Cognitive, Affective, & Behavioral Neuroscience
https://doi.org/10.3758/s13415-025-01359-0

RESEARCH ARTICLE

Decision context and neurobehavioural disturbance in Huntington's disease

Lee-Anne Morris[1,2] · Kyla-Louise Horne[1,2] · Laura Paermentier[2] · Christina Buchanan[3,4] · Daniel Myall[2] · Sanjay Manohar[5,6] · Matthew Apps[7] · Richard Roxburgh[3,4] · Tim Anderson[1,2,8] · Masud Husain[5,6] · Campbell Le Heron[1,2,8]

Received: 5 June 2025 / Accepted: 1 October 2025

Abstract

Value-based decision-making provides a theoretical framework to investigate apathy and impulsivity—two notable disturbances in Huntington's disease (HD). Whilst existing work has examined decisions requiring comparison between two options, many everyday choices involve a different class of decision: whether to continue to pursue a current course of action or switch to an alternative. We investigated whether reward and cost sensitivity in a 'stay or leave' foraging task would be associated with HD apathy and/or impulsivity. People with HD ($n=37$) and controls ($n=40$) performed a foraging task where the costs of leaving were effort (low and high) and time (short and long). Apathy and impulsivity were measured using questionnaires, and their associations with patch-leaving times were examined using linear mixed models. People with HD and controls stayed longer as costs to leave increased, in line with theoretical predictions. There was also a significant positive association between individual sensitivity to effort and delay costs. Apathy in HD was not associated with altered effort or delay cost sensitivity. Impulsivity in HD was associated with increased sensitivity to delay—but not effort—costs. Sensitivity to changing effort and time costs in a foraging context differs as a function of apathy and impulsivity in HD. The effects of these costs on foraging decisions also differ from previous work assessing cost sensitivity in HD using binary choice tasks, underlying the importance of decision context in interpreting associations with clinical syndromes in a value-based decision-making framework.

Keywords Huntington's disease · Foraging · Decision context · Apathy · Impulsivity

✉ Lee-Anne Morris
leeanne.morris@nzbri.org

1 Department of Medicine, University of Otago, Christchurch, New Zealand

2 New Zealand Brain Research Institute, Christchurch, New Zealand

3 Department of Neurology, Auckland City Hospital, Te Whatu Ora Health New Zealand, Auckland, New Zealand

4 Centre for Brain Research Neurogenetics Research Clinic, University of Auckland, Auckland, New Zealand

5 Department of Experimental Psychology, University of Oxford, Oxford, UK

6 Nuffield Department of Clinical Neurosciences, University of Oxford, Oxford, UK

7 Centre for Human Brain Health, School of Psychology, University of Birmingham, Birmingham, UK

8 Department of Neurology, Christchurch Hospital, Te Whatu Ora Health New Zealand, Christchurch, New Zealand

Have you observed a zebra grazing in the wild? You may have noticed that partway through the current clump of grass, it wanders over to the next clump. An astute observer will note that lush, closely spaced clumps are nibbled at, whereas fewer sparser clumps are grazed down to stubble. The zebra is in fact following a fundamental behavioural principle—maximising overall gain whilst minimising time and effort costs, by adjusting feeding behaviour as a function of environmental richness. This principle is ubiquitous across species, with the *environmental context* in which reward-maximising decisions are made being paramount. Whether disruption to this core principle in the setting of brain disease underlies clinically apathetic and/or impulsive phenotypes is the subject of the present work.

Neurobehavioural disturbances such as apathy and impulsivity are common in Huntington's disease (HD), but their underlying cognitive signatures are not yet fully understood (Morris et al., 2022). Apathy is well documented

Published online: 18 November 2025

in Huntington's disease, present in up to 70% of people, and emerging both prior to and after motor disease onset (Craufurd et al., 2001; Martinez-Horta et al., 2016; Paulsen et al., 2001; Tabrizi et al., 2013). On a descriptive level, the relationship between apathy and Huntington's disease (HD) is closely intertwined, with apathy worsening in parallel to disease progression, underpinning its conceptualization as an intrinsic part of HD (Connors et al., 2023; Ruiz-Idiago et al., 2023; Thompson et al., 2012; van Duijn et al., 2014). Impulsivity too, although less well characterised, is evident in HD (Paulsen et al., 2001), with 45% of people scoring above clinical cut-offs for impulsivity (Johnson et al., 2017). Of note, impulsivity appears intrinsically linked to apathy, with their co-occurrence common across populations, including Huntington's disease (Morris et al., 2024c; Passamonti et al., 2018; Petitet et al., 2021; Sinha et al., 2013). Efficacious treatments for apathy and impulsivity are limited, in part due to poor understanding of the disrupted brain processes underlying them. Mechanistic work, which aims to understand neurobehavioural disturbances by teasing apart which cognitive processes are altered and which remain intact, is emerging. However, an understanding of the cognitive processes disrupted to give rise to apathy and/or impulsivity—in Huntington's disease and more broadly—is far from complete.

The neuroscience of value-based decision-making, which describes the interaction between rewards and costs of actions in motivating behaviour towards goals, has provided a framework within which to investigate the mechanisms underpinning behavioural disturbances such as apathy and impulsivity. Using experimental tasks derived from this framework, apathy, but not impulsivity, in HD is associated with increased sensitivity to both physical effort and time delay costs, in the setting of deciding between two options (Morris et al., 2024a).

Whilst studying situations where people decide between two options of varying reward and cost is an important method to probe goal-directed behaviour, many decisions in everyday life do not present as such binary 'a' versus 'b' style choices. Instead, they take the form of deciding whether and when to switch from a current activity to an alternate option. Such decisions may guide much of our day-to-day behaviour, such as whether to keep swimming in the sea for a little longer or to get out; whether to leave a restaurant after a meal or enjoy the company for a bit longer; or whether to stop reading an increasingly disappointing novel and try another. These types of decisions—often called foraging decisions after the behavioural ecology literature in which they have been described—require continuous integration and updating of reward and cost decision variables *over time* (Gabay & Apps, 2021; Gabay et al., 2024; Mobbs et al., 2018). Specifically, they depend on an accurate representation of the background reward rate in the environment—crudely, 'what else is out there', which can be compared with the current (foreground) reward associated with present behaviour. One crucial unanswered question is whether the hypersensitivity to effort and time costs evident in the behaviour of people with Huntington's apathy performing binary choice tasks would be evident in value-based decisions made in a foraging decision context.

Foraging theory provides an experimental framework to examine these sorts of decisions, where rewards and cost variables change over time (Hayden et al., 2011; Pearson et al., 2014; Stephens, 2008). It is closely related to the concept of opportunity cost—what (alternative) rewards are foregone by the current behavioural choice (Niv et al., 2007). The patch-leaving problem is a specific type of foraging situation that captures a crucial ecological decision that all animals must face and solve: Whether to maintain a current behaviour or switch to an alternative. Typically, the decision involves weighing whether to stay and exploit the current (foreground), but depleting, resource or leave, incurring costs of time and effort, to explore the background environment (Charnov, 1976; Constantino & Daw, 2015; Le Heron et al., 2020; Rutledge et al., 2009).

The marginal value theorem (MVT) provides the optimal general solution to this patch-leaving problem: Leave the current patch when the foreground reward rate equals the average background reward rate (Charnov, 1976). Thus, in theory a forager's actions could be determined simply by a comparison between their current instantaneous reward accrual and the background average reward rate available in their environment, which could be conceptualised as a 'threshold' for switching. Importantly for this framework, costs associated with leaving a patch (for example, physical effort to move between patches; travel time between patches), reduce the average background reward rate of the environment (Bernstein et al., 1991). Behaviourally therefore, as costs associated with patch-leaving increase, patch residency times should also increase as it takes longer for the foreground reward rate to drop to the background average. Manipulating patch-leaving costs and measuring the effect on patch-leaving times therefore provides an experimental approach to examine both how people estimate their background reward environment and their intrinsic sensitivity to changing costs and rewards. Despite its clear ecological importance, this experimental framework has not been widely applied to examine motivational disturbances.

Time is a variable of great interest in the field of impulsivity research, including the devaluing of reward by time delay, known as temporal discounting (Ainslie, 1975; Dalley & Ersche, 2019). When deciding between options, more impulsive people tend to select smaller, sooner-available rewards over larger rewards available after a time delay, showing increased sensitivity to the cost of time delay (Amlung et al., 2019; Moreira & Barbosa, 2019; Paasche et al., 2019). However, evidence for this effect in HD impulsivity is mixed (Doridam et al., 2014; McLauchlan et al., 2022; Morris et al., 2024a). Furthermore, decisions to select smaller-sooner rewards may actually be an optimal strategy if an individual is unable to accurately represent background reward information (for example, due to a neurological disorder such as HD). Thus, the observed phenomenon of temporal discounting, whilst potentially being explained by heightened sensitivity to time costs, can also be explained by degraded representation of, or difficult to estimate, background reward rate (Stephens & Anderson, 2001; Stevens & Stephens, 2010). Investigating impulsivity within a patch-leaving context allows dissociation of these two possibilities within the same experimental paradigm; however, this has not been examined previously either in HD or in other clinical populations.

In the present work, we investigated the mechanisms underlying neurobehavioural disturbances in Huntington's disease using a foraging patch-leaving framework. Specifically, in light of a cost-general hypersensitivity in HD apathy when deciding between two options (Morris et al., 2024a), we examined whether hypersensitivity to time and effort costs in apathy would also be evident in a different decision context—whether to stay in a rewarding location or move on. Concurrently we used patch-leaving behaviour to examine whether impulsivity in HD was associated with the time cost hypersensitivity or reduced ability to estimate the background reward rate. Participants with Huntington's disease ($n = 37$) and healthy controls ($n = 40$) performed a novel patch-leaving task where effort and time costs associated with patch leaving were manipulated.

We hypothesised that i) all participants would stay longer in patches as costs to leave increased, in line with the marginal value theorem predictions; ii) HD apathy would be associated with increased sensitivity to effort and delay costs associated with patch-leaving, leading to even longer patch residency times as these costs increased; iii) HD impulsivity would be associated with increased delay cost sensitivity, rather than reduced ability to compute the background reward rate; and iv) effort and delay cost sensitivity would be associated (people more sensitivity to effort costs would also be more sensitive to delay costs).

Methods

Ethics

The study was approved by the Health and Disability Ethics Committee of the New Zealand Ministry of Health (21/CEN/242), and the local ethics committee in Oxford, UK. Written consent was obtained from all subjects in accordance with the New Zealand National Ethical Standards and the Declaration of Helsinki.

Participants

People with confirmed expansion of the Huntington's gene were recruited as part of a wider Huntington's disease study, from three specialist Huntington's disease clinics (Auckland and Christchurch, New Zealand; Oxford, UK) between 2015–2017 (UK) and in 2022 (NZ). Exclusion criteria included inability to voluntarily squeeze a hand-held dynamometer, or inability to provide informed consent. Age and gender matched controls, with no significant history of neurological or psychiatric illnesses, were recruited via local databases. Participants performed a number of behavioural tasks, one of which is presented in this paper. Here, we report clinical, demographic, and behavioural data for the participants who performed a foraging task—called the Milk Collection Task (HD $n = 37$, controls $n = 40$; Fig. 1; Table 1). For comparison with binary choice effort and delay cost sensitivity, we used data from (Morris et al., 2024a) for this subset of HD participants. Power analysis details are shown in Supplementary Box 1.

Disease, cognitive and questionnaire measures

Apathy was assessed using the Apathy Evaluation Scale self-report version (AES; Clarke et al., 2007; Marin et al., 1991). Additionally, the Short Problem Behaviours Assessment (sPBA) apathy subscale and the Lille Apathy Rating Scale (LARS) were administered in New Zealand and Oxford, respectively (Callaghan et al., 2015; Sockeel et al., 2006). People were classified as apathetic if their self-reported AES score was ≥ 37, the clinician-rated sPBA score was ≥ 2, or the LARS was ≥ -21, indicating at least mild-moderate apathy, in line with previous work (Le Heron et al., 2018a; Martinez-Horta et al., 2016; Santangelo et al., 2014). Motor disease severity was assessed using the Unified Huntington's Disease Rating Scale Total Motor Score (UHDRS-TMS; Huntington Study Group, 1996). Cognition was screened using the Montreal Cognitive Assessment in New Zealand, and the Addenbrooke's Cognitive Examination–Revised (ACE-R) in Oxford (Hsieh et al., 2013; Nasreddine et al., 2005). To enable comparison across sites, cognition scores were z-scored using previously published normative data for each tool (Cheung et al., 2015; Kourtesis et al., 2020). Depressive symptoms were assessed using the Beck Depression Inventory II (BDI-II), and its Dysphoria subscale (Beck et al., 1996; Kirsch-Darrow et al., 2011). Impulsivity was assessed using the UPPS-P Impulsive Behaviour Scale (Whiteside et al., 2005). Impulsivity scores were available for a subset of HD participants only (HD $n = 26$). Demographic and clinical data were analysed in R (R Core Team,

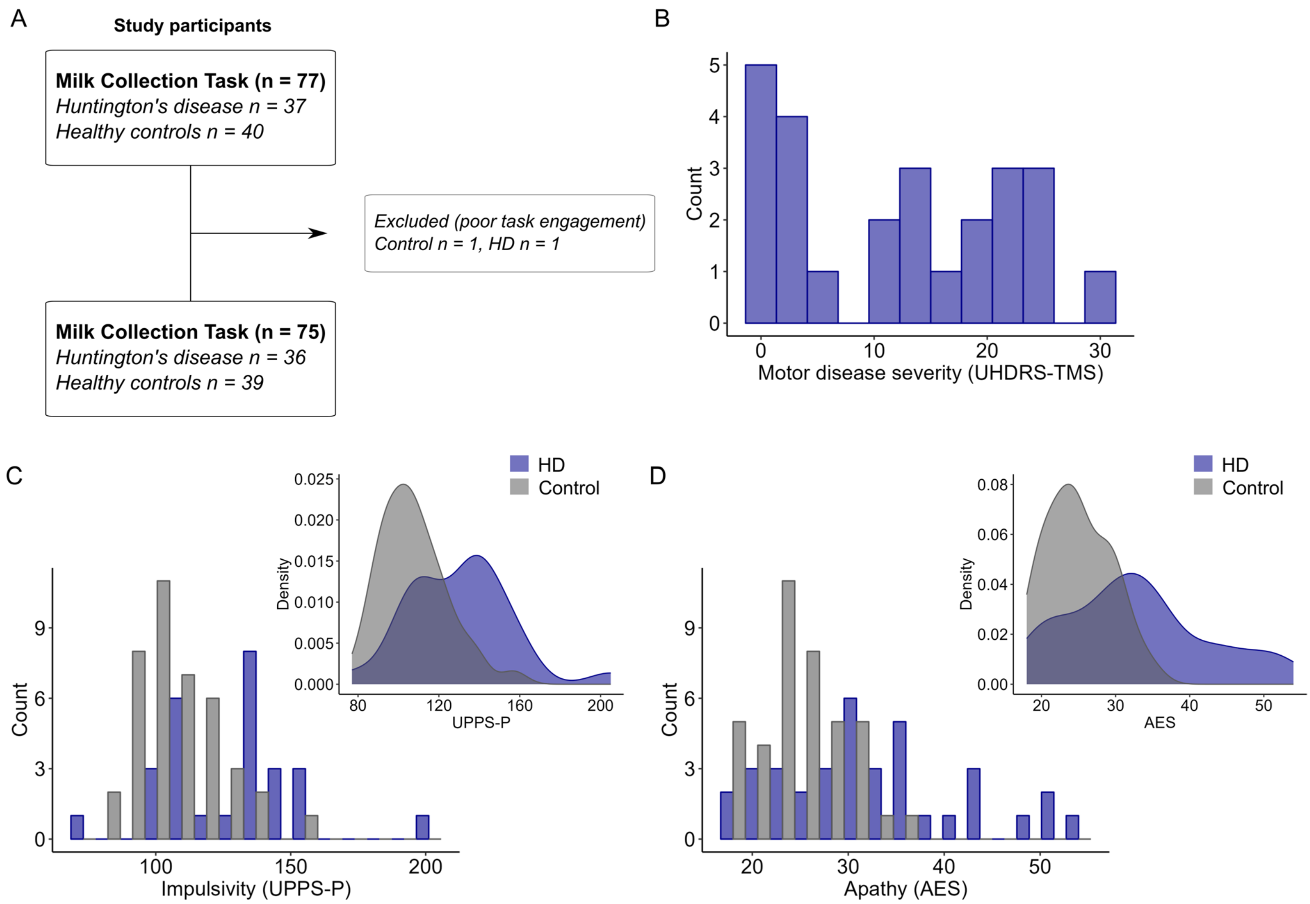

Fig. 1 Study participants. **A** Flowchart of study participants who performed the Milk Collection Task. HD participants were part of a larger behavioural study, reported elsewhere (Morris et al., 2024a). **B** Motor disease severity (UHDRS-TMS) of participants with Huntington's disease. **C** UPPS-P Impulsivity scores, with inset showing density distribution. **D** Apathy evaluation scale scores, with inset depicting density distribution. To note, in this study participants with HD were classified as either apathetic or not based on clinical cut-offs on the AES (≥37), sPBA apathy (≥2) or LARS (≥−21), depending on which scale had been used. AES = Apathy Evaluation Scale; LARS = Lille Apathy Rating Scale; sPBA = Short Problem Behavioural Assessment; UHDRS-TMS = Unified Huntington's Disease Rating Scale Total Motor Score; UPPS-P = UPPS-P Impulsive Behaviour Scale. (Colour figure online)

2024) using Welch's *t* tests or chi-squared tests, depending on the variables (Table 1).

Foraging decisions: The milk collection task

This patch-leaving task was developed to investigate the effects of manipulating *costs associated with patch-leaving* on human patch-leaving behaviour (Le Heron et al., 2020). The task was framed as a dairy farming task. The aim was to collect as much milk as possible in an allocated time period (21 min), from an unlimited number of fields ('patches'). Within a field, milk was accrued by depressing the spacebar, and displayed on-screen as a bucket filling. The foreground reward rate (i.e. the rate of milk accrual), exponentially decayed with increased patch residency time, with decay rate kept constant across the task. The key experimental manipulations were the time and effort costs associated with leaving each field. Time costs involved a waiting period, described to participants as travel time to the next field, of either 6 s (short delay), or 12 s (long delay). Physical effort costs, described as climbing fences between fields, involved squeezing a handheld dynamometer to 30% (low effort) or 60% (high effort) of each participant's maximal voluntary contraction. Low and high effort and delay costs were varied by block, such that there were three combinations: low effort and short delay (Block 1), low effort and long delay (Block 2) and high effort and short delay (Block 3). The task thus comprised three blocks of 7 min each. Cost information was displayed continuously on-screen alongside milk accrual, with effort indicated by red colouring on a rectangular bar, and time delay indicated by red colouring on a clock. During transit time, a displayed clock ticked down the seconds to the next field whilst participants were prompted to squeeze the dynamometer with real-time feedback of performance (a

Table 1 Clinical and demographic characteristics of participants, showing mean (*sd*)

	Controls	HD	Statistic
Participants	40	37	
Age	61.2 (14.5)	50.6 (12.6)	$t(74.67) = 3.41, p = .001$
Male:Female (% Male)	16:24 (40%)	22:15 (60%)	$\chi^2(1, n = 77) = 2.19, p = .139$
Education (years)	16 (4)	15 (3)	$t(70.63) = 1.30, p = .199$
UHDRS total motor Score /124	*NA*	12 (10)	
Medication			
Antidepressant Use	6 (15%)	15 (41%)	$\chi^2(2, n = 77) = 8.17, p = .017$
Antipsychotic Use	0	6 (16%)	$\chi^2(2, n = 77) = 6.87, p = .032$
Behaviour & mood			
Apathy Evaluation Scale /72	25.0 (4.34)	32.9 (9.65)	$t(47.52) = -4.54, p < .0001$
Impulsivity [1]UPPS-P /236	108.0 (16.5)	130.0 (25.5)	$t(40.56) = -4.07, p < .001$
Beck Depression Inventory II /63	5.5 (4.98)	10.3 (9.28)	$t(52.36) = -2.75, p = .008$
BDI dysphoria Subscale /33	2.6 (2.73)	4.65 (5.04)	$t(29.59) = -1.81, p = .081$
Cognition			
MoCA /30	27.5 (2.32)	26.6 (2.90)	$t(38.22) = 1.26, p = .216$
ACE-R /100	*NA*	88 (10)	

ACE-R = Addenbrooke's Cognitive Examination–Revised; BDI-II = Beck Depression Inventory II; MoCA = Montreal Cognitive Assessment; UHDRS = Unified Huntington's Disease Rating Scale; UPPS-P = UPPS-P Impulsiveness Scale

[1] UPPS-P scores were available for 26 HD participants only

green rectangular bar indicating actual effort exerted superimposed on the target effort level; Fig. 2).

Task implementation

Participants performed the task in a quiet research office, with a trained researcher. After standardised task explanation, participants completed a practice task of ~ 12 min, followed by the task itself. Each task block (7 min) was followed by a rest period, to minimize possible fatigue effects. The task was run using Pyschtoolbox (http://psychtoolbox.org), implemented within MATLAB (The MathWorks). Trials with leaving times 3 standard deviations or more from individual mean leaving times per block were regarded as outliers and removed; this equated to < 1% of trials overall.

Statistical analysis

We used linear mixed effects models (*lmer* in R) to investigate predictors of patch-leaving time. Predictors were *z*-scored. We first fitted a model including all subjects, with a grouping variable (*HD/control*), to determine whether there were any fundamental disease-related differences in task performance. Fixed effects were delay, group, and their interaction, and effort, group and their interaction, with subject as a random effect to account for repeated trials per subject:

$$\textit{patch leaving time} \sim \textit{effort} * \textit{group} + \textit{delay} * \textit{group} + (1|\textit{subject})$$

Our primary model of interest was a model fitted to only HD participants' data, with apathy status (*apathetic/not apathetic*):

$$\textit{patch leaving time} \sim \textit{effort} * \textit{apathy} + \textit{delay} * \textit{apathy} + (1|\textit{subject})$$

Modelling random slopes for effort and delay did not significantly change the results and are shown in Supplementary Box 2.

Separate to linear mixed models, individual 'sensitivities' to costs were calculated by subtracting individual mean leaving times from high-effort and low-effort conditions (Block 3 – Block 1) and long delay and short delay conditions (Block 2 – Block 1), in line with previous work (Bustamante et al., 2023). The influence of other factors on individual effort and delay sensitivity was examined

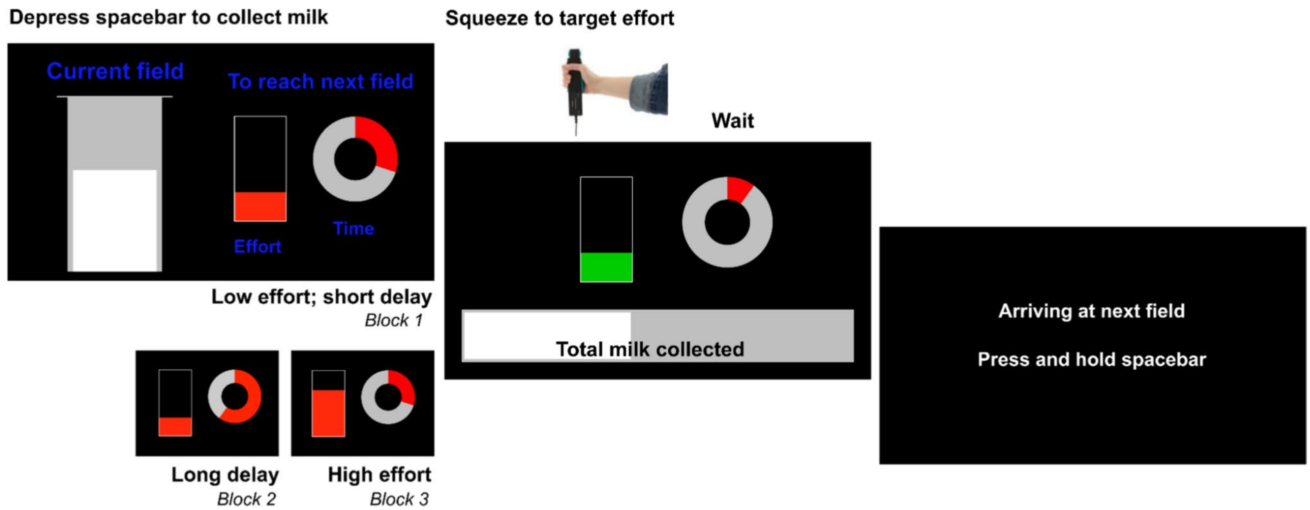

Fig. 2 The Milk Collection Task. A novel patch-leaving task. Framed as a farming game, participants needed to collect as much milk as possible from unlimited fields (patches), within a set time. Milk collection rate diminished with increased time spent in a field. Leaving each field had low or high time and effort costs associated, which, according to predictions made by the marginal value theorem, devalue the background reward rate to different extents. Within foraging theory, patch-leaving time is the point at which foreground reward rate drops to an individual's estimate of the background average reward rate. Thus, the paradigm allows inference of background reward rate representation and individual effort and delay cost sensitivity. (Colour figure online)

using multiple regression models, with covariates apathy, dysphoria, motor disease severity, cognition, medication usage, age and sex.

Variability in patch-leaving times was measured as the standard deviation of leaving times per individual per task block. To determine whether variability was increased as a function of apathy and/or impulsivity, an indirect metric of reduced ability to compute the background reward rate, a linear mixed model was fitted to scaled individual variability in leaving times per block, with apathy (*yes/no*), block, and their interaction as fixed effects, accounting for three repeated measures within subject by including random effect of subject.

Lastly, as an exploratory analysis, for the subset of HD participants with impulsivity scores ($n = 26$), we fitted a model similar to the HD apathy model above, but with continuous impulsivity scores:

$$\textit{patch leaving time} \sim \textit{effort} * \textit{impulsivity} + \textit{delay} * \textit{impulsivity} + (1|\textit{subject})$$

We also examined variability in patch-leaving behaviour as a function of impulsivity in HD.

Data availability

Anonymized data are available upon reasonable request.

Results

At group level, people with HD were significantly more apathetic and impulsive than healthy controls (AES apathy: mean difference = 8, $t(47.5) = -4.5$, $p < .0001$, 95% CI [$-11.5, -4.4$]; impulsivity: mean difference = 23, $t(40.6) = -4.1$, $p = .0002$, 95% CI [$-33.9, -11.4$]). Of note, mean education level, MoCA scores and dysphoric mood did not significantly differ between controls and people with HD. A greater number of people with HD were taking antidepressant and antipsychotic medications compared to controls. The control group was on average older than the HD group (Table 1).

Foraging decision-making: Milk Collection Task

Costs lengthened patch residency times

In this task, participants decided when to switch between fields to maximise overall milk gain, taking into account the changing effort and delay costs associated with leaving. For both HD and controls, increased effort and delay costs were associated with significantly longer patch residency times (effort: $\beta = 0.88$, $t = 7.5$, $p < .001$; delay: $\beta = 2.2$,

$t = 17.0$, $p < .001$), in accordance with marginal value theorem predictions. However, there were significant interactions between group and effort costs, and group and delay costs (Effort × Group: $\beta = -0.41$, $t = -2.5$, $p = .01$; Delay × Group: $\beta = -0.41$, $t = -2.4$, $p = .02$). Increased effort and delay costs had a greater effect on patch residency times in people with HD than controls. There was no significant main effect of group on task performance (group: $\beta = -1.5$, $t = -0.9$, $p = .37$; Fig. 3A–B).

Cost sensitivity not different in HD apathy

In people with HD (no controls), there was no significant main effect of apathy on patch residency time (apathy: $\beta = 0.1$, $t = 0.1$, $p = .95$). Effort and delay cost interactions with apathy were also not significant (Apathy × Effort: $\beta = -0.01$, $t = -0.12$, $p = .91$; Apathy × Delay: $\beta = -0.12$, $t = -0.87$, $p = .39$) Thus, there was no evidence for differences in sensitivity to changing costs as a function of being apathetic or not (Fig. 3C). To determine whether these were, indeed, null effects, equivalence testing was performed. This showed evidence for equivalence for both interactions (Apathy × Effort: 95% CI [−0.22, 0.19], second-generation p value > .999, equivalence accepted, $p < .001$; Apathy × Delay: 95% CI [−0.35, 0.11], second-generation p value > .999, equivalence accepted, $p < .001$).

These null apathy results were further corroborated by separate analyses. Linear regression models fitted to

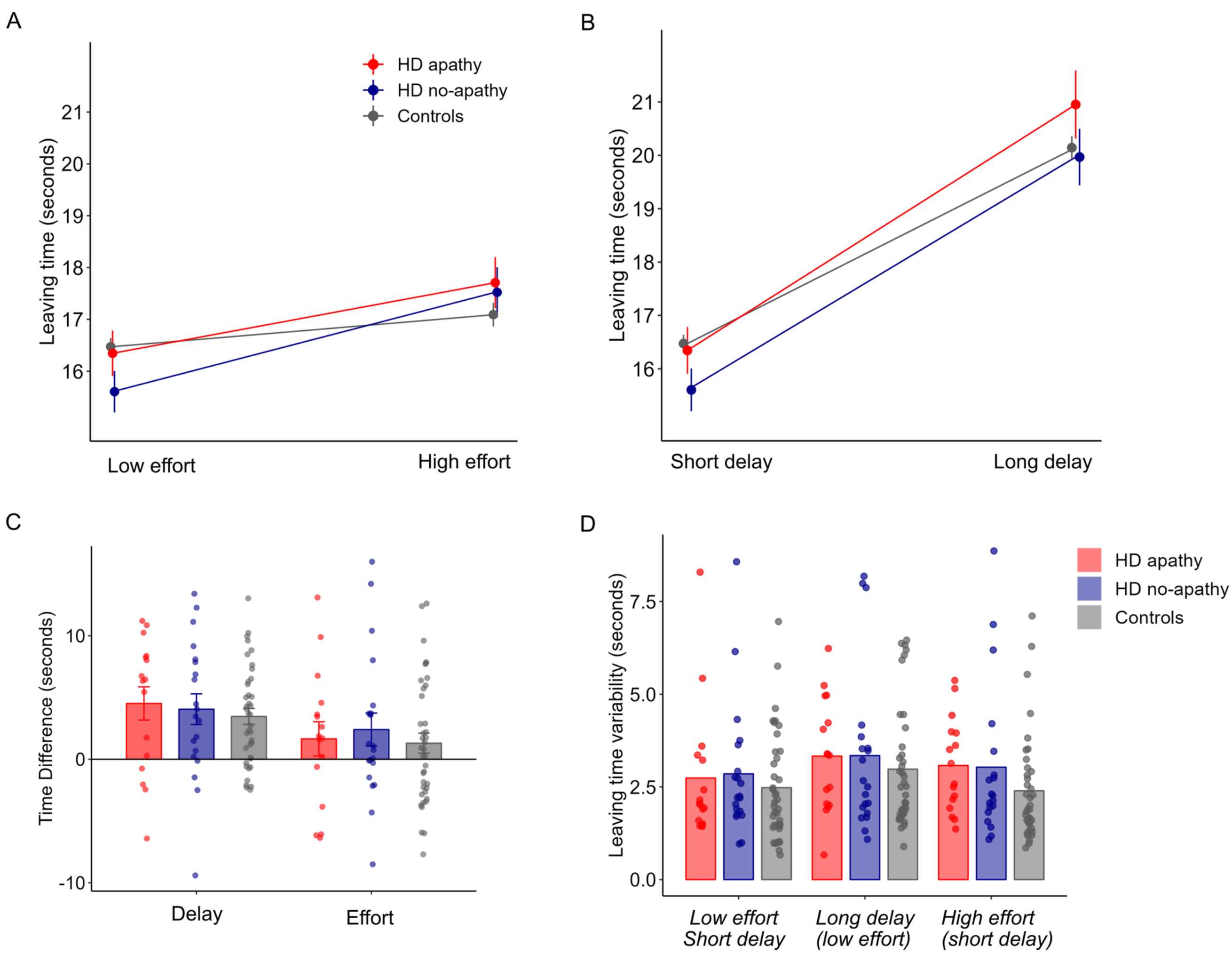

Fig. 3 Patch-leaving behaviour and Huntington's disease apathy. **A** HD and control participants stayed longer in patches as effort, and **B** delay costs associated with patch leaving increased, in line with theoretical predictions that increasing costs lowers the average background reward rate, leading to longer patch residency times. The effect of increasing effort and delay on patch-leaving times was greater in people with HD than controls ($p < .05$), but not significantly different between apathetic and nonapathetic people with HD. **C** Cost sensitivity, calculated as the individual mean difference in leaving times between low and high costs. There were no significant differences in cost sensitivity as a function of apathy in HD. **D** Variability in patch-leaving times did not differ significantly between blocks, groups, or as a function of apathy in Huntington's disease. Error bars show standard error of the mean. (Colour figure online)

individual effort and delay cost sensitivity, respectively, showed no significant associations with apathy, or other clinical variables.

There were no significant differences in variability of patch-leaving times across the task blocks, between groups (controls, HD no-apathy, HD apathy), or their interaction (all p values > .05). Thus, there was no evidence to suggest that ability to estimate the background reward rates differed as a function of apathy in HD, or between HD and controls. Although an indirect marker of ability to estimate background reward rates, decisions would appear more variable ('noisy') should this ability be reduced (Fig. 3D).

HD impulsivity associated with increased delay sensitivity

For the exploratory analysis pertaining to the subset of people with HD with impulsivity scores ($n = 26$), there was no significant main effect of impulsivity on patch-leaving times (impulsivity: $\beta = -1.7$, $t = -1.1$, $p = .3$). The interaction between impulsivity and delay was significant (Impulsivity × Delay: $\beta = 0.39$, $t = 2.2$, $p = .03$). More impulsive people adjusted their patch-leaving times significantly more as delay increased, suggesting that impulsive people found the increase in delay *more costly*. The interaction between impulsivity and effort was not significant (Impulsivity × Effort: $\beta = 0.2$, $t = 1.4$, $p = .16$). Variability in leaving times was not significantly different as a function of impulsivity (impulsivity: $\beta = -044$, $t = -1.48$, $p = .14$; Impulsivity × Block: $\beta = 0.08$, $t = 0.68$, $p = .5$). People with higher impulsivity scores showed a nonsignificant trend towards less variability in leaving times, not more variability (Fig. 4).

Cost sensitivities associated within but not across decision contexts

Sensitivity to changing effort and delay costs was significantly correlated in participants with HD on the patch-leaving task ($r = .55$, $p = .0005$). That is, people who stayed longer in a patch when effort was high, also stayed longer when the patch-leaving delay was long. In these same HD participants, we have previously shown that binary choice effort and delay sensitivity were significantly associated ($r = .36$, $p = .036$; Morris

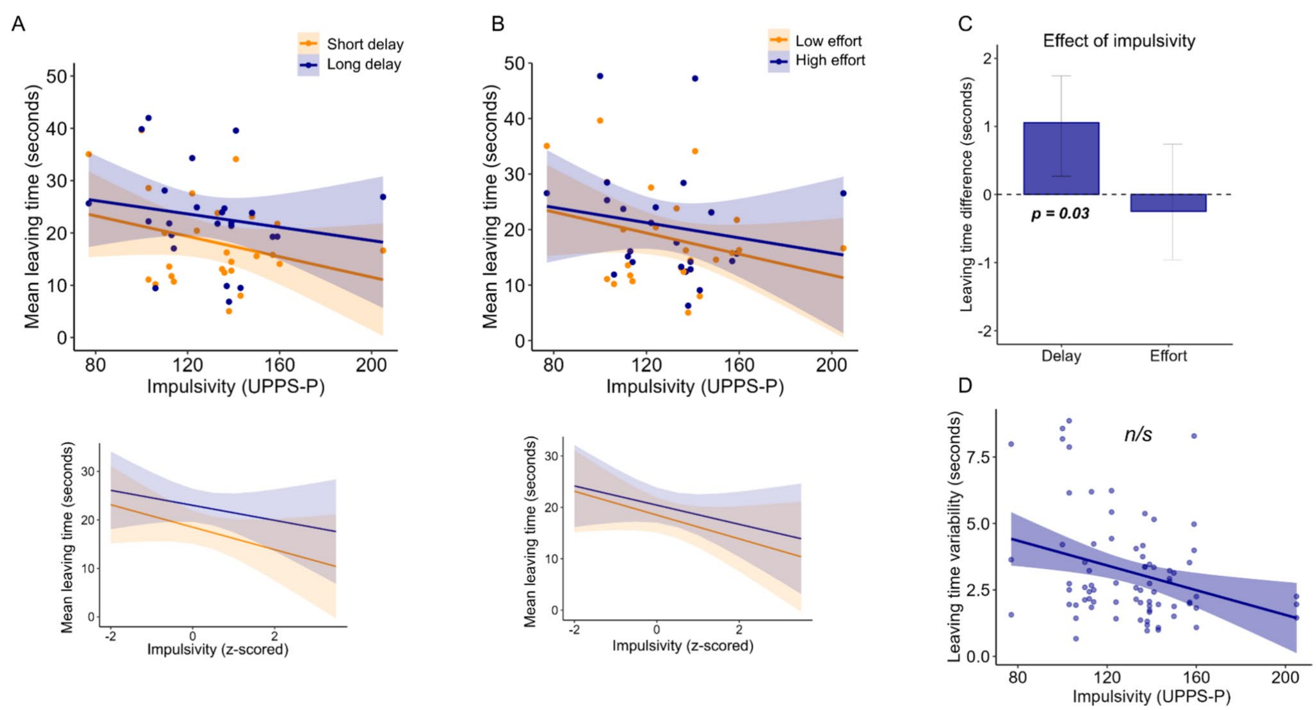

Fig. 4 Patch-leaving behaviour and Huntington's disease impulsivity. **A** Mean patch-leaving times for short and long patch-leaving delay costs, plotted over impulsivity scores. Higher impulsivity was significantly associated with a greater adjustment of patch-leaving times as delays increased (model inset depicted below). **B** Mean patch-leaving times for low and high patch-leaving effort costs, plotted over impulsivity scores. Impulsivity did not have a significant effect on patch-leaving times as effort costs to leave increased (model inset depicted below). **C** The effect of impulsivity on patch-leaving times as a function of changing delay and effort costs. Higher impulsivity was associated with longer patch residency times as delay costs to leave patches increased, relative to short delay patch-leaving times, with no significant effect of impulsivity on effort sensitivity (high − low impulsivity scores, based on mean split, for graphical display purposes). **D** Variability in leaving time did not significantly differ as a function of impulsivity in HD. People with higher impulsivity scores showed a nonsignificant trend towards less variability in leaving times. n/s = not reaching statistical significance of $p < .05$. (Colour figure online)

et al., 2024a). Thus, within each decision context, effort and delay cost sensitivities were associated (Fig. 5 A–B).

An examination of the same costs, but across different *decision contexts* revealed that patch-leaving effort sensitivity and binary choice effort sensitivity were not significantly correlated in people with HD ($r = -.09$, $p = .61$). Similarly, patch-leaving and binary choice delay sensitivity were also not significantly correlated ($r = -.03$, $p = .87$).

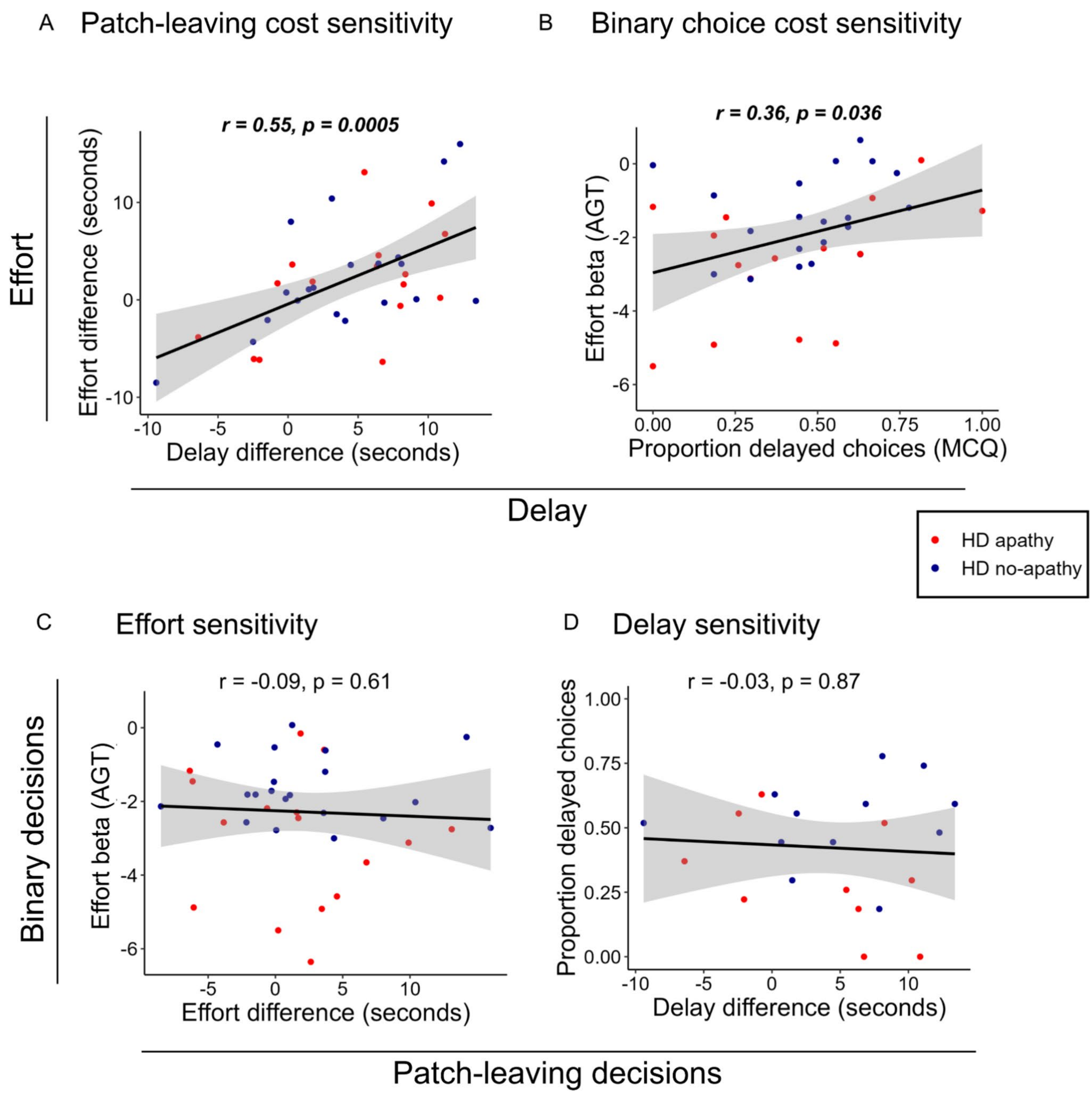

Fig. 5 Cost sensitivities within and across decision types. **A** Effort and delay sensitivities (difference in patch-leaving times as a function of changing effort and time costs) from a patch-leaving task (Milk Collection Task) were significantly correlated in HD. **B** Individual effort sensitivity parameter estimates from an effort-based decision-making task (Apple Gathering Task: more negative = higher sensitivity to effort) and proportion delayed choices from a delay discounting task (Money Choice Questionnaire) were significantly correlated. That is, people more averse to effort also selected fewer delayed options, indicating aversion to time delay as well. **C** Effort sensitivities across binary and patch-leaving decision contexts were not significantly associated, and neither were delay sensitivities (**D**). Overall, cost computations were associated within but not across decision-making contexts in HD. AGT = Apple Gathering Task; MCQ = Money Choice Questionnaire. Data from binary choice tasks shown in panels B–D are from (Morris et al., 2024a), reused with permission. (Colour figure online)

Thus, there was no evidence of a significant association between either effort sensitivity or delay sensitivity metrics in HD across task paradigms that probed these variables in different decision contexts (Fig. 5 C–D).

Discussion

Emerging work suggests that disruptions of value-based decision-making processes may underlie common neurobehavioural disturbances such as apathy and impulsivity in Huntington's disease. However, studies to date have mainly focussed on one particular class of value-based decisions, where two or more options must be weighed against each other. In day-to-day life however, it is often important to decide whether to persist with a current behaviour or switch to another potentially more rewarding one. These types of decisions are well described within the behavioural ecology foraging literature and rely on comparisons between foreground (what you are currently doing) and background (environmental richness—what else you could be doing) reward rates. Here we used a foraging patch-leaving task to determine whether the changes in decision-making associated with neurobehavioural disturbances in Huntington's disease extended to alternative decision contexts—contexts that may be particularly relevant for the everyday behaviours that are often disrupted in HD. Specifically, we examined whether sensitivity to effort and time costs associated with foreground/background decisions would be increased as a function of apathy in Huntington's disease. We also examined whether sensitivity to time delay would be increased in HD in more impulsive people. People with HD performed a patch-leaving task in line with theoretical predictions, broadly showing increased patch-residency times as costs associated with patch-leaving increased. Effort and delay sensitivity were also correlated within people with HD. Contrary to our hypothesis, and in contrast to results seen in binary choice tasks, apathy in HD was not significantly associated with either effort or delay cost hypersensitivity on this task. Impulsivity, however, was associated with longer patch residency times as delay costs to leave patches increased, but not increased variability of decisions, suggesting more impulsive people with HD do experience waiting as more costly. Overall, this study provides evidence that *decision context* plays a key role in sensitivity to cost and reward variables in value-based decision-making, and the relationship of these changes to common behavioural disturbances that arise with brain pathology.

Studies of value-based decision-making in patient populations have led to important advancements in understanding of the mechanisms underlying common neurobehavioural disruptions such as apathy and impulsivity (Blouzard et al., 2023; Dalley & Ersche, 2019; Le Heron et al., 2025). However, the context in which a decision is being made—and specifically the influence of background environmental richness—is an important factor for many day-to-day decisions that is often not incorporated into value-based decision-making paradigms (Hayden, 2018; Mobbs et al., 2018). Previous work in HD has shown apathy is associated with increased sensitivity to both effort and time delay costs, when deciding between two options, although not across all studies (McLauchlan et al., 2019; Morris et al., 2024a), whilst HD more generally has also been associated with increased sensitivity to cognitive effort for these types of decisions (Atkins et al., 2020, 2024). However, despite these findings, in this study we found no evidence for an association between apathy and cost sensitivity in a foreground/background decision-making paradigm, where participants had to decide whether to stay or leave a patch with diminishing rewards. Within a foraging context, costs to 'move on' influence the background environmental reward rate and thus, more broadly, we did not find evidence for altered computation of foreground or background reward rate computations in HD apathy. Interestingly, a previous study examining apathy mechanisms in the context of traumatic brain injury did find a significant association between apathy and altered background reward rate computation, using a similar though not identical foraging paradigm (Quang et al., 2023). Additionally, reduced (rather than increased) sensitivity to costs was associated with apathy in a large online sample, whereby people chose to continue search behaviour for longer than optimal, despite incurring search costs (Scholl et al., 2022). Taken together, and acknowledging the small number of studies examining this question to date, no clear foraging signature for apathy has yet emerged, despite relatively convergent associations between apathy and reward and cost processing in other types of decision contexts (Attaallah et al., 2024; Lafond-Brina et al., 2023; Le Bouc et al., 2022; Le Heron, Plant, et al., 2018a, 2018b). There is a clear need for further studies, across different populations, to further explore this question, particularly because of the importance of this class of decision-making for many of the daily activities that are disrupted by apathy in HD and other brain disorders.

The lack of association between cost sensitivity and apathy in a foreground/background decision-making context—as distinct from a binary choice context—requires explanation. It is possible that binary and patch-leaving decisions fundamentally differ, with different underlying cognitive mechanisms, despite both requiring cost–reward integration (Carter et al., 2015). Thus, in HD, apathy may be driven by changes in one—but not another—type of decision-making. Whilst relatively little to no work in humans has examined cost sensitivity across decision contexts, in the present study effort and delay cost sensitivities were not significantly correlated across decision contexts in HD. In line with this, dissociable sensitivity to physical effort costs across different decision contexts has been previously demonstrated in rodents (Holec et al., 2014; Schweimer & Hauber, 2005). In particular, amygdala and basolateral amygdala lesions (and inactivations) in monkeys and rats are associated with increased effort sensitivity on choice tasks between options (Floresco & Ghods-Sharifi, 2007; Ostrander et al., 2011) but not on progressive ratio tasks (choice to stay on task, or leave; Baxter et al., 2000; McGregor & Roberts, 1993). Whilst not specific to costs, binary choice and patch-leaving behaviour has also been dissociated in humans, dependent upon the glutamate-GABA (excitatory-inhibitory) balance in the ventromedial prefrontal cortex for binary decisions, and in the anterior cingulate cortex for patch-leaving decisions (Kaiser et al., 2021). Taken together, this points to the likelihood that binary and patch-leaving decisions may not utilise the same cognitive processes, but rather that computing of cost information for each decision *context* may be distinct. However, *within* decision contexts, cost sensitivities are significantly associated (Bustamante et al., 2023; Morris et al., 2024a). Speculatively, then, apathy in HD may arise from disruption to processes associated with cost computation in binary, but not patch-leaving contexts. It is also possible that binary choice and patch-leaving cost sensitivities may in fact be associated, but our particular study population did not show evidence for this, or that cost sensitivities may be associated across decision contexts but our novel foraging task failed to capture this effect.

In the exploratory analysis, more impulsive people with HD showed increased sensitivity to time delay costs in the patch-leaving task. Specifically, impulsivity was associated with a greater adjustment in patch-leaving times as delay varied, relative to less impulsive people. Previous attempts to understand impulsive behaviours have focussed on the concept of delay discounting within binary choice tasks. However, this has been criticised as theoretically increases in delay discounting associated with impulsivity could be explained either by increased delay sensitivity OR altered computation of background environmental reward rates. In this study, we were able to assess both these factors, clearly showing that impulsivity in people with HD was associated with increased sensitivity to time costs, but not changes in perception of background reward rate (indexed by the variability of their decisions). This could be explained by a direct effect of HD pathology on cost processing. Another possibility is that the effect is mediated by changes in time perception in HD. Recent work has shown that higher impulsivity in HD is associated with altered perception of time—specifically, thinking that more time has passed than really has (Morris et al., 2024b). In theory, if time is perceived as passing more slowly, waiting may feel longer, leading to an overestimation of time as a cost when integrated with reward decision variables. This hypothesis is consistent with the results seen in the patch-leaving task. One strength of using a patch-leaving paradigm in this context is that time costs are experienced (actual waiting whilst 'traveling' between patches) whereas in binary choice tasks, time delays are generally hypothetical.

It is important to consider limitations in interpreting the results of this study. The sample size in this work, whilst in line with other work in the field, was still relatively small, and it will be important to demonstrate these findings can be replicated in a different sample. However, our null apathy results were strengthened by including two separate analyses, both of which showed no evidence for increased effort or delay cost sensitivity in apathetic people with HD.

In addition, because we only had impulsivity scores for a subset of participants, it was difficult to directly compare apathy and impulsivity results. The impulsivity finding, considered exploratory, should be interpreted with caution due to the small sample size and requires replication in a larger cohort. To minimize possible fatigue effects, rest breaks were provided between task blocks, and the maximal effort required on a trial was capped at 60% of an individual's maximal voluntary contraction. A proxy for fatigue—variability in leaving times—was not significantly different between blocks, suggesting fatigue was not an issue. Nonetheless it is important to consider the potential effects of cognitive and motor fatigue on task performance. Future work would also benefit from neurophysiological markers of reward and cost processing to accompany the behavioural results, in order to probe the neural underpinnings of behavioural changes seen in HD. A strength of this study is the application of a strong theoretical framework, developed and validated across multiple species, to understand neurobehavioural disturbances in Huntington's disease—that of animal foraging theory.

In conclusion, we show that whilst people with Huntington's disease performed a patch-leaving task in line with normative predictions, performance did not differ as a function of apathy. Specifically, and in contrast to previous work examining different types of decisions, people with apathy did not show heightened sensitivity to effort or time costs associated with patch-leaving. In contrast, impulsivity in HD was significantly associated with increased sensitivity to delay—but not effort—costs, providing evidence for differing decision variables being affected by these behavioural phenotypes, in a context where foreground and background reward rates must be compared to drive optimal behaviour.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.3758/s13415-025-01359-0.

Acknowledgements The authors would like to thank all study participants.

Authors contributions **L.-A.M.**: conceptualization, formal analysis, writing–original draft.

K.-L.H.: project administration, resources.

L.P.: project administration, resources.

C.M.B.: project administration, resources.

D.M.: resources, software, writing–reviewing and editing.

S.M.: supervision, writing–reviewing and editing.

M.A.: supervision, conceptualization, writing–reviewing and editing.

R.R.: project administration, resources.

T.A.: project administration, resources.

M.H.: supervision, writing–reviewing and editing.

C.LH.: conceptualization, formal analysis, writing–review and editing, supervision.

Funding This work was funded by a University of Otago doctoral scholarship (L.M.).

Data availability De-identified data is available from the corresponding author upon reasonable request. None of the experiments were preregistered.

Code availability Code is available from the corresponding author upon reasonable request.

Declarations

Conflicts of interest The authors declare no conflicts of interest.

Ethics approval This study was approved by the Health and Disability Ethics Committee of the New Zealand Ministry of Health (21/CEN/242) and the local ethics committee in Oxford, UK.

Consent to participants Written consent was obtained from all participants, and research was conducted in accordance with the Declaration of Helsinki and the New Zealand national ethical standards.

Consent for publication The manuscript does not contain identifying information.

References

Ainslie, G. (1975). Specious reward: A behavioral theory of impulsiveness and impulse control. *Psychological Bulletin, 82*(4), 463–496.

Amlung, M., Marsden, E., Holshausen, K., Morris, V., Patel, H., Vedelago, L., Naish, K. R., Reed, D. D., & McCabe, R. E. (2019). Delay discounting as a transdiagnostic process in psychiatric disorders: A meta-analysis. *JAMA Psychiatry, 76*(11), 1176–1186. https://doi.org/10.1001/jamapsychiatry.2019.2102

Atkins, K. J., Andrews, S. C., Stout, J. C., & Chong, T.T.-J. (2020). Dissociable motivational deficits in pre-manifest Huntington's disease. *Cell Reports Medicine, 1*(9), Article 100152. https://doi.org/10.1016/j.xcrm.2020.100152

Atkins, K. J., Andrews, S. C., Stout, J. C., & Chong, T.T.-J. (2024). The effect of Huntington's disease on cognitive and physical motivation. *Brain,* , Article awae023. https://doi.org/10.1093/brain/awae023

Attaallah, B., Toniolo, S., Maio, M. R., & Husain, M. (2024). Apathy and effort-based decision-making in Alzheimer's disease and subjective cognitive impairment. *Alzheimer's & Dementia: Diagnosis, Assess Disease Monit, 16*(4), e70013. https://doi.org/10.1002/dad2.70013

Baxter, M. G., Parker, A., Lindner, C. C. C., Izquierdo, A. D., & Murray, E. A. (2000). Control of response selection by reinforcer value requires interaction of amygdala and orbital prefrontal cortex. *Journal Of Neuroscience, 20*(11), 4311–4319. https://doi.org/10.1523/JNEUROSCI.20-11-04311.2000

Beck AT, Steer RA, Brown GK (1996) *Manual for the Beck Depression Inventory–II* [Dataset]. Psychological Corporation. https://doi.org/10.1037/t00742-000

Bernstein, C., Kacelnik, A., & Krebs, J. R. (1991). Individual decisions and the distribution of predators in a patchy environment. II. The influence of travel costs and structure of the environment. *Journal of Animal Ecology, 60*(1), 205–225. https://doi.org/10.2307/5455

Blouzard, E., Pouchon, A., Polosan, M., Bastin, J., & Dondé, C. (2023). Effort-cost decision-making among individuals with schizophrenia: A systematic review and meta-analysis. *JAMA Psychiatry, 80*(6), 548–557. https://doi.org/10.1001/jamapsychiatry.2023.0553

Bustamante, L. A., Oshinowo, T., Lee, J. R., Tong, E., Burton, A. R., Shenhav, A., Cohen, J. D., & Daw, N. D. (2023). Effort foraging task reveals positive correlation between individual differences in the cost of cognitive and physical effort in humans. *Proceedings of the National Academy of Sciences of the United States of America, 120*(50), Article e2221510120. https://doi.org/10.1073/pnas.2221510120

Callaghan, J., Stopford, C., Arran, N., Boisse, M.-F., Coleman, A., Santos, R. D., Dumas, E. M., Hart, E. P., Justo, D., Owen, G., Read, J., Say, M. J., Durr, A., Leavitt, B. R., Roos, R. A. C., Tabrizi, S. J., Bachoud-Levi, A.-C., Bourdet, C., van Duijn, E., & Craufurd, D. (2015). Reliability and factor structure of the short problem behaviors assessment for Huntington's disease (PBA-s) in the TRACK-HD and REGISTRY studies. *The Journal of Neuropsychiatry and Clinical Neurosciences, 27*(1), 59–64. https://doi.org/10.1176/appi.neuropsych.13070169

Carter, E. C., Pedersen, E. J., & McCullough, M. E. (2015). Reassessing intertemporal choice: Human decision-making is more optimal in a foraging task than in a self-control task. *Frontiers in Psychology, 6*, Article 95. https://doi.org/10.3389/fpsyg.2015.00095

Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology, 9*(2), 129–136. https://doi.org/10.1016/0040-5809(76)90040-X

Cheung, G., Clugston, A., Croucher, M., Malone, D., Mau, E., Sims, A., & Gee, S. (2015). Performance of three cognitive screening tools in a sample of older New Zealanders. *International Psychogeriatrics, 27*(6), 981–989. https://doi.org/10.1017/S1041610214002889

Clarke, D. E., van Reekum, R., Simard, M., Streiner, D. L., Freedman, M., & Conn, D. (2007). Apathy in dementia: An examination of the psychometric properties of the apathy evaluation scale. *The Journal of Neuropsychiatry and Clinical Neurosciences, 19*(1), 57–64. https://doi.org/10.1176/jnp.2007.19.1.57

Connors, M. H., Teixeira-Pinto, A., & Loy, C. T. (2023). Apathy and depression in Huntington's disease: Distinct longitudinal trajectories and clinical correlates. *The Journal of Neuropsychiatry and Clinical Neurosciences, 35*(1), 69–76. https://doi.org/10.1176/appi.neuropsych.21070191

Constantino, S. M., & Daw, N. D. (2015). Learning the opportunity cost of time in a patch-foraging task. *Cognitive, Affective, & Behavioral Neuroscience, 15*(4), 837–853. https://doi.org/10.3758/s13415-015-0350-y

Craufurd, D., Thompson, J. C., & Snowden, J. S. (2001). Behavioral changes in Huntington disease. *Neuropsychiatry, Neuropsychology, and Behavioral Neurology, 14*(4), 219–226.

Dalley, J. W., & Ersche, K. D. (2019). Neural circuitry and mechanisms of waiting impulsivity: Relevance to addiction. *Philosophical Transactions of the Royal Society B: Biological Sciences, 374*(1766), Article 20180145. https://doi.org/10.1098/rstb.2018.0145

Doridam, J., Roussel, M., Simonin, C., Benoist, A., Tir, M., Godefroy, O., & Krystkowiak, P. (2014). H14 evaluation of impulsivity in Huntington's disease with a delay discounting task. *Journal of Neurology, Neurosurgery & Psychiatry, 85*(Suppl 1), A56–A56. https://doi.org/10.1136/jnnp-2014-309032.159

Floresco, S. B., & Ghods-Sharifi, S. (2007). Amygdala-prefrontal cortical circuitry regulates effort-based decision making. *Cerebral Cortex, 17*(2), 251–260. https://doi.org/10.1093/cercor/bhj143

Gabay, A. S., & Apps, M. A. J. (2021). Foraging optimally in social neuroscience: Computations and methodological considerations. *Social Cognitive and Affective Neuroscience, 16*(8), 782–794. https://doi.org/10.1093/scan/nsaa037

Gabay, A. S., Pisauro, A., O'Nell, K. C., & Apps, M. A. J. (2024). Social environment-based opportunity costs dictate when people leave social interactions. *Communications Psychology, 2*(1), 1–13. https://doi.org/10.1038/s44271-024-00094-5

Hayden, B. Y. (2018). Economic choice: The foraging perspective. *Current Opinion in Behavioral Sciences, 24*, 1–6. https://doi.org/10.1016/j.cobeha.2017.12.002

Hayden, B. Y., Pearson, J. M., & Platt, M. L. (2011). Neuronal basis of sequential foraging decisions in a patchy environment. *Nature Neuroscience, 14*(7), 933–939. https://doi.org/10.1038/nn.2856

Holec, V., Pirot, H. L., & Euston, D. R. (2014). Not all effort is equal: The role of the anterior cingulate cortex in different forms of effort-reward decisions. *Frontiers in Behavioral Neuroscience, 8*, Article 12. https://doi.org/10.3389/fnbeh.2014.00012

Hsieh, S., Schubert, S., Hoon, C., Mioshi, E., & Hodges, J. R. (2013). Validation of the Addenbrooke's cognitive examination III in frontotemporal dementia and Alzheimer's disease. *Dementia and Geriatric Cognitive Disorders, 36*(3–4), 242–250. https://doi.org/10.1159/000351671

Huntington Study Group. (1996). Unified Huntington's disease rating scale: Reliability and consistency. *Movement Disorders, 11*(2), 136–142. https://doi.org/10.1002/mds.870110204

Johnson, P. L., Potts, G. F., Sanchez-Ramos, J., & Cimino, C. R. (2017). Self-reported impulsivity in Huntington's disease patients and relationship to executive dysfunction and reward responsiveness. *Journal of Clinical and Experimental Neuropsychology, 39*(7), 694–706. https://doi.org/10.1080/13803395.2016.1257702

Kaiser, L. F., Gruendler, T. O. J., Speck, O., Luettgau, L., & Jocham, G. (2021). Dissociable roles of cortical excitation-inhibition balance during patch-leaving versus value-guided decisions. *Nature Communications*. https://doi.org/10.1038/s41467-020-20875-w

Kirsch-Darrow, L., Marsiske, M., Okun, M. S., Bauer, R., & Bowers, D. (2011). Apathy and depression: Separate factors in Parkinson's disease. *Journal of the International Neuropsychological Society, 17*(6), 1058–1066. https://doi.org/10.1017/S1355617711001068

Kourtesis, P., Margioti, E., Demenega, C., Christidi, F., & Abrahams, S. (2020). A comparison of the Greek ACE-III, M-ACE, ACE-R, MMSE, and ECAS in the assessment and identification of Alzheimer's disease. *Journal of the International Neuropsychological Society: JINS, 26*(8), 825–834. https://doi.org/10.1017/S1355617720000314

Lafond-Brina, G., Pham, B.-T., & Bonnefond, A. (2023). Initiative apathy trait underlies individual differences in the ability to anticipate and expend cognitive effort in cost-benefit decision-making tasks. *Cerebral Cortex, 33*(12), 7714–7726. https://doi.org/10.1093/cercor/bhad074

Le Bouc, R., Borderies, N., Carle, G., Robriquet, C., Vinckier, F., Daunizeau, J., Azuar, C., Levy, R., & Pessiglione, M. (2022). Effort avoidance as a core mechanism of apathy in frontotemporal dementia. *Brain*. https://doi.org/10.1093/brain/awac427

Le Heron, C., Kolling, N., Plant, O., Kienast, A., Janska, R., Ang, Y.-S., Fallon, S., Husain, M., & Apps, M. A. J. (2020). Dopamine modulates dynamic decision-making during foraging. *Journal Of Neuroscience, 40*(27), 5273–5282. https://doi.org/10.1523/JNEUROSCI.2586-19.2020

Le Heron, C., Manohar, S., Plant, O., Muhammed, K., Griffanti, L., Nemeth, A., . . . Husain, M. (2018). Dysfunctional effort-based decision-making underlies apathy in genetic cerebral small vessel disease. *Brain*, *141*(11), 3193–3210. https://doi.org/10.1093/brain/awy257

Le Heron, C., Morris, L.-A., & Manohar, S. (2025). Understanding disrupted motivation in Parkinson's disease through a value-based decision-making lens. *Trends in Neurosciences*. https://doi.org/10.1016/j.tins.2025.02.008

Le Heron, C., Plant, O., Manohar, S., Ang, Y.-S., Jackson, M., Lennox, G., Hu, M. T., & Husain, M. (2018b). Distinct effects of apathy and dopamine on effort-based decision-making in Parkinson's disease. *Brain, 141*(5), 1455–1469. https://doi.org/10.1093/brain/awy110

Marin, R. S., Biedrzycki, R. C., & Firinciogullari, S. (1991). Reliability and validity of the apathy evaluation scale. *Psychiatry Research, 38*(2), 143–162. https://doi.org/10.1016/0165-1781(91)90040-v

Martinez-Horta, S., Perez-Perez, J., van Duijn, E., Fernandez-Bobadilla, R., Carceller, M., Pagonabarraga, J., . . . Kulisevsky, J. (2016). Neuropsychiatric symptoms are very common in premanifest and early stage Huntington's disease. *Parkinsonism & Related Disorders*, *25*, 58–64. https://doi.org/10.1016/j.parkreldis.2016.02.008

McGregor, A., & Roberts, D. C. S. (1993). Dopaminergic antagonism within the nucleus accumbens or the amygdala produces differential effects on intravenous cocaine self-administration under fixed and progressive ratio schedules of reinforcement. *Brain Research, 624*(1), 245–252. https://doi.org/10.1016/0006-8993(93)90084-Z

McLauchlan, D. J., Lancaster, T., Craufurd, D., Linden, D. E. J., & Rosser, A. E. (2019). Insensitivity to loss predicts apathy in Huntington's disease. *Movement Disorders, 34*(9), 1381–1391. https://doi.org/10.1002/mds.27787

McLauchlan, D. J., Linden, D. E. J., & Rosser, A. E. (2022). Excessive response to provocation rather than disinhibition mediates irritable behaviour in Huntington's disease. *Frontiers in Neuroscience*. https://doi.org/10.3389/fnins.2022.993357

Mobbs, D., Trimmer, P. C., Blumstein, D. T., & Dayan, P. (2018). Foraging for foundations in decision neuroscience: Insights from ethology. *Nature Reviews. Neuroscience, 19*(7), 419–427. https://doi.org/10.1038/s41583-018-0010-7

Moreira, D., & Barbosa, F. (2019). Delay discounting in impulsive behavior. *European Psychologist, 24*(4), 312–321. https://doi.org/10.1027/1016-9040/a000360

Morris, L.-A., Horne, K.-L., Manohar, S., Paermentier, L., Buchanan, C., MacAskill, M., Myall, D., Apps, Roxburgh, R., Anderson, T. J., Husain, M. & Le Heron, C. (2024a). Decision cost hypersensitivity underlies Huntington's disease apathy. *Brain*. https://doi.org/10.1093/brain/awae296

Morris, L.-A., Horne, K.-L., Manohar, S., Paermentier, L., Buchanan, C. M., MacAskill, M., Myall, D., Roxburgh, R., . . . Heron, C. L. (2024b). *Disrupted time perception underlies motivational disturbances in Huntington's disease*. Timing & Time Perception. Advance online publication. https://doi.org/10.1163/22134468-bja10115

Morris, L.-A., Horne, K.-L., Paermentier, L., Buchanan, C. M., MacAskill, M., Myall, D., Husain, M., Roxburgh, R., Anderson, T., & Heron, C. L. (2024c). Apathy and impulsivity co-occur in Huntington's disease. *Brain and Behavior, 14*(10), Article e70061. https://doi.org/10.1002/brb3.70061

Morris, L.-A., O'Callaghan, C., & Le Heron, C. (2022). Disordered decision making: A cognitive framework for apathy and impulsivity in Huntington's disease. *Movement Disorders: Official Journal of the Movement Disorder Society, 37*(6), 1149–1163. https://doi.org/10.1002/mds.29013

Nasreddine, Z. S., Phillips, N. A., Bédirian, V., Charbonneau, S., Whitehead, V., Collin, I., Cummings, J. L., & Chertkow, H. (2005). The Montreal Cognitive Assessment, MoCA: A brief screening tool for mild cognitive impairment. *Journal of the American Geriatrics Society, 53*(4), 695–699. https://doi.org/10.1111/j.1532-5415.2005.53221.x

Niv, Y., Daw, N. D., Joel, D., & Dayan, P. (2007). Tonic dopamine: Opportunity costs and the control of response vigor. *Psychopharmacology, 191*(3), 507–520. https://doi.org/10.1007/s00213-006-0502-4

Ostrander, S., Cazares, V. A., Kim, C., Cheung, S., Gonzalez, I., & Izquierdo, A. (2011). Orbitofrontal cortex and basolateral amygdala lesions result in suboptimal and dissociable reward choices on cue-guided effort in rats. *Behavioral Neuroscience, 125*(3), 350–359. https://doi.org/10.1037/a0023574

Paasche, C., Weibel, S., Wittmann, M., & Lalanne, L. (2019). Time perception and impulsivity: A proposed relationship in addictive disorders. *Neuroscience and Biobehavioral RevieWs, 106*, 182–201. https://doi.org/10.1016/j.neubiorev.2018.12.006

Passamonti, L., Lansdall, C., & Rowe, J. (2018). The neuroanatomical and neurochemical basis of apathy and impulsivity in frontotemporal lobar degeneration. *Current Opinion in Behavioral Sciences, 22*, 14–20. https://doi.org/10.1016/j.cobeha.2017.12.015

Paulsen, J. S., Ready, R. E., Hamilton, J. M., Mega, M. S., & Cummings, J. L. (2001). Neuropsychiatric aspects of Huntington's disease. *Journal of Neurology, Neurosurgery & Psychiatry, 71*(3), 310–314. https://doi.org/10.1136/jnnp.71.3.310

Pearson, J. M., Watson, K. K., & Platt, M. L. (2014). Decision making: The neuroethological turn. *Neuron, 82*(5), 950–965. https://doi.org/10.1016/j.neuron.2014.04.037

Petitet, P., Scholl, J., Attaallah, B., Drew, D., Manohar, S., & Husain, M. (2021). The relationship between apathy and impulsivity in large population samples. *Scientific Reports*. https://doi.org/10.1038/s41598-021-84364-w

Quang, H., Le Heron, C., Balleine, B., Nguyen, T.-V., Nguyen, T.-Q., Nguyen, M.-N., & McDonald, S. (2023). Reduced sensitivity to background reward underlies apathy after traumatic brain injury: Insights from an ecological foraging framework. *Neuroscience, 528*, 26–36. https://doi.org/10.1016/j.neuroscience.2023.07.026

R Core Team. (2024). *R: The R Project for Statistical Computing*. https://www.r-project.org/

Ruiz-Idiago, J., Pomarol-Clotet, E., & Salvador, R. (2023). Longitudinal analysis of neuropsychiatric symptoms in a large cohort of early-moderate manifest Huntington's disease patients. *Parkinsonism and Related DisordeRs, 106*, Article 105228. https://doi.org/10.1016/j.parkreldis.2022.11.020

Rutledge, R. B., Lazzaro, S. C., Lau, B., Myers, C. E., Gluck, M. A., & Glimcher, P. W. (2009). Dopaminergic drugs modulate learning rates and perseveration in Parkinson's patients in a dynamic foraging task. *The Journal Of Neuroscience, 29*(48), 15104–15114. https://doi.org/10.1523/JNEUROSCI.3524-09.2009

Santangelo, G., Barone, P., Cuoco, S., Raimo, S., Pezzella, D., Picillo, M., Erro, R., Moccia, M., Pellecchia, M. T., Amboni, M., Franco, S., Grossi, D., Trojano, L., & Vitale, C. (2014). Apathy in untreated, de novo patients with Parkinson's disease: Validation study of apathy evaluation scale. *Journal of Neurology, 261*(12), 2319–2328. https://doi.org/10.1007/s00415-014-7498-1

Scholl, J., Trier, H. A., Rushworth, M. F. S., & Kolling, N. (2022). The effect of apathy and compulsivity on planning and stopping in sequential decision-making. *PLoS Biology, 20*(3), Article e3001566. https://doi.org/10.1371/journal.pbio.3001566

Schweimer, J., & Hauber, W. (2005). Involvement of the rat anterior cingulate cortex in control of instrumental responses guided by reward expectancy. *Learning & Memory, 12*(3), 334–342. https://doi.org/10.1101/lm.90605

Sinha, N., Manohar, S., & Husain, M. (2013). Impulsivity and apathy in Parkinson's disease. *Journal Of Neuropsychology, 7*(2), 255–283. https://doi.org/10.1111/jnp.12013

Sockeel, P., Dujardin, K., Devos, D., Denève, C., Destée, A., & Defebvre, L. (2006). The Lille apathy rating scale (LARS), a new instrument for detecting and quantifying apathy: Validation in Parkinson's disease. *Journal of Neurology, Neurosurgery, and Psychiatry, 77*(5), 579–584. https://doi.org/10.1136/jnnp.2005.075929

Stephens, D. W. (2008). Decision ecology: Foraging and the ecology of animal decision making. *Cognitive, Affective, & Behavioral Neuroscience, 8*(4), 475–484. https://doi.org/10.3758/CABN.8.4.475

Stephens, D. W., & Anderson, D. (2001). The adaptive value of preference for immediacy: When shortsighted rules have farsighted consequences. *Behavioral Ecology, 12*(3), 330–339. https://doi.org/10.1093/beheco/12.3.330

Stevens, J. R., & Stephens, D. W. (2010). The adaptive nature of impulsivity. In G. J. Madden & W. K. Bickel (Eds.), *Impulsivity: The behavioral and neurological science of discounting* (pp. 361–387). American Psychological Association. https://doi.org/10.1037/12069-013

Tabrizi, S. J., Scahill, R. I., Owen, G., Durr, A., Leavitt, B. R., Roos, R. A., Borowsky, B., Landwehrmeyer, B., Frost, C., Johnson, H., Craufurd, D., Reilmann, R., Stout, J. C., & Langbehn, D. R. (2013). Predictors of phenotypic progression and disease onset in premanifest and early-stage Huntington's disease in the TRACK-HD study: Analysis of 36-month observational data. *The Lancet Neurology, 12*(7), 637–649. https://doi.org/10.1016/S1474-4422(13)70088-7

Thompson, J. C., Harris, J., Sollom, A. C., Stopford, C. L., Howard, E., Snowden, J. S., & Craufurd, D. (2012). Longitudinal evaluation of neuropsychiatric symptoms in Huntington's disease. *The Journal of Neuropsychiatry and Clinical Neurosciences, 24*(1), 53–60. https://doi.org/10.1176/appi.neuropsych.11030057

van Duijn, E., Craufurd, D., Hubers, A. A. M., Giltay, E. J., Bonelli, R., Rickards, H., . . . European Huntington's Disease Network Behavioural Phenotype Working Group. (2014). Neuropsychiatric symptoms in a European Huntington's disease cohort (REGISTRY). *Journal of Neurology, Neurosurgery & Psychiatry*, *85*(12), 1411–1418. https://doi.org/10.1136/jnnp-2013-307343

Whiteside, S. P., Lynam, D. R., Miller, J. D., & Reynolds, S. K. (2005). Validation of the UPPS impulsive behaviour scale: A four-factor model of impulsivity. *European Journal of Personality, 19*(7), 559–574. https://doi.org/10.1002/per.556