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Computational mechanisms underlying the dynamics of physical and cognitive fatigue

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ABSTRACT

The willingness to exert effort for reward is essential but comes at the cost of fatigue. Theories suggest fatigue increases after both physical and cognitive exertion, subsequently reducing the motivation to exert effort. Yet a mechanistic understanding of how this happens on a moment-to-moment basis, and whether mechanisms are common to both mental and physical effort, is lacking. In two studies, participants reported momentary (trial-by-trial) ratings of fatigue during an effort-based decision-making task requiring either physical (grip-force) or cognitive (mental arithmetic) effort. Using a novel computational model, we show that fatigue fluctuates from trial-to-trial as a function of exerted effort and predicts subsequent choices. This mechanism was shared across the domains. Selective to the cognitive domain, committing errors also induced momentary increases in feelings of fatigue. These findings provide insight into the computations underlying the influence of effortful exertion on fatigue and motivation, in both physical and cognitive domains.

1. Introduction

Fatigue - a feeling of exhaustion induced by the exertion of effort - is a common feature of many of our daily activities (Chaudhuri & Behan, 2004; Herlofson & Larsen, 2002; Müller & Apps, 2019). Demanding tasks putatively increase sensations of fatigue, both when the required effort is physical or cognitive in nature (Kuppuswamy, 2017; Lorist, Boksem, & Ridderinkhof, 2005; McMorris, Barwood, & Corbett, 2018; Mockel, Beste, & Wascher, 2015; Müller & Apps, 2019; Stein, Jacobsen, Blanchard, & Thors, 2004). Theoretical accounts posit that the subjective feeling of fatigue increases the cost of continuing to exert effort. As a result, larger incentives are required to persist on a task when one is fatigued as compared to well-rested (Boksem, Meijman, & Lorist, 2006; Boksem & Tops, 2008; Massar, Csathó, & van der Linden, 2018; Müller & Apps, 2019; Richter, Gendolla, & Wright, 2016). However, despite being a cornerstone of theoretical accounts of physical and mental fatigue, and the motivation to exert effort, few studies have simultaneously measured people's sensations of fatigue and willingness to exert effort on a moment-to-moment basis (Müller & Apps, 2019). As a result, whether the same computational processes underpin momentary changes in subjective sensations of fatigue induced by physical or cognitive effort, and how they impact on motivation, is unknown.

Recently, computational accounts have formalised how fatigue might fluctuate on a momentary basis, and how such fluctuations could reduce the motivation to exert effort (Blain, Hollard, & Pessiglione, 2016; Massar, Csathó, & van der Linden, 2018; Meyniel et al., 2016;

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Meyniel, Sergent, Rigoux, Daunizeau, & Pessiglione, 2013; Müller & Apps, 2019; Müller, Klein-Flügge, Manohar, Husain, & Apps, 2021). One component of fatigue is recoverable, increasing after the exertion of effort, but subsides after short amounts of time spent resting (Meyniel et al., 2013; Meyniel & Pessiglione, 2014; Müller et al., 2021). A second, unrecoverable component gradually increases across a task, but is not ameliorated by short periods of rest (Blain et al., 2016; Müller et al., 2021). Increases in both recoverable and unrecoverable fatigue similarly increase the cost of effort and reduce the value placed on rewards that require effort (Müller et al., 2021; Müller & Apps, 2019). However, most tasks that take self-reported fatigue ratings only do so after extended periods of exertion (Ito, Kimura, & Gomi, 2022; Mockel et al., 2015; Müller & Apps, 2019), which does not offer the temporal resolution required to examine the computational mechanisms that govern momentary fluctuations in fatigue. Indeed, most experiments treat the effects of fatigue as a confound to avoid in an experimental design, do not account for it, or only include time on task as a regressor (Müller & Apps, 2019). As a result, it is unknown whether fluctuations in fatigue and motivation are underpinned by the same mechanisms, each influencing the other. Furthermore, it is unclear how such mechanisms may generalise across both physical and cognitive effort (Müller et al., 2021).

Humans are typically averse to exerting effort. People will often choose to undertake less effortful behaviours for less reward, rather than higher effort for more reward (Apps, Grima, Manohar, & Husain, 2015; Chong et al., 2017; Hull, 1943; Kool & Botvinick, 2018; Pessiglione, Vinckier, Bouret, Daunizeau, & Le Bouc, 2018; Shenhav et al., 2017; Westbrook & Braver, 2015). Such "effort discounting" of rewards is often examined with effort-based decision-making (EBDM) tasks where people make choices of whether to tackle easier or more difficult versions of the same task for more or less reward (Chong, Bonnelle, & Husain, 2016). Using EBDM paradigms it has been possible to show that people are averse to both cognitive and physical exertion for many different types of underlying task. This includes studies manipulating effort costs through varying difficulty in the numbers of switches of attention (Apps et al., 2015; Chong et al., 2017), number of task switches (Kool & Botvinick, 2014; Otto & Vassena, 2020), complexity of mathematical operations (Vassena, Deraeve, & Alexander, 2019), number of finger movements (Bächinger et al., 2019), number of mouse-button clicks (Contreras-Huerta, Lockwood, Bird, Apps, & Crockett, 2020), and levels of grip-force (Chong et al., 2017; Klein-Flugge, Kennerley, Saraiva, Penny, & Bestmann, 2015; Lockwood et al., 2017; Pessiglione et al., 2018). However, it is unclear how subjective feelings of fatigue develop as we perform such tasks. Previous work using computational approaches has shown that the motivation to exert physical effort fluctuates with the theorised recoverable and unrecoverable components (Blain et al., 2016; Meyniel et al., 2013; Meyniel & Pessiglione, 2014; Müller et al., 2021). However, it is plausible that in EBDM paradigms fatigue may not similarly fluctuate, as people can prevent increases in fatigue through choices to avoid effort. Since such paradigms have not simultaneously measured both fatigue and the willingness to exert effort for reward, it is unclear how fatigue develops over time.

While both physical and cognitive effort have been shown to discount rewards, it is also unclear whether they depend on the same computational mechanisms and whether the fatigue experienced is similar (Boksem & Tops, 2008; Marcora, Staiano, & Manning, 2009). Previous work has shown that different computations might underlie decisions of whether to exert physical and cognitive effort (Atkins, Andrews, Stout, & Chong, 2020; Chong et al., 2017). Moreover, there are often differences between physical and cognitive effort that might influence motivation and fatigue. Specifically, physically effortful tasks typically set difficulty levels as percentages below a participant's maximum grip strength, thus controlling for capacity (Chong et al., 2017; Müller et al., 2021). As a result, participants do not typically make errors, and are successful almost all of the time at the higher effort levels (Chong et al., 2017; Müller et al., 2021). In contrast, the difficulty levels of cognitively effortful tasks are not usually constrained to participant capacity. As a result, as well as higher difficulty levels being more effortful, they also lead to participants making significantly more mistakes. Errors in cognitive processes have been shown to be aversive (Dunn, Inzlicht, & Risko, 2019; Hajcak & Foti, 2008), and people will avoid them even if they do not impact on the extrinsic rewards that can be obtained from a task (Apps et al., 2015; Birnbaum, 2008; Desender et al., 2021; Desender, Van Opstal, & Van den Bussche, 2017; Kool, McGuire, Rosen, & Botvinick, 2010; Otto & Vassena, 2020; Westbrook et al., 2020; Westbrook, Lamichhane, & Braver, 2019). However, it is unclear whether they also impact upon people's self-reported momentary assessments of fatigue. As a result, it is not known whether the theorised recoverable and unrecoverable components of fatigue can account for fluctuations induced by both physical and cognitive effort, or whether additional computational features are needed to explain fatigue in tasks where people make errors.

Here, we tested whether: (1) fatigue fluctuates on a momentary basis when people make both physical and cognitive effort-based decisions, and (2) fatigue and motivation are driven by both exerted effort and committed errors. To do so, we performed two studies using modified versions of commonly deployed EBDM tasks. In both, participants were required to make a series of choices between two options – one of which required effort, but offered high reward (between 6 and 10 credits), and a second which permitted rest, but only resulted in 1 credit. On each trial, participants chose their preferred option, and then had to exert effort or rest. If successful at the task they received the reward, but if unsuccessful they received nothing. On every trial, before being informed of the outcome but after completing the task or resting, participants were required to rate their level of fatigue between 0 and 100. Using this design, we could measure trial-by-trial changes both in fatigue and effort-based decision-making. In Study 1 we manipulated physical effort (grip-force), increasing the difficulty of the task by requiring higher percentages of participants' maximum voluntary contraction (MVC). In Study 2, we manipulated cognitive effort by varying the levels of complexity of mathematical operations. Using computational modelling we could then test the hypothesis that effort-based decisions and fatigue ratings fluctuate with recoverable and unrecoverable components in both the physical and cognitive domain. In addition, we predicted that in the cognitive effort task, errors in mathematical performance would influence both decisions to exert effort and self-reported ratings of fatigue.

2. Materials and methods

2.1. Participants

Two experiments examined the factors that underlie moment-to-moment fluctuations in fatigue in an effort-based task. We recruited 108 healthy young participants across two studies. Study 1, investigating effort-based decisions in the physical domain (N = 59 participants, 39 female, 20 male, age range 19–37), was approved by The University of Oxford Research Committee. 2 participants were excluded due to a failure to follow task instructions. Study 2, investigating effort-based decisions in the cognitive domain (N = 49 participants, 31 female, 18 male, age range 18–34) was approved by the Monash University Human Research Ethics Committee. 9 participants were excluded due to a failure to follow task instructions. Informed consent was obtained from all participants. For both studies, participants were compensated a flat rate of £12 for their time and were also told that they would receive a bonus of up to £4 based on their responses in the task.

2.2. Design

Across both studies, the same design was used to examine how the willingness to exert effort to obtain rewards changes over trials. The critical difference between each experiment was whether the task required physical or cognitive effort. Both studies comprised a *training* *phase*, in which participants were familiarised with each level of physical or cognitive effort, followed by a *pre-task* (that minimised fatigue), and the *main task*. Study 1 also involved an initial *calibration* phase.

2.3. Effort levels

In Study 1, participants were required to deploy physical effort through the exertion of force on a hand-held dynamometer. Participants undertook an initial *calibration* phase to measure their maximum voluntary contraction (MVC) in order to normalise force levels across participants and avoid variability due to differences in strength.

2.3.1. Calibration

Participants had three attempts to squeeze the dynamometer as hard as they could, receiving strong verbal encouragement throughout. During each attempt, a bar presented on the screen provided live feedback of the force level being generated. In the second and third attempts, a benchmark representing 105–110% of the previous best attempt (displayed with a “target” yellow line on the screen) was used to encourage the participants to improve on their score. Participants were not instructed that this yellow line indicated a higher force level than their previous attempts. The maximum level of force generated during the three attempts was used as that participant’s MVC.

The levels of force required throughout the experiment were then computed as percentages of each participant’s MVC. We defined 6 effort levels corresponding to 0 (rest option), 30%, 39%, 48%, 57%, 66% of MVC.

In Study 2, participants were required to exert cognitive effort to solve mathematical operations of increasing complexity. We determined the levels of cognitive effort in a pilot experiment, and they remained fixed for all participants. Operations in each level were designed to be achievable but require an increasing degree of cognitive demand. Level 1 (rest option) required only a token amount of cognitive effort — the addition of 6 zeros. Participants were still required to select the correct option (zero) from three options displayed during the response window (see 2.5 Cognitive task). Levels 2 through 6 were distinguished by increasingly challenging combinations of operands (addition and subtraction), and by manipulating how numerically close the incorrect alternatives were to the correct response. Fifty unique mathematical operations were designed for levels 2 through 6 (comprising 250 operations in total). Participants were only rewarded for correct responses. Subjective ratings of mental load confirmed that the task levels successfully modulated cognitive effort (see Supplementary material and Suppl. Fig. 6).

2.3.2. Training

In both studies, the pre-task and main task were preceded by an initial training phase. In the first part of training, participants were familiarised with how much physical or cognitive effort was required at each level. Participants were presented with the rest option and the 5 effort levels in an ascending order, 3 times through this sequence (18 trials in total). Participants exerted physical or cognitive effort to complete each trial. If the participant successfully exerted physical force, or made a correct response to the mathematical operation, they were awarded 1 credit. Thus, participants were familiar with how much effort would be required for each level of effort prior to making decisions about whether exerting effort was worth it for the offered reward.

In the second part of training, participants were introduced to the choice to work or not. Participants completed 6 trials, selecting between the fixed rest option for 1 credit and work offers of different levels of reward and effort. Work offers included “good” offers (maximum reward for minimum effort) and “bad” offers (minimum reward for maximum effort). Participants freely chose between “work” or “rest”, and were required to exert effort if they elected to “work”.

2.4. Physical task

A yellow line was shown representing the required level of effort while a fluctuating vertical red bar represented the instantaneous effort exerted by the participant on the hand-held dynamometer. Participants had 5 s to reach the required effort threshold by squeezing the dynamometer. The response was considered correct if the effort exerted was above the required level for at least 3 out of 5 s.

2.5. Cognitive task

A sequence of six operands appeared on the screen, one at a time for 750 ms each and separated by a 400 ms interstimulus interval (ISI). Each operand was paired with an operator (either addition or subtraction). After the final ISI, three response options appeared on the screen. One option was the correct answer to the operation and the other two options were foils. Participants had 1500 ms to register their response, using either the left, up, or right arrow key on a standard computer keyboard to select the option on the left, centre, or right of the screen. Once an option was selected, the participant’s choice was highlighted in yellow and the screen paused for any remaining time in the 1500 ms response window. The total duration of a trial was 8400 ms.

2.6. Pre-task

In order to estimate the degree to which people devalued rewards by effort in the absence of fatigue, participants performed 75 trials of an effort-based task prior to the main task. While in the main task choices on every trial influenced whether force was required or not, in the pre-task only 10% of choices required effort exertion after choice. On 90% of trials, no effort was required irrespective of what was chosen. Participants indicated their choices by pressing one of two keys on the keyboard to select the “work” or “rest” offer, presented on the corresponding left or right of the screen. After the participant made a choice, “no force required” (physical task) or a countdown (cognitive task) was displayed on the screen for a duration identical to trials that required effort in order to avoid the effects of temporal discounting. The 10% of trials that required effort were pseudo-randomly selected. Participants were also given four breaks during this task, to minimise any possible effects of fatigue. Taking this approach allowed us to measure the degree to which people devalue rewards by effort in a task where the total demands were low and thus participants were unlikely to become significantly fatigued. In the pre-task, the work options were sampled from five reward levels (2, 4, 6, 8, 10 credits) and five effort levels; for the physical task this corresponded to force intensity (30, 39, 48, 57, 66% MVC) and to mathematical complexity in the cognitive task (see 2.3 Effort levels). Effort levels were represented by the number of elements in a pie chart (Fig. 1b). Effort and reward levels were chosen based on pilot and previous experiments that controlled for fatigue (Chong et al., 2017; Lockwood et al., 2017). Having such high value work offers ensured that participants would not be naturally inclined to avoid those effort levels in the main experiment prior to becoming fatigued. The pre-task was always followed by the main fatigue task.

2.7. Main task

This was the main phase of the experiment, in which most of the primary outcome measures were taken and related to fatigue. On each trial, participants chose between “work” or “rest” (Fig. 1a). The rest option was always worth 1 credit, but gave participants a 5 s time window to pause and, in the cognitive task, only required a token amount of exertion (Fig. 1c). Work offers varied in terms of both the rewards on offer and the effort required on every trial. For the work option we selected 9 combinations of reward and effort levels for which acceptance in the pre-task was higher (Fig. 2). This corresponded to the three highest rewards (6, 8, 10 credits) and three lowest effort level

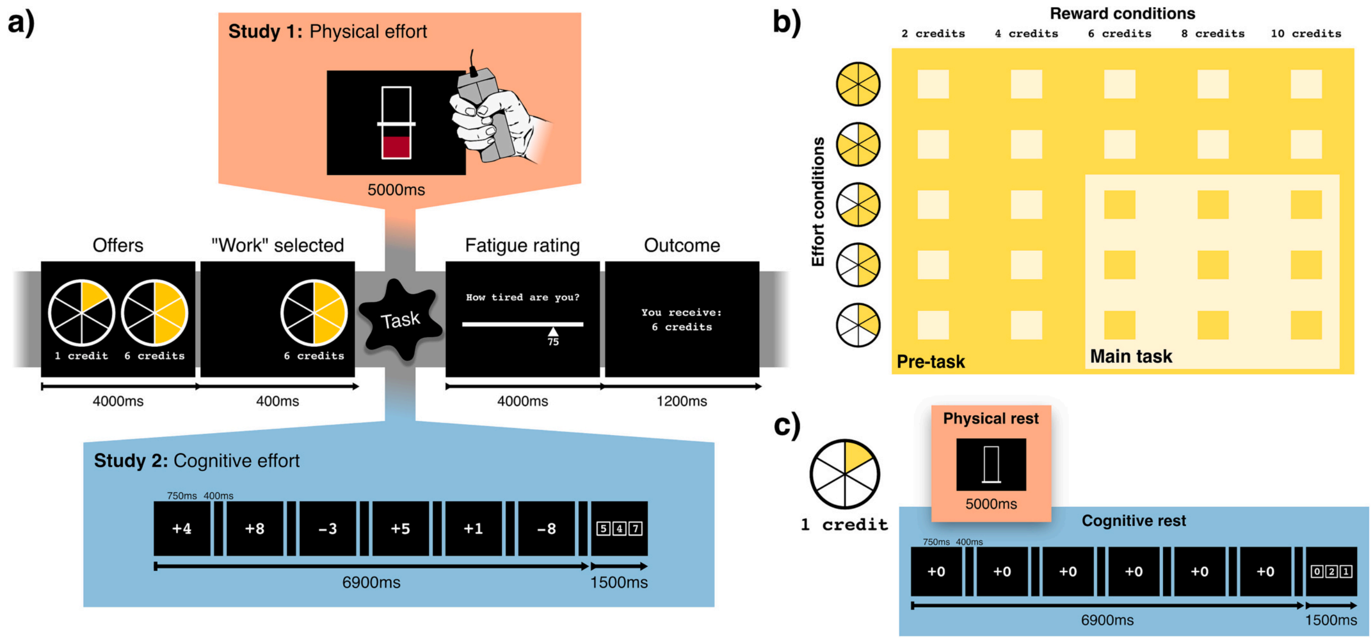

Fig. 1. Methods. a) Trial structure in the main task for Study 1 (physical effort) and Study 2 (cognitive effort). Participants chose between a fixed "rest" offer for 1 credit and variable "work" offers that paired different levels of effort with different rewards. In this example, the participant chooses a work offer that requires the successful exertion of intermediate effort (level 3) for 6 credits in reward. After working or resting, participants rated their fatigue on a 0–100 point scale. Finally, the outcome of the trial was revealed. Participants received no reward if they did not sustain physical effort at the required force level for 3 out of 5 s (Study 1), or gave an incorrect answer (Study 2). b) Effort and reward conditions. In the Pre-task, work offers included 5 levels of effort and 5 levels of reward. In the Main task, work offers paired the 3 highest levels of reward with the 3 lowest levels of effort. c) Declining the work offer. In Study 1, decisions to decline the work offer afforded the participant a 5 s window where no physical effort was required, they were required only to hold the grip-force device without squeezing it. In Study 2, decisions not to work required the participant to respond to a fixed mathematical operation (a sum of zeros) where the trivial answer (zero) was known in advance.

Fig. 2. Proportion of decisions to work for (E)ffort and (R)eward conditions appearing in both the pre-task and main task. Decisions are contrasted between the pre-task, where only 10% of decisions required the exertion of effort, and the main task where effort was required on every decision to work. See Suppl. Fig. 8 for an expanded plot that includes all conditions in the pre-task. Group means are centred in each cell together with standard errors. a) Study 1 (physical domain). b) Study 2 (cognitive domain).

(2–4). Participants were instructed that more credits equated to a greater financial remuneration for their participation. They were instructed that there would be no breaks, and, if they felt the need to rest, they would have to choose the rest option. Shifts in preferences towards resting rather than working would therefore be indicative of changes in motivation and potentially the effects of fatigue. Participants had 4 s to make their choice. Participants indicated their choices by pressing one of two keys on the keyboard corresponding to the option on the left or right of the screen. If the choice was to work, participants exerted the corresponding level of either physical (Study 1) or cognitive (Study 2) effort. If they failed to do so, they received 0 credits. All trials lasted the same duration, to avoid the effects of temporal discounting (Green, Fristoe, & Myerson, 1994). If the choice was to rest, participants either observed a blank screen for the same five-second duration (Study 1), or performed a mathematical operation containing only zeros and provided a response within 1.5 s (Study 2).

Participants also provided a rating between 0 and 100 of how "tired, exhausted or fatigued they felt", immediately after the exertion of force (or rest). They had a fixed four-second period to register their response using the left and right arrow keys, with the initial position of the cursor positioned on their previous rating. A rating taken prior to the main task of the experiment provided the initial position on trial 1. The reward outcome of the trial was then shown for one second. In the cognitive task, the outcome screen could be used to infer whether the selected response was correct or incorrect. For both studies, the main task comprised 234 trials, equally distributed amongst the nine conditions (three effort x three reward levels).

2.8. Apparatus

Physical exertion was measured using a hand-held dynamometer (SS25LA, BIOPAC Systems, USA) that participants squeezed using their dominant hand. The task was programmed and presented using MATLAB 2012 (MathWorks, USA) and Psychtoolbox (http://psychtoolbox.org). Choices were made on the keyboard using their non-dominant hand. The cognitive task was also programmed and presented using MATLAB (MathWorks, USA) and Psychtoolbox. All choices and responses were made on the keyboard using the dominant hand.

2.9. Computational modelling

To study and compare fluctuations in the motivation to exert effort, as well as changes in the subjective feeling of fatigue in the cognitive and physical domain, we developed several computational models based on theories of fatigue and error-based learning. These models share the assumption that when engaging in a task, subjective fatigue sensations fluctuate continuously based on both the effort exerted and the outcome of the trial, and that this in turn affects the motivation to exert effort in the future. We built on previous work that established the presence of two components, a recoverable one, in which fatigue increases after effort, but declines through rest, and a long-term unrecoverable component that can only be restored by long-term disengagement in the task (Müller et al., 2021).

We fit these models to choices and trial-by-trial ratings of fatigue. In order to fit choices, we input the fatigue ratings into a computational model of effort discounting, shifting how much rewards were devalued by effort on a trial-by-trial basis. By separately fitting these models both to choices to work and ratings of fatigue, we could determine whether the subjective feeling of fatigue and the effect of fatigue on the motivation to exert effort are underpinned by similar factors and operate on the same timescales.

2.10. Modelling choices in the absence of fatigue

We first fit choices in the pre-task to estimate the choice model parameters in the absence of fatigue. We used an effort discounting model which has been used to accurately characterise how people trade off rewards against effort (Chong et al., 2017; Hartmann et al., 2015; Lockwood et al., 2017). The model assumes that the subjective value of a choice is proportional to the reward on offer, discounted by the effort associated with it. The shape of this discounting function reflects how effort affects choice behaviour. For example, linear models predict that the discounting will grow at a constant rate as effort increases. In contrast, a hyperbolic or exponential model predicts that changes from low effort will have greater impact than changes at a higher level of effort, whereas a parabolic model would predict the opposite. These functions have been used in several previous studies to fit effort discounting in the physical and cognitive domain (Lockwood et al., 2017; Chong et al., 2017; Lockwood et al., 2022).

We made a preliminary comparison of four models with linear, hyperbolic, parabolic, and exponential effort discounting functions. For each model we fit participants' choices in the cognitive and physical effort pre-task. We found that the best-fitting effort discounting function for both the cognitive and physical domains was one with a parabolic function:

$$SV_{(t)} = R_{(t)} - k_0 {*} E_{(t)}{}^2 \tag{1}$$

Here we estimate the subjective value (SV) of a choice as the value of the reward (R) offered on a trial discounted by the associated effort (E). This trade-off is dictated by a free parameter (k_0) estimated for each participant. As k_0 increases, it leads to lower subjective values. To fit choices we used a *softmax* transformation:

$$P_{work(t)} = \frac{e^{SV_{(t)}{*}\beta}}{e^{\beta} + e^{SV_{(t)}{*}\beta}} \tag{2}$$

This estimates the probability (P_{work}) of the participants choosing to accept the offer to work (exert the effort) to obtain the reward. β is a free parameter that estimates the degree of stochasticity present in participants' choices. The probability of the participant choice under the model is therefore defined as

$$P_{choice(t)} = \begin{cases} P_{work(t)} \ if \ choice(t) = work \\ 1 - P_{work(t)} \ if \ choice(t) = rest \end{cases} \tag{3}$$

Fitting this model to the choices in the pre-task we could estimate the two free parameters (k_0, β) for each participant using the *fminsearch* function in MATLAB. Each model was fit 50 times using different parameter starting values to ensure that the optimisation function had not settled on a local minimum. The parameters of this model allowed us to estimate the degree to which participants devalued rewards by effort when not fatigued. k_0 and β were then used as fixed values when fitting all models to the main task data.

2.11. Modelling subjective fatigue

In the main task participants became increasingly fatigued. To estimate how fatigued a participant was at any trial (t) in the experiment, we built models from the history of exerted effort and trial-by-trial outcomes. Based on previous studies (Massar, Csathó, & der Linden, 2018; Müller et al., 2021; Müller & Apps, 2019) we assumed that, on any given trial (t) the level of fatigue (F) was a function of a recoverable (RF) and unrecoverable (UF) component:

$$F_{(t)} = RF_{(t)} + UF_{(t)} \tag{4}$$

Both components change over the course of the experiment. RF increases after trials where participants had made a decision to work:

$$RF_{(t+1)} = RF_{(t)} + \left(\alpha {*} E_{(t)}^2\right) \tag{5}$$

This increase depends quadratically on the amount of effort (E) required on the trial, such that higher amounts of effort would increase RF by larger amounts, weighted by a free parameter α. This parameter scales the degree to which exerting effort increases recoverable fatigue idiosyncratically for each subject. A higher α would reflect someone who shows greater fatigability. RF also decreases for all times when participants choose to rest or when they timed out without making a decision:

$$RF_{(t+1)} = RF_{(t)} - (\theta {*} T_{Rest}) \tag{6}$$

RF here declines by the amount of time (T_{rest}) spent resting on the last trial. How much someone recovers through rest is determined by the free parameter θ, which scales the degree to which rest reduces fatigue. A higher θ reflects greater recovery through rest. As all trials are equally long within as task, we took a notional value of $T_{Rest} = 1$.

As outlined in (1), fatigue is also assumed to be a function of a long-term unrecoverable component UF reflecting the fact that people tend to always be exhausted after extended periods of work and are unable to fully recover unless they receive primary rewards or extensive periods of rest (e.g. sleep). This "unrecoverable" component of fatigue increases throughout the task:

$$UF_{(t+1)} = UF_{(t)} + \left(\gamma {*} E_{(t)}^2\right) \tag{7}$$

UF on trial t + 1 increases as a function of the effort (E), multiplied by the free parameter γ which idiosyncratically quantifies the build-up of unrecoverable fatigue throughout the experiment. When effort is exerted, UF increases on the next trial; when participants rest, UF remains unchanged, as it can only be reduced through extensive rest. A model defined by Eq. (1)–(4) therefore accounts for a trial-by-trial fluctuating level of subjective fatigue, given by the sum of a fluctuating recoverable component and an unrecoverable one that can only increase or remain stable.

To test whether both components of the model were necessary to fit the fatigue ratings in our cognitive and physical effort tasks, we ran three different versions of this model. *Model F1* included both components as defined by Eqs. (1)–(4); *Model F2* included only the long term, unrecoverable fatigue component defined in (4), i.e.:

$$F_{(t)} = UF_{(t)} \tag{8}$$

Model F3 included only the short term, recoverable fatigue defined in (2–3), i.e.:

$$F_{(t)} = RF_{(t)} \tag{9}$$

2.12. Modelling changes effort-based decisions through fatigue and trial-by-trial outcomes

To estimate changes in effort-based decisions in the main fatigue task, we adapted Eq. (7) to allow rewards to be discounted by effort on a trial-by-trial basis:

$$SV_{(t)} = R_{(t)} - \left(k_{(t)} * E_{(t)}{}^2\right) \tag{10}$$

Here, the subjective value (*SV*) of a work offer on a trial is a function of the reward on offer (*R*), discounted by the effort required (*E*) as weighted by the discount factor (*k*) which varies over time. Therefore, the trade-off between reward and effort varies trial-by-trial as a function of *k*. The evolution over time of the discount factor distinguishes how our models fit choices. For *Model F1*, *Model F2* and *Model F3,* $k_{(t)}$ increases with the accumulated fatigue $F_{(t)}$:

$$k_{(t)} = k_0 \left(1 + F_{(t)}\right) \tag{11}$$

where k_0 is the effort discounting in the absence of fatigue estimated in the pre-task. Next, we tested the hypothesis that the motivation to work varies together with participants' capacity to successfully implement the required action. In *Model 4* and *Model 5*, we hypothesised that an individual's effort discounting parameter increases following a trial in which participants are not rewarded:

$$k_{(t)} = k_{t-1} - \varepsilon \left(\widehat{R}_{(t-1)} - R_{(t-1)}\right) \tag{12}$$

where ε is a learning parameter and $R_{(t-1)}$ and $\widehat{R}_{(t-1)}$ are the reward chosen and obtained in the previous trial, respectively. The latter can either be equal to the chosen reward (when a subject is successful in the trial) or equal to 0 (following an error). In *12* we therefore implement a delta-learning rule, with an error-driven component whereby $k_{(t)}$ increases following every trial in which a participant makes a mistake. In these two models, therefore, it is the trial outcome and not the subjective feeling of fatigue that drives increases in sensitivity to effort over time.

Model 4 (L1 in figure labels) and *Model* 5 (L2 in figure labels) differed in how they modelled subjective fatigue. Both models had a recoverable and a non-recoverable component, but while *Model 4* had fatigue increase at the same pace after every trial, *Model 5* further allowed $RF_{(t)}$ to increase at a different rate after a correct trial or a mistake.

$$RF_{(t+1)} = \begin{cases} RF_{(t)} + \left(\alpha * E_{(t)}^2\right) \ if \ \widehat{R}_{(t)} = R_{(t)} \\ RF_{(t)} + \left(\varepsilon * E_{(t)}^2\right) \ if \ \widehat{R}_{(t)} = 0 \end{cases} \tag{13}$$

Importantly*, Model 5* had the further constraint that mistakes increased both subjective fatigue and effort sensitivity at the same rate, so that the same parameter ε scaled how fatigue should increase after a mistake, and also how the discount factor increased in Eq. (12).

2.13. Model fitting

To fit the models outlined above to trial-by-trial ratings of fatigue $\widetilde{FR}_{(t)}$ we minimised an error ERR_{fat} defined by the sum of squared residuals between the ratings of fatigue and the estimated subjective fatigue $F_{(t)}$ on each trial:

$$ERR_{fat} = \sum_t \left(F_{(t)} - \widetilde{FR}_{(t)}\right)^2 \tag{14}$$

Ratings were first normalised to account for variability in scale usage between participants using

$$\widetilde{FR}_{(t)} = \frac{FR_{(t)} - min\left(FR_{(t)}\right)}{std\left(FR_{(t)}\right)} \tag{15}$$

where *min* and *std* are computing the minimum and standard deviation of each subject ratings. To fit the models outlined above to choices $C_{(t)}$ we minimised an error ERR_{choice} defined by the negative log likelihood of the choice model with

$$ERR_{choice} = -\sum_t log\left(P_{choice(t)}\right) \tag{16}$$

where $P_{choice(t)}$was obtained through Eq. (9). Time out trials were excluded from this analysis.

A single error function was obtained as

$$ERR = ERR_{fat} + ERR_{choice} \tag{17}$$

The model parameters ($\alpha, \gamma, \theta, \epsilon$) for each subject were optimised using MATLAB *fminsearch* function under the constraint they should all be positive. Initial parameter values were set randomly in the open interval (0,1). Each model was fit 50 times using different parameter starting values to ensure that the optimization function had not settled on local minima.

We compared models using the Bayesian Information Criterion (BIC) and Akaike Information Criteria (AIC), which punishes models for their number of free parameters. To do so we converted ERR_{fat} to a likelihood under the assumption of normally distributed errors and obtained the criteria as

$$AIC = 2k + 2ERR_{choice} + n * log\left(ERR_{fat}\right) \tag{18}$$

$$BIC = klog(n) + 2ERR_{choice} + n * log\left(ERR_{fat}\right) \tag{19}$$

Computing exceedance probabilities we could test which model outperformed the others. To do so, we used the MATLAB function *spm_BMS* from the *spm12* toolbox. Schematics of the models and the model comparison is included in Fig. 5 while differential results for choice and fatigue ratings fitting are shown in Suppl. Fig. 5.

All data, code to produce figures and computational modelling code are available.

3. Results

The aim of this project was to examine how self-reported fatigue fluctuated on a momentary basis, and in turn how that affected the value of exerting either physical or cognitive effort to obtain rewards. In two studies, we used a decision-making task in which participants exerted either physical (Study 1) or cognitive (Study 2) effort to obtain rewards (Fig. 1a). In the main task, participants were not given an opportunity to take breaks. Rather, on each trial, participants chose to either "work" or "rest". Work offers varied on every trial in both the magnitude of the reward (6, 8, 10 credits) and the amount of physical or cognitive effort required to obtain it (Fig. 1c). Declining to work resulted in a token amount of effort in exchange for a small reward of 1 credit, providing an opportunity to rest (Fig. 1b) In Study 1, physical effort was operationalised through grip-force on a handheld dynamometer. Effort levels were calibrated to each participants' maximum grip strength (30, 39, 48% of the maximum voluntary contraction [MVC]). In Study 2, cognitive effort was operationalised using arithmetic operations. Participants responded to unique operations by choosing the correct solution between three possible alternatives. On each trial they were offered work options with different effort levels corresponding to operations of higher or lower mental demand. Mental demand was manipulated by the choice of operands (addition and/or subtraction), and by manipulating how numerically close the incorrect response alternatives were to the correct response. To examine trial-by-trial changes in fatigue, we instructed participants to rate their level of fatigue on a scale from 0 to 100 at the start of the main task, and again on each trial. Fatigue ratings were given after exerting effort -or resting - but before the participant was informed about the reward they had obtained (i.e., ratings were made prior to receiving reward feedback).

3.1. *Fatigue fluctuates on momentary basis after physical exertion, and predicts choices to work*

In Study 1, we hypothesised that physical effort would induce fatigue over time, diminishing the value of exerting physical effort to obtain rewards. Our framework predicts that: (1) participants will be more inclined to work, when their fatigue is low; (2) participants will change their valuation of physical effort, such that higher effort/lower reward work offers will increasingly be declined; and (3) ratings of subjective fatigue will fluctuate with unrecoverable and recoverable components of fatigue, and predict subsequent choices. To test these predictions, we used mixed-effects models and computational modelling.

Our first prediction was that participants would be more inclined to work when their fatigue was low. To test this hypothesis, we compared choices in the main part of the experiment, where every choice of work resulted in the requirement to exert force for reward, with a pre-task in which only a random 10% of trials resulted in the requirement to exert force. We start with our analysis of the pre-task where decisions were made under conditions of low fatigue.

In the pre-task, to ensure that participants were discounting rewards by effort we analysed choices to work or rest. Choices were entered into a logistic mixed model together with effort levels, reward levels, and subject-specific intercepts. We observed a significant main effect of effort ($\chi^2(4) = 197.11$, $p < .001$) and reward ($\chi^2(4) = 16.20$, $p = .003$) with an interaction between effort and reward ($\chi^2(16) = 54.43$, $p < .001$). Consistent with effort discounting, participants worked most often when rewards were high and when effort demands were low (Fig. 2a, Suppl.Fig. 8a). Critically, participants worked on a high proportion of trials (M = 96.9%, SEM = 1.6%) for all the effort levels (i.e., 2, 3, 4) and reward levels (i.e., 6, 8, 10) included in the main task suggesting that these offers were regarded as good value under conditions of low fatigue.

But did people's preference change in the main task designed to induce fatigue? To directly contrast behaviour in the pre-task and main task, we first examined the subset of trials in the pre-task which matched the effort levels (2, 3, 4) and reward levels (6, 8, 10) from the main task. We entered these trials together with all trials in the main task into a logistic mixed model predicting choices to work or rest. We included effort levels, reward levels, and experiment phase (pre-task or main task) as fixed factors together with subject-specific intercepts. Interaction terms were included for all fixed effects, and we tested the significance of main effects after interactions (type III sums of squares). We observed a significant main effect of effort ($\chi^2(2) = 8.49$, $p = .014$) and experiment phase ($\chi^2(1) = 9.66$, $p = .002$) that was moderated by a two-way interaction between effort and experiment phase ($\chi^2(2) = 47.56$, $p < .001$). All remaining effects and interactions were not significant (main effect of Reward: $\chi^2(2) = 0.64$, $p = .724$; Reward x Effort: $\chi^2(4) = 1.35$, $p = .853$; Reward x Experiment Phase: ($\chi^2(2) = 5.11$, $p = .078$); Reward x Effort x Experiment Phase: $\chi^2(4) = 0.44$, $p = .979$). The same pattern of results was observed when contrasting the first and last halves, or first and last quarters, of trials in the main task, minimising the possibility that a change in behaviour was driven by a change in the frame of options available and not changes due to fatigue (see Supplementary material and Suppl. Fig. 3). Thus, when repeated effortful exertion has to be made, the motivation to exert higher levels of effort is reduced.

To examine our second prediction that choices would change over trials, we included cumulative physical effort into the model (a running sum of effort exerted from all previous trials). Choices were entered into a logistic mixed model together with effort levels, reward levels, cumulative effort, and subject-specific intercepts as random effects. Interaction terms were included for all fixed effects. We observed a significant main effect of effort ($\chi^2(2) = 283.47$, $p < .001$), reward ($\chi^2(2) = 27.81$, $p < .001$), and an interaction between effort and cumulative effort ($\chi^2(2) = 8.97$, $p = .011$). All remaining effects were not significant including the main effect of cumulative effort ($\chi^2(1) = 2.98$, $p = .084$), two-way interaction between reward and cumulative effort ($\chi^2(2) = 0.62$, $p = .735$), as well as the three-way interaction between reward, effort, and cumulative effort ($\chi^2(4) = 1.03$, $p = .906$). These results suggest that a build-up of fatigue is induced by the efforts exerted over time.

Our third prediction was that self-reported fatigue would change over trials and participants would change their decisions to work as fatigue increases. We first used a linear mixed model, fitting trial-by-trial fatigue ratings as a function of trial count in the main task (together with subject-specific intercepts as random effects). Although participants could freely choose to rest, and thus prevent substantial build-up of fatigue, ratings increased significantly during the main task ($\beta = 0.168$, 95% CI [0.165, 0.171], $F(1,13,280) = 14,471$, $p < .001$; Fig. 3a). In addition, we found that fatigue ratings significantly decreased on the trials where they declined the work offer, and significantly increased as a function of effort exerted on the trials where they chose to work (Suppl. Fig. 4). The average change in fatigue was significantly lower following rest (M = -1.65, SEM = 0.31) compared to physical exertion at Effort level 2 (M = 0.20, SEM = 0.13; $t(218) = -5.07$, $p_{holm} < 0.001$), Effort level 3 (M = 1.06, SEM = 0.18; $t(218) = -7.45$, $p_{holm} < 0.001$), and Effort level 4 (M = 2.66, SEM = 0.33; $t(218) = -11.78$, $p_{holm} < 0.001$). Effort level 3 was associated with significantly higher fatigue than Effort level 2 ($t(218) = 2.44$, $p_{holm} = 0.016$), and Effort level 4 was significantly higher than level 3 ($t(218) = 4.47$, $p_{holm} < 0.001$).

To test whether these increases predicted choices to exert effort, we examined choices to work in the main task together with effort levels, reward levels, and trial-by-trial fatigue ratings in a mixed model. Interaction terms were included for all fixed effects. We observed a significant main effect of reward ($\chi^2(2) = 17.33$, $p < .001$) and effort ($\chi^2(2) = 133.09$, $p < .001$), as well as a two-way interaction between Effort and Fatigue ratings ($\chi^2(2) = 9.04$, $p = .011$). All remaining effects were not significant (main effect of Fatigue: ($\chi^2(2) = 1.80$, $p = .179$); Reward x Effort interaction ($\chi^2(2) = 3.86$, $p = .425$); Reward x Fatigue ($\chi^2(2) = 5.30$, $p = .071$); Reward x Effort x Fatigue ($\chi^2(4) = 5.25$, $p = .263$)). Thus, as self-reported fatigue increased it was associated with subsequent reductions in the willingness to choose to exert higher levels of effort. This is consistent with an increase in effort-discounting driven by increased fatigue.

In summary and consistent with our hypotheses, we found that fatigue increased as a function of time, and particularly after high effort trials. Furthermore, increases in fatigue were related to subsequent reductions in the willingness to exert higher levels of effort for reward.

3.2. *Computational modelling reveals fatigue and motivation fluctuate on a momentary basis*

To better understand the relationship between fatigue and physical effort-based decisions we developed several computational models

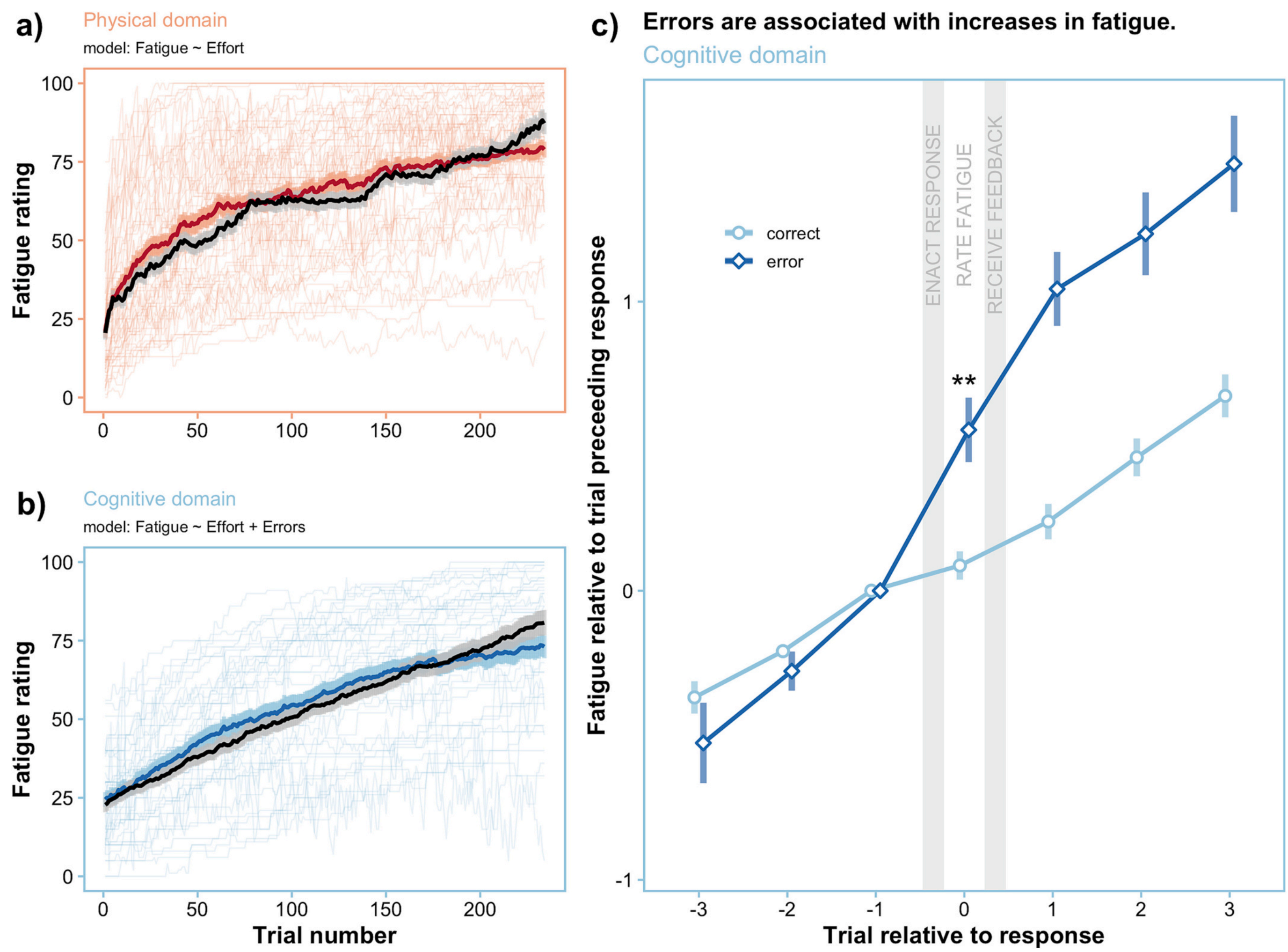

Fig. 3. Fatigue ratings fluctuate from trial to trial and depend on errors in the cognitive task. a) Study 1 (physical domain). Individual participants' fatigue ratings are plotted in orange with the group mean in red together with standard error. Fatigue ratings predicted by the winning model (where ratings are determined by physical effort alone) are plotted in black. b) Study 2 (cognitive domain). Individual participants' fatigue ratings are plotted in pastel blue with group mean in blue together with standard error. Fatigue ratings predicted by the winning model (where ratings are determined by cognitive effort as well as error history) are plotted in black. c) Incorrect decisions are associated with increases in fatigue in the cognitive domain. Here, we plot fatigue relative to the preceding trial separately for incorrect and correct responses. We observed that fatigue ratings were relatively higher following incorrect decisions than correct decisions. Notably accuracy was high in the physical effort (Mean = 99%) task. This result cannot be explained by feedback since participants observed the outcome only after rating fatigue. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

based on theories of fatigue (Müller et al., 2021; Müller & Apps, 2019) and fit them to the choice and ratings data from Study 1. These models test the notion that the subjective sensation of fatigue fluctuates continuously based on the effort previously exerted, and that this in turn affects the motivation to exert effort in the future (Müller et al., 2021; Müller & Apps, 2019). We predicted that ratings of fatigue and effort-based decisions would fluctuate in line with unrecoverable and recoverable components. In addition, although errors were rare in this task, we also compared a class of models that included an error-driven mechanism that tracks trial outcomes using a simple delta-learning rule. However, we first modelled the pre-task choices to examine whether choice data were best explained by a linear, quadratic, or hyperbolic discount function. Consistent with previous reports (Chong et al., 2017), we found that the best computational model of effort discounting was one where efforts discount rewards quadratically (BIC = 47). By fitting the choices in the no-fatigue task we could also estimate the baseline level of effort aversion and choice stochasticity for each participant, which we then used in our modelling of the main task.

For the main task, computational models were fit to both fatigue ratings and effort-based decisions simultaneously to ensure our models could explain fluctuations in both fatigue and choices. These models therefore assumed that effort discounting increased with fatigue, thus reducing reward value and decreasing the probability of working. Three models were developed to account for how exerting effort would subsequently increase effort discounting (F1-F3; Fig. 4) which differed in how they accounted for increases in fatigue after effort. In addition, we developed two learning models (L1-L2 in Fig. 4), in which the trial outcome updated the effort discounting parameter, which did not depend on the effort-level. For trials in which participants were successful, the effort discounting parameter remained unchanged. In contrast, trials in which participants were not successful resulted in an increase in this parameter. This had the subsequent effect of reducing motivation to work in successive trials. L1 and L2 differed in whether they allowed trial outcomes to have an impact on just choices or on both fatigue ratings and choices. Specifically, L1 assumed that fatigue simply varied with effort, while L2 assumed that fatigue would increase proportionally to the effort exerted but with a different rate dependant on whether the trial was successful or not.

Consistent with our predictions, we found that both choices and fatigue ratings were best explained by a model of fatigue comprising both

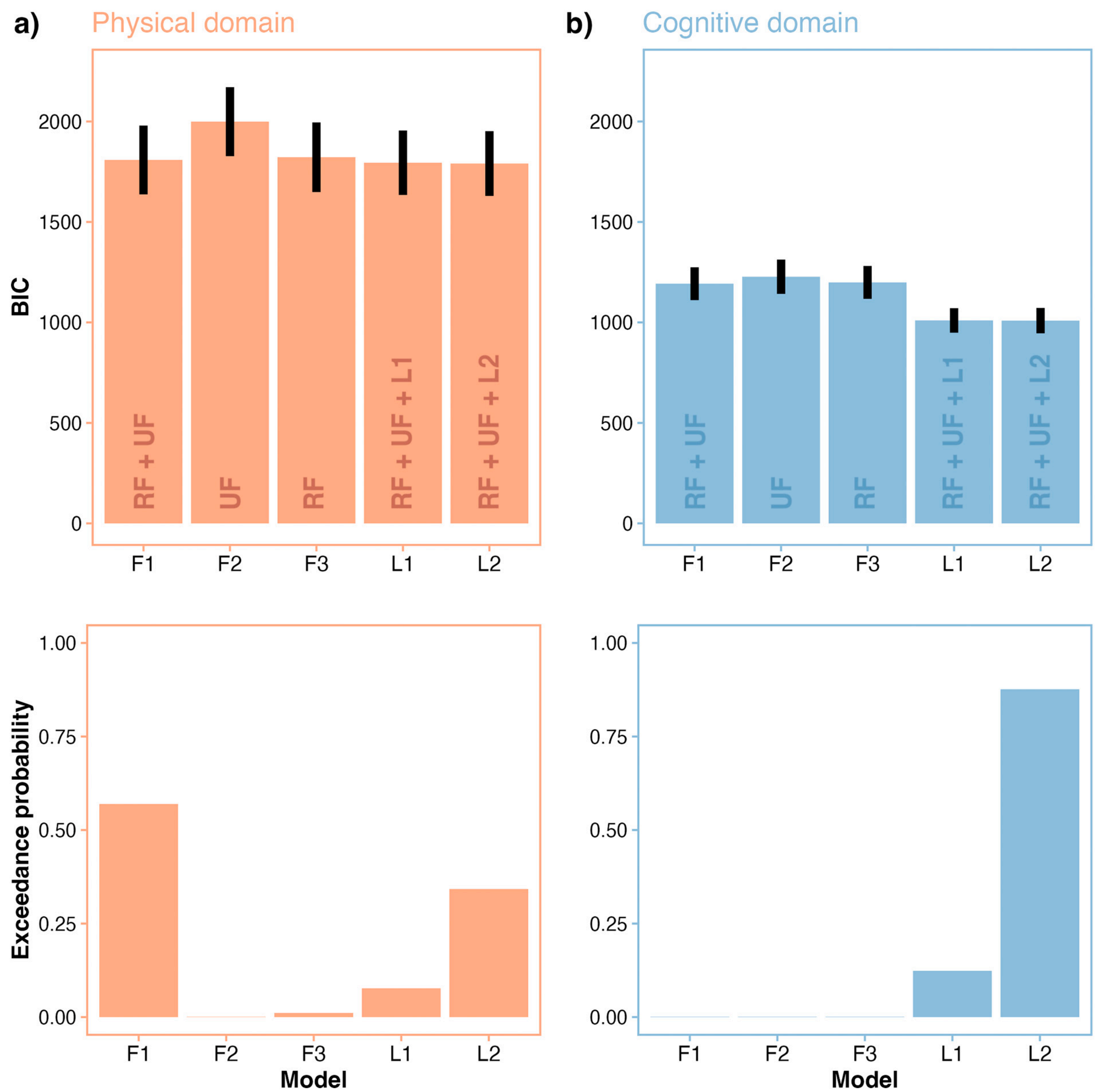

Fig. 4. Model fits on decisions to work a) Experiment 1 (physical domain). Decision and rating data were best fit by a model where motivation is entirely driven by physical effort. b) Experiment 2 (cognitive domain). Decision and rating data were best fit by a model that included cognitive effort as well as error history. Models labelled as 'F' modelled changes in effort-based decisions through changes in fatigue. Models labelled as 'L' modelled changes in effort-based decisions through an error driven learning component. F1 is the full model containing both recoverable and unrecoverable components. F2 contains only the unrecoverable component and F3 only the recoverable component. L1 includes the components of F1 to explain fatigue ratings, with the addition of errors impacting upon choices of whether to exert effort. L2 includes the components of F1 and L1, but also explains fluctuations in fatigue ratings with an additional error-driven component.

a recoverable and unrecoverable component of fatigue (Model F1). The winning model fit well both fatigue ratings and choices for both studies: the median R^2 for fatigue ratings fit was 0.99 both for the physical and cognitive effort tasks while the median point-biserial correlation values for explaining choices was 0.77 and 0.78 respectively. This model outperformed alternatives both in terms of model fit and in exceedance probabilities (BIC = 1808 AIC = 1798 Exceedance probability (XP) = 0.57, Fig. 4a, Suppl.Fig. 1). The winning model therefore did not include errors, consistent with the fact that participants were successful on 99% of trials and that fatigue primarily affected their decisions to work. It should be noted that the unrecoverable parameters were an order of magnitude lower than that of the recoverable parameters (S), this is because the unrecoverable parameter scales the effects of fatigue gradually over trials, whereas the RF parameters constantly fluctuate, and as such they are not directly comparable (Suppl. Fig. 5). Thus, our results demonstrate that fatigue fluctuates constantly during physical effort-based decision-making, influencing both self-reports of fatigue and choices to exert effort. This fatigue is partially recoverable, increasing after effort and decreasing after rest, but also contains an unrecoverable component that simply increases over time.

3.3. *Momentary fluctuations in fatigue and cognitive effort-based decisions*

In Study 2, we hypothesised that fatigue fluctuates with recoverable and unrecoverable components as in Study 1. However, in addition we predicted that the nature of the arithmetic task, like other cognitive effort tasks, meant participants would make errors and that these would influence both choices and fatigue ratings.

We analysed choices to work in the pre-task to ensure participants'

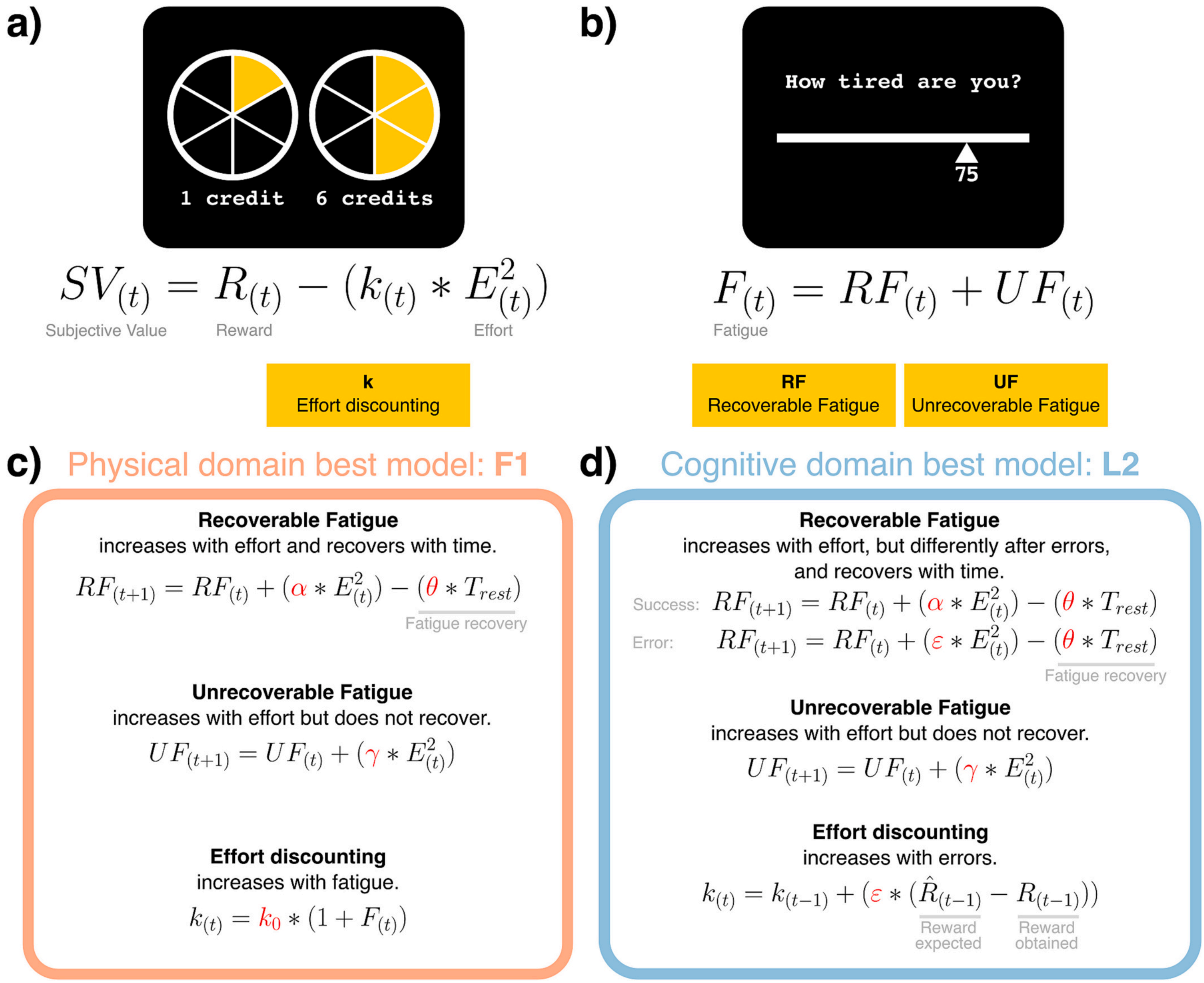

Fig. 5. Winning models a) In both domains, choices were fit computing the subjective value (SV) of the work offer. SV is proportional to the reward (R) offered and discounted by the effort (E) through the effort discounting parameter k(t). b) In both domains, fatigue ratings were fit by the sum of two components: a recoverable component, which increases after efforts but recovers with time when resting, and an unrecoverable component, which does not. c) Best model for physical domain. Fatigue ratings are best fit by a model with two components. Effort discounting is entirely driven by fatigue. d) Best model for cognitive domain. Fatigue ratings are best fit by a model with two components. However, recoverable fatigue has different rates of increase following either successful or error trial outcomes. Effort discounting increases after errors.

choices were consistent with effort discounting. Choices were entered into a logistic mixed model together with effort levels, reward levels, and subject-specific intercepts as random effects. Consistent with Study 1, we observed a significant main effect of effort ($\chi^2(4) = 168.06$, $p < .001$) and reward ($\chi^2(4) = 26.47$, $p < .001$), which were qualified by an interaction between effort and reward ($\chi^2(16) = 48.89$, $p < .001$). Participants worked most often when rewards were high and when effort demands were low (Fig. 2b, Suppl.Fig. 8b) (M = 87.6%, SEM = 4.0%).

To contrast behaviour in the pre-task and main task, we considered the subset of trials in the pre-task matching the effort levels and reward levels from the main task. These trials and all trials in the main task were entered into a logistic mixed model on choices to work. We included Effort, Reward, and Experiment Phase (pre-task or main task) as fixed factors together with subject-specific intercepts. Interaction terms were included for all fixed effects. We observed the same pattern of effects as in Study 1, significant main effects of Effort ($\chi^2(2) = 32.74$, $p < .001$) and Experiment Phase ($\chi^2(1) = 19.90$, $p < .001$) were moderated by a two-way interaction between effort and experiment phase ($\chi^2(2) = 40.14$, $p < .001$). All remaining effects and interactions were not significant (main effect of Reward: $\chi^2(2) = 2.56$, $p = .278$; Reward x Effort: $\chi^2(4) = 5.36$, $p = .253$; Reward x Experiment Phase: ($\chi^2(2) = 3.28$, $p = .194$); Reward x Effort x Experiment Phase: $\chi^2(4) = 1.59$, $p = .811$). The same pattern of results was observed when comparing halves or quarters of the main task (see Supplementary material and Suppl. Fig. 3). It is thus unlikely that decisions are driven by there simply being different offers available in the main task compared to the pre-task. Notably there was also no difference in perceived mental load or accuracy over the course of the experiment (see Supplementary material, Suppl. Fig. 6, and Suppl. Fig. 7). As was the case for physical effort, the motivation to exert higher levels of effort was lower with repeated exertion.

Consistent with Study 1, fatigue ratings increased significantly during the main task (β = 0.205, 95% CI [0.202, 0.208], $F(1,9319) = 19{,}675$, $p < .001$; Fig. 3b). Fatigue increased as a function of Effort, with higher increases in fatigue ratings on more difficult trials (Suppl. Fig. 4). The change in fatigue at effort level 2 (M = -0.10, SEM = 0.13) was significantly lower than at effort level 3 (M = 0.31, SEM = 0.04; t(150) = −2.69, p_{holm} = 0.040) and effort level 4 (M = 0.56, SEM = 0.13; t(150) = −4.36, p_{holm} < 0.001). Changes in fatigue were not significantly different for the other comparisons, including those against rest (M = 0.21, SEM = 0.10). This indicates that effort exertion may not be the only factor that drives changes in fatigue ratings, as we explore below.

To examine whether increases in fatigue predicted subsequent choices to work in the main task we modelled choice as a function of Effort, Reward, and trial-by-trial Fatigue Ratings together with subject-specific intercepts. We observed a significant main effect of Effort ($\chi^2(2)$ = 95.94, $p < .001$) and Fatigue Ratings ($\chi^2(2)$ = 4.01, p = .045), but no two-way interaction ($\chi^2(2)$ = 1.68, p = .431). All remaining effects were not significant (Reward: ($\chi^2(2)$ = 2.61, p = .271); Reward x Effort ($\chi^2(2)$ = 1.62, p = .805); Reward x Fatigue ($\chi^2(2)$ = 0.23, p = .893); Reward x Effort x Fatigue interaction ($\chi^2(4)$ = 3.57, p = .468)). These results highlight that fatigue and effort both impact choices in a cognitively effortful task.

We contrasted fatigue ratings against the alternative measure of fatigue employed in Study 1: cumulative effort (the running sum of effort exerted from all previous trials). Choices were entered into a logistic mixed model together with Effort, Reward, Cumulative Effort, and subject-specific intercepts. We included interaction terms for all fixed effects. Consistent with Study 1 we observed a significant main effect of Effort ($\chi^2(2)$ = 214.13, p < .001) and an interaction between Effort and Cumulative Effort ($\chi^2(2)$ = 6.45, p = .040). Unlike Study 1, we observed a main effect of Cumulative Effort ($\chi^2(1)$ = 9.67, p = .002) but the main effect of reward was not significant ($\chi^2(2)$ = 2.57, p = .277). All remaining effects were not significant (Reward x Cumulative Effort ($\chi^2(2)$ = 0.39, p = .822); Reward x Effort ($\chi^2(4)$ = 4.57, p = .335); Reward x Effort x Cumulative Effort interaction ($\chi^2(4)$ = 7.71, p = .103)). Although the pattern of results for cumulative effort resembled those for fatigue ratings, the presence of an interaction between effort and cumulative effort, but not between effort and fatigue ratings, raised the possibility that self-reported fatigue was not a simple proxy of cumulative effort. We investigated this further by examining the role of trial outcomes (errors) on fatigue.

3.4. Errors are associated with increases in cognitive fatigue

Notably, unlike in Study 1, participants made a significant number of errors in Study 2 (18% across all effort levels, 35% across the highest effort trials) and thus did not obtain the rewarding outcome on many trials. To examine the effect of trial outcome on fatigue ratings in Study 2 we compared two nested, linear mixed models. The null model estimated fatigue ratings as a function of trial number and subject-specific intercepts. The outcome model included an interaction with trial outcome. Despite the increase in model complexity, the outcome model provided a significantly better fit ($\chi^2(4)$ = 19.95, $p < .001$; outcome model AIC = 69,102, BIC = 69,159, loglikelihood = −34,543; null model AIC = 69,113, BIC = 69,142, loglikelihood = −34,553). This suggests that the increase in fatigue ratings that accumulated from trial to trial were moderated by the outcome on each trial.

To further examine how fatigue is related to trial outcomes, we computed changes in fatigue on each trial relative to the trial preceding it. This was entered into a point biserial correlation with accuracy (correct or incorrect). The correlation was significant (r = −0.097, 95% CI [−0.117, −0.076], p < .001) and we observed the same result using a repeated measures correlation (r(9272) = −0.103, p < .001, 95%CI [−0.125, −0.081]) or building a logistic mixed model predicting trial-by-trial accuracy from trial-by-trial changes in fatigue (increases in fatigue predict errors: $\chi^2(1)$ = 76.63,p < .001).

To determine whether trial outcomes were driving the effects above, we pooled trials into correct and incorrect answers to the arithmetic question, and, for each trial, computed the change in fatigue relative to the preceding trial. This allowed us to compute the mean change in fatigue for correct and incorrect trials for each participant in Study 2 and contrast these means with a paired *t*-test. Fatigue was significantly higher following incorrect decisions than correct decisions (t(39) = 3.10, p = .004, 95%CI [0.163, 0.775], Fig. 3c). Taken together, these results suggest that making an incorrect response is associated with rating fatigue higher relative to making a correct response. Critically, these results cannot be explained by the mere appearance of feedback since fatigue ratings are made prior to witnessing the trial outcome.

3.5. Computational modelling reveals both effort and error-driven mechanisms of fatigue in the cognitive domain

To better understand the relationship between fatigue and cognitive effort we developed several computational models based on theories of fatigue (Müller et al., 2021; Müller & Apps, 2019) and fit them to the choice and ratings data from Study 2. We deployed the same set of models used in Study 1 to examine Study 2. Thus, we could compare whether models including recoverable and unrecoverable components (F1-F3) in addition to delta-learning rules to account for the effects of error (L1 and L2) could best explain both fatigue ratings and choices.

We first modelled the pre-task to examine whether choice data were best explained by a linear, quadratic, or hyperbolic discount function. Consistent with Study 1, we found that the best computational model of effort discounting was one where efforts discount rewards quadratically (BIC = 58). By fitting the choices in the no-fatigue task we could also estimate the baseline level of effort aversion and choice stochasticity for each participant, which we then used in our modelling of the main task.

Consistent with our predictions, we found that choices and fatigue ratings were best explained by a model of subjective fatigue comprising both a recoverable and unrecoverable component where effort increases fatigue, as well as a delta-learning rule to explain the impact of errors (Model L2 BIC = 1009 AIC = 0.9951 XP = 0.8763, Fig. 4b, Suppl.Fig. 2). This suggests that cognitive fatigue was dependent on errors as well as on the effort induced by mental exertion. Specifically, errors increased fatigue more than correct responses, and subsequently reduced the value of exerting effort for reward.

3.6. Pooled analysis

Studies 1 and 2 suggest that the effects of fatigue on choice vary across the physical and cognitive domains. Choices to exert physical effort depended on reward and the amount of effort, with the latter modulated by fatigue. In contrast, choices to exert cognitive effort depended primarily on effort and fatigue, in the absence of an interaction between the two. To clarify this statistically, we entered trial-by-trial choice data from both studies into a logistic mixed model with Effort, Fatigue Ratings, and Experimental Domain (physical or cognitive). We included interactions between all fixed effects and subject-specific intercepts as random effects. The main effects of Effort ($\chi^2(2)$ = 185.12, $p < .001$), Fatigue ($\chi^2(1)$ = 27.12, p < .001), and Domain ($\chi^2(1)$ = 7.80, p = .005) were significant. We also found a significant interaction between Effort and Domain ($\chi^2(2)$ = 20.74, p < .001). The remaining two-way interactions were not significant (Effort x Fatigue ($\chi^2(2)$ = 3.32, p = .190); Fatigue x Domain ($\chi^2(1)$ = 0.11, p = .736)). Critically, we observed a three-way interaction between Effort, Fatigue Ratings, and Domain ($\chi^2(2)$ = 9.73, p = .008) (see Supplementary material and Suppl.Fig. 4). This suggests that the precise relationship between effort and fatigue on decisions to work depends on whether the effort being exerted was physical or cognitive in nature.

4. Discussion

Humans are cognitive and physical misers, but when they do exert effort it often induces fatigue (Hull, 1943). By probing fatigue on every trial of two effort-based decision-making tasks, we show that fatigue constantly fluctuates whether the effort required is physical (Study 1) or cognitive (Study 2). In Study 1, we showed that fatigue induced by physical exertion (grip-force) is best explained by a computational model in which fatigue has both recoverable and unrecoverable components. That is, exerting effort increases fatigue, and taking a rest reduces it, but there is also a gradual increase in fatigue which cannot be recovered by short breaks. This model accounted for fluctuations in both effort-based decisions and in ratings of fatigue, with ratings also predictive of choices on the next trial. In Study 2, we showed that self-reported fatigue and its effect on effort-based decisions are similarly increased by the exertion of cognitive effort (mental arithmetic) and are also explained by a model with recoverable and unrecoverable components. However, this is supplemented by an error-driven mechanism that monitors trial outcomes. These results highlight that fatigue: (1) can fluctuate on a momentary basis due to either cognitive or physical effort, (2) impacts the willingness to exert effort for reward, and (3) is sensitive to errors in a cognitive task.

There has been considerable debate surrounding the existence of mental fatigue in cognitive tasks, the antecedents of its development across time, and its relationship to motivation (Boksem & Tops, 2008; S. M. Marcora et al., 2009; Mockel et al., 2015; Müller & Apps, 2019). Notably, our study differed methodologically from many others probing mental fatigue in a number of ways. In particular, studies measuring self-reported fatigue often do so before and after extended blocks with multiple trials of a cognitive task, and use speed and accuracy changes or neurophysiological changes with time-on-task as proxies of fatigue and motivation (Boksem et al., 2006; Lorist et al., 2000, 2005, 2009; Mockel et al., 2015; Wascher et al., 2014). Such methods are useful, but are indirect measures of motivation (i.e., the value of exerting effort) and sensations of fatigue as they are likely to interact with each other. For example, as fatigue increases it may decrease motivation and in doing so reduce task accuracy. Moreover, people may temporarily disengage from trials of the task to reduce fatigue, and in doing so increase the motivation to exert effort in the future. All such processes may occur across a block, and thus a single measurement at the end obscures these processes.

Here, we more directly measured sensations of fatigue and effort-based decisions on a trial-by-trial basis. In doing so, we were able to examine moment-to-moment the dynamics of people's sensations of fatigue and motivation. Such an approach allowed us to show unambiguously that mental fatigue increases over time in demanding tasks, but also changes transiently from moment-to-moment, from even brief, but demanding cognitive processes. In this case, even the short mental exertion required by a difficult mathematical operation induced an increase in self-reported fatigue and lead to reductions in the willingness to perform more effortful operations over time. Moreover, we were able to show that errors in cognitive processes also increase self-reported fatigue and subsequently reduce the willingness to choose to exert effort. Such findings highlight the need to measure fatigue more frequently during tasks than is common in the literature, as error and effort driven mechanisms will otherwise be obscured, and also for effort-based decision-making research to consider how the willingness to exert effort may be constantly fluctuating across a task. Beyond this, by using computational approaches to model trial-by-trial changes we were able to reveal multiple new insights into the dynamics of fatigue, highlighting the utility of formal modelling of such processes and potentially opening new avenues for a computational psychiatry and neurology of fatigue (Chaudhuri & Behan, 2004; Huys, Maia, & Frank, 2016; Huys, Moutoussis, & Williams, 2011; Mars, Shea, Kolling, & Rushworth, 2012; Stephan et al., 2016).

A major debate in research on fatigue has been the extent to which physical and cognitive tasks induce similar sensations and whether they similarly impact on motivation (Boksem & Tops, 2008; S. M. Marcora et al., 2009). Our results suggest that there are some striking similarities in the mechanisms that underlie the development of fatigue, even if the underlying task is different. In particular, we found that similar effort-driven processes influenced sensations of fatigue and effort-based decisions in both tasks. In both, a model containing recoverable and unrecoverable components of fatigue that increased with the amount of effort exerted and partially recovered after rest best explained people's ratings. This suggests similarity between how fatigue develops during physically and mentally demanding tasks, with both induced (at least in part) by effort costs. Moreover, it raises the possibility that previous evidence of recoverable and unrecoverable components of fatigue induced by physically demanding tasks is not driven by peripheral or muscular fatigue, but instead more directly relates to the mental fatigue induced by cognitive tasks that influences the valuation and choice to exert effort (Gallagher et al., 2001; S. Marcora, 2009; McMorris et al., 2018; Müller et al., 2021).

Although there were similarities between the findings between studies, there were some crucial differences. Firstly, ratings of fatigue were broadly speaking higher in the physical effort task. Secondly, the willingness to exert effort for reward was higher in the cognitive effort task. Although it is tempting to draw conclusions about these differences being due to a difference between cognitive and physical effort, it is important to note that there are also differences between the tasks that make broader distinctions between cognitively and physically induced fatigue difficult. In particular, as is commonly the case with cognitive or physically effortful tasks deployed in research, the levels of difficulty in the physical effort task were yoked to participants' capacity – their maximum grip strength – but this was not the case for the cognitive effort task. This difference between the tasks was due to our desire to use paradigms as similar as possible to those used in the literature examining effort-based decisions, such that individuals using such tasks can be aware of additional effects present in people's behaviour (Bonnelle, Manohar, Behrens, & Husain, 2016; Chong et al., 2017; Chong et al., 2016; Kool & Botvinick, 2018; Le Heron et al., 2018; Lopez-Gamundi et al., 2021; McGuigan et al., 2019; Müller, Husain, & Apps, 2022; Scholey & Apps, 2022; Vassena et al., 2014, 2019). However, it does limit the strength of inferences we can yield from direct contrasts between the two studies.

It seems highly likely that one distinct finding between the two tasks, that error-driven processes underlie fatigue in the cognitive task, would become more similar if errors were present in the physical task. There is a wealth of evidence that people's decisions of whether to engage in instrumental behaviour is guided by reinforcement learning (RL) processes that govern the probability of a successful outcome being received following an action (Dayan & Balleine, 2002; Dayan & Daw, 2008; Seymour et al., 2004). People can learn to avoid more effortful actions through RL processes (Hauser, Eldar, & Dolan, 2017; Scholl et al., 2015). In addition, people avoid risks in relation to effort (Apps et al., 2015; Nagengast, Braun, & Wolpert, 2011), and are more averse to physical effort levels close to their capacity, where the probability of success decreases (Bonnelle et al., 2016; Klein-Flugge et al., 2015). Further, errors in physical tasks have been associated with perception of fatigue in the physical domain (Ito et al., 2022) and in turn physical effort can influence RL processes (Jarvis et al., 2022). Thus, whilst the studies differed in terms of the nature of the demanding task, effort-driven and error-driven processes are likely to underlie fatigue and effort-based decisions regardless of whether it is physical or cognitive in nature.

Intriguingly we found that error-driven processes might supplement effort-driven fatigue processes when it comes to the motivation to exert cognitive effort. Previous work has suggested that risky decision-making and effort-related decisions may in part be driven by separate neural circuits (Burke, Brunger, Kahnt, Park, & Tobler, 2013). Given the close links between risk, which is often defined as the fixed probability of receiving a highly rewarding outcome, and RL, which often involves learning the probability of a rewarding outcome being present, partial distinction in their circuits could be interpreted as suggesting they do not have similar effects on behaviour. However, more recent work has shown that RL and effort-based decision-making mechanisms may indeed be intertwined in several different ways. Recently studies have shown that RL-like processes are involved when learning how effortful a behaviour is and when learning how to avoid highly effortful actions

(Hauser et al., 2017; Scholl et al., 2015). In addition, there is at least some overlap in neural mechanisms, with the ventral striatum being linked to RL processes, risky decision-making and integrating fatigue into valuations that guide effort-based decisions (Dayan & Balleine, 2002; Lockwood, Apps, Valton, Viding, & Roiser, 2016; Mohr, Biele, & Heekeren, 2010; Müller et al., 2021). As such, it appears likely that RL based error aversion, and fatigue related effort aversion, are integrated to guide goal-directed decision-making.

Not only do our results suggest that RL mechanisms influence effort-based decision-making, but we also found that people's fatigue ratings can be influenced by whether a trial was successful or not. Strikingly, this was despite the fatigue rating being taken before a participant was informed of the actual outcome of the trial. This removes the possibility that being explicitly informed of the absence, or presence, of a rewarding outcome was increasing or decreasing fatigue ratings. Instead, it suggests that participants were aware of a difference between accurate and inaccurately performed cognitive processes and such awareness was influencing how fatigued they were rating themselves. These results indicate that fatigue may be underpinned by metacognitive processes (De Martino, Fleming, Garrett, & Dolan, 2013; Fleming, Weil, Nagy, Dolan, & Rees, 2010; Müller & Apps, 2019; Stephan et al., 2016; Turner et al., 2021), with people estimating the fidelity of the cognitive process they had just performed, and low confidence in that process leading to an increase in sensations of fatigue. The links between error-driven and metacognitive processes is not surprising. Models of metacognition highlight that estimating confidence in part relies on estimating the error in one's cognitive processes (Müller & Apps, 2019; Stephan et al., 2016) and similar neural circuits have been shown to underlie fatigue and metacognition (Fleming et al., 2010; Müller et al., 2021). Behavioral and neuroscientific evidence supports the involvement of metacognitive mechanisms in decisions to exert effort (Desender et al., 2017, 2021) and in decisions to engage in difficult tasks (Rouault, Dayan, & Fleming, 2019; Rouault & Fleming, 2020). Further, causal evidence shows that disruption of this underlying metacognitive circuitry impairs participants' ability to mediate between these decisions optimally (Miyamoto et al., 2021). As such, it seems likely that monitoring and estimating the state of cognitive systems, a key component of processing one's level of fatigue, may be strongly linked to metacognitive processes that underlie one's estimates of confidence. Overall, this suggests that multiple costs feed into both sensations of fatigue and the effects of fatigue on effort-based decisions. In particular, both rely on estimates of the effort-costs associated with performance of a level of difficulty of a task, and metacognitive, RL processes that estimate one's confidence in the cognitive or physical processes being executed to accurately succeed at a task.

In our experiments, it is likely that higher levels of difficulty (i.e. more force or harder arithmetic) also required participants to exert more effort. This is a common feature of effort-based decision research and is consistent with close connections between effort and difficulty (Massin, 2017). Critically, our design provides sufficient granularity to identify situations where individuals are initially willing but later become unwilling to perform trials of the same difficulty for reward. Through our analyses, we can attribute this phenomenon to fatigue, indicating that fatigue is associated with a diminished willingness to exert the effort that participants were previously willing to invest.

A recent line of work investigates how knowledge of task progress and goal proximity affect the willingness to exert effort (Devine, Roy, Beierholm, & Otto, 2023; Devine & Otto, 2022; Emanuel, Katzir, & Liberman, 2022)). Consistent with the goal-gradient hypothesis (Hull, 1932), these studies show that humans exert more effort when they get closer to a known deadline or finish line. In our studies, we intentionally minimised the amount of information provided to participants about the length of the experiment and their progress. While participants may have occasionally felt the study must be nearing completion, these feelings would not have occurred at systematic points of the experiment. Our analyses found significant effects of fatigue on the willingness to exert effort even in the last quarter of trials in the main task. This suggests that even though participants were nearing the end of the task, as this fact was unknown to them it was not reflected in an increase in the willingness to exert effort as found in goal gradient studies. Thus, our results reflect the dynamics of effort and fatigue when goal-gradient effects are minimised. Future research should explore the curious effects of goal knowledge, and pacing more broadly, on the dynamics of effort and fatigue.

4.1. Conclusion

Fatigue is a major factor influencing our everyday lives. Here, using a combination of two effort-based decision-making tasks, trial-by-trial ratings of fatigue, and computational modelling, we show that the dynamics of fatigue and effort-based decisions depend on effort-driven components of fatigue which hinge on how costly physical or cognitive exertion is. However, when demanding tasks also come at the cost of mistakes, these errors in turn increase the sensation of fatigue, while simultaneously reducing the willingness to exert effort.

CRediT authorship contribution statement

Julian Matthews: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Validation, Visualization, Writing – original draft, Writing – review & editing. **M. Andrea Pisauro:** Conceptualization, Data curation, Formal analysis, Validation, Visualization, Writing – original draft, Writing – review & editing. **Mindaugas Jurgelis:** Conceptualization, Data curation, Investigation, Formal analysis, Methodology, Project administration, Software, Writing – review & editing. **Tanja Müller:** Conceptualization, Methodology, Software. **Eliana Vassena:** Conceptualization, Methodology, Project administration, Software, Supervision, Writing – review & editing. **Trevor T.-J. Chong:** Conceptualization, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – review & editing. **Matthew A.J. Apps:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing.

Data availability

All anonymized behavioral data and code used for the analysis and to generate the figures are available in an Open Science Framework project (https://osf.io/ywn63/). All code used to run the computational modelling is available in an Open Science Framework project (https://osf.io/ywn63/).

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Appendix A. Supplementary data

Supplementary material: All anonymized behavioral data and code used to generate the figures are available in an Open Science Framework project https://osf.io/ywn63/. All code used to run the computational modelling is available in an Open Science Framework project https://osf.io/ywn63/. Supplementary data to this article can be found online at [https://doi.org/10.1016/j.cognition.2023.105603].

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