Title: Stress-sensitive brain computations of task controllability

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Abstract: Estimating environmental controllability enables agents to better predict upcoming events and decide when to engage controlled action selection. How does the human brain estimate environmental controllability? Trial-by-trial analysis of choices, decision times and neural activity in an explore-and-predict task demonstrate that humans solve this problem by comparing the predictions of an "actor" model with those of a reduced "spectator" model of their environment. Neural BOLD responses within striatal and medial prefrontal areas tracked the instantaneous difference in the prediction errors generated by these two statistical learning models. BOLD activity in the posterior cingulate, parietal and prefrontal cortices covaried with changes in estimated controllability. Exposure to inescapable stressors biased controllability estimates downward and increased reliance on the spectator model in an anxiety-dependent fashion. Taken together, these findings provide a mechanistic account of controllability estimation and its distortion in stress-related disorders.

INTRODUCTION

Influential theories suggest that the human brain navigates its environment by building predictive models of the world, which in turn fuel cognitive processes such as directed exploration, goal-directed decisions and forward planning (Bastos et al., 2012; Gläscher et al., 2010; Rao and Ballard, 1999). While these internal models can take diverse mathematical forms, their efficiency always depends on the use of task-relevant and cost-efficient state spaces (Hamid et al., 2019; Kim et al., 2019; Niv, 2019). Most often, these state spaces are actually state-action spaces in which the actions of the agent actively contribute to the prediction of upcoming events. For example, a driver must take into account the movement of their hands in order to predict the future position of their car. By contrast, a passenger worried for their safety should ignore their own hands and instead focus on the hands of the driver in order to anticipate potential hazards.

Determining whether an environment is controllable or not is key to decide to which extent one's actions should influence the prediction process, since only controllable environments afford causal influence over state transitions. Controllable contexts thus prompt the use of "actor" models including one's own actions as predictors, whereas uncontrollable contexts prompt the use of simpler "spectator" models linking past and future states of the environment. By gating the causal influence of action selection, controllability likely plays a central role in the engagement of elaborate action selection mechanisms. Supporting this idea, it is well established that prior exposure to controllable contexts promotes proactive and goal-directed strategies in a variety of cognitive tasks (Maier and Seligman, 2016; Moscarello and Hartley, 2017). Conversely, the lack of perceived control over events, especially stressful ones, constitutes a well-established correlate and a potential predictor of prevalent psychiatric disorders involving an increased influence of reactive and habitual behaviours, such as depression, anxiety,

post-traumatic stress or obsessive-compulsive disorders (Cheng et al., 2013; Diener et al., 2009; Gillan et al., 2014; Hammack et al., 2012; Harrow et al., 2009).

Numerous studies have shown that exposure to uncontrollable stressors can induce a state of learned helplessness characterized by the generalization of passive reactions to subsequent challenges (Maier and Seligman, 2016; Moscarello and Hartley, 2017). Evidence indicates that this maladaptive state largely depends on functional changes within the medial prefrontal cortex (mPFC) and the serotonin system (Amat et al., 2005; Bland et al., 2003; Challis et al., 2013; Kerr et al., 2012; Wood et al., 2015). In humans, a handful of neuroimaging experiments have further suggested that the anterior insula and cingulate cortex contribute to the detrimental effects of uncontrollable stressors (*12*, *13*). Beyond stress induction studies, the sense of being in control of one's own actions and their outcomes is known to modulate hemodynamic responses parietal and prefrontal cortices (Haggard, 2017; Kühn et al., 2013; Spengler et al., 2009) and the right temporoparietal junction (TPJ) was found to track the divergence of action-outcome transitions, a feature of controllable environments (Liljeholm et al., 2013).

Yet, little is known about the algorithms by which the brain estimates dynamically to what degree a task is controllable. A general strategy is to estimate controllability by computing the causal effect the agent's own actions have over the environment. Formally, a task can thus be deemed controllable when the transfer entropy (TE) —a generalization of Granger causality to non-linear and discrete systems— linking state and action time-series is positive (Barnett et al., 2009; Vejmelka and Paluš, 2008). By comparing the entropy of observed states given previous states and actions [H(S'|S,A)] to the entropy of observed states given previous states only [H(S'|S)], this information-theoretic quantity isolates the effective causal influence of actions over state transitions (**Fig. 1A, Supplementary Note**). Here, we develop a computational model that tracks a dynamic approximation of TE and use it to shed light on the neural mechanisms supporting the ability to estimate task controllability and adapt behaviour accordingly.

Based on this information-theoretic formalism, we designed an explore-and-predict task that allowed us to manipulate task controllability and assess the resulting changes in terms of subjective controllability and prediction accuracy. This new task was first used in behavioural (n=50) and fMRI (n=32) experiments which aimed at: (a) demonstrating that humans are sensitive to controllability in the absence of reinforcers; (b) establishing the dissociation of spectator and actor models at the behavioural and neural levels; and (c) unraveling the neural substrates underlying the representation of controllability itself and its influences on behaviour. In a subsequent stress experiment (n=54), we exposed participants to either uncontrollable or controllable electric shocks before administering the explore-and-predict task in order to (d) provide causal evidence supporting a dissociation of the spectator and actor models and (e) test whether learned helplessness can be characterized by an increased reliance on the former relative to the latter.

RESULTS

Experimental paradigm and computational model

Healthy human participants were invited to explore an abstract environment composed of three states (square, circle, triangle) and three actions (yellow, blue, magenta). A hidden transition rule always determined upcoming states, either dependent on the action of the participants (controllable rules, C) or the previous state only (uncontrollable rules, U) (**Figure 1B**). The transition rules were probabilistic and reversed covertly, so participants needed to explore and accumulate evidence in order to tell which rule was operative. From time to time, the participant was asked to predict the most likely upcoming state given a state-action pair (e.g. “blue” action in “circle” state), and its counterfactual (e.g. “yellow” action in “circle” state). This procedure yielded a direct yet implicit assessment of their subjective sense of controllability, because counterfactual predictions should only differ in controllable contexts, where selected actions determine upcoming states (**Figure 1C**). A novel and distinguishing feature of our task is that controllability varied independently of uncertainty (**Figure 1D**), a methodological improvement over earlier paradigms where the two constructs covary systematically (Diener et al., 2009;

Dorfman and Gershman, 2019; Liljeholm et al., 2013). Another key difference from previous studies is that we did not include any reinforcers: participants were merely instructed to explore their environment with the goal of performing accurate predictions when asked to. Here, controllability estimation can interact with, but does not depend on reward and punishment processing (Huys and Dayan, 2009; Ly et al., 2019; Moscarello and Hartley, 2017), the only requirement being to maintain a minimal level of exploration, or noise in the action selection process (**Figure 1E**, **Supplementary Text**).

To untangle the mechanisms of controllability estimation in this task, we designed a computational architecture for dynamically tracking an approximation of TE (for a detailed description, see **Fig. S1A**, **Methods**). Paralleling the standard computation of TE, two sets of transition probabilities were monitored, one corresponding to an "actor" model (tracking state-action-state transition, SAS') and the other to a "spectator" model (tracking state-state transition, SS', **Figure 1F,i**). Following each transition, an approximation of TE (hereafter termed Ω) was updated in proportion to the difference between 'actor' and 'spectator' transition probabilities $p_{SAS'}$-$p_{SS'}$ (**Figure 1F,ii**). Intuitively, this difference term can be understood as an instantaneous causality signal, reflecting how likely the last state transition towards S' was due to the influence of action A rather than state S. By integrating $p_{SAS'}$-$p_{SS'}$ over time, Ω thus reflects the causal influence of actions on recent state transitions (**Figure S1B**).

This causality signal Ω is at the core of the proposed algorithm, which arbitrates between the actor and the spectator model when making predictions about upcoming states. Specifically, the relative weight of the actor versus spectator model is set by an arbitrator (hereafter termed ω) whose value can be interpreted as an estimate of controllability. Two parameters influence the mapping between Ω and ω: a threshold determining how much causal evidence is required to infer controllability and a slope determining how fast controllability estimates change around that threshold (**Figure 1F,iii**). This SAS'-SS'-Ω algorithm was contrasted with a conventional model-based reinforcement learning algorithm monitoring SAS' transitions, as implemented by the actor model alone (Gläscher et al., 2010; Lee et al., 2014). Importantly, this simpler algorithm could still learn

transition probabilities from both uncontrollable and controllable conditions in stable environments, but the lack of controllability-dependent arbitration makes it less efficient in volatile environments alternating rapidly between controllable and uncontrollable rules.

Flexible adjustment of behaviour to changes in controllability

Participants performed well on the task: in all experiments, the average prediction accuracy was substantially above chance [chance level: 1/3; behavioural: $t(49)=12.3$, $p<0.001$; fMRI: $t(31)=13.4$, $p<0.001$; stress: $t(53)=13.2$, $p<0.001$](**Figure 2A**). In the fMRI experiment, for which participants received more training, accuracy was also stable across conditions and time (**Table S1**). Prediction accuracy dropped and then rapidly recovered after covert reversals in transition rules: it already exceeded chance levels on the first prediction trial after reversal for all types of reversals (all $t(49)>5.38$ and all $p<0.001$](**Figure 2B**). Prediction accuracy also correlated positively with working memory capacity as indexed by d-primes in a standard 2-back task [U rules: $\rho=0.37$, $p=0.006$; C rules: $\rho=0.52$, $p<0.001$](**Figure 2C**), consistent with the engagement of a model-based learning process (Otto et al., 2013).

In line with our prediction that humans solve the task by estimating Ω, Bayesian model comparisons demonstrated that SAS'-SS'-Ω schemes outperformed the conventional model-based learning algorithm (SAS' alone) in all experiments (**Figure 3A**; **Figures S2A** and **3**), Simulation analyses confirmed that the model was identifiable and that its parameters could be recovered accurately (**Figures S2B-D**). As expected, the arbitrator ω captured quantitative changes in subjective controllability, indexed by the proneness of participants to predict that different actions would lead to different states in counterfactual prediction trials (**Figure 3B**). Critically, the SAS'-SS'-Ω scheme which included an arbitration mechanism accounted better for the dynamics of subjective controllability changes around reversals than did the SAS' model alone (**Figure 3C**, correct prediction of controllability: 72.7% versus 66.5%, $z(49)=4.69$, $p<0.001$). The benefits of monitoring controllability is further illustrated by the finding that the likelihood of using the SAS'-SS'-

Ω scheme over the SAS scheme increased with accuracy across subjects [behaviour: r=0.58, p<0.001; fMRI: r=0.32, p=0.07; stress: r=0.54, p<0.001] (**Figure S2E-G**).

Behavioural and neural dissociation of the actor and spectator models

Model comparison results are consistent with our proposal that subjects estimate the subjective controllability of an environment by separately tracking and comparing an actor and a spectator model. In order to further test the dissociation of the actor and spectator models, we used subject-level GLMs to assess trial-by-trial fluctuations of decision times. It is known that decision times slow down following state prediction errors (Shahar et al., 2019b, 2019a). The large amount of exploratory trials per participant thus allowed us to analyze decision times as a proxy of model updating and to evaluate to which extent controllability *per se* influences the speed of action selection [behaviour: 562+/-163 trials; fmri: 550+/-115; stress: 519+/-84]. We therefore extracted the prediction errors derived from both the actor and spectator models (hereafter termed $\delta_{SAS'}$ and $\delta_{SS'}$). We found that both type of prediction errors slowed responding [behavioural: betas $\delta_{SAS'}$: t(49)=3.53, p<0.001; betas $\delta_{SS'}$: t(49)=7.93, p<0.001; fMRI: betas $\delta_{SAS'}$: t(31)=3.50, p=0.001; betas $\delta_{SS'}$: t(31)=2.46, p=0.020] (**Figure 3E**) and independently explained variance in decision times (**Figure S4**). We also observed that in periods of higher estimated environmental controllability (i.e. higher ω), decision times were slower [behavioural: t(49)=2.20, p=0.032; fMRI: t(31)=3.78, p<0.001]. This effect suggests that controllable contexts promote a more controlled action selection process even when no reinforcement is at stake.

Separable neural correlates should therefore exist for the prediction errors generated by the actor and spectator probability tracking processes, $\delta_{SAS'}$ and $\delta_{SS'}$. A conjunction analysis first revealed that both types of prediction errors activated the typical set of bilateral brain areas commonly associated with state prediction errors (Gläscher et al., 2010; Lee et al., 2014), such as the frontoparietal network and the pre-supplementary motor area (**Figure 4A**, **Table S2**). When contrasting events where only $\delta_{SS'}$ or only $\delta_{SAS'}$ were above their median value (a contrast circumventing collinearity issues), the mPFC

significantly dissociated the two prediction error terms (**Figure 4B**, **Table S3**, see also **Figures S5A-B** for robustness checks). Mixed-effects ROI analyses indicated that the mPFC encoded $\delta_{SS'}$ more negatively than $\delta_{SAS'}$.

Testing directly the effect of $\delta_{SS'}$-$\delta_{SAS'}$ (mathematically equivalent to $p_{SAS'}$-$p_{SS'}$) using a conventional parametric analysis at the whole brain level showed that the mPFC also negatively encoded this signal required for the update of controllability. Like the mPFC, the nucleus accumbens encoded $\delta_{SS'}$-$\delta_{SAS'}$ negatively, but ROI analyses indicated that this effect stemmed from a positive response to $\delta_{SAS'}$ and an absence of relationship with $\delta_{SS'}$ (**Figure 4C**, **Table S3**). Interestingly, a similar pattern was observed in the dopaminergic nuclei of the brainstem at a more lenient threshold (**Figure S5C**).

Neural correlates of dynamic controllability

Having established the dissociation of $\delta_{SAS'}$ and $\delta_{SS'}$ at the behavioural and neural levels, we next probed the correlates of the prediction error δ_{Ω} governing changes in estimated controllability ($\delta_{\Omega}=\delta_{SS'}-\delta_{SAS'}-\Omega_{t-1}$). This second order learning mechanism is key to accumulate, over time, evidence in favor or against the controllability of the ongoing rule. Whole-brain analyses revealed a significant negative relationship between δ_{Ω} and neurovascular responses in the posterior cingulate (PCC, BA 29/30) and dorsal posterior cingulate cortex (dPCC, BA 23/24), the right dorsal anterior insula (dAI) and the right temporo-parietal junction (TPJ, **Figure 4D**, **Table S4**). Mixed-effects ROI analyses including decision times and Ω confirmed that these effects reflected a genuine response to controllability prediction error, peaking 4-8 seconds after trial onset. Interestingly, we observed a controllability-dependent coupling between the PCC and the mPFC cluster found to encode the difference term $\delta_{SS'}$-$\delta_{SAS'}$ (**Figure S5D**). Moreover, interindividual variability in the proneness to rely on the actor model and to perceive the environment as controllable was partly explained by the strength of δ_{Ω} encoding in this structure [r=-0.47, p=0.007](**Figure 4E, Figure S5E-F**).

In order to unravel the neural correlates of controllability with maximal sensitivity, we performed a multivoxel pattern analysis (MVPA). A support vector machine classifier was trained at predicting whether streaks of consecutive exploratory trials were governed by controllable or uncontrollable rules. Whole-brain maps of classification accuracy were obtained using the searchlight method (leave-one-run-out cross-validation). Objective rule controllability could be decoded above chance from most regions of the frontoparietal control network. Local patterns of activity in the precuneus, the right TPJ, the dlPFC (bilaterally) and the dorsomedial prefrontal cortex (dmPFC) were all sensitive to controllability (**Figure 4F, Table S5**). Interestingly, the sensitivity of the dmPFC to controllability predicted to which extent controllable contexts lengthened decision times from one participant to another [r=0.53, p=0.002](**Figure 4G**).

Uncontrollable stressors promote reliance on the spectator model

We applied this new paradigm to better understand the computational mechanisms underlying learned helplessness. More precisely, we hypothesized that exposure to uncontrollable stressors might bias controllability estimation mechanisms to promote reliance on the spectator model relative to the actor model. We invited participants to perform an active avoidance task exposing them to mild electric shocks prior to completing the explore-and-predict task (**Figure 5A**). Participants in the controllable group learned to avoid the shock following one of the three possible cues by pressing the correct response button (out of six alternatives). Shocks received by participants in the uncontrollable group were yoked to the former, so that their decisions had no influence on shock probability. As expected, this procedure induced a dissociation between actual shock frequency, matched across groups by design, and reported shock expectancy (**Figure 5B**), so that shock expectancy remained high until the end of the induction phase in the uncontrollable group.

Despite the absence of aversive reinforcers in the explore-and-predict task, we observed clear carry-over effects from the shock experiment when analyzing the model parameters governing controllability estimation (**Figure 5C**, **Table S6**). In particular, the threshold

parameter increased significantly in the uncontrollable group compared with the controllable group [t(52)=2.82, p=0.007]. This parameter determines how much causal evidence is required before controllability is inferred. Therefore, when making predictions, participants exposed to uncontrollable stressors relied more on the spectator model, demonstrated by the reduced average value of the arbitrator ω [z=-2.44, p=0.015] as well as the direct analysis of subjective controllability estimates, revealing that counterfactual predictions were more often identical in the uncontrollable group (z=1.69, p=0.045, one-tailed). Importantly, counterfactual predictions did not differ during the training phase, which occurred before stress induction [z=-0.58, p=0.56].

Exposure to uncontrollable stressors thus elicits an imbalance between actor and spectator mechanisms for transition probability learning consistent with a sustained shift in controllability expectations. This finding provides a parsimonious account of the cross-contextual generalization of passive strategies, a core feature of helpless states (Maier and Seligman, 2016; Moscarello and Hartley, 2017). Interestingly, state anxiety, as assessed before the experiment, moderated the induction of controllability estimation biases. It predicted the average value of the arbitrator only in participants exposed to uncontrollable stressors [U: r=-0.47, p=0.014; C: r=0.24, p=0.21, U versus C: z=-2.59, p=0.01](**Figure 5D**).

Since uncontrollable stressors promoted increased reliance on the spectator model and decreased reliance on the actor model, we expected PE-dependent slowing effects to follow a similar pattern. Confirming this prediction, the type of stress induction profoundly altered the slowing of decision times by actor and spectator prediction errors [interaction group by PE type: F(1,52)=9.34]. In the uncontrollable group, $\delta_{SAS'}$ no longer modulated decision times whereas the impact of $\delta_{SS'}$ was increased compared with the controllable group [$\delta_{SS'}$: t(52)=2.08, p=0.042; $\delta_{SAS'}$: t(52)=-3.37,p=0.001]. Similarly, Ω no longer predicted decision times [t(26)=1.04, p=0.15], contrary to what was observed in the controllable group [t(26)=1.98,p=0.029](**Figure 5E**) and in the other two experiments.

DISCUSSION

Taken together, these findings shed light on one of the most fundamental aspects of human experience: the ability to estimate to which extent our actions affect our environment and to adjust our decisions accordingly. Our results demonstrate that this ability involves the comparison of actor and spectator models of the ongoing task, which are dissociable computationally, behaviourally and neurally. In turn, controllability estimates can be used to arbitrate between these models when making predictions about future events. The mPFC and the striatum encode the difference between the prediction errors generated by each model, while signals related to the update of controllability estimates are found in a more posterior brain network encompassing the TPJ and the PCC. Furthermore, exposure to uncontrollable stressors biases this process assessed by the explore-and-predict task, hence establishing its relevance for the study of neuropsychiatric disorders involving altered perceptions of controllability (Cheng et al., 2013; Diener et al., 2009; Gillan et al., 2014; Voss et al., 2017).

Historically, the concept of task controllability has been heavily influenced by learned helplessness studies in which animals granted the ability to actively terminate stressors are compared to yoked animals exposed to the exact sequence of stressors, but whose actions are made independent from stressor termination (Amat et al., 2005; Bland et al., 2003; Maier and Seligman, 2016). In this line of research, focused on the long-lasting consequences of stress exposure, more controllable contexts were defined as those in which the mutual information linking the timings of actions and stressor offsets is higher (Maier and Seligman, 1976). However, a positive mutual information linking an organism's actions and upcoming states of the environment is a necessary but not a sufficient condition to declare a task controllable. For example, the highly positive mutual information linking the statements of a weather forecaster with the occurrence of rain should obviously not be interpreted as a sign that the forecaster controls the weather, because the statements of the forecaster and the occurrence of rain are both conditioned by past meteorological states. Moreover, following this incomplete definition, variations of task controllability were often obtained by manipulating uncertainty about future states

(Bräscher et al., 2016; Dorfman and Gershman, 2019; Kerr et al., 2012), hence leading to ambiguous conclusions regarding the mechanisms underlying the estimation of controllability *per se* and its downstream influence on behaviour.

Formalizing controllability using transfer entropy (TE) rather than mutual information allowed us to design a task in which controllability varied independently from uncertainty. In addition, this approach provided an algorithm for detecting genuine changes in task controllability. Model comparisons showed that, across the three experiments, algorithms monitoring controllability using an approximation of TE (i.e SAS'-SS'-Ω schemes) accounted better for participants' choices than a standard model-based learning algorithm. The analysis of reaction times confirmed that participants were sensitive to the prediction errors generated by the spectator and actor models. These two first-order models, whose comparison governed the update of controllability estimates, can be viewed as two state spaces competing to structure the learning of statistical contingencies. When controllability estimates are low, the spectator model representing only the successive states of the environment dominates. In contrast, when controllability estimates are high, the actor model representing both states and actions takes over.

By defining the most appropriate state space dynamically, controllability estimation improves predictions about the future states of one's environment and can therefore contribute to maximize utility when reward or punishment rates depend on such predictions. By promoting reliance on a simpler spectator model when the environment is deemed uncontrollable, it can also minimize the metabolic cost and subjective effort associated with controlled action selection (Hahn et al., 2020; Westbrook et al., 2020). These hypotheses could be tested directly by introducing reinforcers in the explore-and-predict task, but it is already worth to note that the controllability-dependent arbitration logics can readily explain why Pavlovian (equivalent to SS') and instrumental (equivalent to SAS') learning mechanisms are respectively promoted uncontrollable and controllable contexts (Dorfman and Gershman, 2019). Restricted to the striatum and the mPFC, the limited spatial dissociation of the actor and spectator models reported here is consistent with a recent MEG study showing that the human brain relies on shared "neural codes"

to infer hidden states in controllable and uncontrollable contexts (Weiss et al., 2019). Yet, signatures of the actor and spectator models may ultimately be found within local neural circuits, which are beyond the reach of standard fMRI and MEG techniques. Moreover, the preferential encoding of actor prediction errors by the striatum and dopaminergic midbrain is consistent with earlier findings showing that the mesolimbic pathway preferentially encodes reward prediction errors in instrumental learning tasks (Garrison et al., 2013; Grogan et al., 2020; Hamid et al., 2019; O'Doherty, 2004). Conversely, the preferential encoding of spectator prediction errors by the mPFC is consistent with its more general role in statistical learning (Gilboa and Marlatte, 2017; Klein-Flügge et al., 2019). It may explain why dysfunctions of this structure impair observational learning more profoundly than instrumental learning (Jurado-Parras et al., 2012; Kumaran et al., 2015) and why mPFC lesions can alter the perception of controllability without altering performance of simple instrumental learning tasks (O'Callaghan et al., 2019).

By comparing the predictions emanating from the actor and spectator models, one can derive an instantaneous causality signal (i.e how likely did the last action cause the last state transition). Encoded negatively by mPFC and striatal BOLD responses, this instantaneous signal can then be integrated over time, hence reflecting the causal influence of actions over recent transitions. A signature of the second-order prediction errors supporting this integration was found in the right TPJ, right insula, PCC and dPCC. The right TPJ was the only region sensitive to both these second-order prediction errors as well as to objective controllability as assessed by the decoding analysis. It is thus a strong candidate for the implementation of controllability monitoring in our task. Supporting this view, the right —but not left— TPJ has previously been found to encode the divergence in action-outcome distributions (Liljeholm et al., 2013) and the discrepancy between expected and actual outcome timings in a simple sensorimotor task alternating controllable and uncontrollable trials (Spengler et al., 2009). Other brain areas including the dlPFC and the dmPFC were sensitive to objective controllability, likely reflecting downstream adaptations of brain networks to task controllability (Wanke and Schwabe, 2019). Strikingly, a higher sensitivity of the dmPFC to controllability was associated with a stronger influence of controllability on decision times. This finding suggests that

controllability detection fosters more elaborate action selection processes by potentiating a form of proactive response inhibition previously linked to dmPFC activity (Albares et al., 2014). It might be noted that the dmPFC region discussed here is more dorsal than the dACC region previously implicated in the valuation of control (Shenhav et al., 2016).

Interestingly, the PCC exhibited a controllability-dependent coupling with the mPFC and participants with a more (negative) encoding of controllability prediction errors in the PCC had a higher propensity to rely on the actor model when making predictions. Based on this finding, we may speculate that deactivations of the PCC facilitate the switch towards the actor model whenever the environment is deemed controllable. Supporting this view, electrical stimulation of the human PCC can elicit behavioural idleness and loss of control feelings (Vesuna et al., 2020), a phenomenon possibly due to the sudden blunting of action monitoring mechanisms(Li et al., 2019). Future studies may test whether the heightened metabolic activity of the pCC (Leech and Sharp, 2014) and its unstable connectivity with the mPFC during major depression (Wise et al., 2017) contributes to the lower sense of control observed in this condition (Cheng et al., 2013).

Having described the computational principles and outlined neural correlates of controllability estimation, we sought to test whether an experimental manipulation could alter this process and simultaneously contribute to a better understanding of the learned helplessness phenomenon. Indeed, exposure to uncontrollable stressors is known to induce passive responses to subsequent controllable stressors, but the origins of this maladaptive strategy remain poorly understood. In particular, it is unclear whether prior exposure to uncontrollable stressors induces an increased sensitivity to future aversive events, reduces expectation of control with respect to future stressors or reduces expectations of control in general (Ly et al., 2019; Maier and Seligman, 2016). Our results support the latter hypothesis by showing sustained alterations of controllability estimation in human participants previously exposed to uncontrollable versus controllable stressors. More precisely, the specific increase observed for the threshold parameter implies that the former group needed to integrate more causal evidence before considering a given rule as controllable in the explore-and-predict task. The dorsal anterior insula (dAI) is

involved in the modulation of pain perception by controllability (Bräscher et al., 2016) and it was found to encode controllability prediction errors in our fMRI experiment. Therefore, it is possible that prior exposure to uncontrollable stressors altered dAI excitability to distort subsequent controllability estimation mechanisms. Supporting this idea, a study showed that a lower perception of control mediates the exacerbation of dAI responses to physical threats in more anxious individuals, who also displayed lower controllability estimates following uncontrollable stressors in our data (Alvarez et al., 2015). Yet, this increased reliance on the spectator relative to the actor model following uncontrollable stressors likely involves several other brain areas, including the mPFC and the dorsal raphe nucleus, both highly sensitive to stressor controllability (Amat et al., 2005; Bland et al., 2003; Challis et al., 2013).

In sum, the explore-and-predict task allowed us to isolate the core computations underlying controllability estimation by excluding reinforcers and matching uncertainty across contexts. By showing that the human brain can compute an approximation of transfer entropy, our study may help bridging the gap between neuroscience and artificial intelligence research, where transfer entropy plays an important role in solving unsupervised learning problems (Leibfried et al., 2020; Mohamed and Jimenez Rezende, 2015). More invasive techniques will be required to understand how these computations are implemented within local neural circuits and how neuromodulators such as dopamine or serotonin mediate their broad impact on stress responses and mental health (Amat et al., 2005; Bland et al., 2003; Dickerson and Kemeny, 2004; Moscarello and Hartley, 2017).

METHODS

Participants

For the behavioural experiment, fifty young adult participants (mean age: 24.7, range: 18—43, 27 women) were recruited via the Sona system (human subject pool management system) of the Radboud University (The Netherlands). All participants were included in the data analysis. For the fMRI experiment, thirty-two young adult participants (mean age: 25.1, range: 20—43, 18 women) were recruited through the same system. For the stress experiment, a total of 62 participants (mean age = 21.8; range: 18-27, 52 women) were recruited via the Sona system of Leiden University. One additional participant was excluded a posteriori from the fMRI experiment and four participants were excluded from the stress experiments, together with their yoked counterparts (see Supplementary Methods for details on exclusion and inclusion criteria). The behavioural and fMRI experiments were approved by the local ethics committee (CMO region Arnhem/Nijmegen, The Netherlands, CMO2001/095). The stress experiment was approved by the Psychology Research Ethics Committee (CEP17-0905/282) at Leiden University. All participants provided written informed consent, in line with the declaration of Helsinki.

Explore-and-predict task

In the 3 experiments, the overall structure of the task was identical. Participants performed 6 (fMRI and stress experiment) or 7 (behavioural experiment) exploratory trials before a pair of predictions was required. Pairs of predictions always probed the two actions available for a given state (e.g blue followed by yellow in the circle state), in order to derive subjective control lability from counterfactual responses. Participants received feedback about their predictions in 50 percent (fMRI and stress) or 100 percent (behavioural experiment) of the trails. In the fMRI and stress tasks, feedback was delivered only after one of the two counterfactual predictions in order to prevent participants from inferring whether the rule was controllable or not based on feedback.

On each exploratory trial, two identical geometrical shapes were displayed side by side. The color of each shape determined the action corresponding to left and right button presses (side randomly assigned in each trial). An urgency signal was displayed after 1.5s. Transitions to the next state were always governed by one of the four rules, as displayed in Fig. 1c. In order to maximize the variation of prediction errors, the transitions were stochastic (noise: 0.05 to 0.2).

The first prediction trial of each pair was simply displayed at the end of the ITI of the previous exploratory trial. An urgency signal was displayed after 4s. The hypothetical state action pair was displayed at the center of the screen, just below a question mark, and the 3 possible next states were displayed as white geometrical shapes at the top of the screen. The selected state was then highlighted and the feedback was displayed when applicable.

The ongoing rule was never changed before 4 pairs of predictions were completed. In the behavioural experiment, the rule changed from then as soon as 5 correct responses were provided in the last 6 predictions or if the last 4 predictions were accurate. In the fMRI experiment, the rule was changed as soon as the p-value of a binomial test indicated that accuracy was significantly below chance ($p<0.05$, one-tailed, chance level: 1/3), hence making the accuracy threshold more lenient as the number of predictions made for a given rule increased. In all experiments, the rule changed after 10 pairs of predictions, even if performance did not meet the learning criterion. Prediction trials were pseudo-randomly ordered with the constraint that each state would be tested a similar number of times. An exhaustive description of instructions, counterbalancing, reversal schedules, transition noises and timings is available in Supplementary methods.

Stress induction task

To test the impact of prior controllability over stress on subsequent controllability estimations, participants underwent a stressor controllability manipulation prior to the

explore-and prediction task in a between-subjects design. Critically, we employed a between-subjects yoked control procedure in order to match the amount and order of aversive outcome stimuli between the controllable and uncontrollable conditions. We randomized participants in blocks of four where the controllable condition of a yoked pair was always administered first in order to create the schedule for the yoked counterpart in the uncontrollable condition.

Electric stimuli served as stressors in the manipulation task and were delivered by a Digitimer DS7 stimulator. First, individual levels of intensity of the electric stimulus for the manipulation task were determined using a stepwise procedure in which the intensity of the stimulus was gradually increased until participants reported a 'just bearable, but not yet painful' experience of shock. A yoked control-design with preprogrammed pseudorandomized schedule enabled us to match the amount and order of electric stimuli between the conditions.

In the controllable condition, a total of four cues (different in shape and color) were presented for at least six repetitions each following a preprogrammed pseudorandomized schedule. Participants could learn by trial-and-error the correct response corresponding to the cue (a key between 1 and 6) to avoid the electric stimulus. Critical trials on which participants would be able to prevent the electric stimulus for the first time according to the schedule were repeated until the participants arrived at a correct response. As such, all participants underwent the whole schedule with a minimum of 24 trials, and were able to acquire the correct response for each cue.

The uncontrollable condition was yoked to the controllable condition, such that participants experienced a comparable pattern of events across conditions. However, in the uncontrollable condition, participants were not able to acquire these action-outcome contingencies to prevent the shocks, whose sequences were merely replayed from the yoked participants performing the controllable condition. An exhaustive description of counterbalancing, instructions and procedures is available in Supplementary methods.

Computational modeling

The main purpose of all SAS'-SS'-Ω algorithms is to provide a way to dynamically estimate the causal influence of actions over state transitions by updating a variable termed Ω. In all models, S represents the previous state of the environment, A represents the previous action and S' represents the current state of the environment. The local causality estimate Ω can only be used as a proxy for controllability, which is not a property of actions but of the environment. It is this "inferred controllability" variable, termed ω, which can then be used to decide (arbitrate) whether one should make predictions using learned S-S' transitions or learned SA-S' transitions. Ω is homologous to transfer entropy (TE, which is itself a generalization of Granger causality to discrete and non-linear domains). See Supplementary Methods for a detailed explanation of the differences between TE and Ω.

In order to demonstrate that participants used a dynamic estimate of transfer entropy to solve the task, we systematically compared variants of the SAS'-SS'-Ω algorithm to a standard model based architecture tracking SAS' transitions (Gläscher et al., 2010). This latter algorithm corresponds to the actor model alone. Its asymptotic performance in stable environments is identical to that of SAS'-SS'-Ω algorithms.

The actor model tracks transitions linking state-action pairs to newly encountered states (i.e. SAS'). It updates transition probabilities in the following fashion.
Realized transitions:

$$P(s'|s,a) \leftarrow P(s'|s,a) + \alpha(1 - P(s'|s,a))$$

Unrealized transitions:

$$P(s'|s,a) \leftarrow P(s'|s,a)(1 - \alpha)$$

Where $\alpha \in [0,1]$ controls to which extent learned transition probabilities are determined by the most recent transitions. The prediction error $1-P(s'|\, s,a)$ is noted $\delta_{SAS'}$ in the main text.

The spectator model tracks transitions linking states to newly encountered states (i.e. SS'). Therefore, it updates transition probabilities exactly like the actor model, except that only states are represented: P(s'| s,a) is simply replaced by P(s'| s) in the two equations above, and the prediction error 1−P(s'| s) is noted $\delta_{SS'}$ in the main text.

The variable Ω supports the controllability estimation process by tracking the expected differ ence P(s'| s,a) − P(s'| s) dynamically (or, equivalently, $\delta_{SS'} - \delta_{SAS'}$). The logic of this process is that, in a controllable environment, actions contribute to predicting the upcoming states and therefore P(s'| s,a) > P(s'| s). Higher values of Ω therefore imply higher evidence that the environment is controllable. The update of Ω is governed by the following equation:

$$\Omega \leftarrow \Omega + \alpha_{\Omega}(P(s'|s,a) - P(s'|s) - \Omega)$$

Where $\alpha\Omega \in [0,1]$ is the learning rate controlling to which extent Ω is determined by the most recent observations.

Since Ω reflects the causal influence of one's action over state transition, it can be used as a proxy to infer whether the environment is likely controllable or uncontrollable. In order to form the arbitration term reflecting this inference and accommodate inter individual differences at this step, Ω is thus transformed using a parametrized sigmoïd function:

$$\omega = \frac{1}{1 + \exp(-\beta_{\Omega}(\Omega - thres_{\Omega})}$$

Where $thres_{\Omega} \in [-1,1]$ corresponds to the threshold above which Ω is interpreted as evi dence that the environment is controllable and where $\beta_{\Omega} \in [0,Inf\ ]$ determines to which extent evidence that the environment is controllable (i.e. Ω − thresΩ > 0) favors reliance on learned SAS' transitions when making predictions (and vice-versa for SS' transitions when $\Omega - thres_{\Omega} < 0$). Thus, the variable ω implements the arbitration between the "actor" and the "spectator" model.

When only SAS' learning is considered, the probability that a given state S'=i will be observed given S and A is directly given by:

$$p(S' = i) = p(S' = i|S, A)$$

When the SS'-SAS'-Ω architecture is used, the probability that a given state S'=i will be observed given S, A and ω is directly given by:

$$p(S' = i) = \omega \max_{j=1:3} p(S' = i|S_j, A) + (1 - \omega)p(S' = i|S)$$

The max operation reflects the fact that participants are explicitly instructed that, in this version of the explore-and-predict task, their actions have the same consequences independently of the state in which they are. Thus, it is reasonable to expect that, under the hypothesis that the environment is controllable, participants will select the most likely transition independently of the state in which they are. Obviously, this step cannot be implemented if only SAS' learning is used, as the model would then lose the ability to discriminate amongst different states.

The probability that the participant predicts the next state would be i (e.g. a square) when confronted to the hypothetical state-action pair S,A (e.g. circle state, blue action) is given by:

$$p(prediction = i) = \frac{\exp(\beta_{choice} p(S' = i)}{\sum_{j=1}^{j=3} \exp\left(\beta_{choice} p(S' = i)\right)}$$

Where $\beta_{choice} \in [-\text{Inf}, \text{Inf}]$ determines to which extent the participants will systematically select the most likely transition (i.e. the highest p(S'=i), according to what has been learned) to make their predictions. A very positive β_{choice} implies that the participant systematically selects this most likely transition. A β_{choice} around 0 implies that the participant mostly makes random guesses. And a β_{choice} very negative would imply that the participant mostly goes against what he/she has learned.

The full model space was composed of SAS' alone, SAS'-SS'-Ω balanced and symmetric, SAS'-SS'-Ω unbalanced and symmetric, SAS'-SS'-Ω balanced and asymmetric. SAS'-SS'-Ω unbalanced and asymmetric. Unbalanced algorithms refer to variants allowing different learning rates for the actor and spectator models. Asymmetric algorithms refer to variants allowing different learning rates for upward and downward updates of Ω. The last 3 algorithms were used to test for imbalances or asymmetries which could contribute to biased perceptions of controllability (e.g. illusion of control), independent from Ω. A full

description of these models and of a second model space using a different learning logic is available in Supplementary Methods.

Model fitting procedures

Model fitting was performed using a Variational Bayesian (VB) estimation procedure using the well-validated VBA toolbox(Daunizeau et al., 2014). The fitting procedure only attempted to explain decisions made in prediction trials. In other words, the decisions made in exploratory trials only indirectly constrained the fit by determining the information gleaned between pairs of prediction trials. For the behavioural experiments, the prior distributions of the various learning rates and of the threshold parameter were innately defined as Gaussian distributions of mean 0 and variance 3, which approximates the uniform distribution over the interval of interest after sigmoid transformations. The prior distributions of βchoice and βω parameters were defined as Gaussian distribution of mean 0 and variance 10. For the fMRI and the stress experiments, the prior distributions of every parameter was defined using the posterior mean and variance obtained from the 50 participants who passed the behavioural experiment. Hidden states (i.e values) corresponding to transition probabilities were systematically initialized at 1/3 (equiprobability prior), while Ω was initialized at 0. Detailed information about parameter transformation, model fitting, model comparison and simulation procedures is available in Supplementary Methods.

fMRI: acquisition

All images were collected using a 3T Siemens Magnetom Prismafit MRI scanner (Erlangen, Germany) with a 32-channel head coil. A T2*-weighted multiband echo planar imaging sequence with acceleration factor 8 (MB8) was used to acquire BOLD-fMRI whole-brain covered images (TR = 700 ms, TE = 39 ms, flip angle = 52, voxel size = 2.4 × 2.4 × 2.4 mm3 , slice gap = 0 mm, and FOV = 210 mm). This state-of-the-art sequencing protocol was optimized from the recommended imaging guidelines of the Human Connectome Project, with the fast acquisition speed facilitating the detection and removal

of non-neuronal contributions to BOLD changes (http://protocols.humanconnectome.org/HCP/3T/imaging-protocols.html).

The experiment was divided in 4 blocks lasting on average 7.7+/-2.1 minutes (662+/-179 volumes). We recorded participants' heartbeats using the scanner's built-in photoplethysmograph, placed on the right index finger. Respiration was measured with a pneumatic belt positioned at the level of the abdomen. Anatomical images were acquired using a T1-weighted MPRAGE sequence, using a GRAPPA acceleration factor of 2 (TR = 2300ms, TE = 3.03 ms, voxel size = 1x1x1mm, 192 transversal slices, 8° flip angle). Field magnitude and phase maps were also acquired.

fMRI: preprocessing

fMRI data processing and statistical analyses were performed using statistical parametric mapping (SPM12; Wellcome Trust Centre for Neuroimaging, London, UK). For each session, the first 4 volumes were automatically discarded by the scanner. Functional images were slice-time corrected, unwarped using the field maps and realigned to the mean functional image using a rigid-body registration. Functional images were then coregistered to the anatomical T1. Next, the anatomical images were segmented based on tissue prior probability maps for spatial normalisation using the DARTEL algorithm and the resulting normalization matrix was applied to all functional images. Finally, all images were spatially smoothed with a 6mm Gaussian kernel, except in the decoding analysis for which unsmoothed images were used.

fMRI analyses

Statistical analyses of fMRI signals were performed using a conventional two-levels random effects approach in SPM12. All general linear models (GLM) described below included the 6 unconvolved motion parameters from the realignment step. We also included the eigenvariate of signals from cerebrospinal fluid (CSF) in our GLM (fourth and lateral ventricular). Moreover, we used a retrospective image correction (RETROICOR)

method to regress out physiological noise, using 10 cardiac phase regressors and 10 respiratory phase regressors obtained by expanding cosines and sines of each signal phase to the 5th order. We also included time shifted cardiac rates (lag: +6, +10 and +12s) and respiratory volume (-1 and +5s) as nuisance regressors. All regressors of interest were convolved with the canonical hemodynamic response function (HRF). All GLM models included a high-pass filter to remove low-frequency artifacts from the data (cut-off = 96s) as well as a run-specific intercept. Temporal autocorrelation was modeled using an AR(1) process. All motor responses recorded were modeled using a zero-duration Dirac function. We used standard voxel-wise threshold to generate SPM maps ($p<0.001$ uncorrected), unless notified otherwise. All statistical inferences based on whole-brain analyses satisfied the standard multiple comparison threshold ($p(FWE)<0.05$) at the cluster level unless notified otherwise. Prediction error and (log-transformed) decision time regressors were systematically z-scored to exclude scaling effects.

All GLM models included separate onset regressors for motor responses, for prediction trials and for the first trial of each exploratory sequence (where no prediction error was elicited). All models also included parametric regressors for reaction time and ω (reflecting controllability estimates) on prediction trials. A detailed description of the GLMs used to analyze neuroimaging data is available in Supplementary methods. These GLMs only differ in the way exploratory trials were treated.

In order to verify the robustness of our whole-brain results and inspect the time course of our parametric effects of interest, we performed mixed-effects analyses on BOLD signal filtered and adjusted for nuisance regressors. This adjusted signal was extracted from the functional clusters uncovered by whole-brain analyses and segmented into trial epochs from -3 to +16 seconds around the onset of each exploration trial (excluding the first of each streak). We then estimated the effect of each regressor of interest, at each time point, for all subjects simultaneously. Subject identity was included as a random effect and a subject-specific intercept was included. Parametric regressors were z-scored in the same way as in the mass univariate anal yses. Importantly, this approach was not used

for statistical inference — since doing so would constitute double-dipping — but merely for visualization purposes.

Decoding analyses were performed using the TDT toolbox (Hebart et al., 2015). Each mini-block of 6 exploratory trials was arbitrarily coded as +1 (controllable) or -1 (uncontrollable) based on the rule governing transitions. We used a leave-one-run out cross-validation scheme with 100 permutations per subject, so that classes remained balanced for training. Training was performed on the beta values associated with each miniblock (see previous section) using a Support Vector Machine (SVM) classifier (L2-loss function, cost parameter set to 1, Liblinear, version 1.94), without feature selection or feature transformation. Since we did not constrain the testing sets to have balanced classes, balanced accuracies were used when reporting the results of the searchlight analysis (12mm sphere) at the whole-brain level.

Statistical procedures

Model selections relied on Bayesian model comparisons and exceedance probabilities, as implemented by the VBA toolbox (Daunizeau et al., 2014). The analysis of predictive accuracies relied on a 2-way repeated measure ANOVAs or one-sample t-tests, assuming normal distribution of the data following *arcsin* transformation. The analysis of decision times was performed in two steps: first, a logistic regression was performed on binarized decision times (median-split) ; second, group-level significance was assessed by means of one-sample t-tests. For the analysis of decision times, we excluded trials in which decision times were 3 standard deviations above the mean. Comparison between conditions relied on paired t-tested and comparison between groups (stress experiments) relied on two-sample t-tests, unless normality assumptions were violated, in which case non-parametric equivalents were used (Wilcoxon signed rank and rank sum tests, respectively). All t-tests were two-sided unless notified otherwise. Correlations were based on Pearson coefficients unless normality assumptions were violated, in which case Spearman rank coefficients were used. Statistical procedures related to the fMRI data are described in the fMRI analysis section above.

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AUTHOR CONTRIBUTIONS

Conceptualization: RL, RC, VL. Methodology: RL, VL. Software & formal analysis: RL. Investigation: RL, VL. Resources: RC, ZM. Data Curation: RL, VL. Writing - Original Draft: RL. Writing - Review & Editing: RL, ZM, VL, RC. Visualization: RL. Funding acquisition: RL, ZM, VL, RC.

DECLARTION OF INTERESTS

The authors declare no competing interests.

RESOURCE AVAILABILITY

The behavioural and fMRI data used to generate the figures will be made available upon publication at the following address: https://github.com/romainligneul/controllability. Second-level SPM images will be made available upon publication at the following address: https://identifiers.org/neurovault.collection:8810. Raw behavioral and fMRI data will be made available upon request to the corresponding authors.

The scripts used to collect and analyze data will be made available upon publication at the following address https://github.com/romainligneul/controllability.

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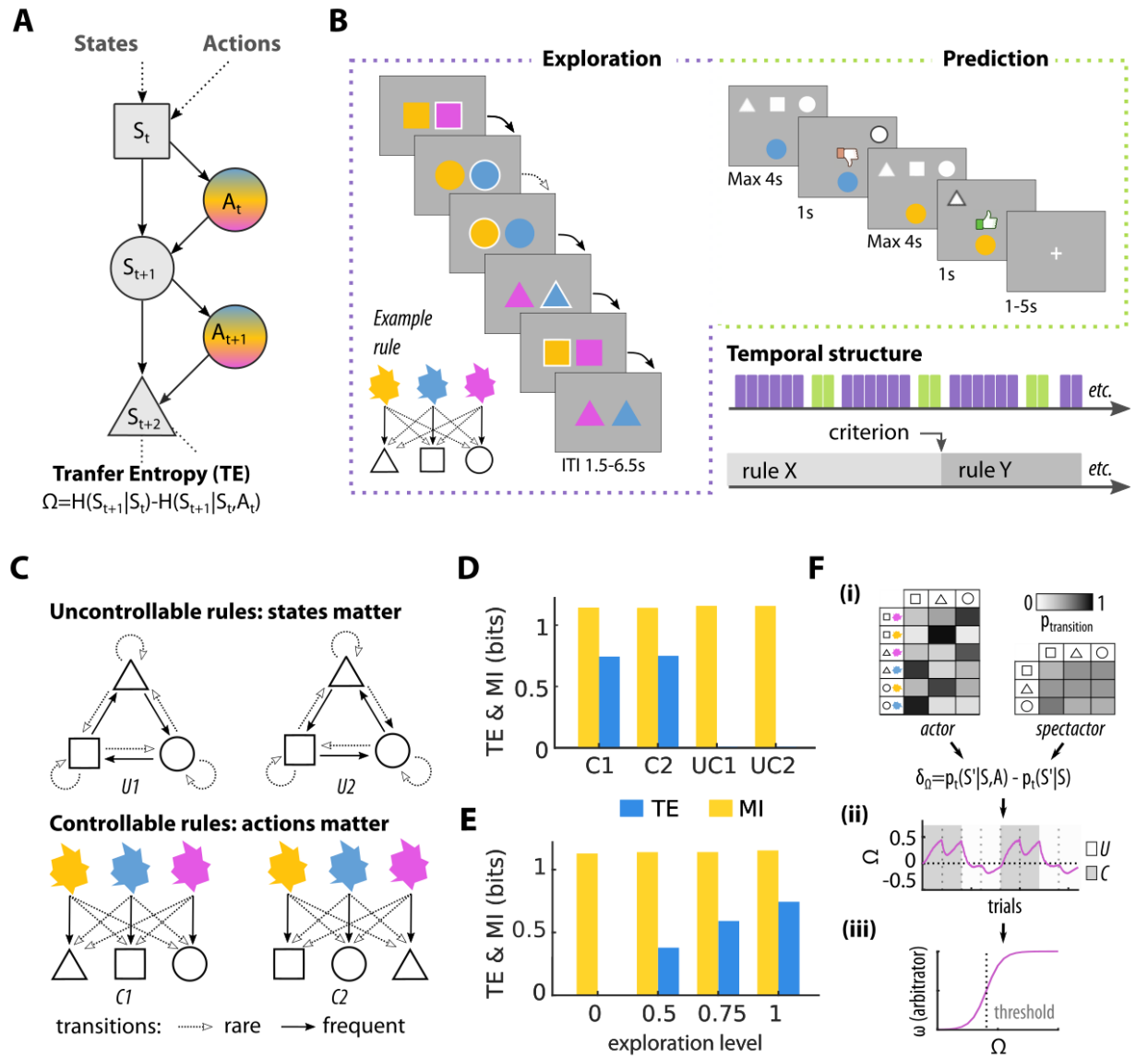

Figure 1. Theoretical framework and experimental protocol.

(A) Controllability can be inferred from transfer entropy, an information-theoretic measure quantifying to which extent a time series causally influences another one.

(B) Time course of a novel explore-and-predict task divided in short mini-blocks. Each miniblock consists of a series of exploratory trials (violet) followed by two counterfactual prediction trials (green) used to assess learning and subjective controllability.

(C) Representation of the 2 uncontrollable rules (U1, U2) and the 2 controllable (C1, C2) rules, which alternate covertly to govern the evolution of the environment.

(D) Simulations showing the dissociation of controllability, as indexed by TE, and predictability, as indexed by the mutual information (MI) shared between successive state-action pairs (random exploration policy).

(E) Simulations under a controllable rule showing that TE requires exploration to be used as a proxy for controllability. Indeed, in the absence of exploration, the conditional

entropies H(S'|S) and H(S'|S,A) are identical (see also Supplementary Text and Supplementary Fig. 1C).

(F) Synthetic overview of the algorithm able to derive an online approximation of TE (termed Ω) by comparing on each trial the transition probabilities of an actor (SAS') and a spectator (SS') model of the world. By thresholding Ω, the algorithm could in turn arbitrate between spectator and actor models when making predictions depending on current controllability estimates (ω).

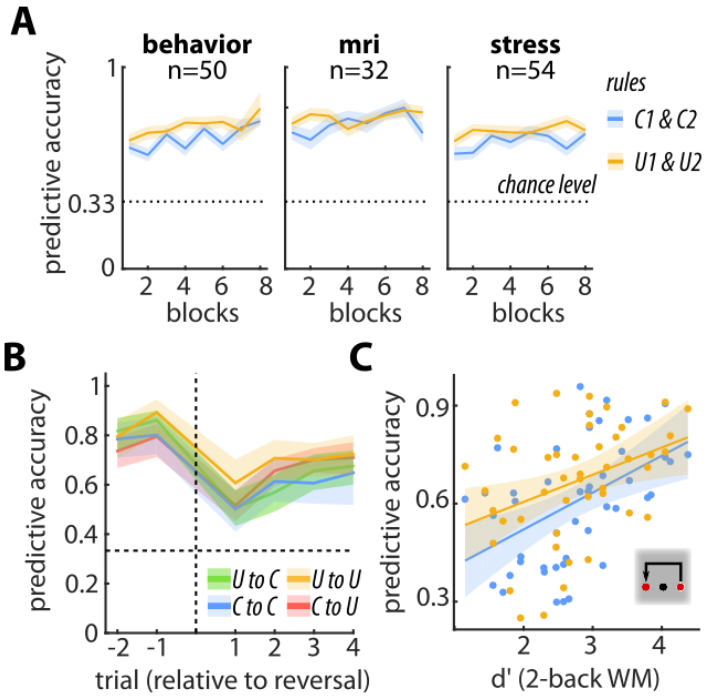

Figure 2. Behavioural performance.

(A) Accuracy in the prediction trials for each of the 3 experiments, split by condition (see also Supplementary Table 1).

(B) Fast recovery of predictive accuracy around reversals.

(C) Positive correlation between working memory capacity indexed by a 2-back task (see Supplementary Methods) and accuracy in the explore-and-predict task for controllable (blue) and uncontrollable (orange) contexts.

Shaded areas represent standard errors of the mean (SEM).

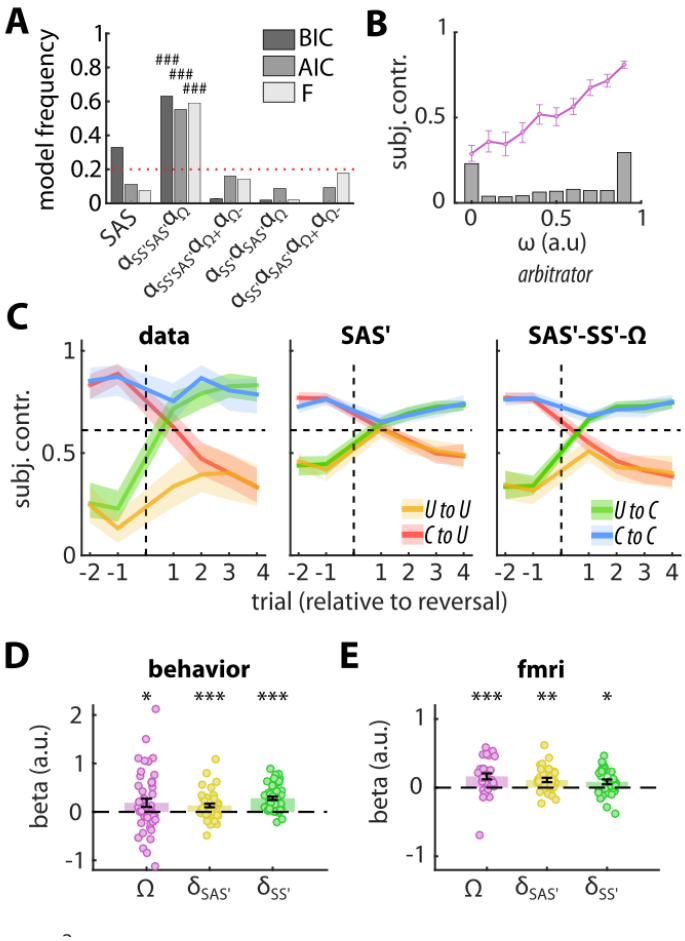

Figure 3. Computational modeling.

(A) Bayesian group model comparison pooled over three experiments showed the advantage of the simplest controllability scheme (SS'-SAS'-Ω) over the actor model (SAS') alone (see Methods and Supplementary Fig. 2a and 3).

(B) Normalized distribution of the arbitrator variable ω (grey bar) and its linear relationship with subjective controllability (pink line). Pairs of prediction trials were labelled as "subjectively controllable" when counterfactual predictions differed (e.g. different responses for blue and yellow actions in the circle state).

(C) The SS'-SAS'-Ω scheme better captured the dynamics of subjective controllability around reversals.

(D-E) Coefficients of the logistic regression predicting binarized reaction times in the behavioural and fMRI experiment using actor and spectator prediction errors (δSAS' and δSS') and Ω.

Error bars and shaded areas represent SEM. *p<0.05,***p<0.005, ***p<0.001. ###$p_{exceedance}$ > 0.999. BIC: Bayesian Information Criterion. AIC: Akaike Information Criterion. F: Free Energy.

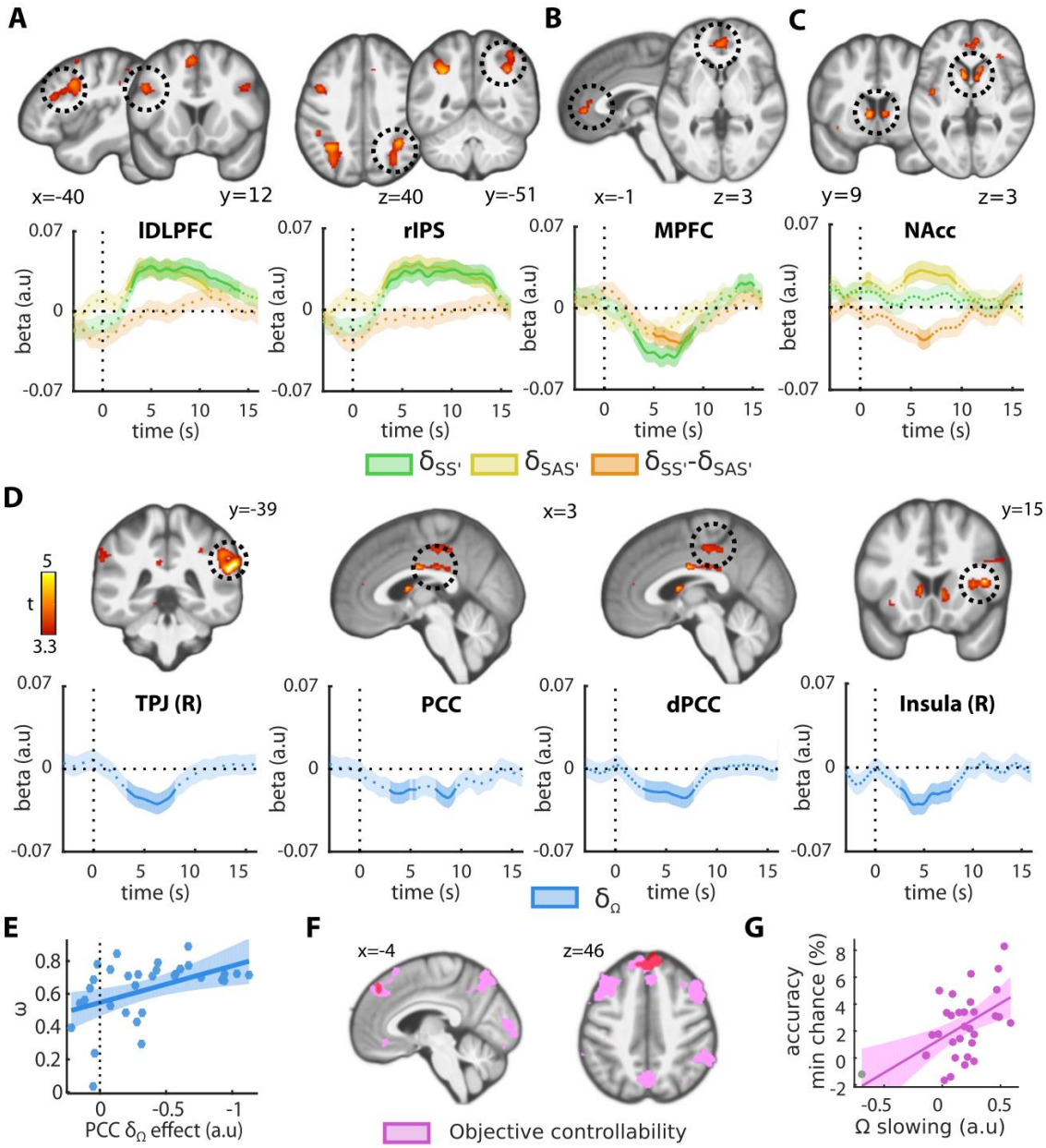

Figure 4. Neural dissociation of the actor and spectator models during exploration. (A) Brain regions whose activity was higher when the prediction error terms ($\delta_{SS'}$ and $\delta_{SAS'}$) were both above their median value, as compared to when they were both below. (B) Paired t-test showing the brain areas whose activity dissociated in response to trials where only $\delta_{SAS'}$ was above median, compared with those where only $\delta_{SS'}$ was above median. This analysis revealed that the mPFC encoded specifically $\delta_{SS'}$ but not $\delta_{SAS'}$. (C) Parametric analysis of BOLD responses showed that the mPFC and the nucleus accumbens encoded negatively the difference term $\delta_{SS'}$ - $\delta_{SAS'}$ used to update controllability. Contrasting with the mPFC pattern, $\delta_{SAS'}$ was encoded positively In the nucleus accumbens whereas $\delta_{SS'}$ was not.

(D) Brain regions encoding signed the second-order prediction errors δ_Ω. All areas surviving correction for multiple comparison showed a negative effect, implying greater activity when an action was less causal than expected.
(E) The degree to which PCC encoded δ_Ω predicted the propensity to rely on the actor model across participants.
(F) Decoding of controllability (rule type) from brain data. A searchlight analysis revealed that the dmPFC, the dlPFC, the right TPJ and the precuneus were sensitive to environmental controllability.
(G) The sensitivity of the dmPFC to objective controllability predicted to which extent periods of higher controllability led to slower decision times.
The time courses shown below (A-D) were only used for robustness checks and visualization. Statistical inferences were based on whole-brain effects at standard thresholds (voxel-wise: $p<0.001$, uncorrected; cluster-wise: $p<0.05^{FWE}$). Shaded areas represent SEM.

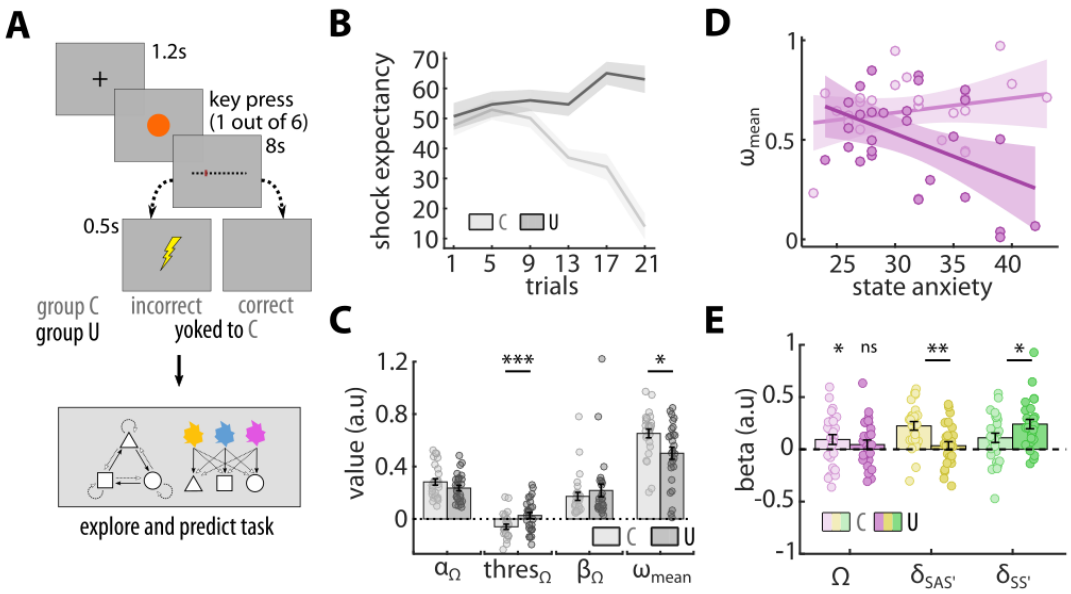

Figure 5. Stress experiment.

(A) Induction of controllable and yoked uncontrollable stress followed by the explore-and-predict task.

(B) Temporal evolution shock expectancy during the induction phase, split by condition.

(C) Impact of induction type on best-fitting parameters related to controllability monitoring as well as on the mean value taken by the arbitrator ω in the explore-and-predict task. The threshold parameter $thres_{\Omega}$ which determined above which value Ω was treated as evidence for a controllable environment increased significantly following uncontrollable stressors and the average value of the arbitrator was reduced, hence leading to increased reliance on the spectator model when making predictions (β_{Ω} and α_{Ω} were unaffected, β_{Ω} was divided by 100 for display purposes).

(D) State anxiety moderated the effect of induction type on the arbitrator variable (ω) reflecting controllability estimation. Higher state anxiety was associated with greater reliance on the spectator model after exposure to uncontrollable stressors.

(E) The impact of induction type on the slowing of decision times induced by $\delta_{SS'}$, $\delta_{SAS'}$ and Ω was consistent with increased reliance on the spectator model. Indeed, the effect of Ω and $\delta_{SAS'}$ vanished whereas the effect of $\delta_{SS'}$ increased in the uncontrollable conditions.

All error bars and shaded areas represent SEM. *p<0.05,**p<0.01.