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► **To cite this version:**

Nils Kolling, Jacqueline Scholl. On the role of behavioural modes during temporally extended decision-making and their neural substrates. *Current Opinion in Behavioral Sciences*, 2024, 58, pp.101404. 10.1016/j.cobeha.2024.101404 . hal-04803676

**HAL Id: hal-04803676**

**<https://hal.science/hal-04803676v1>**

Submitted on 25 Nov 2024

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## Review

# On the role of behavioural modes during temporally extended decision-making and their neural substrates

Nils Kolling<sup>1,3</sup> and Jacqueline Scholl<sup>2,3</sup>

Everyday decision-making is broader than the types commonly studied in the laboratory. For example, food preference or gambling tasks lack many essential elements of decisions frequently faced by animals and humans alike. Those often require self-organization and temporally extended behaviours, resulting in sequential dependencies, a need to adjust for changing environments and an ability to balance behavioural flexibility with consistent decision-making strategies. Here, we highlight how behavioural modes help achieve adaptive decision-making and distinguish between different sequential behaviours, reasons for changing mode and mechanisms for mode shifts and maintenance. We highlight the potential role of emotions as a mechanism for mode changes and an ability to prioritize different behavioural strategies. We suggest changes in experimental design and analyses that could help understand brain and behaviour in more self-organized contexts, which will be crucial for a better understanding of real-world decision-making and prefrontal cortex function.

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**Current Opinion in Behavioral Sciences** 2024, **58**:101404

This review comes from a themed issue on **Cognitive Flexibility**

Edited by **Roshan Cools** and **Lucina Uddin**

For complete overview of the section, please refer to the article collection, "[Cognitive Flexibility \(2024\)](#)"

Available online 31 May 2024

Received: 17 January 2024; Revised: 30 April 2024;  
Accepted: 1 May 2024

<https://doi.org/10.1016/j.cobeha.2024.101404>

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## Introduction

In the real world, much decision-making plays out over extended timescales and requires the agent to self-organize their behaviours. For example, when you leave the house, you need to decide where to go, how long to stay

there and what to do next. However, one key challenge emerging during this kind of decision-making is how to integrate all types of potentially decision-relevant information into coherent decision-making. Here, we propose that a useful way to understand self-organized flexible decision-making is through the idea of internal states that fundamentally shape how and with what systems decisions are being made, that is, an agent's decision strategy or 'behavioural mode'. Thus, behavioural modes go beyond simply changing the subjective value of specific options. Instead, they capture ways to approach an environment, filter information and weigh different value dimensions. For example, shifting between explore and exploit modes has been suggested to come with many implications regarding what to pay attention to [1], how we learn [2] and consider the 'outside world' beyond simply undervaluing high-value targets. Equally, hunger can affect both the valuing of specific food items, for example, 'salt hunger', but if it changes completely how an agent engages with a world when hungry, it can certainly lead to substantial behavioural mode shifts, including not just changed decisions but also overall cognition potentially leading to obsessive thoughts [3]. The best-known example of such a selection is the 'fight or flight' response, where attention, physiology and decision-making are completely reshaped based on overall shift in strategy and goals. In short, behavioural modes ideally generalize across narrowly defined decision options or even task constraints and have larger impacts on how we approach the world, although different modes are likely distinct in how broad their impact is (e.g. fight or flight modes are likely very generalized while more strategic states might be more confined).

However, to be able to measure and understand these processes, we need new types of decision-making experiments that capture temporally extended, often sequentially dependent, decision problems [4,5]. We also need to better track the internal state of participants during those tasks, such as their emotions and physiology as well as their current 'behavioural mode'.

## Why do we need 'behavioural modes' at all?

One key problem for temporally extended decision-making is balancing stability and long-term goal pursuit with flexibility. To do this, one can simply periodically change how one makes decisions. In other words,

switching between different sets of decision weights based on shifting internal or external environments [6]. Examples of this could include shifts from evaluating to implementing goals during goal pursuit, switches to exploration of the environment or shifts between foraging and hunting states. This way, flexibility can be achieved without having to continuously finetune every factor weighing individually. In more realistic decision scenarios, changing one's complete 'behavioural mode' or decision strategies allows evaluation of a whole approach, rather than simply learning on specific outcomes or actions. Being able to organize behavioural modes also vastly simplifies more self-organized behaviours, as it allows the implementation of specific subgoals in a temporally coherent way and enables mode-specific credit assignment. Many advantages of behavioural modes become apparent when an agent needs to self-organize, that is, when an agent does not simply decide between preselected limited options but instead needs to also decide what to do, when, for how long and with how much motivation. Here, we propose that such shifts are not exclusive to extreme scenarios (such as fight or flight) but serve as a general mechanism for dynamically shifting between ways of interacting with the environment as well as a way to learn about new ways of interacting with one's environment. We also hypothesize that such shifts are particularly useful for temporally extended and self-organized behaviours, as it allows an agent to select between internally coherent strategies for larger time without the need for micro-managing.

### When environments shift modes

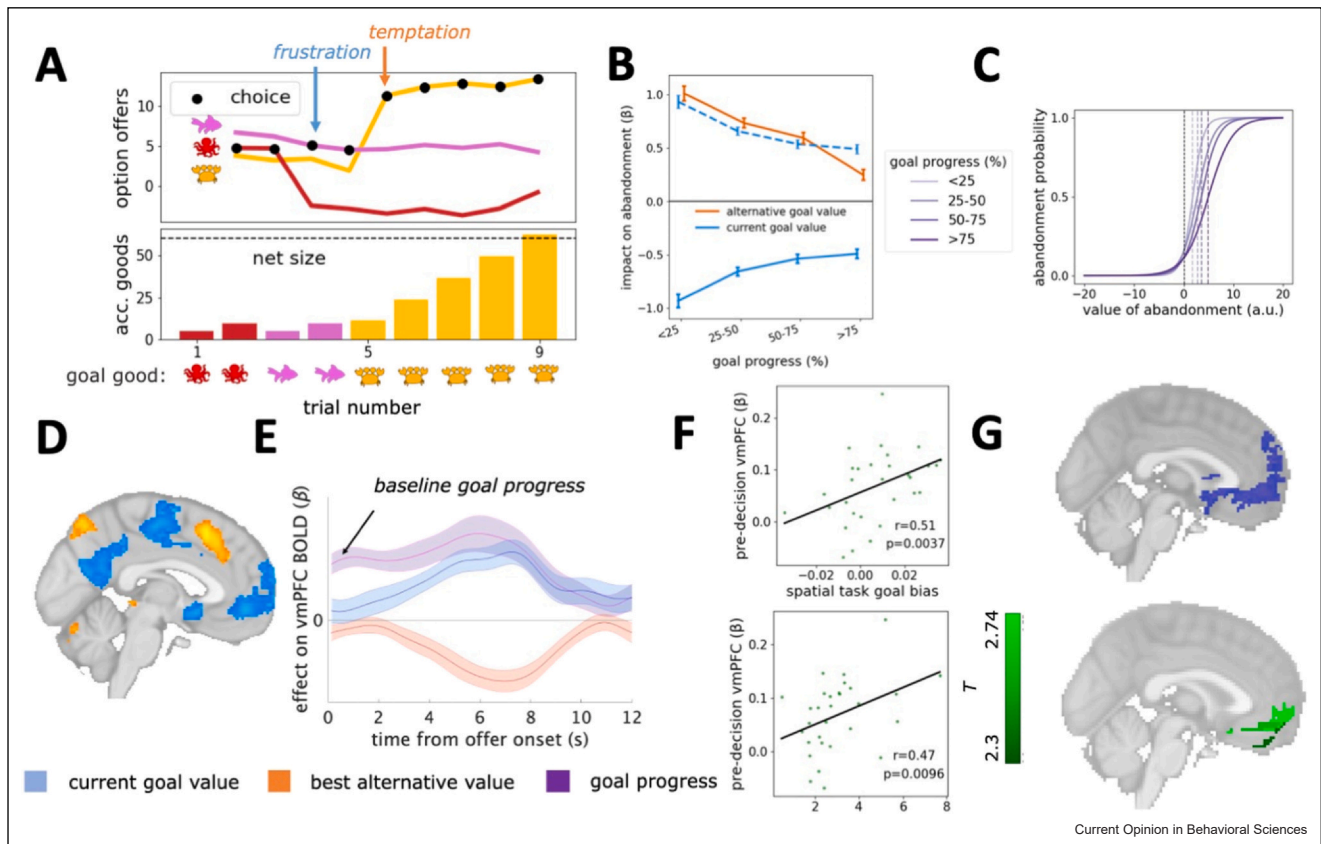
Maybe one of the most well-known behavioural shifts in the literature is the shift between explore and exploit. While many studies consider explore–exploit trade-offs to be singular decisions [7], others have considered them as longer lasting strategies that change how we value information [2], with information being perceived as more valuable when the horizon of usefulness is longer, that is, there is more time to take advantage of information gathered [8,9]. A recent study in mice used cell type–specific optogenetics in the medial raphe nucleus to change the animals' behavioural mode related to explorations. Specifically, they were able to drive distinct modes of exploratory behaviour, choice perseverance or overall task disengagement by suppressing GABAergic, glutamatergic and serotonergic cells, respectively [10]. Explore–exploit can take more sophisticated forms than tuning the value of information, instead humans are capable of shifting into modes of hypothesis testing, making them specifically tuned to certain features of the environment or their actions instead of learning using all information equally [1]. Despite the relevance of other ecological modes, such as food seeking, vigilance or curiosity, other types of potential behavioural modes and mode–environment interactions have been explored a lot less.

### When choices drive mode shifts

Decision-relevant states are not just a passive reflection of the environment an agent is in. Importantly, an agent's goals and actions can drive state changes, which in turn impact the actions an agent takes, creating feedback loops. For example, when an agent pursues a goal, those goal commitment choices themselves can have an impact on the way subsequent decisions are made.

Specifically, in the case of sequential goal pursuit, distinct decision phases have been proposed for evaluation and implementation of goals [6,11]. The most well-known change in decision-making with goal pursuit in psychology and economics is the 'sunk cost fallacy' [12]. It describes an increasing commitment bias in favour of the currently invested goal based on already incurred, retrospective, costs or effort, instead of the rational, prospective future value of the goal. Using a novel sequential goal pursuit task, we were able to quantify such biases, measure their dynamic change throughout goal pursuit and link them to their neural substrates ([11], Figure 1a). Participants had to choose between pursuing one of three options of varying value and mutually exclusive currency, forcing them to repeatedly assess the value of continued goal pursuit (staying with the current option type) or abandonment (pick one of the other two currencies). Concretely, in our incremental goal pursuit task, we asked people to choose between three kinds of sea creatures (octopus, fish and crab) to fill a fishing net. The value of each type of food item changed over time, slowly drifting but sometimes jumping up or down, making a previously plentiful sea creature scarce. Crucially, participants could only fill their net with one type at the time, having to completely abandon their already accumulated gains if they switched, losing all of their goal process. Nonetheless, switching could be optimal if the alternative was sufficiently better so that it filled the net quicker overall. We found that people shifted between goal selection and increasingly biased goal pursuit states, being overly committed to their goal. The more progress, the less flexible, that is, more biased participants were against goal abandonment and the less they took alternatives into accounts. However, while both the value of the goal and alternative impacted decisions less with goal process (downwards trend of regression weights), the impact of the alternative decreased more rapidly, so that participants were more driven by frustration than temptation with high goal progress (Figure 1b, c). As we also measured participants' attentional focus on the goal and alternative items in a separate but interleaved task, we were able to show that goal pursuit also had an impact on attention, making participants less able to remember alternatives compared with the currently chosen goal. This suggests that attentional allocation could serve as a mechanism to change decision influence during goal pursuit but also highlights how mode shifts can have global impact on brain processes beyond changing decision-making

Figure 1



Decision driven behavioural mode shifts and their neural substrates. **(a)** In our incremental goal pursuit task, we asked people to choose between three kinds of sea creatures (octopus, fish and crab) to fill a fishing net. The value of each type of food item changed over time, slowly drifting but sometimes jumping up or down, making a previously plentiful sea creature scarce (see lines). Crucially, participants could only fill their net with one type at the time, having to completely abandon their already accumulated gains (progress) if they switched (see accumulated goods, 'acc. goods'). **(b)** While participants took the value of the chosen goal and alternatives both into account, the impact of the alternative value (orange) diminished quicker with goal progress than the goal (blue, continuous; for better comparison, the dotted blue line is the same sign-reversed). **(c)** Goal progress also made people more biased against abandonment (shift of softmax curve to the right). **(d)** Activity in well-known decision regions vmPFC and dACC reflected the relative value of abandonment (yellow) and goal pursuit (blue). **(e)** Analysis of BOLD timecourse in vmPFC reveals not just signals for current goal value (blue) and alternative value (red) but also a persistent goal progress signal (purple) even at baseline, that is, before the decision. This baseline signal further correlated with attentional capture of the goal and persistence bias **(f)**. **(g)** Furthermore, lesions of vmPFC (green) reduced goal biases at the same location where baseline activity was observed (blue). vmPFC, ventromedial prefrontal cortex.

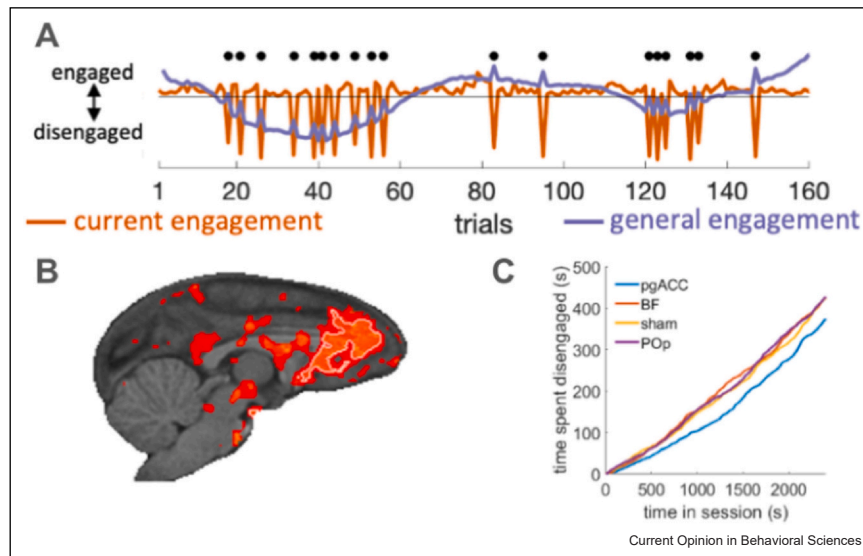
directly. Neurophysiologically, we identified ventromedial prefrontal cortex (vmPFC) as being particularly important for establishing and maintaining goal focus, while anterior cingulate cortex (ACC) continuously signalled the value of abandonment (Figure 1d, e) and lesions of vmPFC reduced goal biases (Figure 1f). Our work links to previous studies showing that changing attention can change decisions [13] and that value signals in vmPFC and striatum can also be impacted by attention [14], suggesting a close relationship between attention, value and vmPFC even in simple one-shot binary choice [15]. Overall, our results suggest a larger scale shift in behavioural mode from one that is more careful and deliberate (comparing options' values) to one that is more focused on the current goal (always choosing the option that is already being collected). Importantly, this

behavioural mode extended to an interleaved spatial working memory task, in which people showed worse memory for the alternative.

While this work shows that people shift between different ways of assessing their options with corresponding shifts in neural mechanisms, future work will need to establish how shifts between different types of decision strategies (e.g. changes from hunting to foraging) are implemented and driven by internal states.

There is, however, evidence that these kinds of approaches have potential for understanding individual differences. For example, we have recently been able to show in a novel sequential decision-making task that apathetic traits increase participants' decision inertia,

Figure 2



Intrinsic motivation as example of spontaneous mode shift. **(a)** Monkeys sometimes give up with the task (black dots), allowing us to build a model that estimates the trial-wise current engagement beyond the manipulated task parameters (orange line). Additionally, we can exploit autocorrelations in current engagement (i.e. the fact it is slowly drifting) to make even better predictions of general engagement levels (blue line) and look at trials with low or high engagement, controlling for current trial behaviours. Panel **(b)** shows the neural signal that is correlated with a highly engaged behavioural mode across events and tasks, with particular focus on pgACC. **(c)** Additionally, pgACC transcranial ultrasound stimulation (TUS) selectively increased engagement.

that is, create an inability to overcome biases to stick with an exploratory mode of behaviour, even when it is more beneficial to settle on an option [16]. Specifically, while most people show such inertia to a certain degree with increasing apathy, previous search decisions keep participants searching despite the diminishing returns, suggesting an inability to adapt and flexibly assess one's options more objectively. Instead, apathy increases reliance on the presumably less cognitively costly heuristic of simply repeating the previous search decision. Our hope is that future tasks that allow for even more behavioural mode flexibility will uncover significantly more individual differences in how people organize their own behaviours with meaningful links to other clinical and nonclinical traits.

### When modes shift spontaneously

Behavioural modes can also be shifted internally. This has been studied as 'motivational states', with a common conceptualization as a depleting resource that is replenished through rest [17,18].

In a macaque brain imaging study [19], we examined task general (i.e. across a diverse set of cognitive tasks), internal (i.e. not task evoked), motivational fluctuation. We specifically focused on motivation to disengage completely from the task. We investigated total task disengagement instead of more common measures, such as vigour (i.e. response speed) or the willingness to

invest effort, as a marker of complete shift in behavioural mode, namely, whether to pursue the task at all. This is in fact, unlikely in humans, a common behaviour in experimental animals, including macaques. Doing this, we could show that the internal motivational state fluctuated slowly and independently from the specific task requirements and trial-wise vigour (response speed while on task). Not only did activity in perigenual ACC (pgACC) correlate with this motivational state index, but stimulation of the region changed the overall duration of disengagement from the task at hand. Overall, this suggests that internally slowly fluctuating brain states can impact participants' willingness to do the task, that is, engage with the task-specified 'behavioural mode' Figure 2).

Another type of intrinsic fluctuation has been observed regarding changes in default preference [20]. Here, the default is defined behaviourally as the generally more preferred option, that is, the one that is more frequently chosen. Increased likelihood of choosing such defaults was linked to a neural substrate, that is, specifically to changes in baseline/predecision vmPFC activity. This again links vmPFC properties to changes in how a person makes decisions (e.g. here reverting to their default and choosing quickly or not) rather than simply what they choose. Both types of findings are consistent with suggestions that the overall Orbitofrontal cortex network (including vmPFC but also more central and

lateral Orbitofrontal cortex) is involved in navigating internal state space [21] but represent specific aspects in which the Orbitofrontal cortex determines internal affective and decision state.

### Emotions as intrinsic states

One implementation of behavioural modes could be through emotions. Emotions can be seen as global states that ready organisms for situation-appropriate behaviour through global changes to perception, cognition and priors on actions. Furthermore, they can be seen as large-scale brain states with their own dynamics, that is, momentum, sensitivity to changes in the environment and diverse impact on behaviour [22]. In fact, emotions provide a computational shortcut that reduces the required computations in any given situation by pruning behavioural options that are not emotion congruent. For example, when seeing a threatening bear, emotions of fear could arise that create a strong prior on perceptions and actions to do with escape, preventing wasting computational resources on assessing how tasty the berries you run by might be. This idea aligns with classic theories of emotions [23,24], mostly based on noncomputational work. In particular, the action-readiness theory [25] provides of emotions that fit well with the computational behavioural modes framework suggested here, highlighting the role of emotions to orchestrate changes across perception, action priors and physiology. In agreement with these theories, emotions have been found to be dispersed throughout the brain in decoding studies ([26], Figure 3a). Notably, these maps were overlapping with prefrontal areas commonly associated with decision-making.

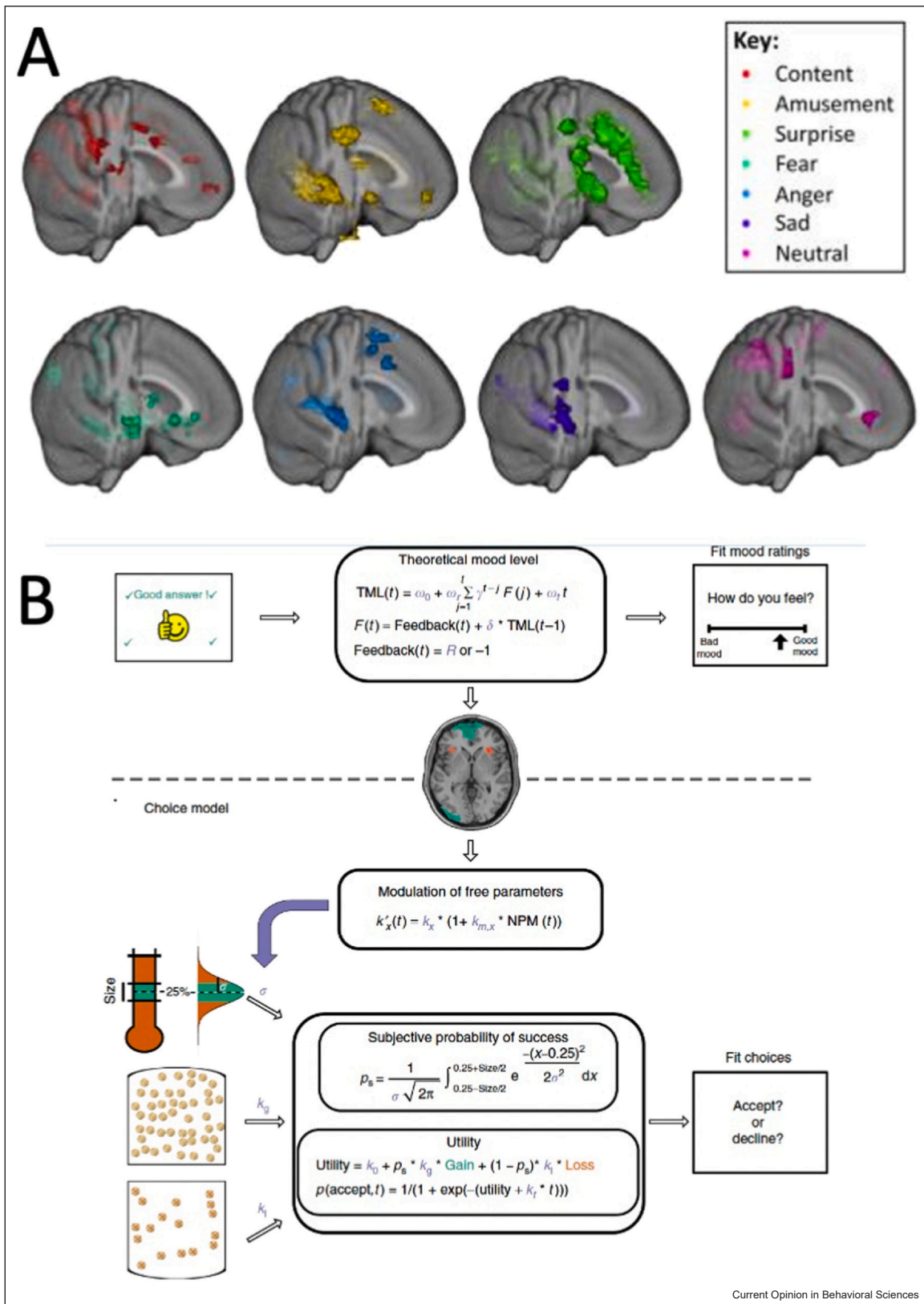
If emotions represent situation-relevant global states, they should track behaviour-relevant computational variables. Indeed, emotions have been found to track computational variables during reward learning, such as reward and punishment outcomes [22,27] and prediction errors making the integration of emotion into computational decision models very appealing. Specifically, Vinckier et al. [27] measured the impact of mood on decision-making (accepting or rejecting a risky effort task) by modulating mood through an incidental task (trivia quiz). They proposed a computational model in which an internal state of mood ('happiness', ranging from 'bad' to 'good') was updated based on feedback in the quiz task (Figure 3b). In turn, emotions then change how the environment is perceived. They influence, for example, how much decisions take into account reward and punishment dimensions or as how rewarding outcomes are perceived [22]. Neurally, Vinckier et al. found both insula and vmPFC to be related to mood, with carrying different information (i.e. explaining unique variance in mood and in the impact of mood on choices). This could mean that, even though mood was measured using a unidimensional scale (happiness), in fact, it is

multidimensional, as would be more aligned with models of distinct emotions.

The tasks considered so far, while computationally tractable, were however less naturalistic, and it was less clear whether states were global. Recently, emotions have also been examined in more naturalistic tasks, that is, with more freedom for participants to self-organize their behaviour over time (Trier et al. [29,30] and Leitao et al. [31]). Trier et al. used a foraging under threat task (Figure 4d), in which participants were asked to self-report their mood intermittently. Unlike other computational studies, mood here was measured using two separate dimensions of stress and excitement. This paper identified a homeostatic feedback loop (Figure 4e) between self-reported stress and behaviour: participants' stress increased as a function of the task (e.g. predator danger), which shifted participants' behavioural mode towards increased hiding from predators and foraging (and less checking). This shift in behaviour in turn decreased stress, revealing a homeostatic process of adapting behaviour in light of emotional response. These findings are in agreement with work in the natural environment using experience sampling, that is, participants completing smartphone prompts throughout the day [32]. Specifically, Taquet et al. found that participants organized their behaviour matching their moods. If they felt more positively, they engaged with behaviours prone to reduce their mood (e.g. cleaning) and vice versa for negative moods (e.g. leading to TV watching).

The most direct test of emotions as global states has been carried out in an functional Magnetic resonance imaging study by Leitao et al. [31]. Here, participants played a Pac-Man game, manipulating valence or 'goal conduciveness' (good, bad, neutral monsters) and control or 'coping potential' (a potion that increased earnings and reduced losses). They measured three distinct aspects of emotions through physiology (heart rate, skin conductance, breathing), facial muscle activity, and behaviour during the task. To assess whether synchronization of different aspects of physiology and behaviour is indeed an important aspect of emotions, they computed two separate synchronization indices, one based on behaviour and one based on brain activity. First, they mapped each of the three features they had measured to their respective neural network to then test which areas are more activated when the neural responses to those features are more synchronized, potentially driving this integration into emotional states. Second, they computed a measure of synchronization from the nonbrain data (i.e. directly from the three components) and mapped moments of high observed synchronization to the brain. Remarkably, both methods revealed a network of similar areas that was active, not specifically when one network or emotion feature was strong or not, but when there was high synchrony or agreement between the networks/features. Those regions included medial PFC, caudate and putamen and posterior

Figure 3



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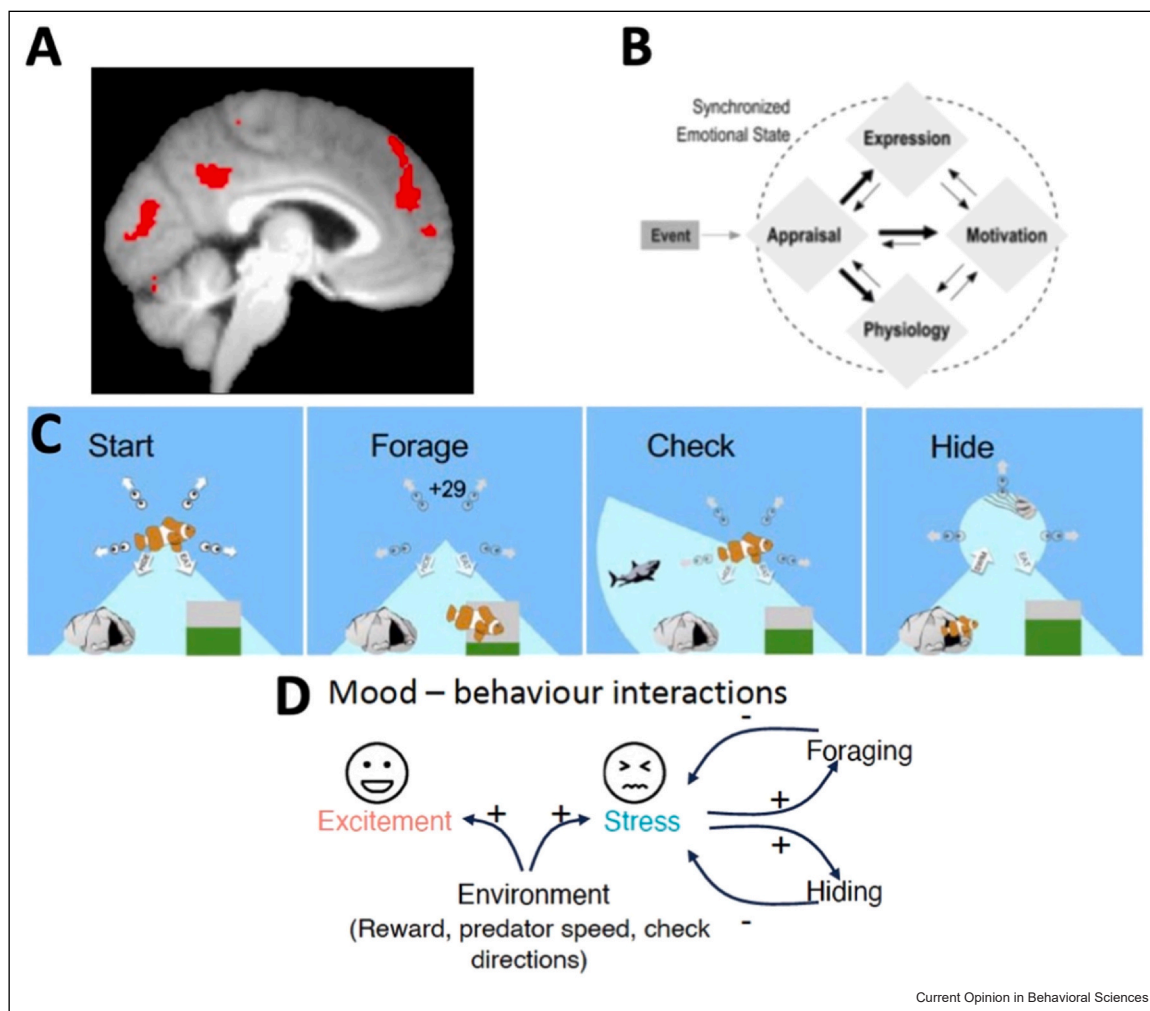
The neural networks of emotion and impact of moods on decision making. **(a)** Decoding shows widespread cortical and subcortical brain networks for emotions (videos and music), overlapping with networks involved in decision-making [26,28]. **(b)** Mood levels are impacted by positive or negative feedback (in an incidental task) [27]. Neural activity at baseline (before making choices, 'NPM', neural proxy of mood) in vmPFC and insula was modulated by mood. This baseline activity in turn modulated how much participants took rewards and losses into account (parameters  $k$ , i.e.  $k_g$  for gain and  $k_l$  for loss) when making effort and reward choices.

insula (see Figure 4a), suggesting these regions might be involved in actively synchronizing behaviour or coordinating the physiological emotional response. This is in agreement with the idea that emotions impact different systems (action, physiology, facial expressions) and when those systems are working together both emotional experiences and situation-appropriate behaviour can emerge.

### Hidden Markov models to extract behavioural modes

In addition to novel task design and concepts for understanding behavioural modes and corresponding brain states, we need corresponding new analysis approaches that can make sense of time series data on different timescales. A particularly promising approach builds on

Figure 4



Emotion driven behavioural mode shifts. **(a)** In an emotional video game (Pacman adaptation), different components of emotions (here behavioural impact, facial expression and physiological measures) were modulated and measured by Leitao et al. [31] during fMRI scanning. Using behavioural and neural markers of emotional synchronization, they were able to localize activity that correlated with synchronization. **(b)** Emotions can be conceived as the moments of such synchronization between the different components that are manifested by the cross regional neural networks shown in **(a)**. **(c)** In another video game 'foraging under threat task', we made participants play a fish collecting rewards (algae) while checking for and avoiding predators [29,30]. **(d)** Here, self-reported stress showed a homeostatic relationship with foraging behaviour, with stress increasing foraging, which, in turn, decreased stress, showing the dynamic nature and the interplay between emotion-behaviour interactions, rather than the integrated response within an emotion. fMRI, functional Magnetic resonance imaging.



Hidden Markov models (HMM) as they can bootstrap idiosyncratic changes in behavioural modes from existing data. In the HMM-GLM (generalized linear model) approaches, state is defined as the way the agent makes decisions, implemented as different sets of regression weights for each state. For example, in state A, reward could have a large and risk a small impact on choice, while in state B, neither could have a large impact on choice. Using this approach, Ashwood et al. [33] could show that rodents shift between being engaged and disengaged or biased decision-making in a simple perceptual decision task by fitting distinct state-specific behavioural GLMs. However, to get the most out of a HMM-GLM, we need a more complex task design that allows for the expression of distinct decisions.

Additionally, HMM analyses can also allow the extraction of specific states from the neural data directly. For example, it has been shown that even in simple working memory tasks, participants' brain states switch between low- and high-load states [34]. Impressively, in *Drosophila*, Calhoun et al. [35] used HMMs to identify distinct states defined by their different sensitivity to feedback and link to distinct song modes. Furthermore, using optogenetic stimulation, they could change the state likelihood, that is, feedback to song mode mapping instead of simply changing specific behaviours or songs directly.

### Developing a new neuroscience for self-organized behaviours and behavioural modes

To summarize, if we want to understand behavioural modes and decision brain states better, we need tasks that allow us to measure shifting behavioural modes behaviourally, analysis methods to extract intrinsic behavioural states and their shifts (such as HMM-GLMs) and record the right kind of neural and pharmacological signals that might shift on larger time scales (minutes rather than the second and milliseconds we look at in event-related analyses) as well as measure the impact of such states on event locked dynamics. To achieve this, we need to find inspiration from relevant behavioural challenges that require temporarily extended, multidimensional and self-organized behaviours, which might require a new 'gamified' approach to experimental design [36] to motivate participants to engage with such complex tasks meaningfully and consistently. While HMM-GLMs are a great start as an analysis approach, we need to find new ways of describing such findings (e.g. in terms of state durations, transition probabilities, etc.) and relating the results to neural activity. For example, state shifts could be implemented differently in the brain than primarily studied event evoked transient neural activity. In fact, given the variable timescales of behavioural modes, we might need to fundamentally rethink how we link behaviour to brain activity in computational models if we want to understand how brain-wide decision states enable behavioural mode shifts. Furthermore, we need to understand

behavioural modes as states with their own dynamics, such as stability and momentum, as well as how they relate to other large-scale states, such as emotional or motivational state. If we assume that behavioural modes are part of how an agent navigates complex and extended internal and external environments, progress in measure, analysis and design is essential. Here, we highlighted dynamic environments, own behaviour, motivation and emotions, as key drivers of behavioural mode shifts and emphasize recent empirical work, suggesting shifts in decision-making states. Future work will also need to address how states are maintained physiologically with neuromodulators being an intriguing candidate known to shift different cognitive trade-offs and can themselves have state-dependent effects [37,38].

### Declaration of Competing Interest

The authors declare no conflict of interest.

### Acknowledgements

Both JS and NK are employed and supported by L'Institut national de la santé et de la recherche médicale (Inserm). NK is funded by the European Research Council (<https://erc.europa.eu/>) grant FORAGINGCORTEX, project number 101076247 (NK). The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript. Views and opinions expressed are those of the author only and do not necessarily reflect those of the funders. Neither the European Union nor the granting authority can be held responsible for them.

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