Reviewed Preprint
v1 • August 12, 2025
Not revised

Reviewed Preprint
v2 • July 1, 2026
Revised by authors

For correspondence:
shuangyi.tong@ndcn.ox.ac.uk
ben.seymour@ndcn.ox.ac.uk

Competing interests: No competing interests declared

Funding: See page 26

Reviewing editor: Markus Ploner, Department of Neurology and TUM-Neuroimaging Center, TUM School of Medicine and Health, Technical University of Munich (TUM), Germany

Phasic and tonic pain serve distinct functions during adaptive behaviour

Shuangyi Tong[1,2], Timothy Denison[1,2], Danielle Hewitt[2], Sang Wan Lee[3], Ben Seymour[1,2]

[1]Institute of Biomedical Engineering, University of Oxford, Oxford, United Kingdom • [2]Nuffield Department of Clinical Neurosciences, University of Oxford, Oxford, United Kingdom • [3]Department of Brain and Cognitive Sciences, Korea Advanced Institute of Science and Technology (KAIST); Kim Jaechul Graduate School of AI, KAIST; KAIST Center for Neuroscience-inspired Artificial Intelligence, Daejeon, Republic of Korea

eLife Assessment

The article presents **important** findings of a dissociation between phasic and tonic pain functions in adaptive behavior, combining immersive VR, computational modeling, skin conductance, and EEG data. The methodology used is **convincing**. Its ecological design and sophisticated computational modeling are major strengths.

https://doi.org/10.7554/eLife.107911.2.sa4

Abstract

Pain drives self-protective behaviour, and evolutionary theories suggest it acts over different timescales to serve distinct functions. Whilst phasic pain provides a teaching signal to drive avoidance of new injury, tonic pain is argued to support recuperative behaviour, for instance by reducing motivational vigour. We test this hypothesis in an immersive virtual reality EEG foraging task where subjects harvested fruit in a forest: some fruit elicited brief phasic pain to the grasping hand, and this reduced choice probability. Simultaneously, tonic pressure pain to the contralateral upper arm was associated with reduced action velocities. This could be explained by a free-operant computational framework that formalises and quantifies the function of tonic and phasic pain in terms of motivational vigour and decision value, and model parameters correlated with physiological and neural responses. Overall, the results show how tonic and phasic pain subserve distinct objective motivational functions that support harm minimisation during ongoing adaptive behaviour.

Introduction

Despite its unpleasantness, pain serves a useful function. This is most clearly the case for phasic pain, where newly incoming nociceptive signals warn of impending tissue damage, elicit rapid defensive responses, and drive learning that reduces future chances of encountering harm. In this context, function can be objectively measured through conditioned responses and avoidance behaviour, which quantify pain in terms of its motivational value (Fields, 2006; Seymour, 2019). However, the adaptive function of tonic pain has been much harder to quantify. In ecological and ethological contexts, tonic pain is generally considered to serve protective and recuperative functions. For instance, in the context of injury, it has been proposed that tonic pain can aid recovery by reducing motivational vigour and hence suppress unnecessary activity until healing occurs (Bolles and Fanselow, 1980; Wall, 1979; Walters and Williams, 2019; Seymour et al., 2023). The goal of this study was to test whether we can formally and quantifiably dissociate these two distinct motivational functions of pain.

One of the challenges in studying adaptive functions of pain is the difficulty of embedding experiments within ecologically meaningful contexts. To solve this, we designed an immersive foraging task using virtual reality (VR), in which humans search a forest to collect fruits from the low-lying bushes at varying heights. A foraging paradigm provides a robust, free-operant framework that captures the core components of adaptive behaviour: it is goal-directed, involves complex movement, and requires the learning of an optimal strategy to maximise rewards. This allows us to computationally dissociate how different types of pain influence the control of action. Our first hypothesis was that phasic pain provides a distinct valuation signal that updates the value of specific actions within complex environments. In our task, this was implemented by associating specific fruit (distinguishable by colour) with a brief electrical stimulus to the grasping hand, emulating thorns. In our computational model, this was defined as an aversive utility term incorporated into the state-action value evaluation process. We predicted that this computational mechanism would manifest behaviourally as a reduction in choice probability for pain-associated targets and an increase in 'choice distance bias' (the willingness to travel further for pain-free options). Neurally and physiologically, we predicted that these aversive values would be tracked by skin conductance responses (SCRs) and the amplitude of nociceptive event-related potentials (ERPs), specifically the N1-P2 complex (Favero et al., 2023).

Second, we hypothesised that tonic pain acts as a coefficient modulating the trade-off between opportunity cost and vigour cost, thereby serving a recuperative function. To test this in Experiment 2, we delivered continuous tonic pressure to the non-dominant arm via an inflated cuff to emulate a background state of injury. Within our free-operant framework, tonic pain was modelled as a weighting factor that shifts the optimal balance toward reduced energy expenditure. Because the stimulus was applied to the non-task limb, we specifically predicted a global reduction in motivational vigour—operationalised as decreased movement velocities and foraging rates—rather than a direct mechanical impairment. By applying this formal computational approach, we move beyond exploratory observations to provide a rigorous, mechanism-based explanation for how distinct pain states adaptively govern choice and action.

Results

Experiment 1: Phasic pain avoidance in a free-operant foraging task

Twenty-five subjects performed a free-operant instrumental foraging task to accrue reward points and avoid pain. The task was embedded into a fully immersive VR context, in which subjects physically moved in a flat open space. A virtual boundary of 4 m × 4 m was displayed when the subject approached the edge of the area. Within the VR context, this space resembled a flat forest (Fig. 1), with trees and vegetation locations randomly generated. The task was structured into one-minute blocks. At the beginning of each block, virtual fruits of varying heights and locations were generated within the virtual space. The spatial coordinates of subjects' heads and hands were tracked, requiring them to physically move towards the fruit, pick it up by reaching with their dominant hand, clicking, and holding the button on the handset. Only the dominant hand was enabled in the virtual environment. Subsequently, subjects could drop the fruit into one of the baskets to earn points. Subjects were told that the total points accrued would be rewarded with an incentive of up to £10. All fruits used in both experiments were pineapples, as their spiky shape naturally matches the pricking pain induced by the Wasp pain stimulation electrodes.

Pineapples were categorised into two visually distinguishable types: 50% were green and 50% were yellow. The green pineapple was aversive, and picking one up immediately elicited a brief painful cutaneous electric stimulation to the proximal medial side of the middle finger of the (grasping) dominant hand. In contrast, picking up a yellow pineapple was always pain-free. The intensity of the electric stimulation was held constant within each block. Experiment 1 consisted of 20 blocks, with the initial 10 blocks designated for practice purposes with a fixed order of stimulation intensities. The subsequent 10 blocks used randomised pain stimulation intensities across five different levels, determined by a pain calibration procedure. After completing the 10 training blocks, all subjects were aware that picking up green pineapples resulted in painful shocks, as confirmed through verbal questioning. However, subjects did not know the exact pain level of a new block until they tried to pick up one green pineapple. Only data from the latter 10 non-training blocks were analysed.

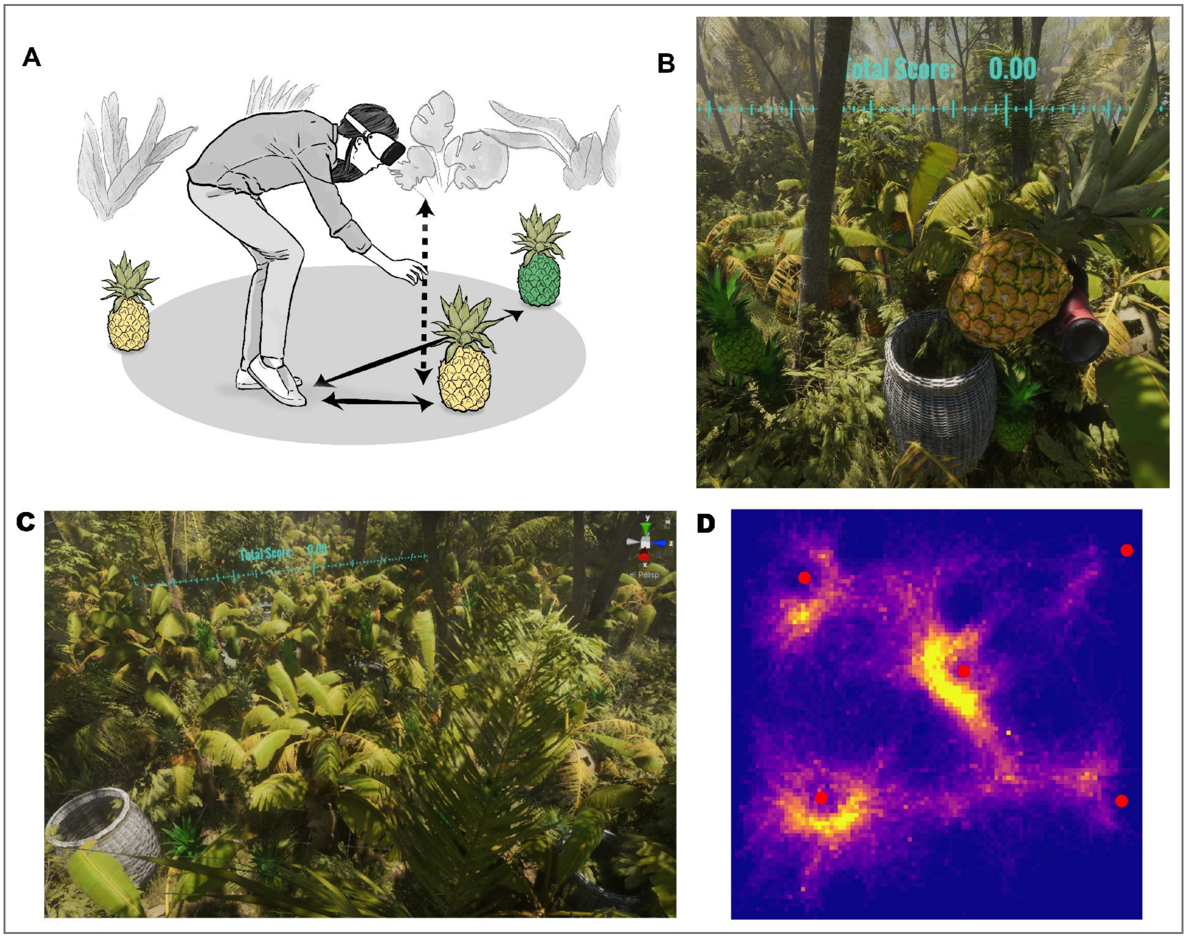


Figure 1. **Task description.**

(**A**) An illustrative figure depicting the foraging task. (**B**) Subjects' view (left eye) in the task. (**C**) A perspective view of the task environment. (**D**) An aggregated top-view heat map of head trajectories of all subjects' data. Red dots denote baskets' preset locations.

Avoidance increases with increasing phasic pain intensity

We found that the probability of choosing a fruit decreased as the pain associated with it increased. For this analysis, both aversive choice probabilities and subjective pain ratings were estimated at the block level. Figure 3A shows an approximately linear decrease in aversive choice probability as a function of visual analogue scale (VAS) rating of pain stimuli, whereby the aversive choice probability is defined as the number of painful fruits collected divided by the total number of fruits collected.

Additional cost of effort associated with movement

Next, since movement itself may carry a small cost related to time and effort (incurring opportunity costs), we investigated whether there is a trade-off relationship between moving distances and pain intensity (i.e., is it worth moving further to avoid a certain amount of pain). We measured the distance from the fruit to the subject at the moment the subject first fixated on the fruit, as estimated from eye-tracking data, after collecting the previous one. We found a significant correlation between the egocentric distance differences between painful and non-painful fruits, and the VAS ratings. As shown in Figure 3B, the vertical axis represents the 'choice distance bias', calculated as the difference between the average egocentric distance to non-painful fruits and the average egocentric distance to painful fruits within each block. The egocentric distance is the fruit distance relative to the participant. This metric was computed to test whether subjects would trade off physical effort for pain avoidance; specifically, a positive bias indicates that subjects were willing to bypass closer painful fruits to reach more distant pain-free ones. As hypothesised, we found that as the pain intensity (VAS) of the aversive fruits increased, this distance bias grew significantly, confirming that subjects exerted greater movement effort to avoid higher levels of pain.

Choice-based computational modelling in RL framework

As noted above, these initial regression results were analysed at the block level. Within each one-minute block, each pickup, which could result in an immediate shock, can be considered an individual trial. By analysing the data at the trial level, we can extract more detailed information and provide a parameterised behavioural description for each individual. This approach laid the groundwork for a robust, objective measure of phasic pain value within an ecologically valid context. In each trial, despite the presence of numerous lower-level controls required to complete the action, the primary decision involved choosing which fruit to pick up. We simplified the problem by assuming that there exists a set of decision points $\mathcal{S}$ as states, where the subject took an action at a state $s \in \mathcal{S}$—choosing to pick up a fruit—and deterministically arrived at another state $s^{'} \in \mathcal{S}$if the block had not concluded. Based on the initial regression results, we assumed that the reward was a linear combination of an internal reward r for each fruit, a negative utility function u representing the phasic pain value, and an effort cost function d. Therefore, the Bellman optimality equation for the action-value function was

$$q_*(s,a) = r + C_p u(a) + C_m \cdot d(a) + \gamma \max_{a^{'}} q_*\left(s^{'}, a^{'}\right)$$

, where C_p and C_m were the parameters to be fitted for each subject.

As fruits were randomly distributed in our task, previous foraging studies suggested that animals may adopt a suboptimal greedy policy, opting for the closest fruit rather than solving the complex travelling salesman problem for a marginally better optimal solution (Anderson, 1983; Jeon et al., 2023). To initially demonstrate the basic effects, we further eschewed learning and future planning by setting the discount factor $\gamma = 0$. Figure 2 shows the conceptual diagram of the computational framework setup. One of the key simplifications was assuming the existence of a set of decision points in this free-operant context. To fit the model, we again utilised the eye-tracking data, setting the decision point as the first time point when the subject saw a new fruit. Nevertheless, the task's available actions were partially observable, and subjects could explore for more actions if they were not satisfied with the currently available ones. This exploration action was not modelled in our formulation. To proceed with model fitting, we retrospectively identified the fruits that were picked up and selected only those time points when the fruits chosen afterwards were first seen as the decision points. We also kept track of the previously seen fruits, storing them in a memory queue, so the decision involved choosing the best option from these items in memory. Figure 3(C, D) shows the parameters fitted to the subjects' behavioural data. This shows the negative utility associated with pain and vertical and horizontal components of movement, and it illustrates how the computational modelling framework can be used to quantify behaviour in a free-operant VR context.

Skin conductance analysis dissociated decision values and subjective ratings for phasic pain

As an objective measure derived from empirical behavioural data, the phasic pain utility function generated by the model can be abstract. To understand its physical implications, we further examined its relationship with subjective pain ratings and their correlations with physiological responses, specifically SCRs. Figure 3(E, F) presents the subjective ratings and decision values of phasic pain across different conditions, while Figure 3G demonstrates a significant correlation between decision values and subjective pain ratings.

Two types of evoked SCRs were analysed: those elicited by the pick-up action (which triggered a shock for painful fruit) and those associated with the fixation action (looking at either painful or non-painful fruit). Figure 4A compares evoked SCRs for painful and non-painful fruit. To quantify the magnitude of evoked SCRs which may overlap in the time domain, given that changes in skin conductance can be approximated by a linear time-invariant system, we fitted the skin conductance data to a constructed time series by convolving the event trigger with a known canonical response function (CRF) (Bach et al., 2010). We selected fixation and pick-up events for painful fruit and extracted their fitted coefficients. Analysis using a multilevel linear mixed-effects model revealed a clear dissociation in the relationship between physiological responses and motivational parameters. Fixation-evoked SCR coefficients were significantly associated with decision values, but not with subjective pain ratings (Fig. 4B). Conversely, shock-evoked SCR coefficients showed a significant association with subjective pain ratings, while the association with decision values was not significant (Fig. 4C). This double dissociation suggests a notable divergence between the physiological correlates of expected utility (at the decision level) and experienced utility (the actual pain experience). Taken together, these findings highlight the composite nature of the overall aversiveness of pain and underscore the benefit of combining subjective ratings with model-based measures to capture its distinct impacts on behaviour.

Experiment 2: Modulation of free-operant foraging by tonic pain stimulation

In the second experiment, we introduced a tonic pain condition by applying an inflatable blood pressure cuff around the non-dominant arm (Graven-Nielsen et al., 2017). We reduced the number of phasic pain levels from five in the first experiment to three (no pain, low pain, and high pain). These three phasic pain levels were then combined with two fixed tonic pain conditions (with and without tonic pain) to form a factorial design experiment with a total of six different combinations. Similar to experiment 1, the experiment was divided into one-minute blocks, and the pain conditions were fixed within each block. The six combinations were initially presented in a fixed order as training blocks, then the order was randomised and repeated three times, resulting in a total of 24 blocks. To obtain a neural measure of pain behaviour, we introduced concurrent EEG recording alongside the VR set-up.

No effect found for tonic pain on phasic pain

We found no significant modulation of phasic pain ratings by tonic pain (Fig. 5(A, B)). We found a basic decrease in aversive choice probability, in terms of the probability of selecting a painful fruit, as in experiment 1. The average aversive choice probabilities were similar in conditions with and without tonic pain (Fig. 5(C-E)), providing evidence that punishment sensitivity was not affected by the presence of tonic pain.

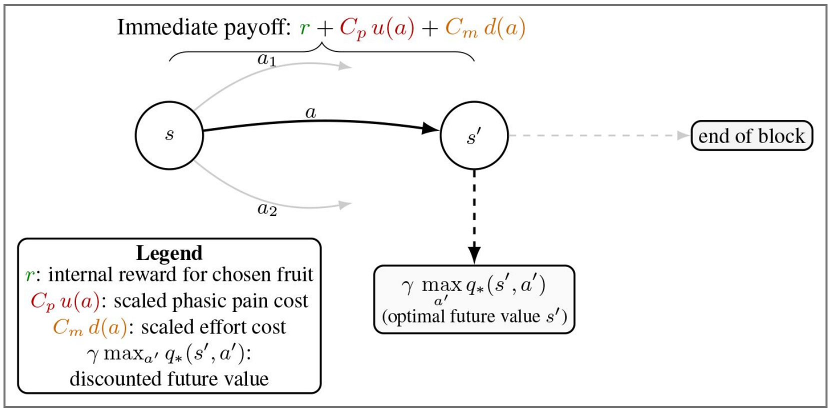


Figure 2. Illustration of the computational setup for a single trial within a block.

From state *s*, the subject chooses an action *a* (picking a fruit), deterministically transitions to $s^{'}$ if the block continues, receives an immediate payoff decomposed into reward, pain, and effort, and then accrues discounted future value.

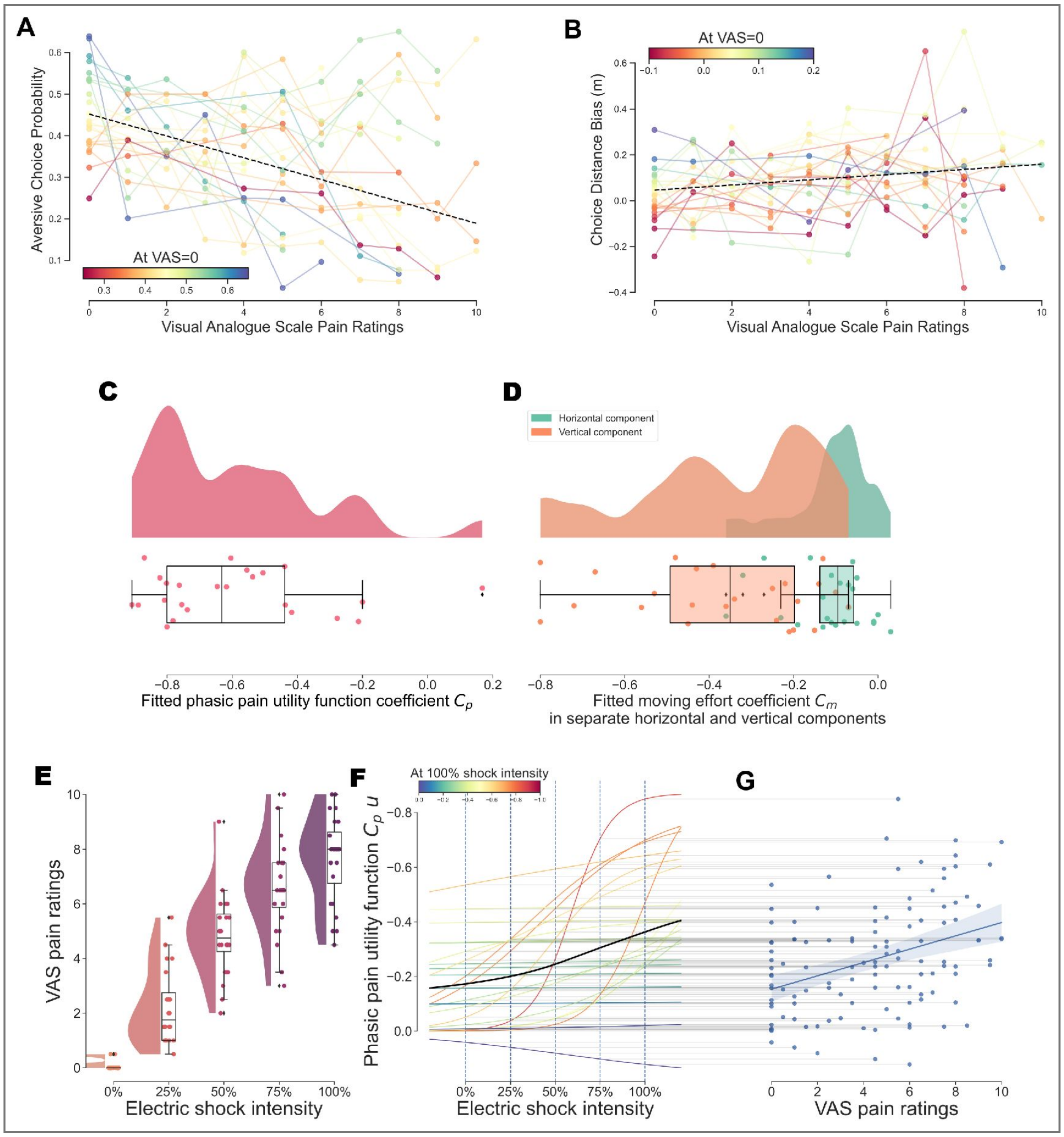


Figure 3. **Experiment 1 behaviour and modelling results.**

(**A**) Each coloured line represents one single subject data with the colour reflecting the value in pain-free condition (VAS=0). The dashed black line's slope and intercepts are fixed effect estimates from a linear mixed model. The slope's estimate shows an inverse relationship between pain choice probability and VAS rating, $\beta = -0.0263$, 95%$CI[-0.0383, -0.0144]$, $t(21.27) = -4.40$, $p < .001$. (**B**) As described in (A), the dashed line's slope is the fixed effect's estimate of choice distance bias, and it shows a positive relationship between the choice distance bias and VAS ratings, $\beta = 0.0113$, 95%$CI[0.00294, 0.0197]$, $t(29.36) = 2.68$, $p = .012$. (**C**) The negative phasic pain coefficients ($M = -0.592$, $SD = 0.261$) showed the model captured the aversiveness of phasic pain stimuli in this free-operant decision-making task, $t(23) = -10.89$, $p < .001$. (**D**) The moving effort coefficient C_m was separated into a horizontal component ($M = -0.115$, $SD = 0.0967$) and a vertical component ($M = -0.370$, $SD = 0.217$). The fitted coefficients showed lower effort cost to move horizontally than vertically, $t(23) = 6.72$, $p < .001$. (**E**) VAS ratings at different electric shock intensities. (**F**) Phasic pain utility values as a function of electric shock intensity. Each coloured line represents one subject's fitted curve. Black line is the average over all subjects. (**G**) A mixed model accounting for hierarchical data (random intercepts and slopes per subject) showed significant correlation between VAS pain ratings and model estimated phasic pain values, $\beta = -0.0227$, 95%$CI[-0.0349, -0.0108]$, $t(20.62) = -3.78$, $p = .001$

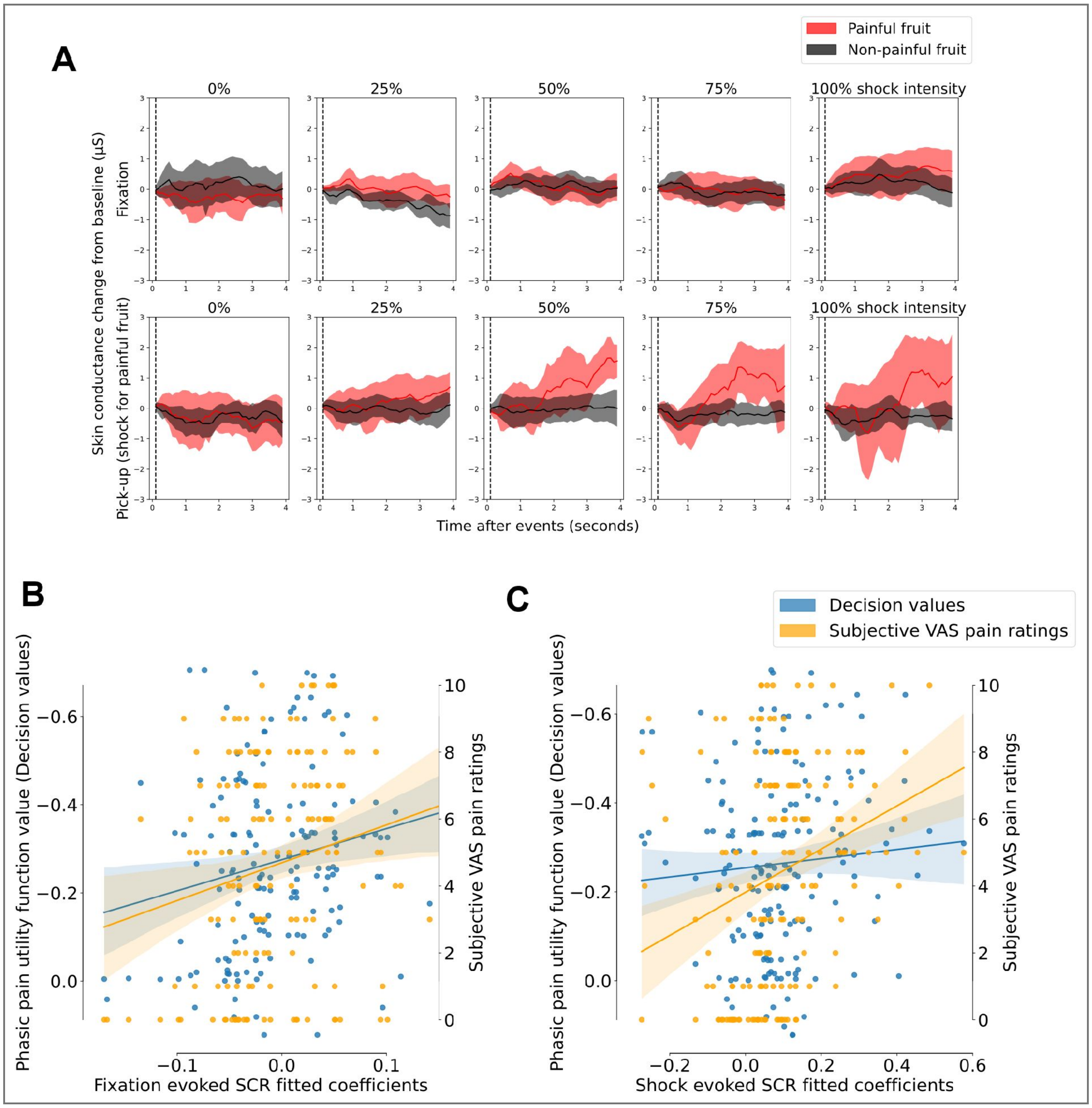


Figure 4. **Skin conductance changes and their correlation with decision values derived from the model.**

(**A**) Evoked SCR for fixation and fruit pick-up events. Compared to seeing the visual cues, shock stimuli induced a greater SCR when the shock intensities were high. Shaded area is the 95% confidence interval. (**B**) Results from a multilevel regression (mixed-effects) model showed that fixation-evoked SCR coefficients were significantly associated with decision values (β = −0.0739, 95% CI [−0.138, 0.015], $t(26.77) = -2.81$, p = .009), but not with subjective pain ratings (β = 0.0037, 95% CI [−0.0006, 0.0081], $t(18.64) = 1.703$, p = .105). (**C**) Conversely, shock-evoked SCR coefficients showed a significant association with subjective pain ratings (β = 0.0154, 95% CI [0.00566, 0.0253], $t(16.98) = 3.174$, p = .006), while the association with decision values was not significant (β = −0.0468, 95% CI [−0.241, 0.147], $t(7.76) = -0.44$, p = .672).

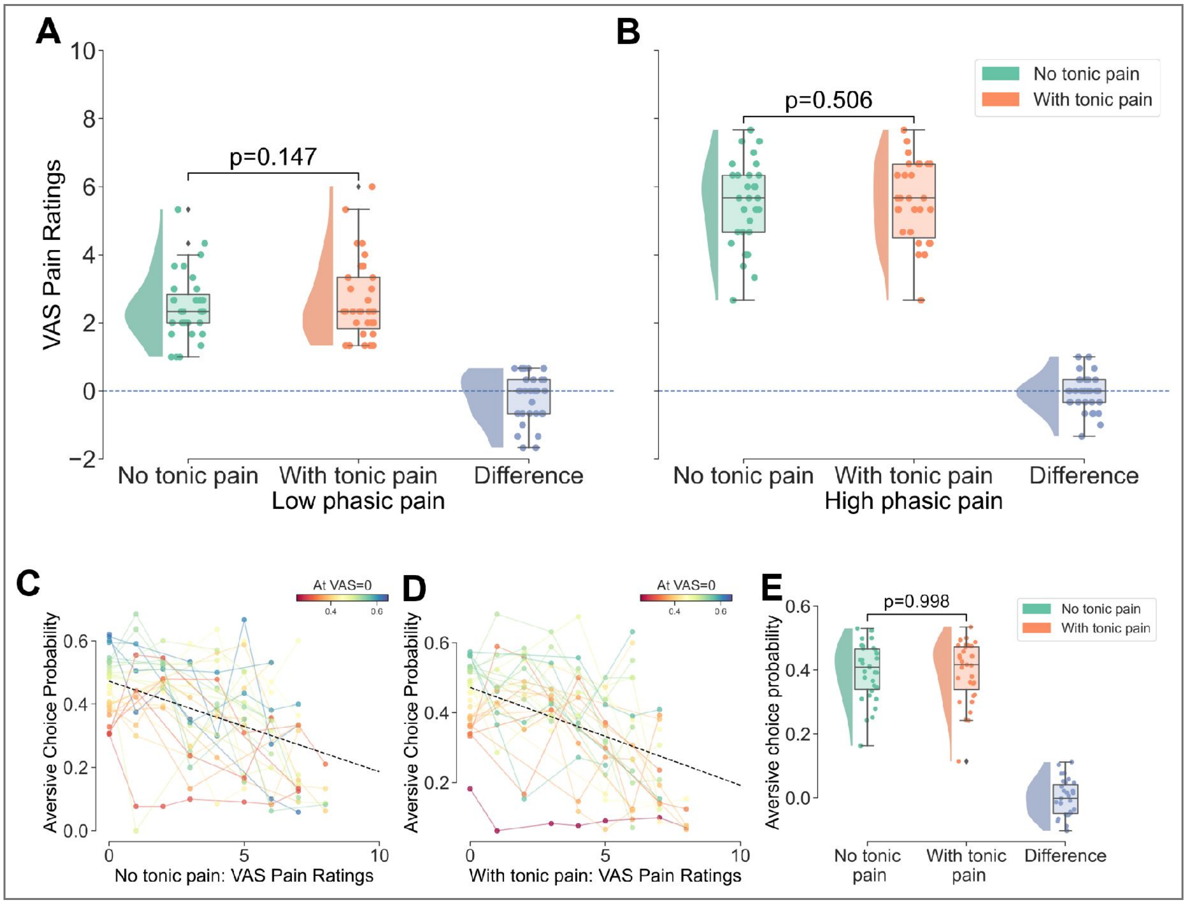


Figure 5. **Effects of tonic pain on phasic pain ratings and aversive choice probabilities.**

(**A, B**), Two-way repeated measures ANOVA showed no statistically significant difference in subject's ratings of phasic pain intensity as a result of tonic pain in low (A) or high (B) phasic pain conditions, F(1,30)=2.01, p=.167, nor was there a significant interaction effect between tonic pain and phasic pain, F(1, 30)=0.87, p=.357. (**C, D**), Similar linear mixed model fitting results for aversive choice probability. No tonic pain condition: $\beta = -0.0286$, $95\% CI = [-0.0372, -0.0198]$, $p < .001$, intercept = 0.473. Tonic pain condition: $\beta = -0.0280$, $95\% CI = [-0.0349, -0.0209]$, $p < .001$, intercept = 0.472. (**E**), Aversive choice probability averaged over phasic pain conditions. Two-way repeated measures ANOVA showed significant effect for phasic pain (including no pain condition), $F(2, 60) = 36.872$, $p < .001$, but no effect for tonic pain, $F(1, 30) = 0.00$, $p = .998$. The interaction effect between tonic and phasic pain was also not significant $F(2, 60) = 0.07$, $p = .930$.

In the neural data, we found that phasic pain intensity modulated the amplitude of phasic pain ERPs, as would be expected. But as in the behavioural results, this was not modulated by the presence/absence of tonic pain (Fig. 6). That is, tonic pain neither facilitated nor inhibited the behavioural or neural responses to the phasic pain. We focused our neural analysis of phasic pain on ERPs as phasic stimuli are well characterised by these time-locked evoked potentials. Nevertheless, to ensure a comprehensive assessment of the neural response, we also examined induced oscillatory responses. These results were consistent with the ERP findings and are detailed in the Supplementary Materials (Fig. S4, S5).

Tonic pain reduced motivational vigour

By analysing the motion tracking data, we found that tonic pain was associated with a reduction in task-related movement velocities (Fig. 7(A, C)) and an associated reduction in fruit collection rates (Fig. 7B).

To quantify this effect in terms of motivational vigour, we extended the computational model to accommodate vigour effects. The model presented for experiment 1 does not consider time, and fitting the model to the collected data requires acausal simulation (see Methods - model-fitting section below). For experiment 2, we took account of the temporal factor and fitted the model causally with high temporal resolution. Niv et al. (2007) proposed that the delay between consecutive actions performed by animals can be formulated as a trade-off between opportunity costs and vigour costs. This framework was developed based on earlier works in average-reward reinforcement learning, showing that this trade-off approach maximises average reward (Niv et al., 2005). In this formulation, animals choose an action pair (a, τ). The first, a, is the common action in discrete decision-making models, and the separate τ represents the time delay between two actions. We built upon this model to suit the requirements of our study. Similar to the model in experiment 1, our action a represents the choice of which fruit to pick up. To account for the different effort costs incurred for each fruit, we again used a distance-based effort cost term $C_m \cdot d(a)$, as in experiment 1. Additionally, a time delay between actions is required to model vigour. We assumed that subjects estimated the time delay by estimating their speed V_{speed} and calculated the delay based on the distance to the fruit and the estimated speed. Hence, for a decision time point state $s \in \mathcal{S}$, if the effort cost is inversely proportional to the time delay, the optimal differential value of an (a, τ) pair is

$$Q^*(s,a,\tau) = r + C_p u(a) - C_v C_m \cdot d(a)\left(\tau + \frac{\|d(a)\|}{V_{\text{speed}}(s)}\right)^{-1} - \bar{R}\left(\tau + \frac{\|d(a)\|}{V_{\text{speed}}(s)}\right) + \gamma \max_{a',\tau'} Q^*\left(s', a', \tau'\right)$$

, where τ is the additional delay accounting for the time waited before committing to execute the action. $s' \in \mathcal{S}$ is the deterministic subsequent state after choosing (a, τ). Q^* is the optimal differential state-action value function. C_v is the vigour constant that scales the vigour cost term. $\bar{R}$ is the average reward and assumed to be constant (Fig. 8).

We fitted vigour constants C_v and other parameters for no tonic pain and with tonic pain conditions separately. We found the fitted vigour constants were significantly higher in tonic pain conditions (Fig. 9A). We further fitted the model with additional separate vigour constants for different levels of phasic pain. Consistent with the fitting results over tonic pain conditions only, tonic pain showed a strong effect on fitted vigour constants, while phasic pain did not show a significant effect (Fig. 9B).

A unified model for tonic and phasic pain for decision-making in free-operant task

This new decision model therefore includes both phasic pain and vigour costs, by which the tonic pain effects can be expressed as change in vigour. Experiment 2 replicated the phasic pain punishment sensitivity effect shown in experiment 1. Using this model, the fitted phasic pain parameters also showed no significant differences in punishment sensitivity (Fig. 9(C-E)), in line

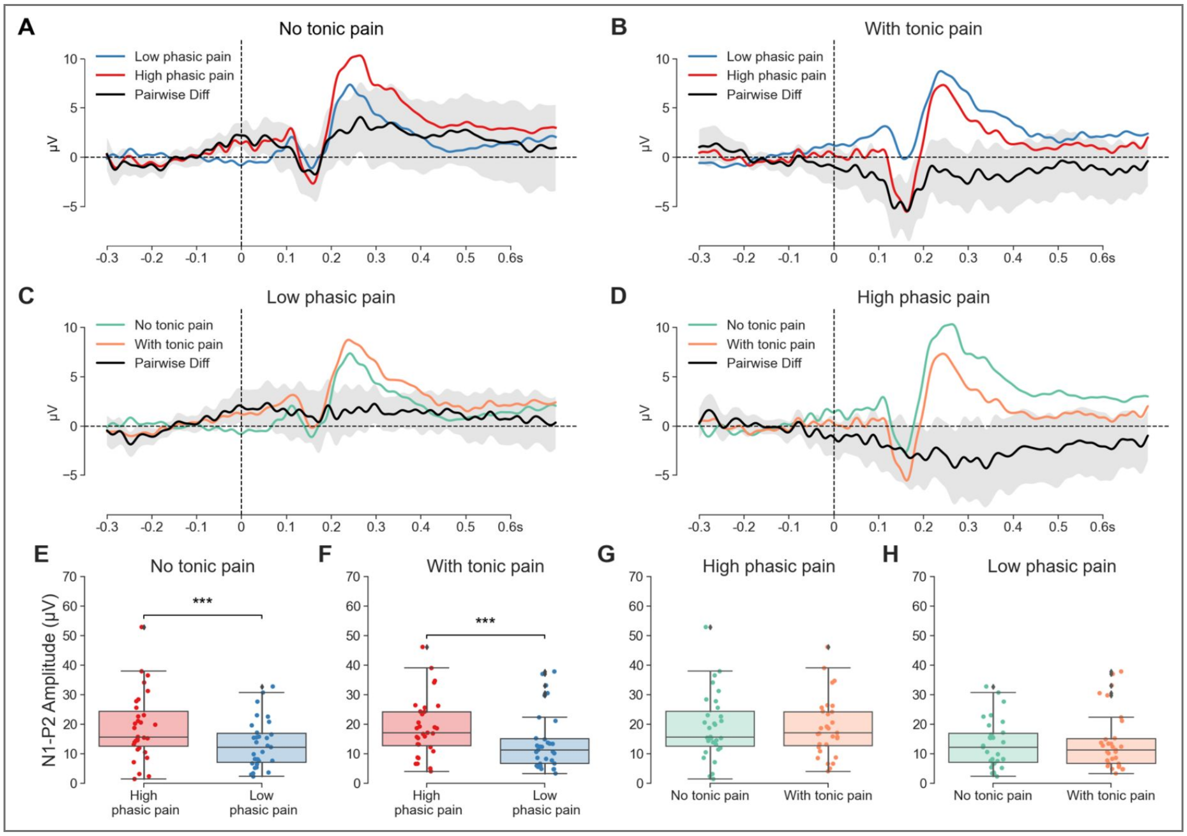


Figure 6. **Phasic pain ERPs in different pain conditions.**

(**A, B**) Phasic pain ERP comparison in the same tonic pain conditions. (**C, D**) Phasic pain ERP comparison in the same phasic pain conditions. (**E, F**) High phasic pain induced a significantly higher N1-P2 amplitude with or without tonic pain. Shaded areas represent the 95% confidence interval across participants. (**G, H**) Tonic pain stimulation does not show a significant effect in phasic pain ERP's N1-P2 amplitude. Two-way repeated measures ANOVA showed the effect for phasic pain was significant, F (1, 30) = 35.42, p < .001. The effect for tonic pain was not significant, F (1, 30) = 0.30, p = .589, and the interaction effect was also not significant, F (1, 30) = 0.58, p = .454.

Figure 7. **Tonic pain reduced action velocity.**

(**A**) Average hand speed. A one-tailed paired t-test was conducted to evaluate whether the hand speed was faster without tonic pain (*M* = 1.01, *SD* = 0.19) than with tonic pain (*M* = 0.99, *SD* = 0.18), *t*(30) = 2.09, *p* = .023, with a small to moderate effect size *d* = 0.37. (**B**) The average fruit collection rate over the one-minute block. A one-tailed paired t-test was conducted to evaluate whether the collection rate was higher without tonic pain (*M* = 18.22, *SD* = 3.45) than with tonic pain (*M* = 17.90, *SD* = 3.35), *t*(30) = 1.93, *p* = .031, with a small to moderate effect size *d* = 0.35. (**C**) A visualisation demonstrating the instantaneous hand speed at different percentages of total distance travelled in reaching to the fruit. Shaded area is the 95% confidence interval of the pairwise difference mean.

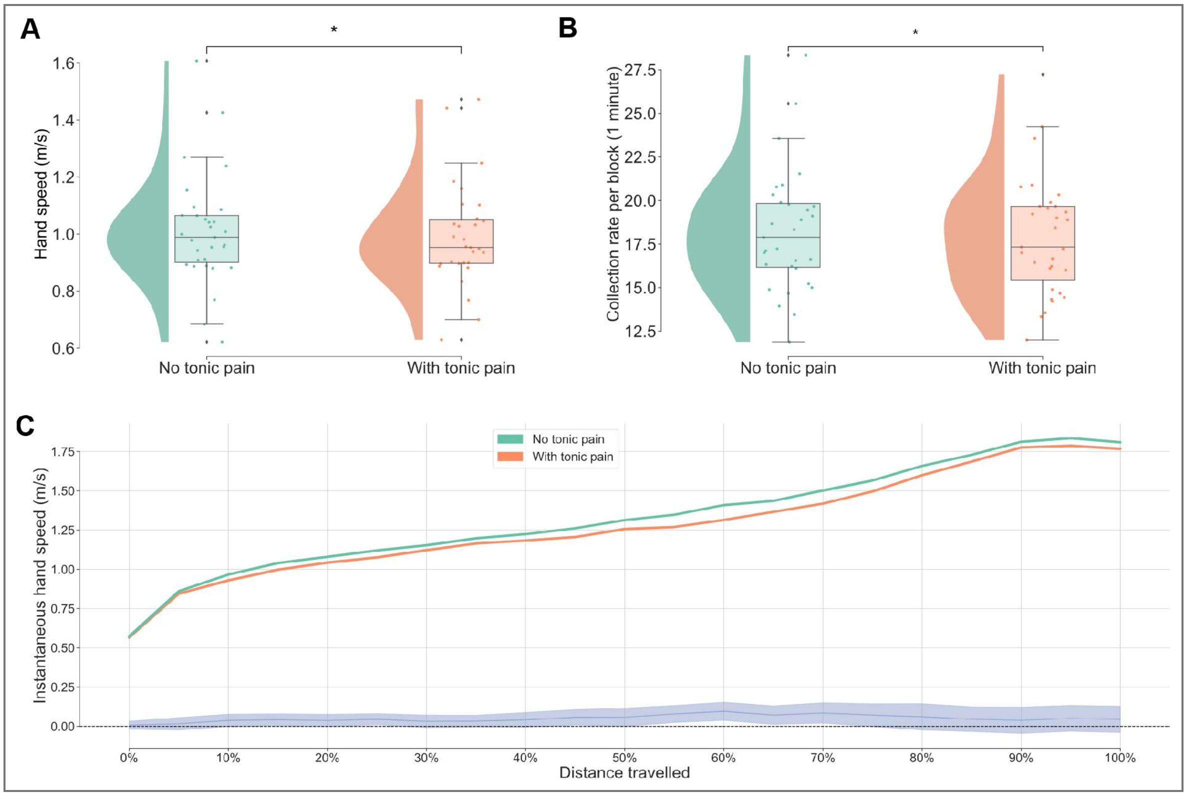
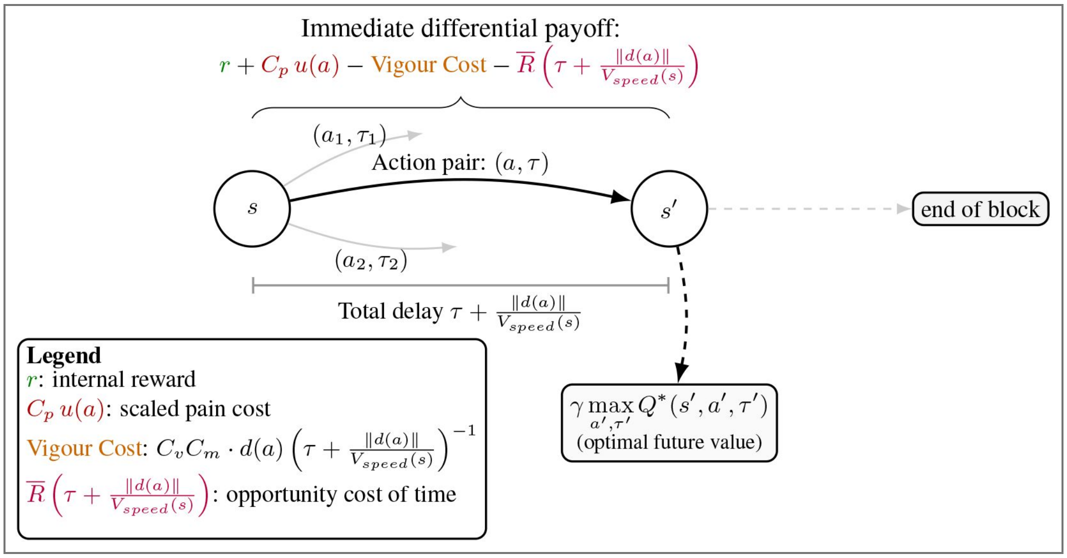


Figure 8. **Computational setup for Experiment 2 incorporating vigour and opportunity costs.**

The subject chooses a fruit *a* and a latency τ. The total delay $\left(\tau + \frac{\|d(a)\|}{V_{\text{speed}}(s)}\right)$ penalises the payoff via both a vigour-dependent effort cost and the opportunity cost of time.



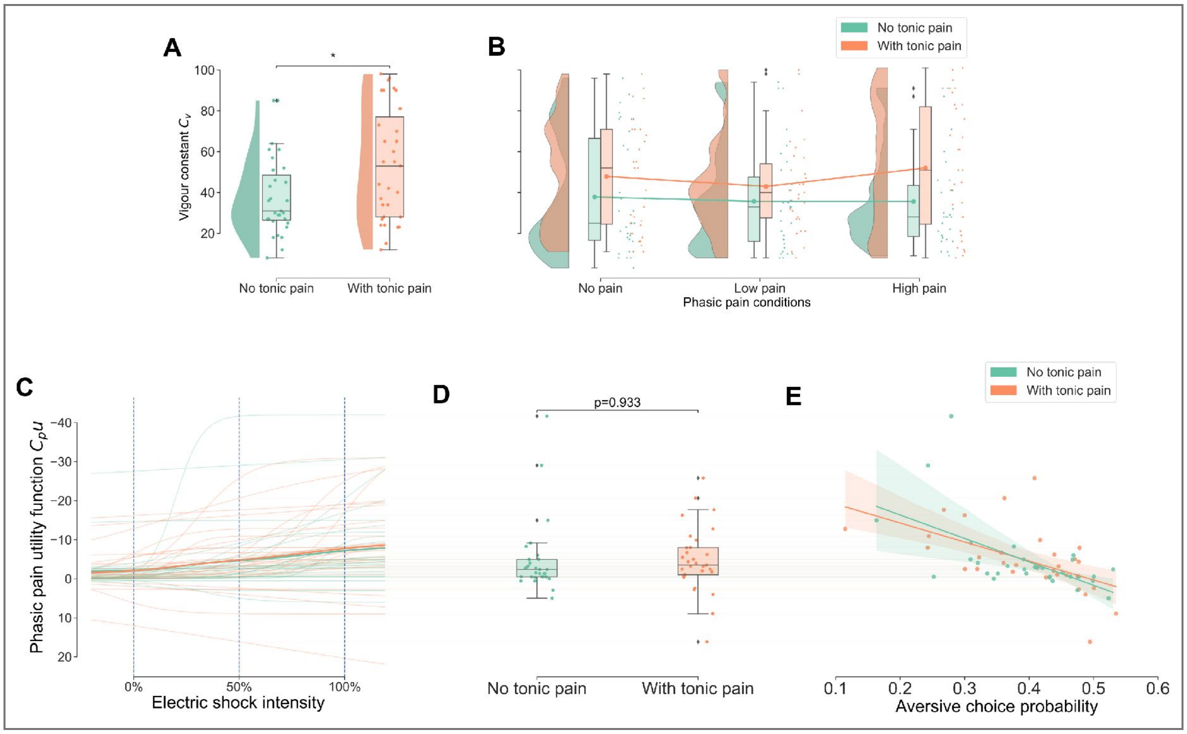


Figure 9. **Experiment 2 model-fitting results.**

(**A**) Fitted vigour constants were greater in tonic pain conditions (*M* = 53.61, *SD* = 27.17) than no tonic pain conditions (*M* = 38.16, *SD* = 18.88), *t*(30) = 2.37, *p* = .024. (**B**) Separate vigour constants fitting for each phasic pain conditions. Repeated measures ANOVA showed the effect for tonic pain was significant, *F* (1, 30) = 6.33, *p* = .017, but the effect for phasic pain was not significant, *F* (2, 60) = 0.40, *p* = .673. The interaction effect was not significant, *F* (2, 60) = 0.67, *p* = .515. (**C**) Phasic pain utility function curves. Solid lines are the average values in each condition. (**D**) Phasic pain utility function values at 50% electric shock intensity. A paired t-test was conducted and found no significant differences between no tonic pain (*M* = −4.645, *SD* = 8.982) and with tonic pain (*M* = −4.807, *SD* = 8.146) conditions, *t*(30) = 0.08, *p* = .933. (**E**) Phasic pain utility function values at 50% electric shock intensity plotted against aversive choice probability. Both conditions show a significant correlation between the fitted model values and behavioural choice probability. In blocks without tonic pain, R^2 = 0.337, *F* (1, 29) = 14.75, *p* < .001; in tonic pain conditions, R^2 = 0.311, *F* (1, 29) = 13.07, *p* = .001.

with the behavioural results presented above. The vigour constants and phasic pain function fitting results illustrate how we can combine two dissociable effects of pain motivation in a single model, consistent with the results from empirical regression.

Characterisation of neural activity during tonic pain

To probe the neural activity associated with the modulation of motivational vigour by tonic pain, we performed LMM-based time-frequency analysis on the EEG data. The data were epoched based on key decision points. Linear mixed models (LMM) were employed to account for random effects across subjects and to control for motion artefacts by including instantaneous head movement speed as an additional predictor. We found that alpha band power overlaying central-parietal and temporal regions (CP6 and T8), as well as beta power in parietal scalp regions (P8), was strongly associated with the presence of tonic pain (Fig. 10A).

To investigate how tonic pain impacts vigour, the vigour constants separately fitted to tonic pain conditions (Fig. 9A) were fit to the EEG data. We found that the alpha band power overlaying the midline parietal region (Pz) was significantly negatively correlated with the vigour constants, but it did not survive the multiple comparison correction (Fig. 10B).

Discussion

The experiments show that tonic and phasic pain serve different motivational functions during adaptive behaviour, in line with ecological and evolutionary theories of pain (Bolles and Fanselow, 1980; Walters and Williams, 2019). Specifically, our findings point towards phasic pain providing a punishment teaching signal that directs avoidance through value-based learning, balancing the cost of future harm alongside potential reward. This is supported by the observation that increasing phasic pain intensity significantly reduced choice probability and increased distance bias between choices, whereby participants were willing to travel further to reach a pain-free fruit. In contrast, we found that tonic pain reduces motivational vigour, which supports energy conservation and recuperation in the context of bodily damage. This claim is directly evidenced by the reduction in task-related movement velocities and fruit collection rates during tonic pain blocks. The experiments are the first to show that these two functions can be formally distinguished and quantified during ongoing behaviour. By utilising a free-operant RL computational framework, we were able to dissociate these roles: phasic pain was quantified as a generally negative utility term affecting choice values, while tonic pain was formalised as a change in vigour constants that were significantly higher (increasing delays between actions) in tonic pain condition. This illustrates how pain simultaneously acts in different ways to serve self-protection.

One notable aspect of our results is that we did not see interactions between tonic and phasic pain at either the behavioural or neural level. Behaviourally, we observed that average aversive choice probabilities remained similar regardless of the presence of tonic pain, with no significant interaction effect on punishment sensitivity. Furthermore, our model-fitting confirmed that tonic pain did not significantly modulate the fitted phasic pain utility values. There are two contexts in which these might be predicted. First, in 'conditioned pain modulation' paradigms (Kennedy et al., 2016), a tonic pain stimulus is sometimes seen to reduce both the perceived intensity and the cortical evoked responses to phasic pain stimuli delivered somewhere else on the body (Höffken et al., 2017; Enax-Krumova et al., 2020). Although we utilised concentric 'Wasp' electrodes designed to selectively activate nociceptive A-delta fibres (Inui et al., 2002), and confirmed that the resulting ERPs (N1-P2) were significantly modulated by phasic intensity, we observed no such attenuation by tonic pain. Indeed, neither subjective pain ratings nor the N1-P2 amplitude showed a significant modulation by the tonic pressure pain stimulus. In contrast, our results were more compatible with a trend in the other direction.

This finding raises the (testable) question as to what extent conditioned pain modulation depends on the task setting: notably, here we utilise an active in contrast to a passive task, which is known to be an important distinction in other contexts of coping behaviour (Bandler et al., 2000). In an active behavioural context, the brain may prioritise the fidelity of phasic pain as a teaching signal

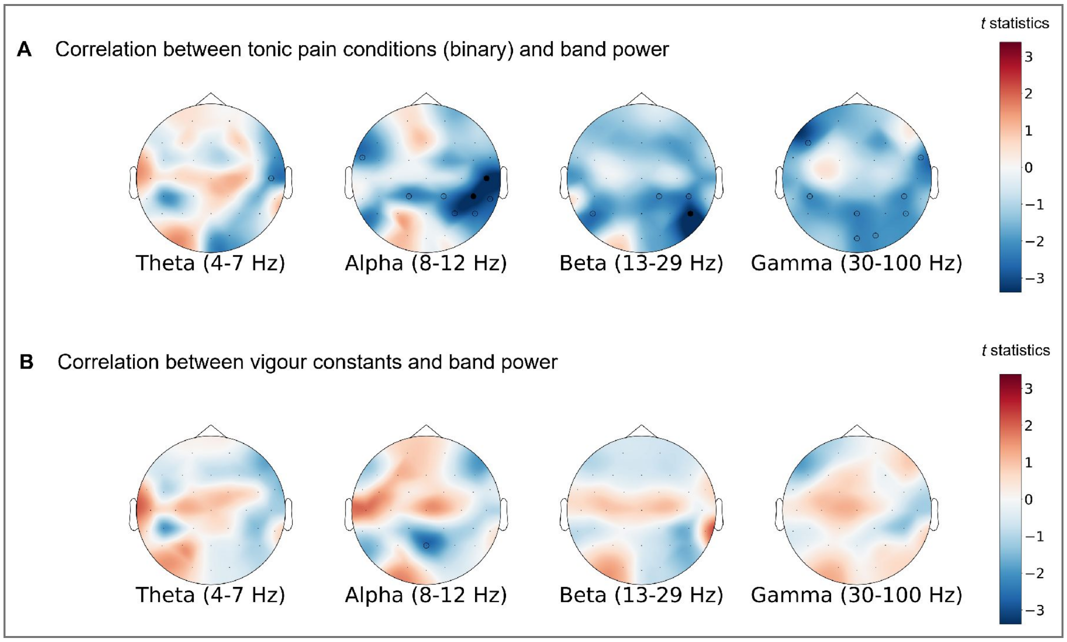


Figure 10.

(**A**) Topography of t-values from the LMM, with binary tonic pain condition as the independent variable and EEG band power 0–0.5 s after the decision point as the dependent variable. Empty circles represent channel power showing a significant association with tonic pain that does not survive Bonferroni correction. Solid circles indicate significant results after correction. Central-parietal and temporal scalp regions (CP6 and T8) showed significant decreases in alpha power predicted by tonic pain, $t = -3.52$ for CP6 and $t = -3.42$ for T8. A significant negative association with beta power was found in parietal scalp regions (P8), $t = -3.58$. (**B**) Topography of t-values from the LMM, with continuous vigour constants as the independent variable and EEG band power 0–0.5 s after the decision point as the dependent variable. Negative correlation was found with alpha band power at midline parietal electrode Pz, $t = -2.59$, $p = .010$.

for learning, potentially overriding modulation seen in passive CPM paradigms. A second context in which phasic-tonic interactions are possible is in punishment sensitivity, where it is proposed that tonic pain signals increase vulnerability to new phasic pain insults (Seymour et al., 2023). Punishment sensitivity is seen in terms of anxiety-like responses to novel threats in animals (Crook et al., 2014; Lister et al., 2020), and also in decision-making tasks in people with chronic pain (Mancini et al., 2024). However, we do not see an increase in the punishment value of phasic pain in relation to tonic pain here.

These two contexts highlight the potential difference between ratings and choice as measures of aversiveness, a concept that is sometimes referred to as experienced utility and decision utility (Kahneman and Tversky, 1984), or disliking and unwanting (the negative version of the liking-wanting distinction (Dayan and Seymour, 2009; Berridge et al., 2009), or put colloquially, ‘what you say’ versus ‘what you do’). In our task we get a further hint of this in the SCR measures in experiment 1, whereby a discrepancy exists between decision values and pain ratings in their respective associations with fixation-evoked SCRs and phasic pain-evoked (shock) SCRs. Taken together, this indicates the composite nature of overall aversiveness of pain, and highlights the benefit of combining subjective ratings with model-based measures of its motivational impact on behaviour.

The experiments show how probing objective motivational functions of pain is facilitated by VR. Conventionally, pain motivation is studied using desktop tasks in which decisions and physiological responses are made by a seated subject, responding via a keyboard with pain stimuli applied to a distant site. VR provides several useful advances. First, the ability to apply pain stimuli in a way that is appropriate to the action, i.e. phasic pain stimuli to a grasping hand, providing sensorimotor congruency. Second, the ability to embed pain within a free-operant and free-moving physical task allows evaluation of full-body responses to a topographic stimulus, and it is this in particular that allows assessment of motivational vigour. Third, the provision of a multisensory immersive environment entirely transforms a pain task into a naturalistic setting that matches the experience of pain in real-life. The importance of naturalistic contexts is well documented in fear learning, although less well studied for pain (Mobbs et al., 2015).

However, the use of VR requires an analysis framework that accommodates the complexity of free-operant and free-moving nature of behaviour. This challenge can be overcome with a computational approach and judicious use of simplifying assumptions where appropriate. The free operant model exploits a theoretical framework developed for animal studies that derives action delays from a trade-off between vigour cost and opportunity cost (Niv et al., 2007). This model has been applied to human studies (Nair et al., 2023), albeit in a much simpler setting involving perfect information and a single instantaneous action. In our task, the environment was partially observable and evolved as subjects interacted with it. By utilising eye-tracking to extract an abstract observation space and a modified version of the model that enabled simulation at high temporal resolution, we demonstrated that it is possible to predict free-operant behaviour in real-time. Compared to overall speed and collection rate, which can be influenced by multiple factors, such as different choice sets available to participants as the fruit locations are randomly generated, the model’s fitted parameters (e.g. vigour constant C_v) in theory serves as a direct, concrete estimate of that internal state. This approach revealed critical insights into a subject’s internal pain and motivational states.

A concern that is sometimes raised in pain experiments is to what extent the impact of pain on other behavioural and cognitive processes might be interpreted as an attentional phenomenon (e.g. distraction, or cognitive load), and therefore not specific to pain per se (Moont et al., 2010), specifically the reduction in vigour observed here. One argument to this point posits that attention is an intrinsic part of what pain is, and therefore it does not make sense to consider pain as an operational system without attention (Van Damme et al., 2010): i.e. tonic pain may mediate vigour effects by using distraction as a functional mechanism, and therefore attention is a core part of pain, and not a confound. One way to test this would be to add an additional condition comprising a tonic salient but non-painful stimulus (such as a continuous salient auditory stimulus), although this introduces other confounds related to the incommensurability of such dissimilar types of stimulation. Attentional arguments have also been proposed in CPM paradigms, but here it has been noted that CPM (and diffuse noxious inhibitory control) operates at least partly at a spinal/brainstem level, at 'lower' levels than those typically associated with attention (Youssef et al., 2016; Kucharczyk et al., 2023).

It is important to acknowledge that the signal-to-noise ratio in both our physiological and neural recordings is lower than that typically observed in conventional, stationary laboratory experiments (Gramann et al., 2011). This is primarily due to the motion artefacts inherent in an immersive and active virtual reality environment. Whilst we utilised robust cleaning and artefact-correction methods (Klug and Gramann, 2021), the elevated noise floor may limit our capacity to detect more subtle neural effects or interactions. These challenges highlight a critical area for future methodological research, particularly in the development of hardware and signal-processing tools designed to isolate neural signals during complex, mobile behavioural tasks.

Despite the greater levels of noise in EEG recordings due to our highly mobile task, an LMM-based approach (that incorporates head-movement speed into the model) revealed that suppression of oscillatory power in the alpha and beta bands in contralateral parietal and temporal regions during tonic pain was consistent with previous studies on tonic pain (Ferracuti et al., 1994; Huishi Zhang et al., 2016; Dowman et al., 2008; Schulz et al., 2015). When comparing how the neural correlates of tonic pain impacted motivational vigour, no oscillatory changes survived correction for multiple comparisons—although a trend towards reduced alpha power was observed at parietal scalp regions. Changes in alpha band power have been shown to affect neural activity in areas associated with sensory integration, attention, and motor planning (Hu et al., 2013; Palva and Palva, 2011), all of which are linked to motivational vigour.

It is also important to consider the spatial configuration of the stimuli used in this study. Phasic pain was delivered to the grasping hand to maintain spatial congruency with the virtual fruit, ensuring a coherent nociceptive feedback signal for the interactive task. Additionally, tonic pain was applied to the contralateral arm to prevent mechanical interference with motor execution, which would have occurred if pressure were applied to the ipsilateral limb used for grasping the controller. Whilst this design promotes spatial congruency and avoids mechanical confounds, future studies might explore how these effects generalise across different body parts, for which VR experiments serve as a promising tool to test relevant hypotheses (Hewitt et al., 2026).

Finally, the methodological framework has clinical applicability as a way to objectively measure pain behaviour in chronic pain. For instance, while conventional clinical trials often rely on Quantitative Sensory Testing (QST), which can deviate from real-world scenarios, our immersive VR task provides an ecologically valid and behaviourally sensitive evaluation of pain as a function of diagnosis or treatment. In addition, it could be implemented using real-time analysis to provide a feedback signal for closed-loop interventions, such as interactive VR rehabilitation or deep brain stimulation.

Methods

The free-operant foraging task

Foraging theory is a broad and well-studied subject within animal behaviour research. Various foraging study paradigms have been established in both laboratory and natural environments (Constantino and Daw, 2015; Charnov, 1976; Lihoreau et al., 2011). A natural foraging task, while simple for a healthy human to perform, encapsulates key components relevant to pain research. Firstly, foraging is goal-directed; subjects actively search for food under varying levels of motivation, allowing for the examination of the interaction between motivation and pain. Secondly, a natural foraging task involves full-body movement. Given that many types of pain are closely linked to movement and exercise, motion capture technology—a fundamental component of immersive VR—allows for precise recording and analysis of movement under different pain conditions. Finally, foraging involves exploring the environment and learning an optimal strategy to maximise rewards, naturally linking pain to cognitive functions. Motivated by these considerations, we designed the free-operant foraging task aimed at simulating realistic foraging behaviours.

At the beginning of each one-minute block, a total of 150 virtual pineapples of varying heights from 0.33 to 1 m were randomly generated in a circle centred around the participant with a diameter of 6.67 m. Five identical baskets were placed within the space. Spatial locations of trees and vegetation were generated using the game engine's default tree painting tool (Unity Technologies, San Francisco, US).

While the colour association (green for painful, yellow for pain-free) was not counter-balanced across subjects, any inherent aversive value of green pineapples (e.g. as 'unripe' fruit) is expected to have a minimal confounding effect on the analysed data. In associative learning frameworks, while mild prior biases may influence initial value estimations, extensive training with a highly salient unconditioned stimulus (e.g. phasic pain) rapidly updates these values, driving them toward an asymptote determined entirely by the explicit task contingencies (Rescorla and Wagner, 1972; Sutton and Barto, 2018). Because participants underwent extensive training (10 blocks in Experiment 1 and 6 blocks in Experiment 2) to establish the explicit pain associations prior to the analysed sessions, the observed avoidance behaviour was predominantly driven by the learned phasic pain contingencies rather than baseline colour preferences.

We used the HTC Vive Pro Eye headset and controllers in combination with Valve's SteamVR platform to track user motion in our Unity-based virtual environment. The system employs Lighthouse tracking, which uses infrared laser-emitting base stations and IR photodetectors to determine the position and orientation of tracked devices. Motion data from the headset and controllers were accessed in Unity via the SteamVR Unity plugin, which maps physical movements to virtual objects in real time. This setup enables accurate and low-latency motion representation in the virtual space, supporting immersive interaction during the experiment (Sansone et al., 2022). Data acquisition in Unity occurred at the rendering frame rate. The average delay between consecutive frames was 22.49 ± 5.82 ms.

Participants

A total of fifty-eight healthy subjects with no significant mobility issues were recruited from community and a pool of university staff and students. Twenty-five subjects were recruited for experiment 1; one subject was excluded due to technical failure. The final sample included 24 subjects (17 female, mean age 25.71 years). Thirty-three subjects were recruited for experiment 2. Two subjects were excluded due to technical failure and compliance failure, respectively. The final sample included 31 subjects (15 female, mean age 24.81 years). An a priori power analysis was not conducted due to the novelty of the investigation and the complexity of the analyses. Instead, we based our target sample size ($N \approx 30$ per experiment) on previous studies using computational modelling of neurophysiological data (Mahajan et al., 2025), as well as EEG, SCR, and pain studies (Schulz et al., 2015; Zhang et al., 2018), and studies from our group using combined neurophysiological recordings and VR (Hewitt et al., 2026). This approach represents a pragmatic balance that ensures the credibility of the results and the stability of model estimates while accounting for the high per-subject cost and depth of data collected from each individual.

The procedure was approved by the Research Ethics Committee of the University of Oxford (CUREC approval reference R58778), and all participants gave written informed consent at the start of the experiment following the Declaration of Helsinki. Participants were reimbursed with £30-£45 depending on the duration of experiment, including a £10 performance incentive. Participants were informed at the start of the experiment that their total points would be rewarded with a monetary incentive of up to £10. To maintain a constant level of motivation throughout the task, the exact point-to-currency exchange rate was not specified. Upon completion of the session, all participants were awarded the maximum bonus of £10.

Statistical Analysis

Statistical analysis was carried out using custom scripts written in Python 3 and R 4.4.2. For LMMs, lme4 and lmerTest packages were used (Bates et al., 2015; Kuznetsova et al., 2017). For LMMs presented in Figure 3, Figure 4, Figure 5, and Figure 10, fixed effects, random effects for intercepts and independent variables (IV) were estimated. The model also estimated the correlation between the intercept deviations and IV effect deviations across subjects. Supplementary materials provide additional details of the formula of the LMMs and their detailed outputs.

Model description and fitting

Experiment 1

As we disregarded planning, the model in experiment 1 compared $C_p u(a)+C_m \cdot d(a)$ for each fruit at a particular time point. The first question was what fruits were available for subjects to choose from. Fruits were abundant in the subjects' reachable area, however, many were not directly in subjects' visual field or hidden behind the trees. Subjects also needed to identify the fruits' colour to know whether the fruit was painful or not. Therefore, there was an additional search (or exploration) process that was not modelled here. We utilised eye-tracking technology (HTC Vive Pro Eye), and assumed only fruits that were in the central visual field were considered by the subject. Fruits that were captured by eye-tracking were saved into a first-in-first-out memory queue (the available choice set). We heuristically set the memory size to be 7, and the memory was cleared each time the subject chose a fruit. Next question was when the subject made a decision. The first time point that the subject looked at a pineapple not seen before could be used as the decision point in this free-operant task. However, we could not evaluate the model when the chosen fruit was not in the memory yet, as the model would never make a correct prediction out of a set of wrong candidates. We could only retrospectively identify the fruit that the subject chose and only fitted the model when the correct choice was in the choice set. This acausal problem is difficult to solve without taking time into consideration. We will show in the experiment 2 model fitting, by quantifying the effort and opportunity costs as a function of time delay, the model-fitting process was made causal.

We had converted the problem into finding a set of hyperparameters so that at each decision point, the maximum value of all choice differential values $C_p u(a) + C_m \cdot d(a)$ predicts the choice that the subject choose. Readers might find the problem similar to the multinomial logistic regression. However, as a decision model, we chose the objective function for the model-fitting to be the error rate (number of correct predictions divided by number of total predictions) rather than weighted least squares. The model is also flexible to take arbitrary parameters other than linear coefficients. As for this experiment, we chose u to be a sigmoid shape function with two additional x scale and translation hyperparameters. Grid search was used as a general method to find the hyperparameters that minimises the error rate. Grid search parameters can be found in supplementary materials.

To provide a detailed description regarding the computational framework, we summarise the properties of the first optimality equation and the underlying state-action space in Table 2.

The simulation and model-fitting process are conducted blockwise. Because the phasic pain intensity x_{stim} for green fruits is fixed for the duration of a single block, this information is treated as a known variable to the model rather than being explicitly encoded into the state space s. A discussion on the choice of constant x_{stim} for the duration of a single block is added in the Supplementary Material section: Discussion of Pain Intensity Information and Model Robustness.

Furthermore, we clarify the distinction between parameters and hyperparameters in this framework. Unlike traditional reinforcement learning models where internal parameters (such as action values or learning rates) may be continuously updated through trial-and-error, we have eschewed learning to maintain simplicity and focus on the steady-state motivational trade-offs.

Result	Dependent variables	Independent variables	Model
Fig. 3A	Aversive choice probability	Pain ratings, Subject (Random slope & intercept)	LMM
Fig. 3B	Choice distance bias	Pain ratings, Subject (Random slope & intercept)	LMM
Fig. 3G	Phasic pain utility values	Pain ratings, Subject (Random slope & intercept)	LMM
Fig. 4B	Phasic pain utility values	Fixation SCR coefficients, Subject (Random slope & intercept)	LMM
Fig. 4B	Pain ratings	Fixation SCR coefficients, Subject (Random slope & intercept)	LMM
Fig. 4C	Phasic pain utility values	Shock SCR coefficients, Subject (Random slope & intercept)	LMM
Fig. 4C	Pain ratings	Shock SCR coefficients, Subject (Random slope & intercept)	LMM
Fig. 5A–B	Pain ratings	Phasic pain, Tonic pain, Subject (Random Factor)	2-way RM ANOVA
Fig. 5C–D	Aversive choice probability	Pain ratings, Subject (Random slope & intercept)	LMM
Fig. 5E	Pain ratings	Phasic pain, Tonic pain, Subject (Random Factor)	2-way RM ANOVA
Fig. 6	N1–P2 amplitude	Phasic pain, Tonic pain, Subject (Random Factor)	2-way RM ANOVA
Fig. 9B	Vigour constant C_v	Phasic pain, Tonic pain, Subject (Random Factor)	2-way RM ANOVA
Fig. 9E	Phasic pain utility values	Aversive choice probability	Linear regression
Fig. 10A	Band power	Tonic pain, Head speed, Subject (Random slope & intercept)	LMM
Fig. 10B	Band power	Vigour constant (C_v), Head speed, Subject (Random slope & intercept)	LMM

Table 1. **Summary of statistical analyses, variables, and corresponding results.**

Table 2. Summary of model properties for the Experiment 1 foraging task

Property	**Description and Mathematical Definition**
State s (Decision Point)	A state $s \in \mathcal{S}$ is identified by the subject's current memory of available fruits. Formally, s is defined by an ordered list $M_s = (m_1, m_2, \ldots, m_n)$ where each m_i is a pair containing a fruit identifier (ID and colour) and its egocentric coordinates (x_i, y_i, z_i). The memory is limited to a maximum of $n = 7$ items and is governed by a first-in-first-out (FIFO) principle.
Action a	The set of actions $\mathcal{A}_s$ available at state s consists of picking up any pineapple currently stored in memory. There is a one-to-one mapping between each item $m_i \in M_s$ and an action $a_i \in \mathcal{A}_s$. Choosing action a_i corresponds to the execution of a reach-and-pickup trajectory towards the i-th fruit in the memory list.
Phasic Pain Utility $C_p u(a)$	The utility cost of phasic pain maps the categorical fruit type (colour) to a continuous value based on the block-specific pain intensity $x_{stim} \in \{0, 0.25, 0.5, 0.75, 1.0\}$. It is defined as: $$C_p u(a) = \begin{cases} \frac{C_p}{1+\exp(-k(x_{stim}-x_0))} & \text{if } a \text{ targets a green pineapple} \\ 0 & \text{if } a \text{ targets a yellow pineapple} \end{cases}$$ where C_p is the pain scaling parameter, k is the logistic growth rate (x-scale), and x_0 is the sigmoid midpoint (x-translation).
Distance $d(a)$	The physical effort associated with movement to the target fruit a, decomposed into horizontal and vertical components: $$d(a) = \begin{bmatrix} \sqrt{x_a^2 + y_a^2} \\ \lvert z_a \rvert \end{bmatrix}$$ where (x_a, y_a) represent the horizontal egocentric coordinates, and z_a represents the vertical egocentric coordinate.
Effort cost $C_m \cdot d(a)$	C_m is a unit vector consists of h and v which represent the horizontal and vertical effort coefficients, respectively. Therefore, the total effort cost is $$C_m \cdot d(a) = \begin{bmatrix} h \\ v \end{bmatrix} \cdot \begin{bmatrix} \sqrt{x_a^2 + y_a^2} \\ \lvert z_a \rvert \end{bmatrix} = h\sqrt{x_a^2 + y_a^2} + v\lvert z_a \rvert$$
Discount factor γ	0 (greedy policy, subsequent states not taken into account)
Hyperparameters	The set of parameters optimised for each subject is $\theta = \{k, x_0, C_p, h, v\}$. These parameters are held constant across all trials and blocks during the individual's simulation.

Table 3. Summary of model properties for the Experiment 2 foraging task (addendum to Experiment 1 Table)

Property	**Description and Mathematical Definition**
Waiting time τ	The time interval during which the subject is stationary or searching, prior to committing to a specific action (moving to the fruit and performing the pick-up action).
Scalar distance $\|d(a)\|$	The Euclidean norm of the distance vector $d(a)$, representing the total spatial displacement required: $\|d(a)\| = \sqrt{x_a^2 + y_a^2 + z_a^2}$.
V_{speed}	The moving speed calculated from historical movement patterns within the virtual environment.
Execution time $\frac{\|d(a)\|}{V_{speed}}$	The calculated duration required to physically reach the target fruit a given the estimated speed.
Total delay between actions	The comprehensive temporal cost associated with an action, which aligns with the opportunity cost of time: $\tau + \frac{\|d(a)\|}{V_{speed}}$.
Hyperparameters	The set of parameters optimised for each subject to describe their stable behavioural preferences: $\{k, x_0, C_p, C_v, h, v\}$.

Consequently, there are no “online” parameters; the hyperparameters listed in Table 2 are the only variables optimised via the fitting procedure to describe the subject’s stable behavioural preferences across the experimental conditions.

Experiment 2

A key assumption in Niv et al. (2007) was that animals chose an action pair of an action and a delay. The delay included both the time waiting and the time executing the action. It was an approximation of real animal behaviour, and in fitting to real human subjects data in this task, we did not have direct access to subjects’ delay decision. Therefore, we tracked the delay and computed the differential value at each time point. The central assumption in this model fitting solution was all differential values for the choices that were not chosen should be less than the value for the final chosen choice. The model-fitting program tracked the model predicted value for each fruit that a subject fixated on. The model’s predicted choice was correct (i.e., fit the data) when the chosen fruit had the highest predicted value (compared to other fruits within the time interval before the last fixation on the chosen fruit). Otherwise, the model’s predicted choice was incorrect. γ is still set to 0 for model-fitting in this experiment.

Experimental pain stimulation

Electric phasic pain

The electric stimulation pulses were generated by a DS5 isolated bipolar constant current stimulator (Digitimer, Letchworth Garden City, UK) and delivered using a Wasp pain stimulation electrode. These electrodes preferentially activate nociceptive A-delta fibres, thereby eliciting ERPs that more accurately reflect nociceptive processing compared to standard bipolar stimulation (Inui et al., 2002; Mørch et al., 2011). The pulses were 200 Hz square waves with a 1 ms pulse width.

Calibration of stimulation intensity was conducted based on subjects’ pain ratings before the task commenced. To maintain consistency in pain ratings, additional calibration could be performed at the end of the 10th block in experiment 1 or at the end of every six blocks in experiment 2. Subjects rated their pain on a 0-10 numerical rating scale while researchers adjusted the stimulation intensities following a staircase procedure. The calibration process was considered complete when subjects provided consistent pain ratings within the desired range, as determined by the experimental design (8/10 in experiment 1 for the max pain condition; 3/10 in experiment 2 for the low phasic pain condition and 7/10 for the high phasic pain condition). At the end of each block, subjects provided a pain rating for that block. Ratings in both procedures were given verbally. During calibration, researchers recorded the subjects’ verbal ratings, whereas in post-block ratings, verbal responses were processed using speech recognition services (Microsoft, Redmond, US) and automatically converted into a visual analogue scale bar displayed in VR. In case of speech recognition failure, researchers wrote down the ratings and manually updated the data for analysis.

Pressure tonic pain

We used pressure cuffs (VBM, Sulz, Germany) to safely induce tonic pain (Graven-Nielsen et al., 2015; Joseph et al., 2022). The cuff was wrapped around the non-dominant arm’s biceps. The cuffs were inflated prior to the start of each required block and immediately deflated after the block ended. Subjects were asked to report verbally when they felt discomfort and when they felt pain as the researcher manually inflated the cuff. Inflation stopped once the subject reported pain. To control for variables associated with wearing the cuff other than pain, pressure cuffs remained wrapped around the subjects’ arms even in blocks without tonic pain.

Skin conductance

Data collection and processing

Experiment 1 was designed to establish the robust behavioural effects of the foraging task while ensuring the collection of reliable physiological data. We chose SCR as it is a well-validated index of autonomic arousal that we were confident would provide a clear peripheral measure of pain-related processing in this novel VR paradigm. In Experiment 1, SCRs were collected using a custom-built wireless sensor. The microcontroller was an Arduino Nano 33 IoT (Arduino SA, Chiasso, Switzerland). The skin conductance sensor was a Grove GSR sensor (Seeed Studio, Shenzhen, China). The firmware was written by the authors of this article with a designated sampling rate of 1000 Hz.

Data was segmented by experimental blocks (60 seconds long each). An entire block of data was removed from further analysis if the data loss was more than 20% of the expected total number of samples due to temporary wireless transmission failure. Each block of data was down-sampled to 10 Hz, and re-centred by the average baseline. A median filter with a window size of 5 was applied to the down-sampled data to further remove artefacts. Further small gaps of missing data were handled in the GLM fitting in R with `na.action` set to `na.omit.` As subjects would only know the intensities of pain stimulation in new blocks after picking up a painful fruit, for fixation events, only events after picking up the first painful fruit were analysed.

Effect coefficient estimate

Generalised linear models (GLM) were used to fit the skin conductance time series data to the constructed time series data. The time series was generated by convolving the event trigger with the CRF, with hyperparameters taken from (Bach et al., 2010). Fixation events that occurred during picking up painful fruit were not included as shock-evoked SCR was strong. For computational practicality, convolutions were truncated between 0 and 60 seconds (the length of an experimental block) (Bach et al., 2009). The GLMs employed a Gaussian distribution with an identity link function. Each GLM was fitted separately to individual blocks, generating its own set of coefficient estimates. Fitted coefficients were thresholded based on a maximum p-value of 0.05. Additionally, coefficients with z-scores greater than 3 were excluded. The remaining coefficients, including negative ones, were used for further correlation analysis, as our focus was on the relationship between decision values, ratings, and coefficients.

EEG

Data collection and processing

Whole-scalp EEG data was continuously recorded with 32-channel LiveAmp system (BrainProducts GmbH, Munich, Germany) at 500Hz. We chose FCz as the reference. To remove ocular artefacts, recordings were first cleaned with EEGLAB (v2023.1) by removing channel drift (linear filter (FIR) transition band from 0.25 to 0.75 Hz). It also automatically removes bad data periods by thresholding max acceptable 0.5 second window standard deviation of 20, max acceptable channel RMS range of 7, and maximum out-of-bound channels of 25%. The ICA was then performed on the cleaned data and the weight matrix was computed and saved separately. Ocular artefact components were identified manually, assisted by automated classifier ICLabel (Pion-Tonachini et al., 2019). We then cleaned ocular artefacts by removing these identified components back projected onto the raw data. By manually inspecting the data, we interpolated up to 10% (3 channels) of electrodes. The output data at this stage served as the input data for ERP and time-frequency analysis separately.

ERP analysis

ERP analysis was conducted on the preprocessed data in Python with MNE-Python 1.7.0 package. The data was re-referenced to the average amplitude of all electrodes. A bandpass filter from 1 to 30 Hz was applied. The high cutoff frequency was chosen because of the presence of strong motion artefacts in our mobile EEG data. Identical analysis was applied at 0.1Hz and 0.5Hz high-pass cutoff frequencies, and significant results remained unchanged (see Supplementary figures). Recordings were processed into 1s epoch with 0.3s baseline before the event trigger. Epochs with peak-to-peak amplitude exceeding 200 μV in Cz channel were excluded (average rate of excluded epochs was 2.81%). We searched for N1 amplitude peaks from 100-170ms and P2 amplitude peaks from 140-300ms at channel Cz (Favero et al., 2023; van den Broeke et al., 2010).

LMM-based time-frequency analysis

Time-frequency analysis was performed on preprocessed data in Python with custom scripts relying on MNE-Python 1.7.0 package. The data was re-referenced to the average amplitude of all electrodes. A notch filter with 4Hz width centred at 50Hz was applied. Data were epoched from 0-0.5s according to the decision points. The decision points were chosen when subjects fixated on the chosen fruit for the first time, or at a re-evaluation point. A re-evaluation point was a subsequent fixation on the chosen fruit when other fruit had higher value than the chosen fruit but the new fixation on the chosen fruit surpassed other fruits' value. These time points were assumed to represent the key moments for decisions and thus chosen for analysing correlated neural activities.

The spectral power was estimated using Welch's method. A Hamming-tapered window was used with the window length equal to the epoch length (250 samples, 0.5 second). The estimated spectral power was separated into four bands: theta 4-7 Hz, alpha 8-12 Hz, beta 13-29 Hz, gamma 30-100 Hz (Levy et al., 2023; Chrastil et al., 2022; Schulz et al., 2015), and averaged within each band range. These band-averaged values formed the basis for the LMM-based time-frequency analysis presented in the main text, which was designed to statistically account for the task's complex noise profile. For each power band, averaged band power was inputted into an LMM for each channel as the dependent variable (Schulz et al., 2015). For each epoch, the z-score of the averaged band power was computed for each channel within the subject, and the epoch would be removed from LMM fitting for this band if any channel had a z-score greater than 3 (Nolan et al., 2010). For tonic pain effect, the binary condition of tonic pain presence was used as an independent variable. Random effects for tonic pain and intercepts were estimated. The model also estimates the correlation between the intercept deviations and tonic pain effect deviations across subjects. Crucially, a single head movement speed variable was added as an additional independent variable to reduce motion artefacts. The head movement speed for a particular epoch was calculated by averaging the speed between 10 Unity frames before the decision point and 10 Unity frames after the decision point. For vigour constants, the LMM had the same structure except replacing the binary tonic pain condition by fitted vigour constants presented in Figure 9A. Source analysis for spectral power was included in the Supplementary materials (section: Source Analysis). Furthermore, the analysis of induced oscillatory responses to phasic pain stimuli which supplement our ERP findings is provided in the Supplementary material (section: Induced oscillatory responses to phasic pain stimuli).

Data availability

Complete analysis code and raw data are released on GitHub: *https://github.com/ShuangyiTong/Phasic-and-tonic-pain-serve-distinct-functions-during-adaptive-behaviour* A series of software tools to replicate the experiment is available for download on GitHub: *https://github.com/ShuangyiTong/PineappleStudy2025ReplicationSoftware*

Acknowledgements

ST would like to thank Pranav Mahajan, Yijia Yan, Suyi Zhang, and Eoin Kelleher for their feedback on the content of this paper during the work-in-progress stage. ST also thanks Kirsty Bannister, Joseph Taylor, Kristian Hennings for sharing valuable knowledge on the safe use of pressure cuffs to induce tonic pain. Special thanks to Eoin Kelleher for providing an exceptional visual representation of the task (Fig. 1A). ST would like to thank the reviewers of IASP 2022, CCN 2023, and COSYNE 2024 for their feedback.

The work was funded by Wellcome Trust (214251/Z/18/Z, 203139/Z/16/Z and 203139/A/16/Z), IITP (MSIT 2019-0-01371, RS-2023-00233251), JSPS (22H04998), and EPSRC (EP/W03509X/1). This work was also funded by the EPSRC and MRC Research Grant Scheme under the reference number UKRI1970. This research was also partly supported by the NIHR Oxford Health Biomedical Research Centre (NIHR203316) and the Royal Academy of Engineering. The views expressed are those of the author(s) and not necessarily those of the NIHR or the Department of Health and Social Care. For the purpose of open access, the author has applied a CC BY public copyright licence to any Author Accepted Manuscript version arising from this submission.

Additional information

Author contributions

ST and BS designed the theory and experimental protocols. ST, BS, and TD developed the VR research platform used for the experiments. ST collected and analysed the data. ST and DH designed the EEG analysis pipeline and methodology. SL and TD provided critical feedback and theoretical insights throughout multiple iterations of the study. ST and BS wrote the first draft. ST, TD, DH, SL, and BS edited and approved the manuscript. TD, SL, and BS acquired funding for the study.

Funding

Funder	Grant reference number	Author
Wellcome Trust (WT)	214251/Z/18/Z	Ben Seymour
Wellcome Trust (WT)	203139/Z/16/Z	Ben Seymour
Wellcome Trust (WT)	203139/A/16/Z	Ben Seymour
MSIT | Institute for Information and Communications Technology Promotion (IITP)	2019-0-01371, RS-2023-00233251	Ben Seymour Sang Wan Lee
MEXT | Japan Society for the Promotion of Science (JSPS)	22H04998	Ben Seymour
UKRI | Engineering and Physical Sciences Research Council (SRC)	EP/W03509X/1	Ben Seymour
NIHR Oxford Health Biomedical Research Centre	NIHR203316	Ben Seymour
Royal Academy of Engineering (RAENG)		Tim Denison
EPSRC and MRC Research Grant Scheme	UKRI1970	Tim Denison Ben Seymour

Author ORCID iDs

Shuangyi Tong: https://orcid.org/0009-0003-4985-6600
Danielle Hewitt: https://orcid.org/0000-0003-2245-4962
Sang Wan Lee: https://orcid.org/0000-0001-6266-9613
Ben Seymour: https://orcid.org/0000-0003-1724-5832

Additional files

Supplementary Materials.

References

Anderson D (1983) Optimal foraging and the traveling salesman. *Theoretical Population Biology* **24**:145-159 https://doi.org/10.1016/0040-5809(83)90038-2

Bach DR, Flandin G, Friston KJ, Dolan RJ (2009) Time-series analysis for rapid event-related skin conductance responses. *J. Neurosci. Methods* **184**:224-234 https://doi.org/10.1016/j.jneumeth.2009.08.005 | PubMed

Bach DR, Flandin G, Friston KJ, Dolan RJ (2010) Modelling event-related skin conductance responses. *International Journal of Psychophysiology* **75**:349-356 https://doi.org/10.1016/j.ijpsycho.2010.01.005 | PubMed

Bandler R, Price JL, Keay KA (2000) Brain mediation of active and passive emotional coping. *Progress in brain research* **122**:333-349 https://doi.org/10.1016/s0079-6123(08)62149-4 | PubMed

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* **67**:1-48

Berridge KC, Robinson TE, Aldridge JW (2009) Dissecting components of reward:'liking','wanting', and learning. *Current opinion in pharmacology* **9**:65-73 https://doi.org/10.1016/j.coph.2008.12.014 | PubMed

Bolles RC, Fanselow MS (1980) A perceptual-defensive-recuperative model of fear and pain. *Behavioral and Brain Sciences* **3**:291-301 https://doi.org/10.1017/s0140525x0000491x

Charnov EL (1976) Optimal foraging, the marginal value theorem. *Theoretical Population Biology* **9**:129-136 https://doi.org/10.1016/0040-5809(76)90040-x | PubMed

Chrastil ER, Rice C, Goncalves M, Moore KN, Wynn SC, Stern CE, Nyhus E (2022) Theta oscillations support active exploration in human spatial navigation. *NeuroImage* **262**:119581 https://doi.org/10.1016/j.neuroimage.2022.119581 | PubMed

Constantino SM, Daw ND (2015) Learning the opportunity cost of time in a patch-foraging task. *Cognitive, Affective, & Behavioral Neuroscience* **15**:837-853 https://doi.org/10.3758/s13415-015-0350-y | PubMed

Crook RJ, Dickson K, Hanlon RT, Walters ET (2014) Nociceptive sensitization reduces predation risk. *Current Biology* **24**:1121-1125 https://doi.org/10.1016/j.cub.2014.03.043 | PubMed

Dayan P, Seymour B (2009) Values and actions in aversion. In: Glimcher PW, Camerer CF, Fehr E, Poldrack RA (Eds). *Neuroeconomics* Elsevier. pp. 175-191

Dowman R, Rissacher D, Schuckers S (2008) Eeg indices of tonic pain-related activity in the somatosen-sory cortices. *Clinical Neurophysiology* **119**:1201-1212 https://doi.org/10.1016/j.clinph.2008.01.019 | PubMed

Enax-Krumova E, Plaga A.-C, Schmidt K, Özgül S, Eitner LB, Tegenthoff M, Höffken O (2020) Painful cutaneous electrical stimulation vs. heat pain as test stimuli in conditioned pain modulation. *Brain Sciences* **10** https://doi.org/10.3390/brainsci10100684 | PubMed

Favero JD, Luck C, Lipp OV, Nguyen AT, Marinovic W (2023) N1-p2 event-related potentials and perceived intensity are associated: The effects of a weak pre-stimulus and attentional load on processing of a subsequent intense stimulus. *Biological Psychology* **184**:108711 https://doi.org/10.1016/j.biopsycho.2023.108711 | PubMed

Ferracuti S, Seri S, Mattia D, Cruccu G (1994) Quantitative eeg modifications during the cold water pressor test: hemispheric and hand differences. *International Journal of Psychophysiology* **17**:261-268 https://doi.org/10.1016/0167-8760(94)90068-x | PubMed

Fields HL (2006) A motivation-decision model of pain: the role of opioids. In: Proceedings of the 11th world congress on pain. pp. 449-459

Gramann K, Gwin JT, Ferris DP, Oie K, Jung T.-P, Lin C.-T, Liao L.-D, Makeig S (2011) Cognition in action: imaging brain/body dynamics in mobile humans. *Reviews in the Neurosciences* **22**:593-608 https://doi.org/10.1515/rns.2011.047 | PubMed

Graven-Nielsen T, Izumi M, Petersen KK, Arendt-Nielsen L (2017) User-independent assessment of conditioning pain modulation by cuff pressure algometry. *European Journal of Pain* **21**:552-561 https://doi.org/10.1002/ejp.958 | PubMed

Graven-Nielsen T, Vaegter HB, Finocchietti S, Handberg G, Arendt-Nielsen L (2015) Assessment of musculoskeletal pain sensitivity and temporal summation by cuff pressure algometry: a reliability study. *Pain* **156** https://doi.org/10.1097/j.pain.0000000000000294 | PubMed

Hewitt D, Tong S, Schreiber S, Seymour B (2026) Tonic pain modulates neural correlates of associative phasic pain memories. *Pain* **167**:1318-1330 https://doi.org/10.1097/j.pain.0000000000003917 | PubMed

Höffken O, Özgül ÖS, Enax-Krumova EK, Tegenthoff M, Maier C (2017) Evoked potentials after painful cutaneous electrical stimulation depict pain relief during a conditioned pain modulation. *BMC Neurology* **17**:167 https://doi.org/10.1186/s12883-017-0946-7 | PubMed

Hu L, Peng W, Valentini E, Zhang Z, Hu Y (2013) Functional features of nociceptive-induced suppression of alpha band electroencephalographic oscillations. *The Journal of Pain* **14**:89-99 https://doi.org/10.1016/j.jpain.2012.10.008 | PubMed

Huishi Zhang C, Sohrabpour A, Lu Y, He B (2016) Spectral and spatial changes of brain rhythmic activity in response to the sustained thermal pain stimulation. *Human Brain Mapping* **37**:2976-2991 https://doi.org/10.1002/hbm.23220 | PubMed

Inui K, Tran TD, Hoshiyama M, Kakigi R (2002) Preferential stimulation of aδ fibers by intraepidermal needle electrode in humans. *Pain* **96** https://doi.org/10.1016/s0304-3959(01)00453-5 | PubMed

Jeon JY, Shim WM, Yoo SBM (2023) Generative model for explaining spatial regularity detection behavior of humans while foraging. In: Conference on Cognitive Computational Neuroscience 2023. https://doi.org/10.32470/ccn.2023.1496-0

Joseph T, Mansfield M, Cummins T, MacMahon S, Fielding A, Graven-Nielsen T, Bannister K (2022) Does activation of a descending modulatory control impact the development of secondary hyperalgesia. In: The World Congress on Pain (IASP 2022).

Kahneman D, Tversky A (1984) Choices, values, and frames. *American psychologist* **39**:341 https://doi.org/10.1037/0003-066x.39.4.341

Kennedy DL, Kemp HI, Ridout D, Yarnitsky D, Rice AS (2016) Reliability of conditioned pain modulation: a systematic review. *Pain* **157** https://doi.org/10.1097/j.pain.0000000000000689 | PubMed

Klug M, Gramann K (2021) Identifying key factors for improving ica-based decomposition of eeg data in mobile and stationary experiments. *European Journal of Neuroscience* **54**:8406-8420 https://doi.org/10.1111/ejn.14992 | PubMed

Kucharczyk MW, Di Domenico F, Bannister K (2023) A critical brainstem relay for mediation of diffuse noxious inhibitory controls. *Brain* **146**:2259-2267 https://doi.org/10.1093/brain/awad002 | PubMed

Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software* **82**:1-26 https://doi.org/10.18637/jss.v082.i13

Levy A, Enisman M, Perry A, Kleiman T (2023) Midfrontal theta as an index of conflict strength in approach–approach vs avoidance–avoidance conflicts. *Social Cognitive and Affective Neuroscience* **18**:sad038 https://doi.org/10.1093/scan/nsad038 | PubMed

Lihoreau M, Chittka L, Raine NE (2011) Trade-off between travel distance and prioritization of high-reward sites in traplining bumblebees. *Functional Ecology* **25**:1284-1292 https://doi.org/10.1111/j.1365-2435.2011.01881.x | PubMed

Lister KC, Bouchard SM, Markova T, Aternali A, Denecli P, Pimentel SD, Majeed M, Austin J.-S, Williams AC. d. C, Mogil JS (2020) Chronic pain produces hypervigilance to predator odor in mice. *Current Biology* **30**:R866-R867 https://doi.org/10.1016/j.cub.2020.06.025 | PubMed

Mahajan P, Tong S, Lee SW, Seymour B (2025) Balancing safety and efficiency in human decision-making. *eLife* **13**:RP101371 https://doi.org/10.7554/eLife.101371

Mancini F, Mahajan P, Guttesen A. á. V, Onysk J, Scholtes I, Shenker N, Lee M, Seymour B (2024) Enhanced behavioural and neural sensitivity to punishments in chronic pain and fatigue. *bioRxiv* https://doi.org/10.1101/2024.04.04.588151

Mobbs D, Hagan CC, Dalgleish T, Silston B, Prévost C (2015) The ecology of human fear: survival optimization and the nervous system. *Frontiers in neuroscience* **9**:121062 https://doi.org/10.3389/fnins.2015.00055 | PubMed

Moont R, Pud D, Sprecher E, Sharvit G, Yarnitsky D (2010) ‘pain inhibits pain’ mechanisms: Is pain modulation simply due to distraction?. *Pain* **150**:113-120 https://doi.org/10.1016/j.pain.2010.04.009 | PubMed

Mørch CD, Hennings K, Andersen OK (2011) Estimating nerve excitation thresholds to cutaneous electrical stimulation by finite element modeling combined with a stochastic branching nerve fiber model. *Medical & Biological Engineering & Computing* **49**:385-395 https://doi.org/10.1007/s11517-010-0725-8 | PubMed

Nair A, Niyogi RK, Shang F, Tabrizi SJ, Rees G, Rutledge RB (2023) Opportunity cost determines free-operant action initiation latency and predicts apathy. *Psychological Medicine* **53**:1850-1859 https://doi.org/10.1017/s0033291721003469 | PubMed

Niv Y, Daw N, Dayan P (2005) How fast to work: Response vigor, motivation and tonic dopamine. In: Weiss Y, Schölkopf B, Platt J (Eds). *Advances in Neural Information Processing Systems* **18** MIT Press.

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

Nolan H, Whelan R, Reilly R (2010) Faster: Fully automated statistical thresholding for eeg artifact rejection. *Journal of Neuroscience Methods* **192**:152-162 https://doi.org/10.1016/j.jneumeth.2010.07.015 | PubMed

Palva S, Palva JM (2011) Functional roles of alpha-band phase synchronization in local and large-scale cortical networks. *Frontiers in Psychology* **2** https://doi.org/10.3389/fpsyg.2011.00204 | PubMed

Pion-Tonachini L, Kreutz-Delgado K, Makeig S (2019) Iclabel: An automated electroencephalographic independent component classifier, dataset, and website. *NeuroImage* **198**:181-197 https://doi.org/10.1016/j.neuroimage.2019.05.026 | PubMed

Rescorla R, Wagner A (1972) A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement. In: Black AH, Prokasy WF (Eds). *Classical Conditioning II: Current Theory and Research* Appleton-Century-Crofts. pp. 64-99

Sansone LG, Stanzani R, Job M, Battista S, Signori A, Testa M (2022) Robustness and static-positional accuracy of the steamvr 1.0 virtual reality tracking system. *Virtual Reality* **26**:903-924 https://doi.org/10.1007/s10055-021-00584-5

Schulz E, May ES, Postorino M, Tiemann L, Nickel MM, Witkovsky V, Schmidt P, Gross J, Ploner M (2015) Prefrontal gamma oscillations encode tonic pain in humans. *Cerebral Cortex* **25**:4407-4414 https://doi.org/10.1093/cercor/bhv043 | PubMed

Seymour B (2019) Pain: a precision signal for reinforcement learning and control. *Neuron* **101**:1029-1041 https://doi.org/10.1016/j.neuron.2019.01.055 | PubMed

Seymour B, Crook RJ, Chen ZS (2023) Post-injury pain and behaviour: a control theory perspective. *Nature Reviews Neuroscience* **24**:378-392 https://doi.org/10.1038/s41583-023-00699-5 | PubMed

Sutton RS, Barto AG (2018) Adaptive computation and machine learning. In: *Reinforcement learning: An introduction* (2nd Ed) Cambridge, MA, US: The MIT Press.

Van Damme S, Legrain V, Vogt J, Crombez G (2010) Keeping pain in mind: A motivational account of attention to pain. *Neuroscience Biobehavioral Reviews* **34**:204-213 https://doi.org/10.1016/j.neubiorev.2009.01.005 | PubMed

van den Broeke EN, van Rijn CM, Biurrun Manresa JA, Andersen OK, Arendt-Nielsen L, Wilder-Smith OHG (2010) Neurophysiological correlates of nociceptive heterosynaptic long-term potentiation in humans. *Journal of Neurophysiology* **103**:2107-2113 PubMed | https://doi.org/10.1152/jn.00979.2009

Wall PD (1979) Three phases of evil: the relation of injury to pain. *Brain and Mind* **69**:293 https://doi.org/10.1002/9780470720523.ch17 | PubMed

Walters ET, Williams AC. d. C (2019) Evolution of mechanisms and behaviour important for pain. *Philosophical Transactions: Biological Sciences* **374**:20190275 https://doi.org/10.1098/rstb.2019.0275

Youssef A, Macefield V, Henderson L (2016) Pain inhibits pain; human brainstem mechanisms. *NeuroImage* **124**:54-62 https://doi.org/10.1016/j.neuroimage.2015.08.060 | PubMed

Zhang S, Mano H, Lee M, Yoshida W, Kawato M, Robbins TW, Seymour B (2018) The control of tonic pain by active relief learning. *eLife* **7**:e31949 https://doi.org/10.7554/eLife.31949 | PubMed

Peer reviews

Reviewer #1 (Public review):

Summary:

This article presents a study consisting of two experiments, which aim to dissociate and quantify the distinct motivational functions of phasic and tonic pain within a naturalistic and immersive VR setting. Specifically, the Authors test two hypotheses: (i) that phasic pain acts as a punishment signal that drives avoidance learning; (ii) that tonic pain reduces motivational vigor, promoting energy conservation and recuperation. In both experiments, participants performed a free-operant foraging task, where they collected virtual pineapples to earn points.

In Experiment 1, phasic pain was delivered as a brief electric shock to the grasping hand when picking up green pineapples. As phasic pain intensity increased, participants were less likely to choose painful fruits. A reinforcement learning model that incorporated reward, pain cost and effort cost was able to successfully capture behavior.

Experiment 2 combined effects of phasic and tonic pain. Tonic pain was induced by a pressure cuff on the non-dominant arm, simulating sustained discomfort. Interestingly, tonic pain did not affect the perceived intensity or avoidance of phasic pain. However, it significantly reduced movement velocity and pineapple collection rate, interpreted as a reduction of motivational vigor. A temporal decision model incorporating vigor cost successfully captured these effects.

Concomitant EEG recordings showed that tonic pain was associated with reduced alpha and beta power in parietal and temporal areas. Phasic pain ratings and decision values distinctively correlated with skin conductance responses.

Overall, these findings indicate that phasic and tonic pain have distinct and dissociable motivational effects.

Strengths:

This is an ambitious study that provides a quantitative dissociation of the roles of phasic and tonic pain in adaptive behavior, by integrating ecological neuroscience, motivational theory, and computational modeling. The use of immersive VR combined with a free-operant foraging task offers a more ecologically valid context to study pain-related behavior compared to traditional paradigms. Furthermore, the study employs a multimodal approach by combining behavioral data, computational frameworks, physiological signals and EEG. In particular, one of the main strengths of the study is the use of sophisticated computational modeling to capture phasic and tonic pain effects. The experiment codes are available on GitHub, increasing reproducibility.

Weaknesses:

As recognized by the Authors, there is no control condition involving an innocuous salient stimulus to rule out non-specific effects of distraction.

https://doi.org/10.7554/eLife.107911.2.sa3

Reviewer #2 (Public review):

Summary:

The study investigated the distinct roles of phasic and tonic pain in adaptive behavior. Phasic pain was proposed to function as a teaching signal, promoting avoidance of further injury, while tonic pain was hypothesized to support recuperative behavior by reducing motivational vigor. This hypothesis was tested using an immersive virtual reality (VR) EEG foraging task, in which participants harvested fruit in a forest environment. Some fruits triggered brief phasic pain to the grasping hand, which in turn reduced the likelihood of choosing those fruits. Concurrently, tonic pressure pain applied to the contralateral upper arm was associated with reduced action velocities. The authors employed a free-operant computational framework to quantify how phasic and tonic pain modulate motivational vigor and decision value. Importantly, model parameters were found to correlate with EEG responses, providing neurophysiological support for the hypothesized functional distinctions.

Comments on revised version.

All my comments have been well addressed.

https://doi.org/10.7554/eLife.107911.2.sa2

Reviewer #3 (Public review):

Summary:

This study investigates how phasic and tonic pain modulate behaviour in a free-operant foraging paradigm. The authors apply a computational modeling approach to the behavioural data to quantify the decision value of phasic pain, as well as the degree to which tonic pain reduces motivational vigour. EEG assessments showed, e.g., reduced signal power at alpha and beta frequencies in tonic pain conditions compared to no-tonic-pain conditions, but no association between these neural measures and motivational vigour. The authors conclude that tonic and phasic pain serve different motivational functions, with phasic pain acting as a punishment signal promoting avoidance and tonic pain reducing motivational vigour.

Strengths:

The experimental paradigm is highly innovative. Assessing human behaviour in a naturalistic yet highly controlled setting represents a promising approach to pain research. Notably, assessing pain magnitude implicitly, via its motivational value, offers insights about the overall pain experience that are not usually accessible via common pain ratings.

https://doi.org/10.7554/eLife.107911.2.sa1

Author response:

The following is the authors’ response to the original reviews.

> ***Reviewer #1 (Public review):***
>
> *Strengths:*
>
> *This is an ambitious study that provides a quantitative dissociation of the roles of phasic and tonic pain in adaptive behavior, by integrating ecological neuroscience, motivational theory, and computational modeling. The use of immersive VR combined with a freeoperant foraging task offers a more ecologically valid context to study pain-related behavior compared to traditional paradigms. Furthermore, the study employs a multimodal approach by combining behavioral data, computational frameworks, physiological signals, and EEG. In particular, one of the main strengths of the study is the*

> *use of sophisticated computational modeling to capture phasic and tonic pain effects. The experiment codes are available on GitHub, increasing reproducibility.*

We appreciate the reviewers' recognition of the study's ambition, the integration of ecological and computational approaches, and our efforts to support reproducibility through open code.

> *Weaknesses:*
>
> *The main limitations of this article are that it provides insufficient detail on VR implementation. The design of the VR environment is, at this stage, under-described. Crucial information is missing, such as the number of pineapples per block, timing precision, details on how motion is mapped to the virtual movement, etc. This aspect strongly limits the reproducibility of the experiments.*

We thank the reviewer for highlighting the importance of detailed reporting to ensure reproducibility. In response to this valuable feedback, we have taken the following steps:

(1) Open Access to Software and Data: We have now uploaded the full software and hardware specifications used in our study to a public GitHub repository: *https://github.com/ShuangyiTong/PineappleStudy2025ReplicationSoftware*. This includes the complete VR implementation, allowing readers to directly experience the task using a commercially available VR headset. The repository also contains the raw data and analysis scripts to facilitate full replication of our results. These links have been updated in "Data and Code Availability" section.

(2) Expanded Methodological Details: We have revised the Methods section to include the specific details requested, such as:

(a) The number of pineapples presented per block,

(b) The temporal resolution and precision of the data collection,

(c) The mapping between physical motion and virtual movement within the VR environment.

Specifically, the paragraph containing the changes is following: "At the beginning of each one-minute block, a total number of 150 virtual pineapples of varying heights from 0.33 to 1 m were randomly generated in a circle centred around the participant with a diameter of 6.67 m. Five identical baskets were placed within the space. Spatial locations of trees and vegetation were generated using the game engine's default tree painting tool (Unity Technologies, San Francisco, US)."

We hope these updates address the reviewer's concerns and significantly improve the transparency and reproducibility of our experimental design.

> *A second limitation lies in the lack of clarity regarding the study hypotheses. Although two overarching hypotheses can be inferred, they are not explicitly formulated. To this end, it is unclear which analyses were merely exploratory, especially for physiological and EEG outcomes.*

We thank the reviewer for this constructive feedback. We agree that making the hypotheses more explicit—particularly regarding the computational framework and the role of physiological measures—strengthens the manuscript. We have significantly revised the final section of the Introduction to explicitly formulate our two primary hypotheses and operationalise the associated behavioural and neurophysiological measures.

(1) Phasic Pain Hypothesis: We hypothesised that phasic pain serves as a discrete valuation signal that updates the state-action value of specific actions. We predicted this would be evidenced behaviourally by reduced choice probability and increased 'distance bias' for pain-

associated targets. Neurally and physiologically, we predicted that these aversive values would be tracked by skin conductance responses (SCRs) and the amplitude of pain event-related potentials (ERPs), which serve as established markers for the encoding of aversive magnitude and salience.

(2) Tonic Pain Hypothesis: We hypothesised that tonic pain acts as a coefficient modulating the trade-off between opportunity cost and vigour cost. This was tested by applying tonic pain to the non-dominant (non-task) limb to ensure that any observed changes were motivational rather than mechanical. We predicted a global reduction in motivational vigour, operationalised as decreased movement velocities and foraging rates.

By framing the study this way, we clarify that the physiological and EEG outcomes were used to quantitatively test whether the brain and body implement the computations (valuation and vigour-regulation) defined by our model. We have updated the text in the Introduction (see below) to reflect these explicit formulations.

Updated paragraphs: “Our first hypothesis was that phasic pain provides a distinct valuation signal that updates the value of specific actions within complex environments. In our task, this was implemented by associating specific fruit (distinguishable by colour) with a brief electrical stimulus to the grasping hand, emulating thorns. In our computational model, this was defined as an aversive utility term incorporated into the state-action value evaluation process. We predicted that this computational mechanism would manifest behaviourally as a reduction in choice probability for pain-associated targets and an increase in ‘choice distance bias’ (the willingness to travel further for pain-free options). Neurally and physiologically, we predicted that these aversive values would be tracked by skin conductance responses (SCRs) and the amplitude of nociceptive event-related potentials (ERPs), specifically the N1-P2 complex (Favero et al., 2023).

Second, we hypothesised that tonic pain acts as a coefficient modulating the tradeoff between opportunity cost and vigour cost, thereby serving a recuperative function. To test this in Experiment 2, we delivered continuous tonic pressure to the non-dominant arm via an inflated cuff to emulate a background state of injury. Within our free-operant framework, tonic pain was modelled as a weighting factor that shifts the optimal balance toward reduced energy expenditure. Because the stimulus was applied to the non-task limb, we specifically predicted a global reduction in motivational vigour—operationalised as decreased movement velocities and foraging rates—rather than a direct mechanical impairment. By applying this formal computational approach, we move beyond exploratory observations to provide a rigorous, mechanism-based explanation for how distinct pain states adaptively govern choice and action.”

> *In Experiment 2, the reduction in vigor during tonic pain could plausibly reflect attentional load rather than pain per se. As recognized by the authors, there is no control condition involving an innocuous salient stimulus to rule out non-specific effects of distraction. Perhaps a tonic non-painful but salient somatosensory stimulus (e.g., a strong vibrotactile stimulus applied on the same arm) could have been used as a control stimulus.*

We agree that examining the potential role of attentional load on the interaction between tonic and phasic pain is an important area of future investigation. The inclusion of additional control conditions matched for attentional salience with additional experiments is possible but introduces other confounds related to their different qualities (e.g. a salient vibrotactile stimulus might invigorate behaviour). More fundamentally, attentional processes are a core part of pain function, and should not necessarily be viewed as a confound (i.e. the way that pain mediates some of its core functional effects may directly be through its salient attentional nature). This view is formalised in Wall and Melzack’s classical tripartite model of pain, and distinguishes pain from purely sensory systems such as somatosensation, vision and so on.

> ***Reviewer #1 (Recommendations for the authors):***
>
> *(1) Computational models may be difficult to follow without prior familiarity. Including simplified explanations could make the approach more accessible.*

We thank the reviewer for this constructive suggestion. To make the computational framework more accessible to a broader audience, we have added two new schematic diagrams (Figure 2 and Figure 8) that provide a visual overview of the models used in Experiment 1 and Experiment 2, respectively. These figures illustrate the state-action transitions and provide a clear decomposition of the payoff components—including reward, pain, and temporal costs. We believe these additions significantly clarify the modelling logic and help ground the mathematical descriptions in a more intuitive visual context.

> *(2) Lines 220-222: I don't think it is possible to talk about "objective measures of pain" as pain is, by definition, subjective. I suggest rephrasing the sentence.*

We thank the reviewer for this thoughtful observation regarding our terminology. We recognise that the phrase ‘objective measures of pain’ may be misintepreted. Our intention was to highlight the distinction between the internal, reported experience and the behavioural manifestations of pain that our computational method reveals.

To avoid ambiguity and to better align the text with the core focus of our study, which is the motivational function of pain, we have rephrased the sentence as suggested. We have shifted the emphasis from ‘measuring pain’ to quantifying its specific impact on behaviour.

Original lines 220-222 have been revised as follows:

"Taken together, this indicates the composite nature of overall aversiveness and highlights the benefit of combining subjective ratings with model-based measures of its motivational impact on behaviour."

We believe this revision more accurately reflects our approach of using choice and movement as objective indices of the motivational value of pain.

> *(3) The explanation for choosing the foraging task is very interesting, but should be provided in the Introduction rather than in the Methods section. In contrast, the Methods section should include the details of the VR implementation.*

We thank the reviewer for these constructive suggestions regarding the manuscript structure.

Regarding the rationale for the foraging task: We agree that providing the theoretical justification for the task earlier in the manuscript improves the narrative flow. We have revised the Introduction to explicitly outline why a foraging paradigm was chosen by added the following sentences:

“A foraging paradigm provides a robust, free-operant framework that captures the core components of adaptive behaviour: it is goal-directed, involves complex movement, and requires the learning of an optimal strategy to maximise rewards. This allows us to computationally dissociate how different types of pain influence the control of action.”

We believe this addition clarifies the link between our computational hypotheses and the experimental design.

Regarding the VR implementation: We have updated the Methods section to include the specific experimental parameters requested in the reviewer's previous comments (e.g., timing precision, stimulus counts, and motion mapping) to ensure full reproducibility.

However, we have opted not to include the exhaustive engineering details of the underlying software architecture and communication protocols. To ensure complete transparency, the full software and firmware source code, which allows for the exact replication of the environment, is available in our public GitHub repository shown in the code and data availability section.

> *(4) It is unclear how the sample size was determined. This information should be included.*

We thank the Reviewer for this comment. For the present study, an a priori power analysis was not conducted due to the novelty of the investigation and the complexity of the analyses. Standard power analyses are not commonly conducted for studies where computational modelling is the primary focus, as results would be potentially misleading. Instead, we based our sample size estimate of N ≈ 30 participants on previous studies using computational modelling of neurophysiological data [6], as well as EEG, SCR and pain studies [7, 8] and studies in our group using combined neurophysiological recordings and VR [9]. This approach represented a pragmatic balance which ensured the credibility of our results and the stability of our model estimates while accounting for the high persubject cost and the depth of the data collected from each individual. This has now been described more accurately in the Method section:

“An a priori power analysis was not conducted due to the novelty of the investigation and the complexity of the analyses. Instead, we based our target sample size (N ≈ 30 per experiment) on previous studies using computational modelling of neurophysiological data (Mahajan et al., 2025), as well as EEG, SCR, and pain studies (Schulz351 et al., 2015; Zhang et al., 2018), and studies from our group using combined neurophysiological recordings and VR (Hewitt et al., 2026). This approach represents a pragmatic balance that ensures the credibility of the results and the stability of model estimates while accounting for the high per-subject cost and depth of data collected from each individual.”

> *(5) Please clarify how / when the monetary performance incentive was provided.*

We thank the reviewer for the opportunity to clarify the incentive structure. The monetary performance incentive is detailed below:

Participants were informed at the start of the study that they would earn a performance-based bonus of up to £10, determined by the points they collected during the foraging task. To ensure that motivation remained consistent across the entire session for all individuals—regardless of their baseline foraging speed—the specific exchange rate between points and currency was not disclosed. This prevented potential 'ceiling effects', where a high-performing subject might stop exertive effort after reaching the maximum bonus early, or 'floor effects', where a subject might perceive the reward for an individual action as too small to be motivating.

Following the completion of the experimental session, all participants were compensated with the full £10 bonus in addition to their base payment for participation.

We have updated the Methods section to reflect these details:

“Participants were informed at the start of the experiment that their total points would be rewarded with a monetary incentive of up to £10. To maintain a constant level of motivation throughout the task, the exact point-to-currency exchange rate was not specified. Upon completion of the session, all participants were awarded the maximum bonus of £10.”

> ***Reviewer #2 (Public review):***
>
> *Strengths:*

> *Overall, this study aims to address an important topic and is generally well written.*

We thank the Reviewer for the generally positive evaluation of our work.

> *Weaknesses:*
>
> *First, phasic pain was induced using electrical stimulation, which typically elicits somatosensory evoked potentials (SEPs). These responses may not reflect pain-specific processes and thus complicate interpretation. This issue bears directly on the study's conclusions, especially when discussing interactions between phasic and tonic pain. For example, tonic pain is known to reduce perceived intensity or cortical responses to phasic pain stimuli delivered elsewhere on the body - an effect not expected for SEPs elicited by electrical stimuli.*

We acknowledge the reviewer's concern regarding the specificity of evoked potentials elicited by electrical stimulation. We agree that traditional SEPs— particularly those evoked by large surface electrodes—primarily reflect activation of non-nociceptive A-beta fibres and thus may not reliably index pain-specific processes or be modulated by tonic pain via descending nociceptive control. However, we would like to clarify that phasic pain was administered in the present study using small-diameter concentric 'Wasp' electrodes. These are comparable to intraepidermal electrodes shown to preferentially activate nociceptive A-delta fibres, thereby eliciting ERPs more closely associated with nociceptive processing rather than mixed somatosensory input [1, 2]. Accordingly, our ERP results demonstrated a reliable increase in N1-P2 amplitude with higher phasic pain intensity, suggesting that the evoked responses captured stimulus-evoked nociceptive processing.

We acknowledge that these ERPs may still reflect mixed sensory processing and thus may not be fully modulated by tonic pain. Previous studies have shown that ERPs elicited by nociceptive electrical stimulation can be attenuated during tonic pain using cold-water immersion in CPM paradigms [3, 4]. However, these studies typically employ passive tasks, whereas our paradigm involved continuous voluntary behaviour during sustained tonic pressure pain. This difference in task context may engage distinct modulatory systems, possibly prioritising behavioural adaptation over sensory gating.

We have revised the Discussion and Methods sections to explicitly clarify the electrode design and address the lack of ERP modulation by tonic pain in the context of active behaviour:

Discussion: "Although we utilised concentric 'Wasp' electrodes designed to selectively activate nociceptive A-delta fibres, and confirmed that the resulting ERPs (N1-P2) were significantly modulated by phasic intensity (Figure 6E, F), we observed no such attenuation by tonic pain (Fig. 6G, H)."

Methods: "These electrodes preferentially activate nociceptive A-delta fibres, thereby eliciting ERPs that more accurately reflect nociceptive processing compared to standard bipolar stimulation (Inui et al., 2002; Mørch et al., 2011)."

> *Second, additional control experiments are necessary to rule out alternative explanations. For instance, the authors are suggested to deliver phasic pain to the contralateral arm (e.g., at 1-2 Hz), which might also reduce action velocity. Similarly, tonic pain applied to the grasping hand should be tested to disentangle hand-specific effects.*

We thank the reviewer for these suggestions regarding the spatial configuration of stimuli. The decision to deliver phasic pain to the grasping hand and tonic pain to the contralateral arm was a deliberate feature of our experimental design.

First, delivering phasic pain to the grasping hand ensured spatial congruency between the virtual stimulus (the fruit) and the physical consequence (the pain). This congruency is essential for subjects to form a coherent representation of the 'painful' object; a contralateral delivery would have introduced a sensory-motor mismatch that could complicate the interpretation of the learning and choice data.

Second, tonic pain was applied to the contralateral arm specifically to avoid mechanical interference with the grasping action. Applying sustained pressure to the ipsilateral limb would likely have impeded the manual dexterity and fine motor control required to operate the controller buttons. This would have introduced a physical confound, making it difficult to determine if changes in behaviour were due to motivational vigour or simply the mechanical difficulty of performing the grasp while the arm was under pressure.

We agree that exploring the spatial generalisation of these effects is an important future direction, and we have added a paragraph to the Discussion to clarify these design choices:

“It is also important to consider the spatial configuration of the stimuli used in this study. Phasic pain was delivered to the grasping hand to maintain spatial congruency with the virtual fruit, ensuring a coherent nociceptive feedback signal for the interactive task. Additionally, tonic pain was applied to the contralateral arm to prevent mechanical interference with motor execution, which would have occurred if pressure were applied to the ipsilateral limb used for grasping the controller. Whilst this design promotes spatial congruency and avoids mechanical confounds, future studies might explore how these effects generalise across different body parts, for which VR experiments serve as a promising tool to test relevant hypotheses (Hewitt et al., 2026).”

> ***Reviewer #2 (Recommendations for the authors):***
>
> *(1) First, the abstract mentions only EEG, yet Experiment 1 employed skin conductance response (SCR) measures while Experiment 2 utilized EEG. Also, the rationale for using SCR in Experiment 1 and EEG in Experiment 2 is not provided and should be explicitly stated.*

We thank the reviewer for identifying the discrepancy between the physiological signals reported in Experiment 1 and Experiment 2. We have revised the Abstract and Methods section to clarify the rationale for these measures.

In Abstract, the following sentence has been revised: This could be explained by a free-operant computational framework that formalises and quantifies the function of tonic and phasic pain in terms of motivational vigour and decision value, and model parameters correlated with EEG “physiological and neural responses.”

Regarding the rationale for the measurements, the following sentences were inserted into the Methods section: “Experiment 1 was designed to establish the robust behavioural effects of the foraging task while ensuring the collection of reliable physiological data. We chose SCR as it is a well-validated index of autonomic arousal that we were confident would provide a clear peripheral measure of pain-related processing in this novel VR paradigm.”

For Experiment 2, we aimed to build on these findings by adding EEG. This was intended as a complementary piece of neural evidence to provide insights into the underlying central neural mechanisms of phasic and tonic pain interactions.

> *(2) Second, the quality of both SCR (Figure 3A) and EEG/ERP data (Figure 5A-D) appears compromised by low SNR. For instance, ERP signals show baseline drift at low frequencies, potentially due to movement-related artifacts. The authors are encouraged to enhance data quality and provide cleaner, more interpretable results.*

We thank the reviewer for this observation. We acknowledge that our recordings exhibit a lower SNR compared to conventional, stationary EEG studies. This is a recognized characteristic of Mobile Brain-Body Imaging (MoBI), particularly in immersive VR experiments where participants are physically active [10]. However, previous research has demonstrated that it is possible to recover valid, interpretable neural signals in active settings using modern cleaning methods including trained ICA labels which we have adopted for artefacts cleaning [11]. We also believe we should be restrained from over cleaning the EEG data as pointed out by Delorme in the paper ‘EEG is better left alone’ [12]. Therefore, we have added a new paragraph in the Discussion:

“It is important to acknowledge that the signal-to-noise ratio in both our physiological and neural recordings is lower than that typically observed in conventional, stationary laboratory experiments (Gramann et al., 2011). This is primarily due to the motion artefacts inherent in an immersive and active virtual reality environment. Whilst we utilised robust cleaning and artefact-correction methods (Klug and Gramann, 2021), the elevated noise floor may limit our capacity to detect more subtle neural effects or interactions. These challenges highlight a critical area for future methodological research, particularly in the development of hardware and signal-processing tools designed to isolate neural signals during complex, mobile behavioural tasks.”

Another factor contributing to the appearance of the raw signal is the "free-operant" nature of our task. Unlike conventional neurophysiological study paradigms with fixed, sufficient intervals between trials, our participants were free to move and interact with fruit at their own pace. This means that neurophysiological signals from successive actions (e.g., picking up one fruit followed quickly by another) can overlap. For the SCR analysis, we addressed this by using a canonical response function (CRF) to model and "unfold" the overlapping signals with GLM to produce our final results [13]. While we did not perform a similar deconvolution for the EEG data, we focused our analysis on the early, salient components (N1-P2 and early time-frequency changes < 500ms) which are less susceptible to overlap from subsequent actions than the much slower SCR.

In summary, while significant efforts representing the state-of-the-art approach for MoBI analyses have been taken to minimise the contributions of noise to the dataset, residual noise does remain in the final data. We have employed a combination of robust preprocessing and model-based analytical methods to account for the complexities of a free-operant task. We believe these results represent the best possible balance between signal clarity and the ecological validity of an active foraging task, and we have called for future research to continue improving these tools for immersive VR environments.

> *(3) Third, although the authors state that time-frequency analysis was conducted on the EEG data, no corresponding results are presented in Figure 8 or elsewhere. Furthermore, the statistical maps shown appear noisy and require further clarification and possible denoising.*

We thank the reviewer for pointing this out. The time-frequency results are indeed presented in Figure 8 (now Figure 10); however, they are depicted as topographic maps of the t-statistics derived from our LMM rather than raw power change plots.

The application of EEG to a novel, free-operant task represents a significant methodological development in this study. Unlike conventional EEG experiments where variables are strictly controlled and a "clean" pre-stimulus baseline is easily obtained, our task involves continuous participant engagement and movement. In this context, for the decision-making event, a stable baseline is unattainable as multiple variables, most notably head movements, are constantly in effect.

Therefore, we believe that presenting the LMM statistical maps in the main text is the most appropriate and rigorous interpretation of the time-frequency results, as these maps represent the signal after accounting for these complex fixed and random effects. This approach was also adopted in previous pain studies [7]. We also updated the figure legend and caption specifically saying that the figure represented correlation between band power and variables we were investigating to improve clarity.

Second, for more salient stimuli like phasic pain stimulation, we can indeed obtain a highly interpretable time-frequency analysis without further LMM analysis. We have added induced oscillatory responses to phasic pain stimuli to the Supplementary Material (section: Induced oscillatory responses to phasic pain stimuli). The results showed that, consistent with our ERP findings, the intensity of phasic pain significantly modulated induced responses, while the background tonic pain state did not significantly alter the induced oscillatory response to the phasic pain stimulus.

Regarding the SNR and Denoising Strategy, we acknowledge that the statistical maps appear noisier than those from stationary studies. This is a direct consequence of the lower signal-to-noise ratio (SNR) inherent in mobile VR. Moving EEG from strictly controlled laboratory settings to ecologically valid, "real-world" VR scenarios introduces higher levels of noise, which we believe represents a key frontier for future methodology research. Regarding the denoising process, the maps in the main text represent the data after our full pipeline (including ICA-based artifact rejection and high-pass filtering). Regarding further denoising, we have deliberately chosen not to apply excessive spatial or temporal smoothing [12]. Also, it is important to note that the LMM framework itself serves as a powerful statistical "filter." By including head movement velocity as a regressor and accounting for random intercepts across subjects, the model effectively "cleans" the signal by partitioning out noise components not related to the task conditions.

> ***Reviewer #3 (Public review):***
>
> *Strengths:*
>
> *The experimental paradigm is highly innovative. Assessing human behaviour in a naturalistic yet highly controlled setting represents a promising approach to pain research. Notably, assessing pain magnitude implicitly, via its motivational value, offers insights about the overall pain experience that are not usually accessible via common pain ratings.*
>
> *Weaknesses:*
>
> *Despite these strengths, the manuscript would benefit significantly from more precise definitions of key concepts and an overall clearer, more coherent presentation of its main arguments. The writing, in its current form, often presents claims that are too vague or insufficiently connected with the experimental findings. Moreover, certain aspects of the computational modeling and statistical analysis appear flawed or inadequately justified.*

We thank the Reviewer for the generally positive evaluation of the manuscript.

> ***Reviewer #3 (Recommendations for the authors):***
>
> *(1) The analyses presented in the section*
>
> *"Results/Additional cost of effort associated with movement" require clearer explanations. The intention here appears to be to assess the association between moving distances and pain intensity to test the hypothesis that the higher the average pain ratings within blocks, the longer the distances moved (i.e., the higher the effort to avoid*

> *pain). It is unclear why and how exactly "egocentric distance differences between painful and non-painful fruits" were computed.*

We thank the reviewer for pointing out the need for a clearer definition of the egocentric distance calculation. As the reviewer correctly identified, this analysis tests the hypothesis that subjects would trade off physical effort (distance) for pain avoidance. To compute this, we used a blockwise approach: for each one-minute block, we calculated the average egocentric distance travelled to pick up non-painful fruits and subtracted the average distance travelled to pick up painful fruits. This difference (labelled as "Choice Distance Bias" in Figure 3B) represents the additional effort subjects were willing to exert to reach a pain-free option. We have clarified the computation method and our motivation for using it in the revised text:

“As shown in Figure 3B, the vertical axis represents the 'choice distance bias', calculated as the difference between the average egocentric distance to non-painful fruits and the average egocentric distance to painful fruits within each block. The egocentric distance is the fruit distance relative to the participant. This metric was computed to test whether subjects would trade off physical effort for pain avoidance; specifically, a positive bias indicates that subjects were willing to bypass closer painful fruits to reach more distant pain-free ones. As hypothesised, we found that as the pain intensity (VAS) of the aversive fruits increased, this distance bias grew significantly, confirming that subjects exerted greater movement effort to avoid higher levels of pain.”

We have also updated the text in the beginning of " Avoidance increases with increasing phasic pain intensity" section to emphasize the calculation is analysed at the block level to clarify the computation procedure:

“For this analysis, both aversive choice probabilities and subjective pain ratings were estimated at the block level.”

> *(2) In its current form, the explanation of the first optimality equation lacks precision and transparency. Consider the following improvements:*
>
> *(a) Precisely define the features that characterize a state/decision point: e.g., i) memory of available options (= set of 7 fruits that were seen but not picked up) and ii) subject's current position, iii) pain intensity associated with green fruit in the current block.*
>
> *(b) Precisely define the set of values the action variable a can assume.*
>
> *(c) Precisely define the function u(a) in mathematical notation, including its hyperparameters. The fact that a is likely a categorical variable, while u(a) is later described as a sigmoid function (i.e., as a function of a continuous variable), is confusing. In my understanding (see Figure 2F), u is actually a function of the stimulus intensity associated with a given fruit. Since the stimulus intensity depends on the current state s (and varies from block to block), the phasic pain utility function technically also depends on s.*
>
> *(d) Precisely define the function d(a) in mathematical notation, including its hyperparameters.*
>
> *(e) Precisely describe how the separate horizontal and vertical components of C_m enter the equation.*
>
> *(f) Provide a summary of all parameters and hyperparameters being optimized. Are parameters and hyperparameters optimized jointly? What distinguishes parameters and hyperparameters practically?*

We thank the reviewer for this insightful critique. We agree that the original presentation of the optimality equation was insufficiently formal. We have now added a dedicated subsection, "Experiment 1 model summary", which includes a comprehensive table (Table 2) and supporting text to address these points with mathematical precision.

Specifically, we have implemented the following clarifications in the revised manuscript:

State and Action Space (a, b): We have formally defined the state s as an ordered memory list M_s of up to 7 items, governed by a FIFO principle. The action a is now explicitly defined as a one-to-one mapping from these memory items to physical reach trajectories.

Utility and Cost Functions (c, d, e): We have provided the full mathematical notation for the phasic pain utility u(a) and the effort cost d(a). We have clarified that while the choice of fruit (a) is categorical, it serves as an indicator variable that determines the application of a continuous sigmoid utility function based on the block-level pain intensity (x_stim). We have also explicitly decomposed the effort cost into its horizontal (C_h) and vertical (C_v) egocentric components.

Parameters and Hyperparameters (f): We have clarified that because our model focuses on steady-state motivational trade-offs rather than online learning, the hyperparameters listed are the only variables subject to optimisation. These are fixed for each subject across the duration of the experiment.

We believe these additions, centred around the new Table 2, provide the transparency and precision requested.

Furthermore, we would like to clarify a subtle caveat regarding the assumption of a fixed x_stim for the entirety of a block. While participants were aware that green pineapples were aversive, the specific stimulation intensity for a given block was only fully revealed upon picking up the first green pineapple.

To ensure our model-fitting remains robust despite this 'information lag', we considered several computational alternatives:

(1) Prior Estimation Modelling: Modelling a participant's prior estimation of pain stimulation based on previous blocks. We found this unsuitable due to the independent block design and the limited number of trials available to establish a stable prior.

(2) Data Trimming: Excluding all decisions made before the first green pineapple pickup. While theoretically 'cleaner', this approach introduces significant data imbalance and ignores blocks where a participant—dissuaded by high pain— only picked up a single green fruit before ceasing (approx. 8.75% of blocks).

Crucially, we performed a sensitivity analysis by re-running the model-fitting procedure using only the data collected after the first green pineapple was harvested in each block. This analysis yielded the same qualitative statistical results as the full-block model presented in the main text. We have added a detailed discussion of this caveat and the alternative study designs we explored (such as pre-block stimulation or stochastic choice paradigms) to the Supplementary Material (Section Discussion of pain intensity information and model robustness). We believe this confirms that our current approach provides a faithful representation of the underlying motivational trade-offs.

> *(3) The statistical method selected for assessing the association between decision values and pain ratings is problematic (Figure 2G): Since there are multiple data points from multiple subjects, which introduces dependence between data points, a multilevel instead of a single-level linear regression should be employed.*

We appreciate the reviewer's suggestion to utilise a multilevel modelling approach. We agree that a single-level regression does not fully account for the nested structure of our data.

In response, we re-analysed the association using a linear mixed-effects model with a maximal random effects structure. Specifically, we included both random intercepts and random slopes for Ratings grouped by Subject (in R syntax: PainFunc ~ Ratings + (1 + Ratings | Subject)).

The results of this mixed effect model are consistent with our original findings, showing a significant relationship between decision values and pain ratings (p = .001). We have updated the Figure caption (now Figure 3G) to reflect these multilevel model statistics. We believe this addition addresses the concern regarding data dependence and provides a more rigorous validation of our conclusions.

> *(4) The statistical method selected for assessing how decision values/pain ratings relate to SCR coefficients is problematic (Figures 3B and C): Again, a multilevel regression method should be used.*

We thank the reviewer for this important point. We agree that a multilevel approach is more appropriate for our nested data structure, and that the interpretation of the SCR data required more explicit justification in the context of the divergence between decision values and ratings.

We have now re-analysed the relationship between SCR coefficients (both fixationevoked and shock-evoked), decision values, and subjective ratings using a multilevel (mixed-effects) regression model. This model included random intercepts and random slopes for each participant to account for individual variability. We have updated Figure 4 (previously Figure 3) caption and the corresponding Results and Discussion sections to reflect these findings (revised text are copied to the response to next comment (5) below. This more rigorous approach provided a clearer and more nuanced picture of the data. Specifically, while the simple regression previously suggested that both measures correlated with fixation-evoked SCR, the multilevel model reveals a dissociation: fixationevoked SCR is significantly associated with decision values, but not with subjective ratings.

> *(5) The interpretation of the skin conductance analysis results as evidence of "dissociation between expected and experienced utility" is vague and not well-supported given the presented data and statistical shortcomings. The low R2 in Figure 2G already indicates divergence between decision values and pain ratings. It is unclear what the decision values' differential association with shock-evoked SCR coefficients adds to this insight.*

The reviewer correctly notes that the low R^2 in the correlation between decision values and pain ratings (Figure 3G) already suggests a divergence between these two measures. We agree that this is one of the key findings, as it highlights that decision values provide a dimension of pain assessment that is not fully captured by subjective report. However, we believe the SCR results add crucial physiological evidence to explain why and how these measures diverge. The updated multilevel results provide a more concrete double dissociation that aligns with the distinction between decision utility and experienced utility:

Experienced Utility (Shock-evoked SCR): This measure of physiological arousal during the painful event was significantly predicted by subjective pain ratings (beta = 0.0154, p = .006) but not by decision values (p = .672). This suggests that ratings are more closely tied to the immediate, experienced aversiveness of the stimulus.

Decision Utility (Fixation-evoked SCR): In contrast, arousal during the period of evaluation/fixation was a significant predictor of decision values (beta = -0.0739, p = .009) but was not significantly associated with subjective ratings (p = .105).

By using a more rigorous statistical method, we found that decision values are actually a more robust predictor of anticipatory/evaluative arousal (fixation) than subjective ratings are. This supports our interpretation that decision values and ratings capture different temporal and functional aspects of pain processing— specifically, the evaluation of potential outcomes (decision utility) versus the reaction to the outcome itself (experienced utility). We have revised the Discussion to be more conservative regarding the strength of this evidence while clearly articulating how these physiological results provide a mechanistic grounding for the divergence observed in the behavioural data.

Summary of changes in the manuscript:

Figure 4 Caption: Updated to report multilevel regression statistics (beta, 95% CI, t, and p-values) instead of R^2 from simple linear regression.

Results Section: Updated the text to describe the mixed-effects model results, highlighting the dissociation between fixation-evoked and shock-evoked SCRs. Revised text:

“Analysis using a multilevel linear mixed-effects model revealed a clear dissociation in the relationship between physiological responses and motivational parameters. Fixation-evoked SCR coefficients were significantly associated with decision values, but not with subjective pain ratings (Fig. 4B). Conversely, shock-evoked SCR coefficients showed a significant association with subjective pain ratings, while the association with decision values was not significant (Fig. 4C). This double dissociation suggests a notable divergence between the physiological correlates of expected utility (at the decision level) and experienced utility (the actual pain experience). Taken together, these findings highlight the composite nature of the overall aversiveness of pain and underscore the benefit of combining subjective ratings with model-based measures to capture its distinct impacts on behaviour.”

Discussion Section: Revised the paragraph discussing decision versus experienced utility to include the "further hint" provided by the divergent SCR correlations.

Revised text:

“In our task we get a further hint of this in the SCR measures in experiment 1, whereby a discrepancy exists between decision values and pain ratings in their respective associations with fixation-evoked SCRs and phasic pain-evoked (shock) SCRs. Taken together, this indicates the composite nature of overall aversiveness of pain, and highlights the benefit of combining subjective ratings with model-based measures of its motivational impact on behaviour.”

> *(6) When investigating the effects of tonic pain on the neural processing of phasic pain (Figure 5), why were only ERPs analyzed and not induced oscillatory responses?*

We thank the reviewer for this insightful suggestion. We initially focused our analysis on Event-Related Potentials (ERPs) because the N1-P2 amplitude is an established and robust marker in pain research, providing a clear and reliable metric for comparing phasic pain processing across conditions.

However, we agree that induced oscillatory responses provide a more comprehensive view of cortical dynamics. Following your suggestion, we have performed a Time-Frequency Representation (TFR) analysis at electrode Cz. These results, now included in the Supplementary Material (Figure S4, S5), are entirely consistent with our ERP findings. Specifically:

Phasic Modulation: Both ERP amplitudes and induced oscillatory power (notably in the theta and gamma bands) were significantly modulated by the intensity of the phasic pain stimulus.

Tonic Independence: Consistent with the ERP results, the presence of background tonic pain did not significantly modulate the induced oscillatory responses to phasic stimuli.

We believe this additional analysis significantly strengthens the manuscript by demonstrating that the observed effects are consistent across both phase-locked and non-phase-locked neural domains. We have amended the ERP results section to reflect the addition of induced oscillatory responses in supplementary materials: “We focused our neural analysis of phasic pain on ERPs as phasic stimuli are well characterised by these time-locked evoked potentials. Nevertheless, to ensure a comprehensive assessment of the neural response, we also examined induced oscillatory responses. These results were consistent with the ERP findings and are detailed in the Supplementary Materials (Fig. S4, S5).”

> *(7) The explanation of the second optimality equation (involving motivational vigour) requires substantial clarification. Besides the points mentioned for the previous optimality equation, specific opportunities to improve the explanations include the following:*
>
> *- In the provided formula, C_v and C_m appear indistinguishable given they are multiplied together, rendering this an ill-posed optimization problem. This should be clarified.*
>
> *- In my understanding, d(a)/V_speed corresponds to the temporal delay associated with picking fruit a. Then, what is tau, and why compute the sum tau + d(a)/V_speed?*
>
> *- V* is not introduced properly. Is V*(s') = Q*(s', a, tau)? If so, why introduce V*? Moreover, the notational similarity between V_speed and V* is confusing.*
>
> *- Gamma = 0 still holds?*
>
> *- Summarize all parameters and hyperparameters that are optimized to model the data and more precisely describe the method used for optimization.*

We thank the reviewer for these insightful comments. We agree that the transition from a standard reinforcement learning framework to one incorporating motivational vigour requires precise definitions to ensure the model is well-posed and interpretable. We have addressed these points as follows:

(1) Clarification of C_v and C_m: We have clarified C_m and d(a) in the newly added Experiment 1 model summary table. Specifically, C_v is the scalar vigour constant and C_m is a unit vector representing the horizontal and vertical components. Because C_m is a unit vector, the optimization does not suffer from a collinearity issue from the scalar multiplication between C_v and C_m.

(2) Bridging Theory to Practice (tau and Total Delay): In the theoretical framework of Niv et al. (2007), "delay" is an abstract sum encompassing both waiting and execution. In practice, when fitting to real-world VR data with variable execution times , we must distinguish between the waiting time tau (time spent stationary or searching) and the execution time (||d(a)|| / V_speed). This is necessary because participants take time to look around the forest to search for fruits before deciding to commit to an action. The sum tau + ||d(a)|| / V_speed represents the total delay between two actions, which directly aligns with the notion of opportunity cost of time. We have added a table (Table 3) and added a new Figure 8 to clarify these distinctions.

(3) V*, Q*, and gamma: The reviewer is correct that V*(s') = max_{a’, tau’} Q*(s', a', tau'). We previously used V* for simplicity. Since the notation of V* and V_speed was confusing, we have updated the term to max_{a’, tau’} Q*(s', a', tau') in the optimality equation. We confirm that gamma = 0 (a greedy policy) still holds for the Experiment 2 framework to maintain

focus on steady-state motivational trade-offs. We have added this statement to the method section.

(4) Summary of Parameters and Optimization: We have summarized the hyperparameters {k, x_0, C_p, C_v, h, v} in the new summary table for Experiment 2.

> *(8) It is not clear what the results of the modelling approach presented in Figure 7a+b concretely add to the comparison of movement velocities and collection rates in Figure 6.*

We appreciate the reviewer's comment regarding the relationship between the raw behavioral metrics and the computational results. While both sets of findings support the argument for reduced motivational vigour in the tonic pain condition, we believe the modeling approach provides distinct and essential value:

(1) Finer-Grained Analysis Tool: The computational model acts as a more sophisticated analysis tool than simple velocity or rate averages. Unlike Figure 9a+b (in the revised manuscript, previously Figure 7), which summarizes overall performance, the model accounts for the trial-by-trial trade-off between opportunity costs, movement effort, and choice values. This allows us to isolate vigour from other confounding components.

(2) Direct vs. Indirect Measurement: If we assume that motivational vigour in a free-operant task can be quantified through an RL framework, as established in animal studies, then the model's vigour constant (C_v) serves as a direct, concrete estimate of that internal state. In contrast, overall speed and collection rates are indirect markers that can be influenced by multiple factors, such as different choice sets available to the participants as the fruits locations are randomly generated.

In summary, the computational approach provides a rigorous, parameterized bridge between observable behavior and the underlying neuro-computational mechanisms of recuperative pain. We have updated the Discussion section to more explicitly state how the computational approach provides a controlled measure that is isolated from the other confounders of the task. Added text to the Discussion:

“Compared to overall speed and collection rate, which can be influenced by multiple factors, such as different choice sets available to participants as the fruit locations are randomly generated, the model's fitted parameters (e.g. vigour constant C_v) in theory serves as a direct, concrete estimate of that internal state.”

> *(9) Claims made in the discussion should be more thoroughly and closely linked to the results presented previously. Specifically, experimental outcomes supporting the following claims should be directly referenced:*
>
> *- "tonic and phasic pain serve different motivational functions".*
>
> *- "phasic pain provides a punishment teaching signal that directs avoidance".*
>
> *- "tonic pain reduces motivational vigour".*
>
> *- "these two functions [punishment teaching signals and reduction of motivational vigour?] can be formally distinguished and quantified".*
>
> *- "We did not see interactions between tonic and phasic pain".*

We have revised the Discussion to more explicitly link these claims to our experimental results. Revised text:

“The experiments show that tonic and phasic pain serve different motivational functions during adaptive behaviour, in line with ecological and evolutionary theories of pain (Bolles and Fanselow, 1980; Walters and Williams, 2019). Specifically, our findings point towards phasic pain providing a punishment teaching signal that directs avoidance through value-based learning, balancing the cost of future harm alongside potential reward. This is supported by the observation that increasing phasic pain intensity significantly reduced choice probability and increased distance bias between choices, whereby participants were willing to travel further to reach a pain-free fruit. In contrast, we found that tonic pain reduces motivational vigour, which supports energy conservation and recuperation in the context of bodily damage. This claim is directly evidenced by the reduction in taskrelated movement velocities and fruit collection rates during tonic pain blocks. The experiments are the first to show that these two functions can be formally distinguished and quantified during ongoing behaviour. By utilising a free-operant RL computational framework, we were able to dissociate these roles phasic pain was quantified as a generally negative utility term affecting choice values, while tonic pain was formalised as a change in vigour constants that were significantly higher (increasing delays between actions) in tonic pain condition. This illustrates how pain simultaneously acts in different ways to serve self-protection.”

“One notable aspect of our results is that we did not see interactions between tonic and phasic pain at either the behavioural or neural level. Behaviourally, we observed that average aversive choice probabilities remained similar regardless of the presence of tonic pain, with no significant interaction effect on punishment sensitivity. Furthermore, our model-fitting confirmed that tonic pain did not significantly modulate the fitted phasic pain utility values. There are two contexts in which these might be predicted. First, in c̀onditioned pain modulation' paradigms (Kennedy et al., 2016), a tonic pain stimulus is sometimes seen to reduce both the perceived intensity and the cortical evoked responses to phasic pain stimuli delivered somewhere else on the body (Hoffken et al., 2017; Enax-Krumova et al., 2020). Although we utilised concentric ‘Wasp’ electrodes designed to selectively activate nociceptive A-delta fibres (Inui et al., 2002), and confirmed that the resulting ERPs (N1-P2) were significantly modulated by phasic intensity, we observed no such attenuation by tonic pain. Indeed, neither subjective pain ratings nor the N1-P2 amplitude showed a significant modulation by the tonic pressure pain stimulus. In contrast, our results were more compatible with a trend in the other direction.”

> *(10) The paragraph in the discussion "A concern that is sometimes raised..." (lines 243 - 254) raises interesting points, but its particular relevance to the study at hand is unclear.*

We appreciate the reviewer's feedback. The motivation for including this discussion is to address a common critique we received for the study: whether the observed reduction in vigour under tonic pain is "simply" due to distraction or cognitive load, rather than being a specific functional output of the pain system. We have revised this paragraph to link the concern to our paper’s specific finding.

Our central argument is that for tonic pain, distraction is not a confounding "sideeffect" but rather the primary mechanism of action. By being inherently "distracting," tonic pain successfully withdraws resources from ongoing tasks (like foraging) to promote the energy conservation required for recuperation.

> *(11) The clinical perspective of the methodological framework presented at the end of the discussion is interesting and could be expanded.*

We thank the reviewer for this encouraging comment. We have expanded the final paragraph of the Discussion to more explicitly state the clinical utility of our framework. Specifically, we now contrast our approach with standard clinical assessments such as Quantitative Sensory Testing (QST). We highlight that while QST is a valuable tool, it can lack ecological validity; in contrast, our VR-based task allows for a more realistic, behaviourally sensitive assessment of how pain impacts a patient’s daily functional activities and motivational state. We believe this represents a significant step towards more objective and "real-world" clinical pain phenotyping.

> *(12) The statistical analyses part in the methods section should provide a clear definition of dependent and independent variables and clearly state which test was used for which analysis, e.g., by referencing the corresponding subfigure in the main text.*

We agree that a more structured summary of the statistical approach would improve the clarity of the Methods section. We have now included a comprehensive summary table (Table 1) in the Statistical Analysis subsection. This table explicitly defines the dependent and independent variables for each analysis, identifies the specific statistical model used (e.g. Linear Mixed Models or repeated measures ANOVA), and directly maps these to the corresponding figures in the results section.

> *Minor comments:*
>
> *(1) Introduction:*
>
> *(a) The introduction should elaborate more on the advantages of employing an "ecologically meaningful context".*

We thank the reviewer for suggesting further elaboration on the advantages of employing an "ecologically meaningful context". We have updated the introduction to provide additional reasoning of choosing an ecologically valid context for the study:

“One of the challenges in studying adaptive functions of pain is the difficulty of embedding experiments within ecologically meaningful contexts. To solve this, we designed an immersive foraging task using virtual reality (VR), in which humans search a forest to collect fruits from the low-lying bushes at varying heights. A foraging paradigm provides a robust, free-operant framework that captures the core components of adaptive behaviour: it is goal-directed, involves complex movement, and requires the learning of an optimal strategy to maximise rewards. This allows us to computationally dissociate how different types of pain influence the control of action.”

> *(b) It would be helpful to clarify why tonic pain applied to a limb not involved in the task is expected to influence the motivational vigour with respect to the task.*

We thank the reviewer for pointing out additional clarification for applying tonic pain to the non-dominant arm. We have added the following text to the introduction clarifying our hypothesis and why it was applied to the non-task limb:

“Second, we hypothesised that tonic pain acts as a coefficient modulating the tradeoff between opportunity cost and vigour cost, thereby serving a recuperative function. To test this in Experiment 2, we delivered continuous tonic pressure to the non-dominant arm via an inflated cuff to emulate a background state of injury. Within our free-operant framework, tonic pain was modelled as a weighting factor that shifts the optimal balance toward reduced energy expenditure. Because the stimulus was applied to the non-task limb, we specifically predicted a global reduction in motivational vigour—operationalised as decreased movement velocities and foraging rates—rather than a direct mechanical impairment.”

> *(2) Results/Experiment 1:*
>
> *(a) How were monetary rewards implemented exactly? How much money per fruit?*

We thank the reviewer for the opportunity to clarify the incentive structure. Participants were informed at the start of the study that they would earn a performance-based bonus of up to £10, determined by the points they collected during the foraging task. To ensure that motivation remained consistent across the entire session for all individuals—regardless of their baseline foraging speed—the specific exchange rate between points and currency was not disclosed. This prevented potential 'ceiling effects', where a high-performing subject might stop exertive effort after reaching the maximum bonus early, or 'floor effects', where a subject might perceive the reward for an individual action as too small to be motivating.

Following the completion of the experimental session, all participants were compensated with the full £10 bonus in addition to their base payment for participation. We have updated the Methods section to reflect these details:

“Participants were informed at the start of the experiment that their total points would be rewarded with a monetary incentive of up to £10. To maintain a constant level of motivation throughout the task, the exact point-to-currency exchange rate was not specified. Upon completion of the session, all participants were awarded the maximum bonus of £10.”

> *(b) A green pine apple is not ripe and, in a naturalistic context, possesses some aversive value, even in the absence of phasic pain stimuli. Why was the color coding not counterbalanced across individuals? To what degree could this have confounded the results?*

We thank the reviewer for this insightful point. We acknowledge that the lack of counter-balancing for fruit colour (green vs. yellow) is a limitation of the current study design. However, we believe the potential confounding effect of "unripe" green pineapples on the final analysed data is minimal due to the principles of associative learning.

While a naturalistic heuristic (green = unripe) might establish a weak prior bias, fundamental associative learning [14] and reinforcement learning models [15] demonstrate that extensive training with a highly salient unconditioned stimulus (such as pain) rapidly overrides mild initial priors. The task objective focused strictly on maximizing reward points, and participants underwent extensive training (10 blocks in Experiment 1; 6 blocks in Experiment 2) before the analysed sessions began. During this time, the strong, explicit contingencies (green = pain, yellow = safe) were learned and verbally verified. Therefore, by the time the main experimental data was collected, any weak baseline aversion to green had been overshadowed by the explicit task contingencies, making the learned associative value the primary driver of behaviour. We have added a statement acknowledging this limitation and outlining this theoretical rationale in the Methods section.

“While the colour association (green for painful, yellow for pain-free) was not counter-balanced across subjects, any inherent aversive value of green pineapples (e.g., as 'unripe' fruit) is expected to have a minimal confounding effect on the analysed data. In associative learning frameworks, while mild prior biases may influence initial value estimations, extensive training with a highly salient unconditioned stimulus (e.g. phasic pain) rapidly updates these values, driving them toward an asymptote determined entirely by the explicit task contingencies (Rescorla & Wagner, 1972; Sutton & Barto, 2018). Because participants underwent extensive training (10 blocks in Experiment 1 and 6 blocks in Experiment 2) to establish the explicit pain associations prior to the analysed sessions, the observed avoidance behaviour was predominantly driven by the learned phasic pain contingencies rather than baseline colour preferences.”

> *(c) In the "Avoidance increases with increasing phasic pain intensity" section, clarify upfront that pain ratings and choice probabilities were estimated at the block level. This information is provided only in a later section.*

We agree with the reviewer that this information should be stated earlier for clarity. We have updated the beginning of the "Avoidance increases with increasing phasic pain intensity" section to specify that these metrics were estimated at the block level:

“For this analysis, both aversive choice probabilities and subjective pain ratings were estimated at the block level.”

> *(3) Results/Experiment 2:*
>
> *(a) ERP visualizations (Figure 5) should include standard error indicators.*

We have updated Figure 5 (now Figure 6) to include 95% confidence intervals for standard error of the mean across subjects for all ERP traces. This provides a clearer visualization of the variance in the neural response.

> *(b) In the section "A unified model...", clarify what is meant by saying that the unified model is "validated by the behavioural data", since behavioral data is what is being modeled in the first place.*

We clarify that "validation" in this context refers to the consistency between the parameters estimated by our generative unified model and the results obtained from the independent, model-free regression analysis of the raw behavioural data. While both approaches use the same source data, the unified model provides a finer-grained analysis of latent internal states (like motivational vigour), whereas the regression provides a direct empirical benchmark (more details were discussed in the response to major comment (8)). We have rephrased this section to better describe this as a consistency check against empirical regression results.

> *(c) In the context of Figure 8a, the term "correlations" is misleading if referring to pairwise comparisons.*

We appreciate the opportunity to clarify our terminology. The results presented in Figure 8a (and the associated text) are derived from a Linear Mixed Model (LMM) where the tonic pain condition was treated as a binary independent variable. The term "correlation" was used to describe the statistical association (represented by the t-values) between the presence of tonic pain and EEG band power, accounting for subject-level random effects. It does not refer to simple pairwise comparisons (like t-tests). However, we agree that "correlation" can be ambiguous when applied to a binary predictor. We have revised the text and figure legends to use the terms "associated with" or "predicted by" to more accurately reflect the LMM framework.

> *(d) Based on the presented data, there is no evidence for the section headings claim "Neural activities link to vigour".*

We agree with the reviewer that our results primarily provide evidence for a significant neural association with the tonic pain condition rather than a direct, statistically robust correlation with the vigour parameter itself (after Bonferroni correction). While tonic pain is associated with reduced vigour behaviourally, the EEG markers we identified are more accurately described as signatures of the pain state. We have revised the section heading and the corresponding text to focus on the characterisation of the tonic pain state to ensure our claims are strictly supported by the statistical evidence.

> *(4) Methods:*
>
> *In the supplementary materials, the headings pertaining to different LMMs are confusing and not consistent with the Figure labeling in the manuscript (e.g., 4(ii)b likely corresponds to Figure 4d).*

We thank the reviewer for identifying these inconsistencies in the supplementary material. We apologize for the confusion caused by the labelling errors during reformatting the manuscript. We have now thoroughly audited the supplementary headings and updated them to ensure they correspond directly and consistently with the figure labels in the main manuscript.

References

(1) Inui, K., Tran, T. D., Hoshiyama, M., & Kakigi, R. (2002). Preferential stimulation of Adelta fibers by intra-epidermal needle electrode in humans. Pain, 96(3), 247–252. *https://doi.org/10.1016/S0304-3959(01)00453-5*

(2) Mørch, C.D., Hennings, K. & Andersen, O.K. Estimating nerve excitation thresholds to cutaneous electrical stimulation by finite element modeling combined with a stochastic branching nerve fiber model. Med Biol Eng Comput 49, 385–395 (2011). *https://doi.org/10.1007/s11517-010-0725-8*

(3) Höffken, O., Özgül, Ö.S., Enax-Krumova, E.K. et al. Evoked potentials after painful cutaneous electrical stimulation depict pain relief during a conditioned pain modulation. BMC Neurol 17, 167 (2017). *https://doi.org/10.1186/s12883-017-0946-7*

(4) Enax-Krumova, E., Plaga, A.-C., Schmidt, K., Özgül, Ö. S., Eitner, L. B., Tegenthoff, M., & Höffken, O. (2020). Painful Cutaneous Electrical Stimulation vs. Heat Pain as Test Stimuli in Conditioned Pain Modulation . Brain Sciences, 10(10), 684. *https://doi.org/10.3390/brainsci10100684*

(5) Enrico Schulz, Elisabeth S. May, Martina Postorino, Laura Tiemann, Moritz M. Nickel, Viktor Witkovsky, Paul Schmidt, Joachim Gross, Markus Ploner, Prefrontal Gamma Oscillations Encode Tonic Pain in Humans, Cerebral Cortex, Volume 25, Issue 11, November 2015, Pages 4407–4414, *https://doi.org/10.1093/cercor/bhv043*

(6) Mahajan Pranav, Tong Shuangyi, Lee Sang Wan, Seymour Ben (2024) Balancing safety and efficiency in human decision making eLife 13:RP101371 *https://doi.org/10.7554/eLife.101371.2*

(7) Enrico Schulz, Elisabeth S. May, Martina Postorino, Laura Tiemann, Moritz M. Nickel, Viktor Witkovsky, Paul Schmidt, Joachim Gross, Markus Ploner, Prefrontal Gamma Oscillations Encode Tonic Pain in Humans, Cerebral Cortex, Volume 25, Issue 11, November 2015, Pages 4407–4414

(8) Suyi Zhang, Hiroaki Mano, Michael Lee, Wako Yoshida, Mitsuo Kawato, Trevor W Robbins, Ben Seymour (2018) The control of tonic pain by active relief learning eLife 7:e31949

(9) Hewitt, D., Tong, S., Schreiber, S., & Seymour, B. (2026). Tonic pain modulates neural correlates of associative phasic pain memories. PAIN. DOI: 10.1097/j.pain.0000000000003917

(10) Gramann, K., Gwin, J. T., Ferris, D. P., Oie, K., Jung, T.-P., Lin, C.-T., Liao, L.-D., and Makeig, S. (2011). Cognition in action: imaging brain/body dynamics in mobile humans. Reviews in the Neurosciences, 22(6):593–582.

(11) Klug, M. and Gramann, K. (2021). Identifying key factors for improving ica-based decomposition of eeg data in mobile and stationary experiments. European Journal of Neuroscience, 54(12):8406–8420.

(12) Delorme, A. EEG is better left alone. Sci Rep 13, 2372 (2023). *https://doi.org/10.1038/s41598-023-27528-0*

(13) Bach, D. R., Flandin, G., Friston, K. J., and Dolan, R. J. (2010). Modelling event-related skin conductance responses. International Journal of Psychophysiology, 75(3):349–356.

(14) Rescorla, R. and Wagner, A. (1972). A theory of Pavlovian conditioning: Variations in the effectiveness of reinforcement and nonreinforcement, volume Vol. 2

(15) Sutton, R. S. and Barto, A. G. (2018). Reinforcement learning: An introduction, 2nd ed. Adaptive computation and machine learning. The MIT Press, Cambridge, MA, US.

https://doi.org/10.7554/eLife.107911.2.sa0