criterion, which
605   translated into a threshold of approximately 1200 ms. Most participants failing this criterion
606   had reaction times longer than 2.5 seconds, with some reaching 15 seconds. As a result,
607   these set of analyses included 274 participants, comprising 78% of the original dataset.
608
609   In our analyses, we first computed the optimal policy for the task, by using the SciPy
610   optimisation package, maximising reward with respect to stay durations. We defined a
611   reward function mirroring that used in the task, which was parameterised by a fixed total
612   experiment time of 6e5 ms, an inter-patch travel time of 4000 ms, the experimental rates of
613   return for each condition, and a fixed response latency of 650 ms across all patches (roughly
614   the median participant latency, which has no effect the optimal policy within reasonable
615   bounds, as opposed to the total reward). Optimisation used an initial policy estimate with
616   stay durations of 6 s, 5 s, 4.5 s and 3.5 s, and was robust to changes in this initialisation.
617
618   To examine the structure of foraging behaviour, we conducted Principal Component Analysis
619   (PCA) on stay durations and exit thresholds, where exit thresholds were the patch reward
620   rate at the time people switched patches. The first two principal components (PC1 and PC2)
621   were used in subsequent analyses. We decomposed PC1 into 1) baseline stay duration
622   offset, measuring how much longer a participant stayed compared to optimal durations. This
623   was calculated as the mean stay duration across all conditions; 2) condition-difference
624   scaling, measuring how much a participant exaggerated the differences between conditions.
625   This was calculated as the projection of mean-subtracted stay durations onto the normalised
626   optimal policy.
627
628   To assess task measure stability, we computed split-half reliability by comparing PCAs and
629   exit deviations between first and second halves of the experiment. Correlations between
630   halves were calculated using Pearson's r for PC scores and rank correlations for exit
631   deviations.
632
633   Finally, we investigated the relationships between foraging behaviour and age, AES, and
634   PHQ-9, while controlling for cognitive variables. We first residualised task exogenous
635   variables against age, before entering them into two separate linear regression models,

636   predicting PC1 and PC2. This allowed us to identify independent contributions of each
637   variable, while controlling for cognitive performance. Statistical significance was assessed at
638    $α$=0.05, with specific p-values reported for key comparisons. Effect sizes were reported as
639   Cohen's d for group comparisons and Pearson's r for correlations.
640

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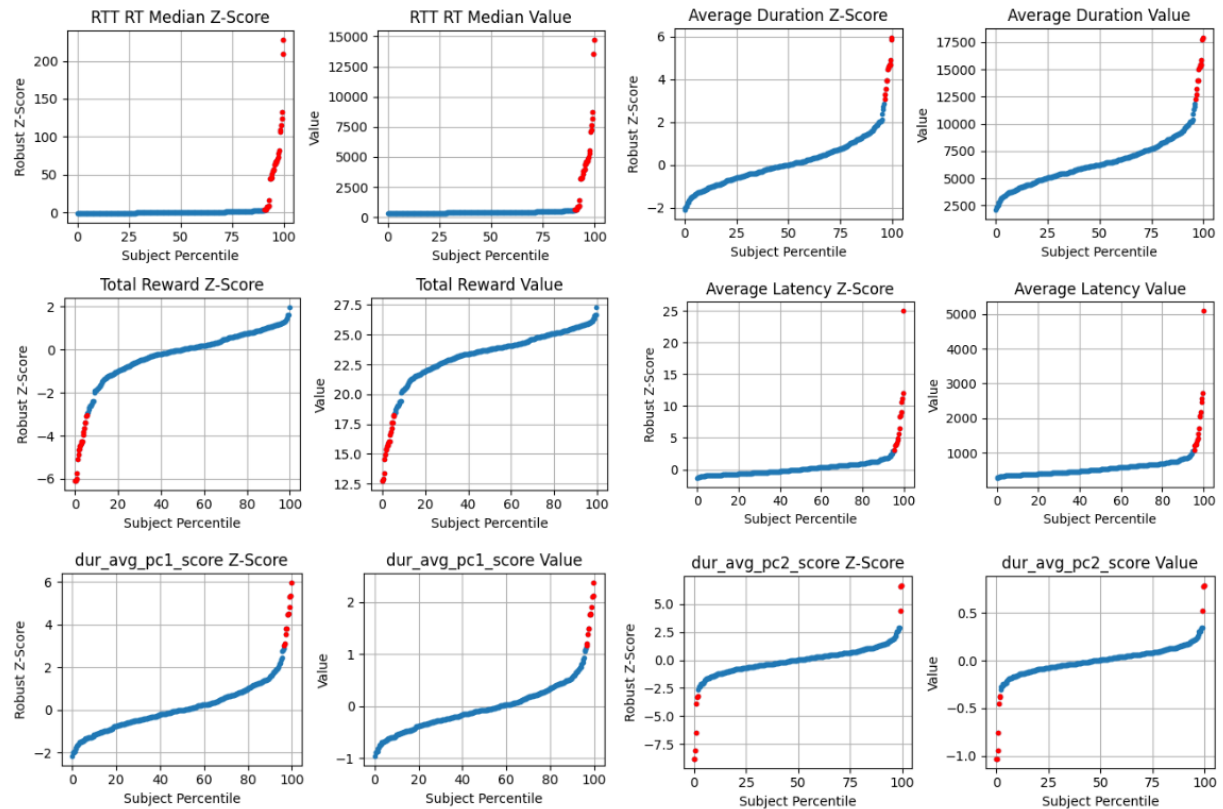851   https://doi.org/10.1016/j.biopsych.2024.01.022

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Supplementary Figures

Supplementary Figure 1: Participant reaction time, stay duration, latency, total reward, and Principal Component (PC) scores. Blue points are participants included in the analyses. Red points are outliers removed using a robust 3-SD cutoff for outlier detection.

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Quality Control Failures

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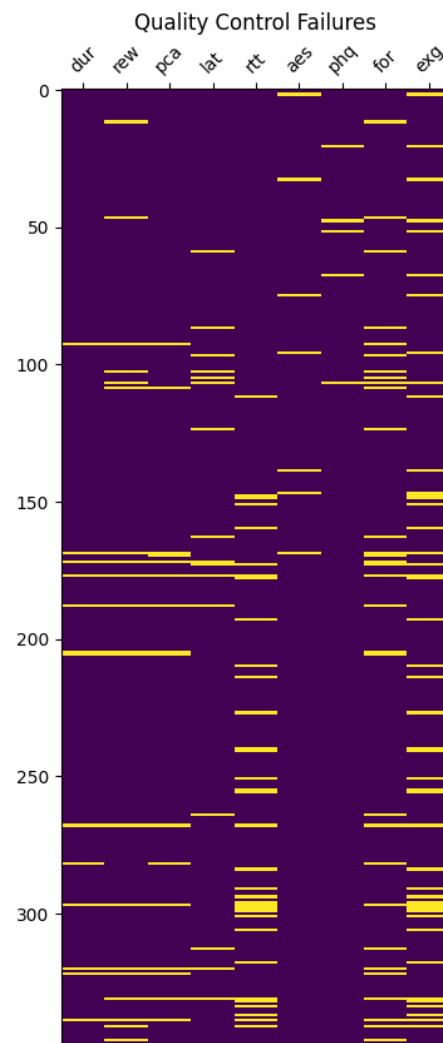
Supplementary Figure 2: Participant quality control failures. Y-axis denotes participant number, x-axis denotes quality control metric, and a yellow bar indicates failure in a quality control check. Duration, reward, Principal Component Analysis (PCA) scores, and latency (first 4 columns) were used to remove participants for the foraging task analyses (PCs were subsequently recomputed). The reaction time task (RTT), Apathy Evaluation Scale (AES), and Patient Health Questionnaire-9 (PHQ) columns show participants who failed our task exogenous quality control, with most exclusions taking place because of implausibly high average reaction times in the reaction time task. The columns "for" and "exg" are aggregated exclusions from the foraging and exogenous task analyses.