

Experimental Brain Research

The cortical oscillatory patterns associated with varying levels of reward during an effortful vigilance task.

--Manuscript Draft--

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Abstract:	<p>We explored how reward and value of effort shapes performance in a sustained vigilance, reaction time (RT) task. It was posited that reward and value would hasten RTs and increase cognitive effort by boosting activation in the sensorimotor cortex and inhibition in the frontal cortex, similar to the horse-race model of motor actions. Participants performed a series of speeded responses while expecting differing monetary rewards (0 pence (p), 1 p, and 10 p) if they responded faster than their median RT. Amplitudes of cortical alpha, beta, and theta oscillations were analysed using the event-related desynchronization method. In experiment 1 (N = 29, with 12 females), reward was consistent within block, while in experiment 2 (N = 17, with 12 females), reward amount was displayed before each trial. Each experiment evaluated the baseline amplitude of cortical oscillations differently. The value of effort was evaluated using a cognitive effort discounting task (COGED).</p> <p>In both experiments, RTs decreased significantly with higher rewards. Reward level sharpened the increased amplitudes of beta oscillations during fast responses in experiment 1. In experiment 2, reward decreased the amplitudes of beta oscillations in the ipsilateral sensorimotor cortex. Individual effort values did not significantly correlate with oscillatory changes in either experiment.</p> <p>Results suggest that reward level and response speed interacted with the task- and baseline-dependent patterns of cortical inhibition in the frontal cortex and with activation in the sensorimotor cortex during the period of motor preparation in a sustained vigilance task. However, neither the shortening of RT with increasing reward nor the value of effort correlated with oscillatory changes. This implies that amplitudes of cortical oscillations may shape upcoming motor responses but do not translate higher-order motivational factors into motor performance.</p>	
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Response to Reviewers:	<p>Explanation of changes made in the revised ms. EXBR-D-19-00605R1 We are grateful to the Reviewer for their constructive and helpful feedback, and to the Editors for the opportunity to amend our work. We are thankful for and have accepted every point raised by the Reviewer and hope that our ms may now receive acceptance. Response: Please find our detailed responses to each of the Reviewer's points below.</p> <p>Reviewer #1</p> <p>Summary: In their revision, Byrne and colleagues have addressed a number of points I raised in my prior review. I appreciate the efforts they took to more clearly articulate several methods and analyses.</p> <p>Unfortunately, I am still concerned about key analytical methods and inferences which I don't think the Authors have addressed adequately. In particular, I am worried that the permutation test might have been done incorrectly in a way that undermines key analyses. I am also still concerned about the process of selecting individual electrodes and what we can infer from that.</p> <p>***</p> <p>I should note that unless some of these concerns can be addressed, I am currently unconvinced that Experiment 1 reveals anything about how incentives impact oscillatory dynamics and how those in turn impact performance beyond showing that oscillations are different when people react fast and slow. The result in Experiment 2 showing incentive linked effects on oscillatory dynamics are a bit more convincing, by contrast, but need shoring up.</p> <p>Response: We are thankful to Reviewer #1 for their constructive evaluation, and, in the revised ms., we endeavoured to address all points of concern and hope that the ms. can now receive acceptance.</p> <p>Point 1: Regarding the permutation test, the thing that concerns me most is that the Authors state that they conducted tests "with the electrode labels being permuted". The standard practice is to form null distributions on cluster extents by permuting condition labels (e.g. incentive amounts), not electrode labels. If they did permute electrode labels, then the null distribution they created would be artificially liberal because the process of permuting electrode labels would break the spatial dependencies inherent in the data. Thus, they give themselves and unfair chance to find "significant clusters". Perhaps this was just a mistake in writing, though, and the Authors did actually permute condition labels? Also, note that the Authors cannot conduct a permutation test on one effect and use surviving clusters to analyze other effects. For example, it is invalid to conduct permutation tests the effects of RT on RBP, and then select among surviving clusters to analyze the effects of incentives. Instead, if the Authors want to make inferences about the effects of incentives, they need to first conduct permutations on incentive labels.</p> <p>Response: We apologise and take full responsibility for this error in the manuscript. Reviewer 1 is correct that reward conditions, not electrode labels, were permuted in this analysis. We closely followed the algorithm given in the EEGlab-Matlab package by Maris & Oostenveld (2007) and have updated the description given in the ms to describe their method more accurately.</p> <p>See page 14</p> <p>"Further, to tackle the risk of a false positive error due to the large number of tests, a hypothesis-independent permutation analysis, implemented in the statcond.m program in the EEGLab package (Makeig et al., 2004), was used to identify clusters of electrodes with significant main effects of reward or response-speed, or interactions between these conditions, separately (Maris and Oostenveld, 2007). This cluster-based method provides a data-driven approach to assess effects of conditions on RBP in specified frequency bands (8-12 Hz, 16-24 Hz, and 4-7 Hz) across all electrodes without making a priori assumptions, while also controlling for multiple comparisons with no loss in statistical power.</p> <p>"In this analysis, we calculated the test statistics for the main effects and interactions of</p>

both response-speed and reward on RBP in the specified frequency bands over all electrodes. The RBP from all experimental conditions was then collected into a single dataset. Data points were randomly drawn from this set and placed into subsets having the same size as the two response-speed and three reward conditions, forming a 'random partition', or dataset representing randomly shuffled versions of the three reward and two response-speed conditions. The test statistics for the main effects and interactions of reward and response-speed in this random partition were then calculated. Next, the creation and analysis of the random partition was repeated 5000 times, and a histogram of the produced test-statistics was constructed for all electrodes. The proportion of random partitions that resulted in a larger statistic than the test-statistic first calculated for the non-shuffled data was calculated for all electrodes, and this was defined as the p-value. Electrodes that exceeded a predefined threshold on the calculated p-values (uncorrected, $p < .01$) for the main effects of, or interactions between, reward and response-speed were selected and clustered based on spatial adjacency."

Point 2: I also remain concerned about how the Authors select individual electrodes for further analysis and reporting. Key examples include electrode 40 in Fig. 4, 124, 21, and 5 in Fig. 5, 172, 136, and 16 in Fig. 6. How were these selected? Were they just picked at random from among significant clusters? Or, are they representative somehow? Are they peak electrodes (those with strongest statistics)? Or is these instances of cherry-picking where the Authors found individual electrodes showing interesting patterns and chose to highlight those? If it was the latter case, then I think the Authors should drop these, and choose electrodes based on a principled approach (like picking the centroid, the peak, or averaging over all electrodes in the cluster).

Response: We are grateful for this comment and endeavoured to correct it. Electrodes were selected for further analysis based on those which passed a combined threshold based on the difference-from-0 tests and the permutation analysis. Electrode clusters were selected if the electrodes were adjacent and showed similar effects of reward or response speed. However, if only one electrode showed a statistically significant effect, only that electrode was reported. In the result section, electrodes 40, 124, 21 and 5 in experiment 1 showed statistically significant effects of either reward or response speed but none of these electrodes were surrounded by electrodes showing similar statistically significant effect and they are, therefore, reported as single electrodes.

This has been explained in the ms on page 20

"Electrode 40, over the left-central area, was the only electrode found to pass both the difference from 0 t-test and the permutation-based threshold, and was, therefore the only electrode selected for further analysis."

And page 21

"Three electrodes passed both the difference from 0 and the permutation-based threshold, and were therefore selected for further analysis."

In contrast, Fig 6., demonstrated that the ERD/ERS expected to occur, based on previous research, was found in response to the experimental cues in all conditions. Time courses of ERD changes were shown over electrodes selected apriori, over areas of the scalp expected to show ERD effects due to task demands (e.g., ERD in the alpha- and beta-bands was expected over contralateral sensorimotor areas while participants prepared a speeded motor response). This was included to show the replications of previous literature and show the validity of the experimental procedure. This has been explained in the ms on page 26

"Fig 6., shows ERD/ERS scalp topographies over specified time periods (0.5 s, 2 s, 2.5 s, and 3.3 s following the presentation of the cue stimulus) in (A) the alpha-band, (B) the beta band, and (C) the theta band. Time courses of percentage power changes over specified electrodes are also shown. Electrodes were selected apriori at areas of the scalp where band power was expected to be modulated by task demands based on previous research. For example, an ERD was expected over contralateral sensorimotor areas in the alpha- and beta-bands during motor preparation (Rhodes, 2019; Pfurtscheller and Berghold, 1989; Tzagarakis et al., 2010; Tzagarakis et al., 2015; Fox et al., 2016; Ishii et al., 2019)."

Point 3: Relatedly, why did the Authors pick electrode 124 in Fig 4. to analyze the correlation between RT and RBP changes, and not 21 and 5 which were just highlighted in this same section? It is necessary to motivate such choices. It is not okay to just pick strong examples.

Response: We are thankful for this feedback, and we apologise for not making this clear in the manuscript. Correlations were assessed in all electrode clusters selected for further analysis, but only significant correlations were reported.

This has been corrected in the revised ms., page 18

“Bivariate correlations were conducted in all electrode clusters or single electrodes selected for further analysis, however, only statistically significant correlation coefficients are reported.”

Point 4: Concerning representativeness, I am unsure what we are to infer about electrodes from the same cluster showing apparently opposite results. This comes up, for example, for Fig. 5 and the contrast of RT effects on electrode 21 which showed lower beta power on fast trials, while electrode 5 showed higher beta power on fast trials. This pattern of contrasting results seems to undermine the interpretability and the implicit claim that electrodes are representative. If one electrode shows an effect in one direction and another electrode shows the opposite, what should we infer about the cluster overall? And what does it mean that they show opposite effects? More importantly, what did we learn from conflicting results?

Response: We are grateful for Reviewer's feedback. The Reviewer is correct that electrodes 21 and 5 showed contrasting results. This effect was caused by a topographic change of the beta-ERD cluster in prefrontal and frontal-central electrodes with fast movements showing greater ERD in fronto-central electrodes than slow movements.

A similar pattern of changes has been found for beta-band synchronisation (Alegre et al 2004), with beta-band synchronisation over frontal regions of the scalp being more focused around central areas in Go compared to NoGo trials. The researchers interpreted this more central synchronisation as reflecting a signal originating from the anterior cingulate cortex, a neural region associated with motor control or adjustment in response to changing rewards (Heilbronner and Hayden, 2016; Rushworth et al., 2003; Chudasama et al., 2013), as well as the persistence of effortful behaviour (Floden and Stuss, 2006; Warden et al., 2012; Chudasama et al., 2013; Parvizi et al., 2013). While our data do not allow inferences on locations of cortical generators, it is likely that fast and slow movements recruited the medial frontal cortex differently resulting in prefrontal and fronto-central electrodes showing different effects of response speed on beta-band ERD.

This has been expanded on in the discussion.

Please see page 24

“Beta-band increases were stronger and more focused over fronto-central regions preceding fast responses compared to slow responses, reflected in a different pattern of ERD changes in electrodes 5 and 21. A similar pattern of a prominent fronto-central focus of beta-band synchronization due to topographic expansion has been found for Go, compared to NoGo, responses (Alegre et al., 2004). While our data do not allow inferences on underlying cortical generators, the shape differences in the large ERD cluster in prefrontal and fronto-central electrodes suggests that the fast- compared to slow movements were preceded by a stronger activation in premotor regions residing in the medial frontal cortex.”

Point 5: Finally, I am concerned about the disconnect between results and the inferences made in the abstract and discussion. Most notably, the authors found no relationships between incentive effects on brain activity and incentive effects on behavior. Thus we cannot directly infer that incentives altered behavior because of changes in these oscillatory dynamics of interest. This should be stated clearly in the abstract and the discussion. Also, there are some incorrect inferences made at points. In the interim discussion following Experiment 1 results, the Authors state, for example, “the presence of monetary incentives shortened RTs, and increased and focused cortical beta oscillations over frontal scalp regions...” However, incentives had no effects on frontal beta oscillations over frontal (or any regions). They found that RT effects on oscillations were stronger in one incentive condition than another, but this *interaction* is not the same thing as a main effect of reward.

Similarly in the first sentence of the Conclusion, the Authors state that “Decreasing RTs as the result of the presence and magnitude of reward was associated with cortical oscillatory changes in both experiment 1 and experiment 2”, while in the abstract, they state “Reward level increased the amplitude of beta-band oscillations over frontal electrodes in experiment 1” - neither of which is true. The Authors should

ensure that such inferences are directly supported by the data.
Response: We are thankful for Reviewer's comment which allows us to phrase the relevant section of Discussion and Abstract more accurately than in previous version of the ms.

We have modified both the abstract and discussion sections to state that there was no relationship on the effect of reward on RTs and the effect of reward on oscillatory changes.

Please see changes to the abstract on page 2

"However, neither the shortening of RT with increasing reward nor the value of effort correlated with oscillatory changes. This implies that amplitudes of cortical oscillations may shape upcoming motor responses but do not translate higher-order motivational factors into motor performance."

And this is further expanded on in the general discussion on pages 34 and 35

"However, while a significant correlation was found between RTs and oscillatory changes between fast and slow responses, no significant relationship was found between the effects of incentives on oscillatory changes and the effect of incentives on RTs, meaning that it is difficult to directly infer that incentives altered behaviour through oscillatory changes. This may be due to other factors modulating how incentives affected RTs, such as individual or state differences, or due to a low level of statistical power."

For an updated discussion regarding the results of incentive on RBP changes in experiment 1, please see changes to the abstract on page 2:

"and sharpened increased inhibition in the frontal cortex under fast responses (experiment 1)."

And, for changes to the discussion, please see page 23

"fast responses were associated with stronger synchronisation in the alpha band over the left-central area of the scalp and stronger and more focused synchronisation in the beta band over fronto-central regions of the scalp, an effect which was particularly apparent in high-reward conditions."

And page 24

"Both the alpha- and beta-band results suggest faster response speeds, especially under high reward, were associated with increased motor inhibition in the time window preceding movement."

Minor comments:

Line 22 on page 24, says "alpha-band power changes", but I believe the authors meant "RT changes"

Response: Corrected

Line 18 on page 11, says "A Bivariate", but should be "A bivariate"

Response: Corrected

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Dear Editors,

Please find uploaded our ms. "The cortical oscillatory patterns associated with varying levels of cognitive effort."

Cognitive effort has been conceptualised in an economic framework as discounting from the value of an expected reward. Previous research has showed that monetary incentives and individual valuations of cognitive effort can modulate reaction-times (RT) in a sustained vigilance task. However, while cognitive effort has been posited to modulate cortical inhibition and activation, the effect of reward and effort on these processes has yet to be investigated. Changes in oscillatory cortical power has been implicated in the activation and inhibition of relevant cortical areas, providing a measure of these processes.

In the present study, increases and decreases in oscillatory power were analysed using the event-related desynchronization method as participants performed a series of speeded RT responses while expecting one of three monetary rewards (0p, 1p, 10p) if they responded faster than their median RT. Electrophysiological responses were recorded using a 129-channel EEG system. Two experiments are reported; in the first experiment, the reward amount was consistent within each block, and, in the second experiment, participants were informed about the reward before each trial. Each experiment evaluated the baseline amplitude of cortical oscillations differently, providing unique measures of cortical activation and inhibition. Individual effort values were evaluated using a cognitive effort discounting task.

In both experiments, higher rewards caused participants to respond significantly faster. Reward level increased the amplitude of beta band oscillations over frontal electrodes in experiment 1 – an effect associated with cortical inhibition – and decreased the amplitude of beta-band oscillations in the ipsilateral sensorimotor cortex in experiment 2. Individual effort values did not significantly correlate with cortical oscillatory changes or RTs in either experiment.

Our study shows, for the first time, that the amount of reward expected during a sustained vigilance task modulates cortical activation in the sensorimotor cortex (experiment 2) and inhibition in the frontal cortex (experiment 1) while participants prepare a speeded RT response. This provides a novel contribution to the understanding of the cortical role of cognitive effort, demonstrating that it modulates relevant cortical activation and inhibition. It is our hope that you will consider this work worthy for the Journal of Experimental Brain Research.

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Page 1 of 40

1 **The cortical oscillatory patterns associated with varying levels of reward during an**
2 **effortful vigilance task.**

3 **Short title:** Cortical oscillations and cognitive effort

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21 **Keywords:** event-related desynchronization; value; discounting; cognitive effort;

1 ABSTRACT

2 We explored how reward and value of effort shapes performance in a sustained
3 vigilance, reaction time (RT) task. It was posited that reward and value would hasten RTs and
4 increase cognitive effort by boosting activation in the sensorimotor cortex and
5 inhibition in the frontal cortex, similar to the horse-race model of motor actions.

6 Participants performed a series of speeded responses while expecting differing
7 monetary rewards (0 pence (p), 1 p, and 10 p) if they responded faster than their median RT.
8 Amplitudes of cortical alpha, beta, and theta oscillations were analysed using the event-
9 related desynchronization method. In experiment 1 (N = 29, with 12 females), reward was
10 consistent within block, while in experiment 2 (N = 17, with 12 females), reward amount was
11 displayed before each trial. Each experiment evaluated the baseline amplitude of cortical
12 oscillations differently. The value of effort was evaluated using a cognitive effort discounting
13 task (COGED).

14 In both experiments, RTs decreased significantly with higher rewards. **Reward level**
15 **sharpened the increased amplitudes of beta oscillations during fast responses** in experiment 1.
16 In experiment 2, reward decreased the amplitudes of beta oscillations in the ipsilateral
17 sensorimotor cortex. Individual effort values did not significantly correlate with oscillatory
18 changes in either experiment.

19 **Results suggest that reward level and response speed interacted with the task- and**
20 **baseline-dependent patterns of cortical inhibition in the frontal cortex and with activation in**
21 **the sensorimotor cortex during the period of motor preparation in a sustained vigilance task.**
22 **However, neither the shortening of RT with increasing reward nor the value of effort**
23 **correlated with oscillatory changes. This implies that amplitudes of cortical oscillations may**
24 **shape upcoming motor responses but do not translate higher-order motivational factors into**
25 **motor performance.**

1 INTRODUCTION

2 Cognitive effort is prevalent in a number of settings such as education (Von Stumm et
3 al., 2011; Cacioppo et al., 1996), the workplace (Kidwell Jr and Bennett, 1993; Van
4 Iddekinge et al., 2018), and consumer behaviour (Heidig et al., 2017). In psychiatric or mood
5 disorders (e.g., depression), a loss of motivation to face cognitively or physically challenging
6 tasks has been reported (Treadway et al., 2012; Cohen et al., 2001). However, while the
7 decision to make an effort has been extensively researched, and the subjective experience of
8 effort is familiar to most people, the effects of reward and the value of effort on performance
9 in an effortful task and the neural basis of this are not yet fully understood.

10 In behavioural economic theories of decision making, effort is framed as a
11 discounting factor that reduces the value of rewards when an effort is required to achieve
12 them (Inzlicht et al., 2014; Kurzban et al., 2013). The discounting effect of effort can be
13 measured using the COGED method (Westbrook et al., 2013; Westbrook and Braver, 2015),
14 which offers staircase iterated rewards across multiple levels of effort until an indifference
15 point is reached, indicating the amount of money required for participants to agree to put
16 more effort into the task (Westbrook et al., 2013; Massar et al., 2016). The value of effort,
17 determined using COGED, has been shown to correlate with individual engagement
18 (Westbrook et al., 2013) and performance (Massar et al., 2016) in cognitive tasks. Further,
19 the level of engagement in a cognitive task can be manipulated by varying performance-
20 based rewards (Massar et al., 2016; Dinges and Powell, 1985; Knutson et al., 2000).

21 The discounting effect of cognitive effort has been attributed to a number of processes
22 (Gailliot and Baumeister, 2007; Lazarus, 1993; Tooby and Cosmides, 2008; Christie and
23 Schrater, 2015), but is commonly thought to be the consequence of top-down cognitive
24 control (Botvinick and Braver, 2015; Kaplan and Berman, 2010; Shenhav et al., 2013b). This
25 would be required to control task-relevant cortical activation and inhibition at the expense of

1 task-irrelevant activation and inhibition, and may be localised to the dorsal anterior cingulate
2 cortex, which has been implied to mediate cognitive control during attentional tasks (Shenhav
3 et al., 2013a).

4 Processes which may to be controlled during motor actions are proposed by the horse-
5 race theory of motor inhibition in the stop-signal task (Logan and Cowan, 1984; Band et al.,
6 2003; Schultz, 2015). This model posits opposing processes of motor readiness during stop-
7 signal tasks, where motor activation occurs in response to a ‘GO’ signal and motor inhibition
8 occurs in response to a ‘STOP’ signal, and a movement is only successfully inhibited if the
9 inhibitive processes complete before the movement is finished, meaning that successful
10 responses to ‘STOP’ signals are based on the relative speed of these competing processes (for
11 more information see Band et al. 2003, Fig. 1).

12 Visual acuity (Mathewson et al., 2009), visual detection threshold (Ergenoglu et al.,
13 2004), visual discrimination (Hanslmayr et al., 2005) and pain sensitivity (Babiloni et al.,
14 2006) have been shown to be enhanced if stimuli occurred during a period of suppressed
15 alpha-band oscillations. In a similar vein, motor readiness or preparation seconds before a
16 self-paced voluntary movement (Chatrian et al., 1959), or during an imagined, or observed
17 movement (Nagai and Tanaka, 2019; Pfurtscheller et al., 2005), often manifests in amplitude
18 decreases of cortical alpha- and beta-band oscillations (Rhodes, 2019; Pfurtscheller and
19 Berghold, 1989; Tzagarakis et al., 2010; Tzagarakis et al., 2015; Fox et al., 2016; Ishii et al.,
20 2019). This has been found to increase prior to self-paced finger movements requiring large
21 force (Stancak et al., 1997), and during fast compared to slow movements (Stancak and
22 Pfurtscheller, 1996b; a). Suppressions of alpha- beta-band band power may, therefore, be
23 representative of the excitatory processes posited by the horse-race theory.

24 Conversely, inhibitory processes are employed in tasks which require withholding a
25 response under the state of strong motor readiness, for example during a stop-signal task

1 (Leimkuhler and Mesulam, 1985). Cortical inhibition or idling has been found to manifest as
2 an increase in the amplitude of alpha- or beta-band oscillations (Visani et al., 2019; Korzhik
3 et al., 2018; Salmelin and Hari, 1994; Pfurtscheller et al., 1996a; Jensen et al., 2005; Fry et
4 al., 2016), and frontal beta-band synchronisation has been shown to occur during periods of
5 motor inhibition (Alegre et al., 2006; Wessel and Aron, 2013; Swann et al., 2009; Fonken et
6 al., 2016; Wagner et al., 2018). Functional brain imaging studies point to a major role of the
7 right prefrontal cortex in employing the inhibition of motor actions (Feng et al., 2014;
8 Garavan et al., 2002; Simmonds et al., 2008), perhaps through dopaminergic innervations
9 (Miller and D'Esposito, 2005; Fuster, 2015; Chao and Knight, 1995). Moreover, frontal beta-
10 band synchronisation has been shown to occur during periods of motor inhibition (Alegre et
11 al., 2006; Wessel and Aron, 2013; Swann et al., 2009; Fonken et al., 2016; Wagner et al.,
12 2018). These areas may be expected to show an increase in alpha- and beta-amplitudes during
13 increased motor inhibition, representing a temporary withholding of movement under the
14 state of high motor readiness.

15 Theta-band oscillations, in contrast, have been found to increase over mid-frontal
16 electrodes during periods of sustained attention (Angelidis et al., 2018; Rajan et al., 2018;
17 Basar-Eroglu et al., 1992; Klimesch, 1999), and have been hypothesised to be a correlate of
18 cognitive effort or fatigue (Arnau et al., 2017). We, therefore, assumed that oscillatory power
19 in the theta band may be involved in the attentional, or top-down processes required during
20 effortful tasks.

21 The present study combined a modified sustained vigilance task (Massar et al., 2016)
22 with a monetary incentive delay task (Knutson et al., 2000) to examine the effects of varying
23 levels of rewards and the value of effort on cortical activation and inhibition. The vigilance
24 task required participants to execute speeded reaction-time (RT) responses during a stream of
25 visual cues occurring in short iterations, and it has been shown that requiring participants to

1 complete a sustained vigilance task, with each block offering different rewards (no reward,
2 low reward, or high reward) for each fast response (faster than the participant's median RT)
3 results in reward-related changes in task performance and sympathetic arousal (Massar et al.,
4 2016), however the effects of reward on cortical oscillatory activity during this task has not
5 yet been investigated.

6 Experiment 1 aimed to analyse the change in amplitudes of cortical alpha, beta, and
7 theta oscillations in the time-window just preceding the cue prompting a speeded response
8 during a vigilance task, and to test whether individual subjective values of effort, evaluated
9 using a COGED method, would correlate with performance and cortical oscillatory changes.
10 Stimuli were presented in three blocks, with each differing in the incentive for fast responses
11 (0p, 1p, 10p), and EEG data was recorded over a 90-s time window preceding each block to
12 take the baseline into account during the calculation of relative-band power (RBP). Due to
13 this block design, and as participants did not know when the target stimulus would occur, a
14 constant state of motor activation was required, meaning a greater likelihood of observing a
15 modulation of inhibition in cortical oscillatory changes was expected, as the release of
16 inhibition would be required for movement. We therefore hypothesised that reward and
17 response-speed would modulate sensorimotor alpha-band and frontal beta-band
18 synchronisation, with stronger synchronisation being found preceding fast trials and in larger
19 reward blocks, representing stronger inhibition.

20 Since the type of baseline employed in experiment 1 cannot fully account for fast
21 changes in arousal and motivation occurring during a lengthy vigilance task, experiment 2
22 was carried out to analyse the effect of reward on cortical activation in a vigilance task using
23 a standard event-related desynchronization (ERD) paradigm (Pfurtscheller and Aranibar,
24 1977). The time course of the relative band power changes was analysed in a period of time,
25 seconds before each trial. Trials involving no reward (0p), a small reward (1p) and a high

1 reward (10p) were presented in a random order, with a visual cue 2 seconds before the
2 stimulus prompting a speeded response. In this experiment, we aimed to measure the cortical
3 processes associated with motor activation. As the participants knew when the target stimulus
4 would occur, we predicted fast response-speeds and higher rewards would be associated with
5 stronger alpha- and beta-band ERD over sensorimotor regions, as well as stronger theta-band
6 synchronisation over central frontal regions. We also predicted, in both experiments, that
7 participants who showed less effort-discounting in the COGED task would show stronger
8 changes in RT and ERD/RBP as a function of reward.

10 **METHODS**

11 **Experiment 1**

12 **Participants**

13 29 subjects (12 females) were recruited. Five subjects were removed from subsequent
14 EEG analysis due to excessive muscle artefacts. Therefore, the final sample included 24
15 participants (10 females), aged 23.34 ± 2.44 (mean \pm SD). The procedure used was approved
16 by the Research Ethics Committee of the University of Liverpool and all participants gave
17 fully informed written consent at the start of the experiment in accordance with the
18 Declaration of Helsinki.

19 **Procedure**

20 Participants were required to complete two tasks. The participants first completed a
21 modification of the sustained vigilance tasks used by Massar et al. (2016) and Dinges and
22 Powell (1985), while EEG was recorded. The second task was a short discounting task
23 requiring the participants to make a series of 36 choices between a high-effort, high-reward
24 option and a low-effort, low-reward option. The purpose of this task was to estimate the

1 subjective value (SV) attributed to each level of effort offered during the task and to evaluate
2 individual indifference points equalling monetary value and units of effort

3 The vigilance task consisted of 1 five-minute practice block with no EEG recordings
4 and 3 ten-minute experimental blocks with EEG recordings included. The five-minute block
5 consisted of 50 trials, and each ten-minute block consisted of 100 trials. Overall, the
6 participants completed 350 trials throughout the experiment. Participants were offered
7 different rewards for each fast response in each block (0p, 1p, or 10p), and feedback
8 regarding the amount of money and number of points the participants had currently earned
9 was given after each block. Effort was measured behaviourally using the participants' mean
10 RTs and electrophysiologically using the participants' change in RBP in the 1-s epoch
11 preceding the presentation of the target stimulus and during the 90 second baseline period of
12 each block.

13 **Sustained vigilance task**

14 The sustained vigilance task was an adaptation of the Psychomotor Vigilance Test
15 used by Dinges and Powell (1985). This was a 10-minute sustained attention task in which
16 participants were required to respond with a button press (left mouse button) with their right
17 hand as quickly as possible whenever they are presented with a target stimulus. The scheme
18 of the vigilance task is shown in Fig 1A.

19 After the application of the EEG net, participants were taken into a dimly lit, sound
20 attenuated room and were asked to complete the sustained vigilance task. Participants were
21 seated in front of a 19-inch CRT monitor and used their right hand to make responses on a
22 computer mouse. The stimuli were presented using Cogent 2000 software (UCL, London,
23 United Kingdom) for Matlab R2016b. (Mathworks, Inc., USA).

24 Participants were presented with a white fixation cross in the centre of a black screen
25 monitor. The target stimulus occurred when the fixation cross disappeared for 0.5 seconds.

1 The presentation of the target stimuli was separated by uniformly distributed inter-trial
2 intervals which ranged from 3.5 to 9 seconds. Participants first completed a five-minute
3 practice run of the task with no rewards offered. During this baseline run the participants'
4 median RT was calculated, which was then used as the target RT in the following 3 ten-
5 minute blocks.

6 Following the practice block, participants were required to complete three
7 experimental ten-minute blocks of the same task. In one of the experimental blocks the
8 participants were not offered any reward and were instructed to respond as quickly and as
9 accurately as possible whenever the target stimulus occurred, and in the other two
10 experimental blocks the participants were offered a monetary reward whenever they
11 responded to the target stimulus faster than, or as fast as, their previously calculated median
12 RT. In one of these two blocks participants were offered 1p per fast response and were
13 offered 10p per fast response in the other block. Participants were presented with 100 target
14 stimuli in each block, meaning they were offered a total of £1 or £10 in the two reward
15 blocks respectively if they received the reward on every trial. In order to prevent practice or
16 fatigue effects the order of the three experimental blocks was randomly generated by a
17 computer at the start of each experiment, and a one-sample chi-square test was conducted to
18 check the transitional probability of block order, confirming that any block order was not
19 presented significantly more often than the others ($p = .40$).

20 EEG recordings were acquired throughout the study. At the start of each of the three
21 blocks, a 90-second baseline period was recorded, during which participants were instructed
22 to look at the fixation cross presented on the monitor. The cross would not disappear and the
23 participants were not required to make a response.

24 Trials were split in half based on whether participants responded faster than their
25 median RT were encoded as fast trials and trials where participants responded slower than

1 their median RT were encoded as slow trials. Behavioural measures of attention were taken
2 as being the mean RT for each participant in each experimental block (0p, 1p, 10p) and
3 response-speed trials (fast and slow).

4 **Discounting task**

5 The discounting task (Massar et al., 2016; Westbrook et al., 2013) was used to evaluate
6 subjective costs of six levels of effort (5, 10, 15, 20, 25, and 30 minutes) for each participant
7 using a series of monetary decisions.

8 Participants were first told that they would be required to complete the previous
9 sustained vigilance task again for an amount of time (ranging from one minute to thirty
10 minutes) based on the choices made in the discounting task.

11 Following this, participants were presented with 36 pairs of monetary offers, with
12 each pair always consisting of one low-effort, low-reward option, and one high-effort, high-
13 reward option (Fig. 1C). The low-effort option always required participants to complete the
14 task again for only one minute, whereas the amounts of time given in the high-effort option
15 was varied based on which condition the trial was in. Participants were offered a fixed reward
16 of £12 in the high-effort option in every trial. In comparison, the reward offered for the low-
17 effort option was adjusted following a staircase titration method (i.e., the offer was increased
18 if the high effort option was chosen and decreased if the low effort option was chosen). The
19 participants were first offered £6 for the low-effort choice with an extra £2.50 being added to,
20 or taken away from, this amount depending on participant choice. The amount of money
21 added to, or taken away from, the low-effort option was then halved each time the participant
22 made a decision. The participants made six choices during each effort block (5, 10, 15, 20,
23 25, 30 minutes), and the order of conditions was randomly presented for each participant.

24 Following the final choice, one trial was randomly chosen through the generation of a
25 random number between 1 and 36, which would then refer to the chosen trial number. Next,

1 the participant would be required to complete the vigilance task for the amount of time
2 chosen during the selected trial and would receive the amount of money associated with that
3 choice.

4 An indifference point was calculated for each condition, and used as a measure of the
5 subjective value of effort. This was defined as the average of the largest low-effort monetary
6 offer for which the participant chose the low-effort option, and the lowest low-effort
7 monetary offer for which the participants chose the high-effort option (Massar et al., 2016;
8 Westbrook et al., 2013).

9 In order to control for temporal discounting, participants were informed that they
10 would be required to remain in the laboratory for the full 30 minutes in total, including the
11 time spent completing the task. This ensured that the participants made decisions during the
12 discounting task based upon the effort required rather than the time taken to complete the
13 task. The boredom associated with remaining in the laboratory was not explored directly,
14 however all participants discounted higher levels (30 min) more than lower levels (5 min).

15 The area under the curve (AuC) in the function representing associations between
16 units of efforts and requested payoffs was computed in every participant (Myerson et al.,
17 2001). This measure corresponds to SV of effort and has been found to be correlated with
18 need for cognition scores (Westbrook et al., 2013). A bivariate correlation was conducted to
19 assess the relationship between this function to RTs and RBP values.

20 **EEG recordings**

21 EEG data was recorded continuously using a 129-channel Geodesics EGI System
22 (Electrical Geodesics, Inc., Eugene, Oregon, USA) with a sponge-based HydroCel Sensor
23 Net. The net was aligned with reference to three anatomical head landmarks: two preauricular
24 points and the nasion landmark. Electrode-to-skin impedances were kept below 50 k Ω and

1 were kept at equal levels across all electrodes. A recording band-pass filter was set at 0.001-
2 200 Hz with a sampling rate of 1000 Hz. The Cz electrode was used as a reference electrode.

3 **Spectral analysis of EEG signals**

4 EEG data was pre-processed using BESA v 6.1 (MEGIS GmbH, Germany). EEG
5 signals were re-referenced using a common average reference method (Lehmann, 1984)
6 which restored the signal at electrode Cz. Eye blinks and electrocardiographic artefacts were
7 removed using principal component analysis (Berg and Scherg, 1994). Further, data were
8 visually inspected for the presence of any movement or muscle artefacts, and epochs
9 contaminated with artefacts were excluded from subsequent analysis.

10 While participants completed all trials behaviourally, the average number of trials
11 accepted for EEG analysis in each condition was: 0p, 53.9 ± 14.0 (mean \pm SD); 1p, 54 ± 15.5
12 (mean \pm SD); 10p, 55.8 ± 14.3 (mean \pm SD). The average number of accepted trials did not
13 differ across conditions ($p > 0.05$). A recording band-pass filter was set at 0.001-1000 Hz
14 with a sampling rate of 1000 Hz.

15 Continuous EEG data was split into two sets of 1-second epochs. One set of epochs
16 comprised epochs preceding the disappearance of the fixation cross (-1.0 - 0.0 s). This set of
17 epochs was used to evaluate the cortical activation preceding the speeded RT response. The
18 other set of 1-s epochs was selected from the 90-second resting period which was recorded at
19 the start of each block. All artefact-free 1-second non-overlapping epochs were used. This set
20 of epochs was used to evaluate the baseline amplitudes of cortical oscillations and was used
21 further to evaluate RBP changes.

22 EEG signals were down-sampled to 256 Hz. In both epochs, the power spectra were
23 computed in Matlab (The Mathworks, Inc., USA) using Welch's power spectral estimate
24 method. All epochs comprising one set of epochs were aligned to form a quasi-continuous
25 EEG signals. The power spectral densities were computed from non-overlapping 1-second

1 segments (256 points). Each data segment was smoothed using a Hanning window. The
2 power spectral densities were estimated in the range 1-80 Hz with a frequency resolution of 1
3 Hz.

4 The RBP in the alpha (8-12 Hz), beta (16-24 Hz) and theta (4-7 Hz) bands were
5 evaluated in each of three conditions using the classical ERD transformation (Pfurtscheller
6 and Aranibar, 1979):

$$D = \left(100 * \frac{R - A}{R} \right)$$

8 Where D represents the RBP during epochs preceding the disappearance of the
9 fixation cross (A) relative to the rest condition (R). Positive values of D correspond to the
10 relative band power decreases which are considered to signify the presence of cortical
11 activation. In contrast, negative D values refer to the amplitude increases of band power or
12 cortical synchronisation.

13 **Statistical analysis**

14 The differences in the median RT across three blocks and two speed conditions of the
15 vigilance task were compared using a 2×3 repeated measures ANOVA with three levels of
16 reward (0p, 1p and 10p) and two levels of response-speed (fast and slow). As participants
17 were rewarded based on whether they beat their median RTs, the two levels of response
18 speed were an integral part of the experimental procedure. These were included in this
19 analysis to confirm the separation of the two trial types and to allow for the investigation of
20 interaction effects between response speeds and reward. For the choice task, the AuC in the
21 function representing associations between units of efforts and requested payoffs was
22 computed in every participant (Myerson et al., 2001). This measure corresponds to SV of
23 effort and has been found to be correlated with need for cognition scores in a previous study
24 (Westbrook et al., 2013).

1 The RBP changes were investigated separately in alpha (8-12 Hz), beta (16-24 Hz)
2 and theta (4-7 Hz) frequency bands across all 129 electrodes using 2×3 repeated measures
3 ANOVAs.

4 A two-step procedure was used to identify electrodes suitable for further analysis. To
5 remove electrodes with spurious results showing only minimal changes in power from the
6 baseline (e.g., <1% changes) in each frequency band, T-tests with significance thresholds of
7 .01 were used to test whether RBP changes over each electrode were significantly different
8 from 0.

9 Electrode clusters showing statistically significant effects in both the permutation
10 analysis and the t-tests were explored further in SPSS v. 22 (IBM Inc., USA). The
11 Greenhouse-Geisser epsilon correction was used to tackle a violation of the sphericity
12 assumption found in the data. The correlations between individual RTs and individual
13 changes in RBP were calculated to test for possible covariations between behavioural and
14 electrophysiological effects in all significant electrode clusters.

15 Further, to tackle the risk of a false positive error due to the large number of tests, a
16 hypothesis-independent permutation analysis, implemented in the *statcond.m* program in the
17 EEGLab package (Makeig et al., 2004), was used to identify clusters of electrodes with
18 significant main effects of reward or response-speed, or interactions between these conditions
19 separately (Maris and Oostenveld, 2007). This cluster-based method provides a data-driven
20 approach to assess effects of conditions on RBP in specified frequency bands (8-12 Hz, 16-24
21 Hz, and 4-7 Hz) across all electrodes without making a priori assumptions, while also
22 controlling for multiple comparisons with no loss in statistical power.

23 In this analysis, we calculated the test statistics for the main effects and interactions of
24 both response-speed and reward on RBP in the specified frequency bands over all electrodes.
25 The RBP from all experimental conditions was then collected into a single dataset. Data

1 points were randomly drawn from this set and placed into subsets having the same size as the
2 two response-speed and three reward conditions, forming a ‘random partition’, or dataset
3 representing randomly shuffled versions of the three reward and two response-speed
4 conditions. The test statistics for the main effects and interactions of reward and response-
5 speed in this random partition were then calculated. Next, the creation and analysis of the
6 random partition was repeated 5000 times, and a histogram of the produced test-statistics was
7 constructed for all electrodes. The proportion of random partitions that resulted in a larger
8 statistic than the test-statistic first calculated for the non-shuffled data was calculated for all
9 electrodes, and this was defined as the p-value. Electrodes that exceeded a predefined
10 threshold on the calculated p-values (uncorrected $p < .01$) for the main effects of, or
11 interactions between, reward and response-speed were selected and clustered based on spatial
12 adjacency.

13 **Experiment 2**

14 **Participants**

15 17 subjects (12 females), aged 24.05 ± 3.65 (mean \pm SD) were recruited. The
16 procedure used was approved by the Research Ethics Committee of the University of
17 Liverpool, and all participants gave fully informed written consent at the start of the
18 experiment in accordance with the Declaration of Helsinki.

19 **Procedure**

20 The procedures employed in experiment 2 were identical to those used in experiment
21 1 except for the structure of the blocks and the trials. The participants first completed an EEG
22 experiment; completing a sustained vigilance task, which was a modification of the vigilance
23 task used in experiment 1 (Dinges and Powell, 1985; Massar et al., 2016). Participants then
24 completed the same discounting task as the one employed in experiment 1.

1 Participants were first presented with a white fixation cross (baseline period) followed
2 by a cue stimulus which displayed the reward value of the next target stimulus (0p, 1p, or
3 10p) the fixation cross was then displayed in the centre of the screen. After 2.5 seconds the
4 target stimulus occurred (the fixation cross would disappear for 0.5 seconds). The
5 presentation of the baseline period and the cue stimulus was separated by uniformly
6 distributed inter-trial intervals which ranged from 3.5 to 9 seconds and the cue stimulus was
7 presented for 1 second (Fig 1B). The participants first completed a practice block of the test
8 which lasted for 15 trials with no rewards offered. The participants' median RT was
9 calculated during the practice block and was then recalculated separately for each reward
10 condition following each trial in the experimental portion of the task.

11 Following this baseline block, participants were presented with target stimuli in
12 groups of three, containing one trial from each reward condition (0p, 1p, and 10p). The order
13 of trials was pseudo-randomly rearranged at the start of each set of 3 trials, meaning that the
14 participants could not predict the order of presentation of trials and that there were an equal
15 number of trials in each reward condition presented throughout the duration of the
16 experiment. In the 0p condition participants were offered one point rather than a monetary
17 reward whenever they responded to the target stimulus faster than (or as fast as) their
18 previously calculated median RT. In two of the reward conditions participants were offered a
19 monetary reward whenever they responded to the target stimulus faster than (or as fast as)
20 their previously calculated median RT. Participants were offered 1p per fast response in one
21 condition, and were offered 10p per fast response in the other. The participants were
22 presented with 100 target stimuli for each condition, meaning that the participants were
23 offered a total of £0, £1 or £10 across all the trials in each reward condition. During the
24 baseline periods of the experiment, participants were instructed to look at the fixation cross
25 presented on the monitor without making a response.

1 Trials were divided in half, whereby trials which participants responded faster than
2 their median RTs were encoded as fast trials and trials where participants responded slower
3 than their median RTs were encoded as slow trials. Behavioural measures of attention were
4 taken as being the mean RTs for the participants in each experimental block (0p, 1p, 10p) and
5 response speed condition (fast, slow). The average number of trials in each condition was: 0p
6 73.67 ± 14.62 (mean \pm SD); 1p 76.76 ± 12.84 (mean \pm SD); 10p 74.95 ± 11.53 (mean \pm SD).
7 The average number of trials accepted did not differ across conditions ($p > 0.05$). Fewer trials
8 were removed from the EEG analysis in this experiment compared to experiment 1 due to
9 overall cleaner data.

10 **Event-related desynchronization analysis**

11 ERD in alpha, beta and theta bands was computed at every electrode by first calculating the
12 absolute band-power value from 1-s time epochs shifted in 100-ms steps across a 9-s trial
13 window. The trial time window ranged from 2 s before and 7 s after the onset of the cue
14 signalling the amount of reward. The power spectral densities in every one of the 81 time-bins
15 were computed using the Welch method. Each data epoch was smoothed using a Hanning
16 window. The epoch ranging from -1.5 to -0.5 s was used to evaluate rest amplitudes of
17 cortical oscillations and this value was used to compute ERD at every time point across the
18 trial according to the ERD transform (Equation 1). ERD values in the time epoch ranging
19 from 2 to 3 s after the cue onset and immediately preceding the disappearance of the fixation
20 cross were averaged for further statistical analysis.

21 **Statistical analysis**

22 The differences in the median RTs across three blocks and two speed conditions of the
23 vigilance task were compared using a 2×3 repeated measures ANOVA with three levels of
24 reward (0p, 1p and 10p) and two levels of response-speed (fast and slow). For the choice

1 task, each participant's indifference point was calculated for each effort block (5, 10, 15, 20,
2 25, 30 minutes).

3 ERD was investigated in theta (4-7 Hz), alpha (8-12 Hz) and beta (16-24 Hz)
4 frequency bands across all 129 electrodes using 2×3 repeated measures ANOVA. To tackle
5 the risk of a false positive error due to the large number of tests the P values were corrected
6 using a permutation analysis (Maris and Oostenveld, 2007), implemented in the *statcond.m*
7 program in the EEGLab package (Makeig et al., 2004). To prevent multiple comparisons
8 from creating false effects electrode clusters were selected using a permutation analysis with
9 5000 permutations. Electrodes with statistically significant main effects or interactions were
10 selected for further analysis. T-tests with significance thresholds of 0.001 were used to test
11 whether ERD over each electrode was significantly different from 0. Only electrodes which
12 passed significance thresholds in both tests were selected for subsequent analysis. The
13 combined statistical and amplitude threshold ensured that results were extracted only from
14 electrodes showing task-related responses.

15 Electrode clusters showing a statistically significant effects in both the permutation
16 and t-test analyses were explored further in SPSS v. 22 (IBM Inc., USA). Greenhouse-
17 Geisser epsilon correction was used to tackle the violation of the sphericity assumption due to
18 more than two levels in the independent variable.

19 To test possible covariations between band power, RT changes, and individual SVs,
20 difference variables were created. These were defined as the mean difference between fast
21 and slow trials for each participant, which were calculated by subtracting fast trial RTs and
22 RBP from slow trial RTs and RBP power. The RBP and RT difference variables were
23 correlated with each other and individual AuC of SVs using bivariate correlations. **Bivariate
24 correlations were conducted in all electrode clusters or single electrodes selected for further
25 analysis, however, only statistically significant correlation coefficients are reported.**

1 RESULTS

2 Experiment 1

3 Vigilance task

4 Differences in median RTs across the three reward conditions (0p, 1p, 10p), and across fast
5 and slow trials were analysed using a 2×3 repeated measures ANOVA. A statistically
6 significant main effect of reward was found ($F(2,56) = 6.75, p = .003, \eta p^2 = .19$) with a
7 significant negative linear trend ($p = .001$). This was found to be the result of a difference
8 between the 10p reward block and both the 1p ($p = .047$) and the 0p reward blocks ($p = .001$).
9 Median RTs in slow and fast trials in each reward category are shown in Fig. 2A.

10 A statistically significant interaction between reward and response-speed was also
11 found ($F(2,56) = 5.03, p = .012, \eta p^2 = .15$). A test of simple effects showed that this
12 interaction was due to an effect of reward on RTs for slow trials only ($F(2,46) = 7.15, p =$
13 $.003$) with a statistically significant negative linear trend ($p = .002$). The main effect was
14 found to be the result of a difference between the 10p reward block and both the 0p ($p = .001$)
15 reward block. No statistically significant effect of reward was found for fast responses.

16 RT difference variables were correlated with the value of effort evaluated as AuC in
17 individual COGED graphs representing amount of money to be paid for each of the six task
18 durations, with no statistically significant correlation being found between RT changes and
19 individual SVs of effort (see Fig. 3B).

20 Discounting task

21 A linear regression analysis was used to compare the change in SV for each effort condition
22 (5, 10, 15, 20, 25 & 30 minutes). The mean discounting values across offered 5-30 min task
23 durations are shown in Fig. 3A. There was a statistically significant exponential relationship
24 between the levels of effort and SVs ($F(1, 172) = 32.87, p < .001, R^2 = .17$). The regression
25 model showed a negative exponential regression with an equation of:

$$Y = 6 \times \exp (-0.041 \times X) + \varepsilon,$$

where Y is the SV, X is the effort level, and ε is an error element.

Alpha-band changes

Fig 4A shows the grand average topographic maps of RBP over all trials (left), as well as the electrodes found to be different from 0 (right). Electrodes responding with amplitude changes in the alpha band included the posterior parietal and occipital cluster of electrodes, the left central-temporal cluster, and two electrodes over the right frontal and prefrontal region of the scalp. The grand average topographic maps of RBP in each of the three reward conditions are shown for slow (Fig 4B) and fast (Fig 4C) trials, as well as across all trials (Fig 4D).

The topographic maps show widespread increases in alpha RBP, with larger RBP increases preceding fast compared to slow trials over left-central region of the scalp.

Electrode 40, over the left-central area, was the only electrode found to pass both the difference from 0 t-test and the permutation-based threshold, and was, therefore the only electrode selected for further analysis. To investigate RBP changes over this electrode a 2×3 repeated measures ANOVA was conducted, with 3 levels of reward (0p, 1p and 10p) and 2 levels of response-speed (fast and slow). A significant main effect of response-speed was found ($F(1,23) = 4.37, p = .048$), where fast responses were found to elicit significantly stronger synchronisation compared to slow responses. Electrode location is shown in Fig 4E and RBP values for electrode 40 are shown in Fig 4F.

In order to assess the relationship between RBP changes and RTs, difference variables were created. These were defined as the mean difference between fast and slow trials for each participant, being calculated by subtracting fast trial RTs and RBP from slow trial RTs and RBP power. There was a significant positive correlation between alpha RBP and RT difference variables in the 10p reward block ($r(24) = .42, p = .015$), showing that participants

1 with stronger synchronisation in fast relative to slow trials had shorter RTs in fast relative to
2 slow trials. However, no significant correlations were found between the same RT and RBP
3 difference variables created in either the 0p ($r(24) = -.015, p = .95$), or 1p ($r(24) = .29, p = .15$)
4 reward blocks. Results of these correlations are shown in Fig 4G-I.

5 The changes in alpha RBP were also correlated with the value of effort evaluated as
6 AuC in individual COGED graphs representing amount of money to be paid for each of the
7 six task durations. However, no statistically significant correlation was found between alpha-
8 band power changes and individual SVs of effort acquired in COGED task.

9 **Beta-band changes**

10 Fig 5A (right panel) shows the grand average topographic maps of beta RBP over all
11 trials (left), showing strong increases in RBP over frontal regions of the scalp at electrodes
12 surpassing a combined statistical and amplitude threshold highlighted with red circles (left
13 panel). The grand average topographic maps of relative band power in each of the three
14 reward conditions are shown for slow (Fig 5B) and fast (Fig 5C) trials as well as across all
15 trials (Fig 5D). **Three electrodes passed both the difference from 0 and the permutation-based
16 threshold and were, therefore, selected for further analysis.**

17 A statistically significant interaction between reward and response-speed was found
18 over the right-frontal region of the scalp (electrode 124) ($F(2,46) = 4.51, p = .016$). The
19 interaction was found to be due to an effect of response-speed in the 10p reward block
20 ($F(1,23) = 9.37, p = .006$), where fast responses were found to elicit statistically significantly
21 more beta-band synchronisation compared to slow responses. Electrode location is shown in
22 Fig 5E and mean values of beta-band RBP in all conditions are shown in Fig 5F.

23 A statistically significant main effect of response-speed was found over a frontal
24 electrode (electrode 21) ($F(1,23) = 5.64, p = .026$), where fast responses were found to elicit

1 significantly weaker beta band synchronisation compared to slow-responses. In contrast,
2 electrode 5, located in the midline fronto-central area of the scalp (Fig. 5G), showed a
3 stronger beta-band power increase in fast compared to slow responses ($F(1,23) = 9.23, p =$
4 $.006$) (Fig. 5H).

5 To evaluate the relationship between RTs and RBP over right-frontal regions
6 (electrode 124) a difference variable was calculated in both RTs and RBP values representing
7 the differences between fast and slow trials in the 10p reward block only, being calculated by
8 subtracting fast trial RBP and RTs from slow trial RBP and RTs. The Pearson product-
9 moment correlation showed a statistically significant positive relationship between the
10 difference values computed for RTs and RBP over electrode 124 ($r(24) = .44, p = .033$) (Fig.
11 5I). This shows that participants with a stronger increase in beta-band power in fast trials
12 compared to slow trials in the 10p reward block also had a greater difference in RTs between
13 slow and fast trials in this block. No significant correlation was found between RBP changes
14 in the beta band and individual discounting results.

15 Data was also analysed in the theta frequency band, however, no electrodes were
16 found to pass both significance thresholds in this frequency range.

17 **Absolute band power changes**

18 In order to confirm that the effects found within the alpha- and beta-bands were not the
19 results of changes in baseline power, the absolute power of the baseline conditions was
20 compared over relevant electrodes in the alpha- and beta-bands. No significant differences in
21 baseline were found across reward conditions for any of the relevant electrodes ($p > .05$) in
22 either frequency band, confirming that the results of experiment 1 were not the result of
23 variations within the baseline power.

24

1 Discussion

2 The results of experiment 1 show that the presence of monetary incentives shortened
3 RTs, and fast responses were associated with stronger synchronisation in the alpha band over
4 the left-central area of the scalp and stronger and more focused synchronisation in the beta
5 band over fronto-central regions of the scalp, an effect which was particularly apparent in
6 high-reward conditions. Individual values of subjective effort, however, were not associated
7 with band-power increases in either the alpha or beta frequency bands. Thus, we were unable
8 to replicate the correlation of $r = 0.31$ between the value of effort and the shortening of RTs
9 found in previous research (Massar et al., 2016). However, the order of the three reward
10 blocks was randomised in the present study, whereas in previous research the no reward
11 block was always presented first. This procedural difference may explain the lack of a
12 statistically significant correlation between the individual value of effort and performance.

13 The effects of response-speed were seen as modulations of amplitude increases in
14 both alpha- and beta-band power in the 1-s epoch preceding the motor response, compared to
15 the baseline. In the alpha band, a stronger increase in oscillatory power was observed in fast
16 compared to slow trials over a left-central electrode. This effect was significantly correlated
17 with the individual differences between fast and slow mean RTs in the 10p reward block. An
18 effect of reward was present only in the beta band, as a stronger synchronisation of beta-band
19 oscillations prior to fast compared to slow responses in 10p condition but not in 0p or 1p
20 conditions. Individuals with the largest differences between slow and fast RTs also showed
21 the strongest increase in beta-band power at the frontal electrode.

22 Amplitude increases in the alpha-band over central regions have traditionally been
23 associated with motor inhibition (Fry et al., 2016; Jensen et al., 2005; Pfurtscheller et al.,
24 1996b; Salmelin and Hari, 1994). This is thought to be due to the absence of excitatory
25 impulses from lower brain centres (e.g., the reticular formation) (Zaaimi et al., 2018; Steriade

1 and Demetrescu, 1962; Bonvallet and Newman-Taylor, 1967) and due to the synchronised
2 firing of GABAergic neurons (Faust et al., 2016; Tritsch et al., 2016; Jensen et al., 2005;
3 Klimesch et al., 2007).

4 **Beta-band increases were stronger and more focused over fronto-central regions**
5 **preceding fast responses compared to slow responses, reflected in a different pattern of ERD**
6 **changes in electrodes 5 and 21. A similar pattern of a prominent fronto-central focus of beta-**
7 **band synchronization due to topographic expansion has been found for Go, compared to**
8 **NoGo, responses (Alegre et al., 2004). While our data do not allow inferences on underlying**
9 **cortical generators, the shape differences in the large ERD cluster in prefrontal and fronto-**
10 **central electrodes suggests that the fast- compared to slow movements were preceded by a**
11 **stronger activation in premotor regions residing in the medial frontal cortex. This**
12 interpretation is supported by findings of activations in the right frontal cortex during stop-
13 signal and Go/No Go task, and of increased beta-band synchronisation over frontal electrodes
14 during motor inhibition (Alegre et al., 2006; Wessel and Aron, 2013; Swann et al., 2009;
15 Fonken et al., 2016; Wagner et al., 2018). The pattern of cortical oscillations in experiment 1
16 matched the inhibitory processes posited by the horse-race theory (Logan and Cowan, 1984;
17 Logan, 1994; Band et al., 2003), showing that active inhibition was required during motor
18 preparation and that this was modulated by response-speed, especially under conditions of
19 high reward.

20 **Both the alpha- and beta-band results suggest faster response speeds, especially under**
21 **high reward, were associated with increased motor inhibition in the time window preceding**
22 **movement.** This relates to the experimental design, where the target was not cued, so motor
23 activation was required to be maintained throughout each block. The increased inhibition
24 found may relate to higher engagement with the task or be due to a faster motor response, and

1 the correlation found between RTs and RBP in the 10p reward block supports this
2 explanation.

3 4 **Experiment 2**

5 **Vigilance task**

6 Differences in median RTs in response to the target stimulus were assessed across the
7 3 reward conditions (0p, 1p & 10p) in both fast and slow trials using a 2×3 repeated measures
8 ANOVA. A significant main effect of reward was found ($F(2,32) = 12.58, p = .001, \eta p^2 =$
9 $.44$), with a significant negative linear trend ($p = .002$). This main effect was found to be the
10 result of significant differences between the 10p reward condition and both the 1p ($p = .003$)
11 and the 0p ($p = .002$) reward conditions. The mean values of RTs in each reward and
12 response-speed conditions are shown in Fig. 2B.

13 A significant interaction was also found between reward and response-speed ($F(1,32)$
14 $= 10.80, p = .002, \eta p^2 = .40$) and, in order to investigate this interaction one-way repeated
15 measures ANOVAs assessed the effect of reward on RTs during fast and slow trials
16 separately. The interaction was related to the statistically significant modulation of RTs
17 during slow trials only ($F(2,32) = 12.84, p = .001, \eta p^2 = .45$) with a significant negative
18 linear trend ($p = .001$). Further analysis of post-hoc effects revealed a significant difference
19 between the 10p reward condition and both the 1p ($p = .001$) and 0p ($p = .001$) reward
20 conditions. No statistically significant simple effect of reward on RTs were found in fast
21 trials.

22 A difference variable representing the high reward RTs subtracted from low reward
23 RTs (10p-0p) correlated with the AuC in individual COGED graphs. However, no
24 statistically significant correlation was found between RT changes and individual SVs of
25 effort acquired in COGED task (see Fig. 3D).

1 Discounting task

2 A linear regression analysis was conducted to compare the change in SV for each
3 block during the discounting task (5, 10, 15, 20, 25, 30 minutes). There was a significant
4 exponential relationship between the levels of effort and SVs ($F(5, 15) = 6.66, p < .002, R^2$
5 $= .69$) (Fig. 3C). The regression model showed a negative exponential regression with an
6 equation of:

$$7 \quad Y = 7.36X - 0.14 + \epsilon,$$

8 where Y is the SV, X is the effort level, and ϵ is an error element.

9 ERD patterns across trials.

10 Fig 6., shows ERD/ERS scalp topographies over specified time periods (0.5 s, 2 s, 2.5
11 s, and 3.3 s following the presentation of the cue stimulus) in (A) the alpha-band, (B) the beta
12 band, and (C) the theta band. Time courses of percentage power changes over specified
13 electrodes are also shown. Electrodes were selected apriori at areas of the scalp where band
14 power was expected to be modulated by task demands based on previous research. For
15 example, an ERD was expected over contralateral sensorimotor areas in the alpha- and beta-
16 bands during motor preparation (Rhodes, 2019; Pfurtscheller and Berghold, 1989; Tzagarakis
17 et al., 2010; Tzagarakis et al., 2015; Fox et al., 2016; Ishii et al., 2019). Oscillations during
18 the cue interval (0.5 s after cue onset) were featured by an ERD over occipital electrodes in
19 the alpha band (Fig. 6A). This is consistent with the presence of attentional and visual
20 processing of a reward cue. During the period of motor readiness (2-2.5 s after cue onset),
21 alpha-ERD was prominent in left (contralateral) parietal, and central electrodes. After the cue
22 disappeared and during the time of motor response, alpha-ERD was distributed bilaterally in
23 parietal, and central electrodes.

24 In the beta band (Fig. 6B), a comparatively weak ERD appeared in the contralateral
25 central electrodes during the period of motor readiness preceding the disappearance of the

1 fixation cross. A beta-ERS was seen at the vertex electrode during motor preparation (2.5 s
2 after cue onset). This increased during the motor response period (3.3 s after cue onset).

3 Finally, in the theta band (Fig. 6C), activation during the cue interval (0.5 s after cue
4 onset) was confounded by the presence of the phase-locked evoked response causing an
5 increase of theta power over the whole scalp. The period of motor readiness (2.5 s after cue
6 onset) was featured with a theta-ERS at central and precentral midline electrodes.

7 **Alpha-band ERD**

8 The grand average topographic maps showing alpha-band ERD for all trials as well as
9 the electrodes found to be significantly different from zero are shown in Fig 7A. Two clusters
10 of electrodes, one in bilateral parietal and central electrodes and another in frontal electrodes,
11 showed alpha-ERD surpassing both the combined amplitude and statistical thresholds.

12 Topographic maps showing ERD in each of the three reward conditions are shown In
13 Fig. 7B for slow, and Fig 7C for fast trials, and in Fig 7D for all trials irrespective of the
14 speed of the motor response.

15 To investigate the effects of response-speed and reward on ERD values 2×3 repeated
16 measures ANOVAs were computed to assess the significant main effects and interactions of
17 response-speed (fast & slow) and reward (0p, 1p, 10p) on ERD recorded by electrodes which
18 passed the combined statistical and amplitude thresholds. This ensured that only electrodes
19 showing a robust ERD across conditions were analysed.

20 Statistically significant main effects of reward were found in both frontal and occipital
21 regions of the scalp. Over frontal electrodes (cluster 1) ERD grew significantly stronger as
22 reward increased ($F(2,32) = 7.95$, $p = .003$, $\eta^2 = .44$), and a statistically significant positive
23 linear trend was found ($p = .005$). The observed main-effect of reward was due to a difference
24 between ERD in 10p reward trials and both 0p ($p = .005$) and 1p reward trials ($p = 0.008$).

25 There was also a statistically significant effect of reward on ERD found over right-parietal

1 regions (cluster 2) ($F(2,32) = 4.31$, $p = .022$, $\eta p^2 = .31$), with a statistically significant linear
 2 trend ($p = .017$). This effect was found to be the result of a difference between ERD
 3 calculated for 10p trials and for 0p trials ($p = .017$). Electrodes with a main effect of reward
 4 are shown in Fig 7E, and results for both cluster 1 and cluster 2 are shown in Fig 7F.

5 Significant main effects of response-speed were also found over frontal and occipital
 6 electrodes, where fast trials were found to elicit significantly stronger ERD when compared
 7 to slow trials. There was significantly stronger ERD found over electrode 9 (frontal) during
 8 fast trials compared to slow trials ($F(1,16) = 6.21$, $p = .024$, $\eta p^2 = .28$), and stronger ERD
 9 over cluster 3 (occipital) during fast compared to slow trials ($F(1,16) = 5.21$, $p = .037$, $\eta p^2 =$
 10 $.25$). Electrodes with a significant main effect of response-speed are shown in Fig 7G and
 11 ERD results for electrode 9 and cluster 3 are shown in Fig 7H.

12 A difference variable was created to by subtracting fast from slow trials for both
 13 individual ERD values over electrode 9 and individual RTs. A significant negative
 14 correlation was found between these two difference variables ($r(17) = -.55$, $p = .021$),
 15 showing that stronger differences in ERD between fast and slow trials were associated with
 16 larger differences in RTs between these trials (Fig 7I).

17 Difference variables were also created to calculate the mean difference between the
 18 ERD found during 10p reward trials and both 1p and 0p reward trials in cluster 1, and to
 19 calculate the mean difference in the participant's indifference points taken from the COGED
 20 task during 5 min and 30 min effort conditions. There was, however, no statistically
 21 significant correlation between the SV of effort, evaluated as AuC of individual COGED
 22 functions, and alpha-band ERD.

23 **Beta-band ERD**

24 The grand average topographic map for all trials and the distribution of electrodes
 25 showing ERD significantly different from zero are shown in Fig. 8A. The electrodes with a

1 strong beta-ERD across conditions were located primarily in the left, right-central and
2 parietal electrodes. The grand average topographic maps in each of the three reward
3 conditions are shown for slow trials in Fig 8B, for fast trials in Fig 8C, and for all trials in
4 Fig. 8D.

5 ERD in the beta band featured a comparatively weak effect in the contralateral central
6 and parietal electrodes in the 0p and 1p conditions compared to the 10p condition. Beta-ERD
7 was also pronounced over ipsilateral central electrodes, however this effect was only found in
8 the 10p condition. ERS can also be seen over central regions (electrodes Cz to Oz), an effect
9 consistent with the ‘surround ERS’ (Suffczynski et al., 2001) found around areas showing
10 ERD in previous studies (Pfurtscheller, 2003; Pfurtscheller et al., 2000; Neuper et al., 2006;
11 Doyle et al., 2005).

12 There was a significant main effect of reward in the ipsilateral (right) sensorimotor
13 hand area (cluster 1, Fig. 8E) ($F(2,32) = 10.14$, $p = .001$, $\eta p^2 = .58$), with a significant
14 positive linear trend ($p = .004$) (Fig. 8F). The main effect of reward was related to the
15 statistically significant difference between 10p reward and both the 1p ($p < .001$) and 0p
16 reward conditions ($p < .001$).

17 In the contralateral (left) cluster of electrodes (cluster 2, Fig 8G), beta-band ERD was
18 significantly stronger when preceding fast trials compared to slow trials ($F(1,16) = 10.39$, $p =$
19 $.005$, $\eta p^2 = .39$) (Fig. 8H). There was no effect of reward in cluster 2 ($p > .05$).

20 In order to evaluate the relationship between behavioural results and beta-ERD found
21 ipsilateral to the hand movement a difference variable was created where the mean ERD
22 difference between 10p reward trials and both 1p and 0p reward trials was calculated.
23 However, there was no statistically significant correlation between beta-band ERD and RT
24 difference values. Similarly, there was no statistically significant correlation between beta-
25 band ERD and the SV of effort in any of the electrode clusters ($p > 0.05$).

1 Similar to experiment 1, there were no statistically significant effects of reward or
2 speed of response in theta band.

3 **Discussion**

4 Reward level quickened RTs, especially in slow movements. The COGED profiles
5 showed decreasing SVs of reward as the associated effort was increased similar to previous
6 studies (Massar et al., 2016; Westbrook et al., 2013). However, no significant correlation was
7 found between the SV of effort and either RTs or cortical oscillatory changes. We were,
8 again, unable to replicate the correlation between value of effort and RTs found in Massar et
9 al. (2016). It appears that this correlation is difficult to replicate if the order of blocks or trials
10 with different reward levels occurs in a random order, showing independence between the
11 individual value of effort and the way rewards effected the modulation of effort during the
12 vigilance task

13 ERD in the alpha band showed reward-related increases, with the strongest ERD in
14 the 10p condition in two clusters of electrodes, one in the frontal and the other the parietal
15 region of the scalp. Both regions also showed a stronger ERD prior to fast, compared to slow
16 motor responses. In the beta-band, ERD was localised in contralateral central regions of the
17 scalp, purportedly overlaying the sensorimotor hand areas, and was stronger preceding fast
18 compared to slow responses. This ERD response became bilateral during the 10p reward
19 conditions before both fast and slow trials, but not during the 0p or 1p reward conditions.

20 Theta-band oscillations showed fronto-central synchronisation prior to the target
21 stimulus, a response associated with increased attention and effort (Angelidis et al., 2018;
22 Rajan et al., 2018; Basar-Eroglu et al., 1992; Klimesch, 1999). This was, however, not
23 modulated by reward or response speed, showing that it was not related motor preparation or
24 may have a ceiling effect.

1 The alpha-band ERD in posterior parietal regions is likely to refer to the activation of
2 regions involving visual-spatial coordination localised in the posterior parietal cortex (Ibos
3 and Freedman, 2016; Whitlock, 2017; Assmus et al., 2005; Corbetta et al., 2000). ERD in
4 posterior parietal electrodes has also been observed during the preparation of shoulder
5 movements (Stancak et al., 2000). This may indicate more generalised motor readiness
6 during intense effort, which may, initially, involve larger muscle groups even if the target
7 movement is only a hand movement. The alpha-band ERD in the prefrontal regions supports
8 the hypothesis that this region is implicated in motor preparation, or in the activation of
9 cortical areas involved in motor preparation (e.g., motor areas or the basal ganglia) (Aron and
10 Poldrack, 2006). This interpretation is strengthened by the significant correlation between
11 alpha-band ERD and individual RTs, and the present results show that these effects can be
12 elicited by increasing performance-based rewards.

13 Fast compared to slow motor responses were preceded by increased beta-ERD in
14 electrodes overlying the contralateral sensorimotor cortex, which is likely to refer to
15 increased motor preparation during fast trials (Ishii et al., 2019; Rhodes, 2019; Tzagarakis et
16 al., 2015; Fry et al., 2016; Tewarie et al., 2018). The effect of reward on beta-band
17 oscillations is supported by previous research, in which voluntary movements have been
18 shown to be preceded by ERD in bilateral sensorimotor cortical regions (Little et al., 2018;
19 Stancak et al., 1997; Stancak and Pfurtscheller, 1996a; Neuper and Pfurtscheller, 2001; Fry et
20 al., 2016). A similar effect was found by Stancak et al. (1997), where desynchronization in
21 the beta band manifested in the ipsilateral somatosensory region under intermediate, but not
22 zero, external load. The results of the present study adds to the literature by showing that
23 incentive can elicit this effect, possibly relating to a ceiling effect in the contralateral
24 sensorimotor cortex, boosting motor readiness in the ipsilateral sensorimotor cortex under
25 strong effort.

1 Overall, the results of experiment 2 show increases in cortical activation in parietal
2 and central electrodes paralleling increases in reward and shortening of RTs. These
3 associations between amplitude decreases of cortical oscillations, and reward and
4 performance could relate to the heightened level of motor readiness assumed to underlie fast
5 responses in the horse-race theory motor control (Logan and Cowan, 1984).

7 **General discussion**

8 The present results add weight to our current understanding of cognitive effort by **suggesting**
9 that reward **may** modulate effort through the activation or inhibition of relevant cortical areas
10 in the short epoch preceding a speeded motor response in a sustained vigilance task.

11 However, results suggest that the cortical mechanisms employed differ widely depending on
12 the structure of the vigilance task.

13 If the task was conducted as a series of speedy movements executed under the same
14 reward level (experiment 1) a sustained motor preparation was required which lasted
15 throughout the entire block. Optimal motor performance was likely achieved as a
16 combination of high motor readiness and inhibition in the frontal cortex; where the inhibitory
17 component, indexed as increases of beta-band oscillations in frontal electrodes, prevailed.

18 In contrast, if the experiment was conducted with the three reward conditions
19 alternating in a pseudo-random fashion with cues signalling the reward levels at the start of
20 each trial (experiment 2), optimal performance could be achieved by a continuous build-up of
21 activation in task-relevant cortical regions. This version of the sustained vigilance task
22 allowed the cortical regions to reach a resting state after each movement because participants
23 were certain that no motor response was required in the time period preceding the reward cue
24 stimulus. Thus, to achieve a fast response, the activation in the sensorimotor, premotor and
25 other cortical areas would need to increase from a state of low activation and reach a state of

1 high activation within the span of two to three seconds. This process of building activation in
2 the sensorimotor cortex did not require a parallel inhibition like in experiment 1, in which
3 short RTs would be achieved if the sensorimotor cortex was continuously active.

4 A novel result was found in experiment 2, showing that when participants are offered
5 sufficient reward (10p) activations are found bilaterally in the sensorimotor cortex. This
6 indicates that strong enough motivation can lead to motor preparation being employed in both
7 the contralateral and ipsilateral motor areas, and adds to previous research finding bilateral
8 sensorimotor ERD during movement (Little et al., 2018; Stancak and Pfurtscheller, 1996a;
9 Stancak et al., 1997; Neuper and Pfurtscheller, 2001; Fry et al., 2016). This suggests that this
10 effect occurs due to activation from the contralateral region ‘spilling-out’ into, or employing
11 resources from the ipsilateral region. Movement-related ERD has been found to be stronger
12 and more bilateral in elderly compared to younger participants (Derambure et al., 1993;
13 Vallesi et al., 2010). The present results suggest this effect occurs because elderly participants
14 have to make more of an effort to make the same movement compared to younger
15 participants.

16 Taken together, the cortical oscillatory patterns seen in experiment 1 and 2 act
17 according to the horse-race model (Logan et al., 1984). The horse-race model assumes two
18 antagonised processes, one generating a response to the primary task and the other inhibiting
19 it. In experiment 1, the increases of beta-band power in frontal cortical regions preceding fast
20 responses in the high-reward condition could be the manifestation of the inhibition process.
21 This would be expected to be found in the frontal cortex, which has been shown to mediate
22 motor inhibition in stop-signal and go/no-go tasks (Wessel and Aron, 2015; Aron, 2007;
23 Sakagami et al., 2006), perhaps via the subthalamic nucleus in the basal ganglia (Fischer et
24 al., 2017; Aron, 2007; Eagle and Robbins, 2003). This may also relate to an optimization of
25 dopamine levels in the prefrontal cortex, which has been associated with increased cognitive

1 stability (Sharp et al., 2016; Cools, 2016; Cools et al., 2002; Durstewitz et al., 2000), and
2 may, therefore, be required in experiment 1 due to the block design. In experiment 2, the time
3 courses of ERD in the alpha and beta band showed a build-up during the interval preceding
4 the motor response (Fig 6A/B). This was motivationally relevant and occurred in areas
5 associated with motor preparation and visuo-spatial attention (Fry et al., 2016; Tewarie et al.,
6 2018; Ibos and Freedman, 2016; Whitlock, 2017), possibly showing the excitatory
7 components posited by the horse-race theory.

8 The individual value of effort did not correlate with either amplitude increases in
9 beta-band oscillations in experiment 1, or beta-band decreases in experiment 2. It is likely
10 that individual values of effort are implemented during the decision about whether to engage
11 into an effortful cognitive task, but not during an ongoing task. Expected reward level, on the
12 other hand, acted as a modifier of effort by imposing a top-down modulation of the inhibitory
13 and excitatory processes to boost performance. Our results also add weight to the idea of
14 cognitive effort being the result of cognitive control (Shenhav et al., 2013b; Kurzban, 2016),
15 a signal which modulates the task-appropriate inhibition and excitation of cortical response.
16 This ties into to the horse-race model of motor control and shows that these responses can be
17 modulated by monetary incentives. **However, while a significant correlation was found**
18 **between RTs and oscillatory changes between fast and slow responses, no significant**
19 **relationship was found between the effects of incentives on oscillatory changes and the effect**
20 **of incentives on RTs, meaning that it is difficult to directly infer that incentives altered**
21 **behaviour through oscillatory changes. This may be due to other factors modulating how**
22 **incentives affected RTs, such as individual or state differences, or due to a low level of**
23 **statistical power.**

1 **Conclusion**

2 Decreasing RTs as the result of the presence and magnitude of reward was associated
3 with cortical oscillatory changes in both experiment 1 and experiment 2. **Experiment 1**
4 **showed a modulation of response-speeds on cortical inhibition in frontal, prefrontal, and**
5 **central regions, especially under high reward**, suggesting that high reward modulated RTs
6 through the holding and release of inhibition. Experiment 2 showed a modulation of cortical
7 activation over motor, frontal, and posterior-parietal regions, suggesting that reward
8 modulated RTs through changes in motor preparation and visuo-spatial co-ordination in this
9 modified task. Taken together, these results show the dual-processes proposed by the horse-
10 race model of motor action, showing that both inhibition and preparation can be manipulated
11 using performance-based rewards, and ties these to the hypothesis that cognitive effort results
12 from top-down cognitive control, and can be encouraged with monetary incentives.

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1 **Figure legends.**

2 **Fig 1.** A schematic representation of trials presented to participants in the motivated vigilance
 3 task for (A) experiment 1 showing first the inter-trial interval, then the target stimulus,
 4 followed by the inter-trial interval for the following trial; (B) experiment 2, showing first the
 5 cue stimulus, then the period of preparation, followed by the target stimulus; and, finally the
 6 inter-trial interval, and (C) the discounting choice task for both experiments, showing, first an
 7 example choice offered to the participants, followed by feedback confirming the selected
 8 choice.

9 **Fig 2.** A bar chart to show the mean RTs in each reward condition (0p, 1p, 10p) in slow
 10 (grey) and fast (white) trials in experiment 1 (A) and experiment 2 (B). Error bars represent
 11 the standard errors of the mean.

12 **Fig 3.** A line graph to show the discounting curve in the choice task, with the mean subjective
 13 value shown for each block in the task (5, 10, 15, 20, 25, 30 minutes). A discounting curve is
 14 shown for both (A) experiment 1 and for experiment 2 (C). Error bars represent standard
 15 errors of the mean. And scatterplots to show the correlation between the area under the curve
 16 of SVs in the discounting task and the median RTs difference between high-reward and no
 17 reward conditions (0p-10p) for experiment 1 (B) and experiment 2 (D)

18 **Fig 4.** The RBP changes in alpha band in experiment 1. (A) A grand average topographic
 19 map of alpha-RBP averaged across all conditions and subjects. (B) An overhead view of
 20 electrodes showing statistically significant changes in alpha band across all conditions. (C)
 21 Grand average topographic maps of alpha-RBP in 0p, 1p and 10p conditions during trials
 22 with slow RTs. (D) Grand average topographic maps of RBP in three reward conditions in
 23 fast RT trials. (E) Grand average topographic maps of alpha RBP in three reward conditions
 24 across all trials and the location of electrode 40 showing an interaction between reward

1 values and speed of motor response. (F) The mean values of alpha RBP in slow (grey
 2 rectangles) and fast (white rectangles) in three reward conditions at electrode 40. The error
 3 bars represent standard errors of the mean. Scatter plot and linear regression lines
 4 representing correlation between the difference alpha RBP (slow-fast trials) and the
 5 difference RT (slow-fast trials) at electrode 40 in 10p condition (G), the 1p condition (H), and
 6 the 0p condition (I).

7 **Fig 5.** The relative band power changes in beta band in Experiment 1. A. Grand average
 8 topographic map of beta RBP across all conditions and subjects. B. An overhead view of
 9 electrodes showing statistically significant changes in beta band across all conditions. C.
 10 Grand average topographic maps of beta RBP in 0p, 1p and 10p conditions during trials with
 11 slow RT. D. Grand average topographic maps of beta RBP in three reward conditions in fast
 12 RT trials. E. Grand average topographic maps of beta RBP in three reward conditions across
 13 both slow and fast RT trials. E. Location of electrode 124 showing an interaction between
 14 reward values and speed of motor response. F. The mean values of beta RBP in slow (grey
 15 rectangles) and fast (white rectangles) in three reward conditions at electrode 124. The error
 16 bars stand for standard errors of the mean. G. Locations of electrodes 121 and 5 showing a
 17 statistically significant main effect of response speed. H. The left-hand panel shows mean
 18 beta RBP at electrodes 121 and 5 in three reward conditions for slow (grey rectangles) and
 19 fast (white rectangles) trials. I. The scatter plot and linear regression line with 95%
 20 confidence interval lines depicting association between differences in RT (slow-fast trials)
 21 and differences beta-band RBP (slow-fast trials).

22 **Fig 6.** Topographic maps of alpha (A), beta (B) and theta (C) ERD at four time points:
 23 during presentation of visual cue (0.5 s), early period of anticipation of motor response (2 s),
 24 late period of motor response anticipation (2.5 s) and during motor response (3.3 s). In each

1 section (A-C), ERDs at selected electrodes are also shown. The grey rectangles covering the
 2 interval from 2 s to 3 s represent the epoch of interest preceding the motor response.

3 **Fig 7.** Alpha-band ERD during anticipation of motor response A. Topographic map of alpha-
 4 band ERD across all conditions and trials (left), and electrodes showing a prominent alpha-
 5 band ERD across all conditions (right). B. Topographic maps of alpha-band ERD in three
 6 reward conditions during slow ER trials. C. Topographic maps in each of three reward
 7 conditions in fast RT trials. D.
 8 E. Location of electrodes in two clusters manifesting statistically significant effect of reward.
 9 F. Bar charts showing mean alpha-band ERD each of three reward conditions in slow (grey
 10 rectangles) and fast (white rectangles) RT trials. Error bars represent standard error of the
 11 mean. G. Locations of electrodes displaying a statistically significant main effect of speed of
 12 motor response. I. A scatterplot and the linear regression line with 95% confidence lines
 13 illustrating the statistically significant correlation between alpha-band ERD differences
 14 (slow-fast RT trials) and RT differences in electrode 9.

15 **Fig 8.** Topographic maps and statistically significant effects in beta-band ERD. A. Grand
 16 average beta-band ERD across all trials and subjects (left panel) and locations of electrode
 17 clusters manifesting a statistically significant beta-band ERD (right panel). B. Topographic
 18 maps of beta-band ERD in three reward conditions (0p, 1p and 10p) in slow RT trials. C.
 19 Topographic maps of beta-band ERD in fast RT trials. D. Topographic maps of beta-band
 20 ERD in three reward conditions averaged across fast and slow trials. E. Location of the
 21 electrode cluster, labelled C1, showing a statistically significant effect of reward. F. Mean
 22 values of beta-band ERD in the cluster shown in (F) in three reward conditions in slow (grey
 23 rectangles) and fast (white rectangles). The error bars stand for standard errors of the mean.

1 (G.) The location of electrode cluster, labelled C2, showing a statistically significant effect of
2 speed of motor response. (H.) Mean values of beta-band ERD in three reward conditions in
3 slow (grey rectangles) and fast (white rectangles) RT trials.
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