University of Liège

Faculty of Medicine

Where was my mind?

Neurophysiological correlates of mind-blanking

BOULAKIS Paradeisios Alexandros

Supervisor: Dr. DEMERTZI Athena

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In 1915, the Russian avant-garde painter Kazimir Severinovich Malevich painted the “Black Square”, as seen on the title page of this thesis. This painting is Malevich’s attempt to move away from representational art. There is nothing represented on the canvas, but a black square. Various interpretations of this work have emphasized the painter’s intent: the absence of content. What do you get once you strip away the semantics? However, I find the historical evolution of the painting more interesting. Over time, the black square began to crack, and we can vaguely peer behind the painting to the white canvas. I wanted my work to leave the same impression: I wanted to cause some initial cracks in the blank box that is mind-blanking, so we may find what lies beneath it.

To those who have helped me close the gap

between the person I am and the person I want to be.

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When starting a PhD, one is poised to hear the phrase: "Treat your PhD as a marathon, not as a sprint". A PhD is a long and demanding journey, requiring steady progress and careful conservation of energy. Yet, like much folk wisdom, this saying holds a deeper truth. Even Eliud Kipchoge, in his historic sub-2-hour marathon, did not run alone — he had a team of pacemakers, coaches, and supporters who were with him every step of the way. In the same spirit, this dissertation is not the result of my efforts alone, but of the unwavering support, generosity, and guidance from the remarkable people who surrounded me from start to finish.

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Publications as first author:

1. **Boulakis, P. A.** & Demertzi, A. (2025). Relating mind-blanking to the content and dynamics of spontaneous thinking. *Current Opinion in Behavioral Sciences*, 61, 101481. http://doi.org/10.1016/j.cobeha.2024.101481

2. **Boulakis, P. A.**, Demertzi, A., Sitt, J. D., & Andrillon, T. (Forthcoming). Spontaneous thoughts and experiences across wakefulness and sleep. In U. Olcese & L. Melloni (Eds.), *The scientific study of consciousness: Experimental and theoretical approaches.* Springer.

3. **Boulakis, P. A.**, Simos, N. J., Zoi, S., Mortaheb, S., Schmidt, C., Raimondo, F., & Demertzi, A. (2025). Variations of autonomic arousal mediate the reportability of mind blanking occurrences. *Scientific Reports*, 15(1), 4956. https://doi.org/10.1038/s41598-024-81618-1

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Registered reports and preprints:

1. Fort, L. D., **Boulakis, P. A.**, Mortaheb, S., & Demertzi, A. (in principle). Embodied perceptual moderation: How interoceptive and proprioceptive engagement affect perceptual performance [Stage 1 registered report, accepted in principle]. *Scientific Reports.* https://doi.org/10.17605/OSF.IO/8UNZC

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3. Koroma, M., **Boulakis, P. A.**, Raimondo, F., Gialama, V., Blume, C., Strauss, M., & Demertzi, A. (2024). Cardiac responses to auditory irregularities reveal hierarchical information processing during sleep (p. 2024.09.24.614090). *BioRxiv.* https://doi.org/10.1101/2024.09.24.614090

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2. **Boulakis, P. A.**, Mortaheb, S., Calster, L. van, Majerus, S., & Demertzi, A. (2023). Whole-brain deactivations precede uninduced mind-blanking reports. (Version 1.0) [Computer software]. GitLab. http://gitlab.uliege.be/Paradeisios.Boulakis/mb_activation

Glossary

blood oxygen level dependent (BOLD) when neurons require energy and oxygen, local blood flow increases to meet the demand (neurovascular coupling). Not all oxygen is consumed, and the resulting changes in the oxygenated-to-deoxygenated haemoglobin ratio create the BOLD signal detected by fMRI. 31

clustering data analysis technique that groups a set of objects or data points based on their similarities. 32

drift-diffusion modelling (DDM) statistical technique that describes decision-making processes by modelling how evidence accumulates over time until a decision threshold is reached. 29

electrocardiography (ECG) measurement of the electrical activity of the heart. 60

electrodermal activity (EDA) physiological response that measures the electrical conductance of the skin. 60

electroencephalography (EEG) neuroimaging technique that measures scalp level electrical brain activity through a discrete number of electrodes. 31

embodiment philosophical position that posits that cognitive processes are deeply rooted in the body's interactions with the environment. 37

entropy measure of the unpredictability or complexity of a signal. 60

experience sampling a thought-sampling technique where people are asked to report what they are thinking immediately after a probe. 27

exteroceptive relating to stimuli that are external to an organism. 22

family-resemblance definition concept in which members of a category share overlapping features, without requiring that all members have a single defining characteristic. 120

fMRI anticorrelations negative relationship in the BOLD signal of different cortical areas. 32

fMRI global signal the average blood oxygen level-dependent (BOLD) signal across the entire brain. 33

functional connectivity (FC) the statistical relationship between spatially distinct brain regions, measured using correlations in BOLD signal fluctuations during fMRI. 22

functional magnetic resonance imaging (fMRI) neuroimaging technique that indirectly measures brain activity by detecting alterations in blood oxygenation levels. When a brain region becomes active (i.e. in response to cognitive demands), it consumes more oxygen, triggering an increase in blood flow to that area. This leads to a higher ratio of oxygenated to deoxygenated haemoglobin, which is measurable through fMRI. 31

general linear model extension of linear models to data with non-Gaussian distributions. 45

independent component analysis data analysis technique that decomposes a signal to additive and statistically independent components. 59

local sleep EEG pattern of brain activity that resembles slow waves during wakefulness. 33

mental content informational or representational aspect of mental states. 20

mental dynamics fluid and unconstrained cognitive processes that generate new mental states. 20

mental state discrete cognitive or emotional mental events that can be decomposed in terms of content and dynamics. 20

meta-awareness knowledge of one's cognitive processes, including the ability to monitor and control one's thinking. 121

microphenomenology qualitative research method that utilizes phenomenological interviews to uncover the latent structure of an experience while preventing the imposition of preconceptions about the experience. 122

mind-blanking (MB) a mental state where people have no content to report or fail to report any content. 24

mind-wandering (MW) an umbrella term denoting thoughts that are decoupled from the environment. 21

operational definition a specific explanation of how a concept or variable is measured or identified in a study. 120

phase-based coherence measure to quantify the constant phase difference between two signals with the same frequency. 89

pupillometry measurement of pupil size and reactivity. 38

Shapley Additive Explanations (SHAP) method used in machine learning to isolate the unique contribution of a feature in prediction, when accounting for all possible feature interactions. 69

slow-wave activity (SWA) EEG pattern of brain activity characterized by low-frequency, high-amplitude oscillations, typical in NREM sleep. 33

spontaneous thought a thought that arises due to the absence of constraints from previous thoughts or external demands. 20

Summary

Human experience is rich and contentful. At any moment, our thoughts encompass many perceptions, beliefs, emotions, and feelings. Yet, the notion of a contentful mind does not fully capture our experience. Recent paradigms of spontaneous thinking reveal that people sometimes fail to report content or have nothing to report. This experience, termed mind-blanking (MB), contrasts with the assumption that the mind is always filled with content and raises the question: Why does introspection sometimes yield nothing? Neuroscientific research suggests that MB occurs during reduced cortical arousal. Aligning with this view, the present thesis seeks to deepen our understanding of MB by examining how arousal extends beyond cortical correlates to include bodily physiology, highlighting its role in facilitating MB reports.

Specifically, we used a cohort of neurophysiological modalities under different experimental settings to relate MB to an underlying brain-body structure. In Study 1, we examined cortical activity preceding MB reports to identify brain regions engaged when individuals are unable to report their thoughts at rest. In Study 2, we combined experience sampling under different arousal conditions with concomitant brain-body measurements to correlate the frequency of MB reports with different brain-body states. Finally, in Study 3, we examined fMRI-EEG activity during a sustained attention-to-response task to differentiate the neuronal correlates of MB and low arousal and understand the electrophysiological origins of these neuronal correlates.

In summary, we demonstrate that MB is associated with BOLD deactivations spanning the whole brain. Compared to mental states with reportable content, we observed deactivations in frontal and parietal areas. Furthermore, we show that MB is an arousal-mediated mental state, with its occurrence increasing during altered arousal levels. While MB could be decoded from body activity alone, optimal decoding requires both brain and body activity. Lastly, we show that alertness and mental states are neuronally dissociable. In the General Discussion, I outline a roadmap for MB research, focusing on a) exploring the phenomenology of “no thought” and b) creating a psychological model of MB. Taken together, this thesis bridges brain and body rhythms with self-reported experience to reveal moments at the boundaries of consciousness, where being awake does not necessarily translate into conscious thought.

Résumé

L'expérience humaine est riche et remplie de contenu. À tout moment, nos pensées englobent de nombreuses perceptions, croyances, émotions et sentiments. Pourtant, la notion d'un esprit rempli de contenu ne saisit pas pleinement notre expérience. Les paradigmes récents de la pensée spontanée révèlent que les individus, parfois, échouent à rapporter du contenu ou n'ont tout simplement rien à rapporter. Cette expérience, appelée "mind-blanking" (MB), contraste avec l'hypothèse selon laquelle l'esprit est toujours rempli de contenu et soulève la question suivante: pourquoi l'introspection ne donne-t-elle parfois aucun résultat? Les recherches neuroscientifiques suggèrent que le MB se produit lors d'une réduction de l'éveil cortical. En accord avec ce point de vue, la présente thèse vise à approfondir notre compréhension du MB en examinant comment l'éveil s'étend au-delà des corrélats corticaux pour inclure la physiologie corporelle, en soulignant son rôle dans la facilitation des rapports de la MB.

Plus précisément, nous avons utilisé un ensemble de modalités neurophysiologiques dans différents cadres expérimentaux afin de relier le MB à une structure sous-jacente du cerveau et du corps. Dans l'Etude 1, nous avons examiné comment l'activité corticale précédant les rapports de MB révèle les régions cérébrales impliquées lorsque les individus sont incapables de rapporter leurs pensées au repos. Dans l'Etude 2, nous avons combiné l'échantillonnage de l'expérience sous différentes conditions d'éveil avec des mesures concomitantes du corps et du cerveau pour corréler la fréquence des rapports de MB avec différents états du corps et du cerveau. Enfin, dans l'Etude 3, nous avons étudié l'activité fMRI-EEG au cours d'une tâche d'attention soutenue afin de différencier les corrélats neuronaux du MB et du faible éveil, et pour comprendre les origines électrophysiologiques de ces corrélats neuronaux.

En résumé, nous démontrons que le MB est associé à un profil de désactivation BOLD à l'échelle du cerveau. Par rapport aux états mentaux dont le contenu est à signaler, nous avons observé des désactivations dans les zones frontales et pariétales. En outre, nous montrons que le MB est un état mental médié par l'éveil, avec une occurrence accrue lors des niveaux d'éveil altérés. Alors que le MB pourrait être décodée à partir de l'activité corporelle seule, un décodage optimal nécessite à la fois une activité cérébrale et corporelle. Enfin, nous montrons que la vigilance et les états mentaux sont dissociables sur le plan neuronal. Dans la discussion générale, je trace une feuille de route pour la recherche sur le MB, en me concentrant sur a) l'exploration de la phénoménologie de l' "absence de pensée" et b) la création d'un modèle psychologique du MB. Dans l'ensemble, cette thèse établie un lien entre les rythmes cérébraux et corporels et l'expérience auto-rapportée pour révéler des moments aux frontières de la conscience, où le fait d'être éveillé ne se traduit pas nécessairement par une pensée consciente.

Chapter 1

Introduction

This chapter is based on:

1. **Boulakis, P. A.,** & Demertzi, A. (2025). Relating mind-blanking to the content and dynamics of spontaneous thinking. *Current Opinion in Behavioral Sciences*, 61, 101481.
2. **Boulakis, P. A.,** Demertzi, A., Sitt, J. D., & Andrillon, T. (Forthcoming). Spontaneous thoughts and experiences across wakefulness and sleep. In U. Olcese & L. Melloni (Eds.), *The scientific study of consciousness: Experimental and theoretical approaches.* Springer.

1.1 Have you ever experienced a blank ?

"There was nothing. Or rather, a nothing in front of a something."

- Eddie Dean of New York, The Dark Tower

Our thoughts are one of our most intimate and intuitive experiences. It appears almost self-evident that we are aware of what we are thinking. Imagine going for a drive. One moment you are attentively paying attention to the road, ensuring you do not miss an exit or any abrupt movements from the neighbouring cars. Your every thought is about the present experience. However, this might not always be the case. A couple of moments later, your attention may decouple from the environment, and your mind may drift away to topics unrelated to the present. This small moment of decoupling from the present environment generates a cascade of random thoughts unrelated to the current moment. Should I travel next year? Do I have enough money? When is my next salary? This cascade of pictures, smells, sounds and emotions may have been triggered by your environment but has nothing to do with it. The mind wandered away. So you return to attentively driving. However, a couple of moments later, you take a mental step back and realise that you do not recall the last couple of seconds of driving, as if there was a time gap in your experience. You try to piece together what has happened, only to realise that, for a brief moment, *your mind was blank*.

1.2 From contentful to content-less

The example above showcases a key intuition about our experience regarding thoughts. During wakefulness, our mental lives can be characterised as a sequence of different **mental states**, discrete cognitive or emotional mental events that can be decomposed in terms of **mental content** (I am thinking about X or I am thinking about Y) and **mental dynamics** (how mental states evolve over time) (Fig. 1.1).

Indeed, during wakefulness, a mind unconstrained by external demands spends a large amount of its waking time delving into **spontaneous thoughts**, highlighting the centrality of thought exploration in our mental life (Kane et al. (2007); Killingsworth & Gilbert (2010); Seli et al. (2018a); Van Calster et al. (2017), For a meta-analysis please refer to Kawashima et al.

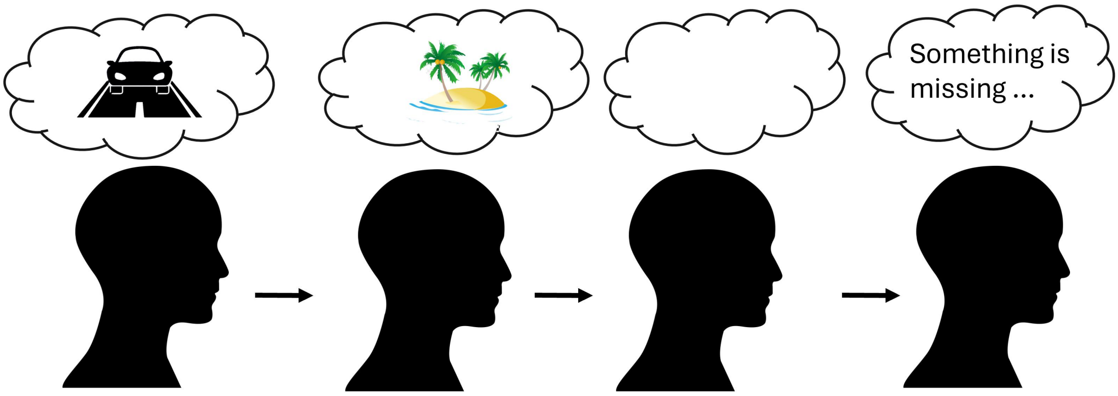

Figure 1.1: The stream of thoughts can be conceptualised as a sequence of mental states. Mental states constitute discrete cognitive or emotional states that can be decomposed in terms of "content" (what the state is about) and "dynamics" (how a mental state transitions to another). For example, during driving, the content is the road, and the dynamics are constrained, ensuring you attend to important environmental cues for driving. However, as our engagement starts to waver, our mental states shift towards mind-wandering (MW), where content reflects non-immediate items in our environment and the thought constraints are weaker, allowing for easier transitions across different thoughts. However, you might find yourself driving and not being able to recall the last few moments of the drive. An introspection yields nothing, as if the mind was briefly empty. What remains is an accompanying feeling that something went missing from the stream of thought. This experience is termed mind-blanking (MB).

(2023)). For example, Killingsworth & Gilbert (2010) examined the frequency of spontaneous thoughts by acquiring people's reports about their thoughts via a phone app as they went by their daily lives. The authors found that people tended to mind-wander about 30-50% of the time in their study. However, more nuanced protocols, providing options that include mixed thoughts, such as simultaneous task engagement and **mind-wandering (MW)**, suggest greater variability in spontaneous thought rates, around 10-60%, depending on what people actually consider a spontaneous thought (Seli et al., 2018a).

Colloquially referred to under the umbrella term "spontaneous thinking" or MW (Seli et al., 2018b; Smallwood & Andrews-Hanna, 2013), these thoughts signal a decoupling of attention from the present environment and current task engagement (Stawarczyk et al., 2011). For example, a spontaneous thought can be about the past or the future (Andrews-Hanna et al., 2013; Cole & Kvavilashvili, 2021; Li & Hills, 2024; Smallwood & O'Connor, 2011; Stawarczyk et al., 2011, 2013, 2014), about oneself or other people (Andrews-Hanna et al., 2013; Kanske et al., 2016; Ruby et al., 2013; Sanders et al., 2017; Smallwood et al., 2011) or about items with differing emotional valence (Killingsworth & Gilbert, 2010; Li & Hills, 2024; Smallwood et al., 2009; Smallwood & O'Connor, 2011). At the same time, spontaneous thoughts can vary depending on their function, serving decision-making (Giblin et al., 2013), creative thinking

(Fox & Beaty, 2019) or autobiographical planning (Stawarczyk et al., 2013). The diversity of content in spontaneous thoughts has given rise to a plethora of mental states: daydreaming (Stawarczyk, 2018), rumination (Nolen-Hoeksema et al., 2008), stimulus-dependent and stimulus-independent thought (Van Calster et al., 2017) and prospective thinking (Girardeau et al., 2022). While these types of spontaneous thoughts are qualitatively different, bearing different emotional valance and content, they all signal how our uninterrupted stream of consciousness organises across time, traversing different content.

At the same time, our thoughts do not arise in a vacuum. They are not solely the product of internal processes but are often influenced by and interconnected with the external environment we find ourselves in. They can be constrained by motivational factors (Seli et al., 2019), goal-oriented thinking (Sripada, 2017) or present task engagement (Andrillon et al., 2021). These examples reflect types of thoughts that revolve around the demands of an organism that engages with a complicated and dynamic world. Such thoughts have been termed “on-task” or “task-relevant”. In experimental settings, these thoughts usually reflect attentional affordances and task engagement with the current experimental task. Similarly, during everyday functioning, these thoughts reflect goal-oriented content or attentional affordances to particularly salient sensory cues.

The apparent dipole of internally-generated and **exteroceptive**-guided thoughts co-evolved alongside the observation that fluctuations in the stream of consciousness in wakefulness are tied to changes in BOLD **functional connectivity (FC)**. One of the most prominent clusters of functionally connected areas is the default mode network (DMN) (Raichle et al., 2001), which comprises the posterior cingulate cortex, the precuneus, the inferior parietal lobule, the medial prefrontal cortex, the inferior temporal cortex, the thalamus and the cerebellum. Although the DMN was originally identified as a set of regions that showed decreased blood flow during task engagement (rest > task), convergent evidence suggests that DMN might be directly implicated in self-referential or internally focused thought processes (Andrews-Hanna et al., 2014), as well as serve auxiliary functions in cognitive flexibility and context-dependent resource allocation during task engagement. Shifts away from external orientation and towards internal mental events are associated with increased activity in DMN areas (Vanhaudenhuyse et al., 2011). Indeed, DMN activity is typically observed during internal mentation, such as prospective or autobiographical thinking, mental simulations, self-referential reflection, and emotional appraisal. However, DMN activity is not exclusive to independent cognition, as recent accounts have extended the relevance of the DMN in task-relevant processes, such as maintaining task-relevant information (González-García et al., 2018; Murphy et al., 2019) and integrating current information with prior knowledge (Konishi et al., 2015). This apparent hetero-modality has lead to the formulation that distinct DMN nodes might support the generation, retrieval and online maintenance of mental representations essential for ongoing cognition (Stawarczyk et al., 2021).

While a classification of thoughts such as internal/external or on-/off-task might be useful in creating umbrella terms with discrete behavioural and neuronal correlates, it might undercut that ongoing thought content is rich and complex, and can be described across many different axes, such as vividness, emotional valance or controllability (Smallwood et al., 2021; Klinger & Cox, 1987). To account for the complexity of thoughts, an alternative line of research has attempted to utilize descriptive experience sampling questionnaires, and by means of dimensionality reduction, create representative thought patterns (Karapanagiotidis et al., 2020; Konu et al., 2020, 2021; Mckeown et al., 2023; Mulholland et al., 2023; Turnbull et al., 2019). These thought patterns describe both how different contents co-vary together (for example, whether future oriented thought may have specific emotional valance) and whether different contents have similar properties (such as apparent vividness). As early as 1987, Klinger & Cox (1987) applied this dimensionality reduction to thought sampling probes and showed that the concept of "daydreaming" could be related to orthogonal thought patterns, ranging from "peculiar and strange" content to "stimulus-independent" content. More recently proposed thought patterns that aim to account for the whole spectrum of ongoing mentation are: a) social episodic cognition, b) task-related processing and c) intrusive, self-relevant thoughts (Konu et al., 2020, 2021; Turnbull et al., 2019). Overall, the descriptive nature of this approach affords a more granular representation of thought content (Smallwood et al., 2021).

Critically, the approaches sketched above aim to answer the question: "What is in your mind?" while eschewing an important step: "Is there anything in your mind?". When given the option, people will infrequently ($\sim$10%) respond that they are thinking of nothing, that they are not thinking of anything or that their mind was simply empty. These are all cases of

mind-blanking (MB). More formally, MB refers to a mental state of no reportable content (Ward & Wegner, 2013; Andrillon et al., 2021; Kawagoe et al., 2019; Mortaheb et al., 2022; Boulakis & Demertzi, 2025). This state is accompanied by a post-hoc feeling that something was lost (Ward & Wegner, 2013; Efklides & Touroutoglou, 2010) (Fig. 1.1). Therefore, MB constitutes a discrete mental state with the unique phenomenology of "absence of thoughts" (Mortaheb et al., 2022; Ward & Wegner, 2013).

Under such a definition, MB poses a unique issue to our current formulations of mental states: does the absence reflect truly no content, bringing this state closer to moments of unconsciousness during wakefulness, where we have no experiences, or is there a failure of memory and confidence in our own mental state reflection (Boulakis & Demertzi, 2025)? In the remainder of this chapter, we will explore how MB manifests during research and whether we can infer what is happening during these blank periods by examining the behavioural, neurophysiological and electrophysiological correlates of MB.

1.3 What is MB?

MB is by no means a novel observation. William James (1890) eloquently and perceptively described the stream of consciousness as

> *... a bird's life, it seems to be made of an alternation of flights and perchings ...*
> (James, 1890, p. 226)

Our mental life is not static. Rather than that, it can described as sequence between different flights. At the same time, there are perchings, content in which we tend to delve in. These observations have been fundamental in the formulation of spontaneous thought.

However, only a few lines before, James (1890) very keenly notes

> *... interruptions, time gaps during which the consciousness went out altogether to come into existence again at a later moment ...* (James, 1890, p. 222)

Based on this description, we can begin to develop an intuition about this phenomenon: it manifests a brief discontinuity between our thoughts. But what can MB represent?

The answer to this question is not straightforward due to the MB definitional heterogeneity across different studies and the low number of performed studies. While the inclusion of "blank" or "empty" reports has increased in recent thought-sampling studies, there is no agreement on what the experience of MB refers to. For example, MB has been referred to as "blank mind" (Van den Driessche et al., 2017; Stawarczyk & D'Argembeau, 2016), "not thinking of anything" (Mortaheb et al., 2022; Robison et al., 2019, 2020), "awareness of absence" (Efklides & Touroutoglou, 2010; Efklides, 2014), "no conscious awareness" (Andrillon et al., 2021; Van den Driessche et al., 2017) or "not attending to anything" (Andrillon et al., 2021; Ward & Wegner, 2013; Stawarczyk & D'Argembeau, 2016). From the diversity of these definitions, we can notice a lack of consensus in the phenomenology of MB (Fell, 2022; Andrillon et al., 2024), which is further evident in the way that MB is described to participants (Table 1.1). At the same time, Fell (2022) correctly notes that definitions focusing on the presence of thoughts do not necessitate the absence of content. As such, under a definition of "moments of no thoughts", a person could still report perceptual content, such as simply noticing the colour of a car or idly listening to music without semantic content about the perceptual experience.

Importantly, this phenomenological heterogeneity can translate to different psychological interpretations of MB. This means that MB could be the result of a) attentional lapses (Andrillon et al., 2021), where instances of attentional decoupling from ongoing tasks fail to orient attention towards any specific content; b) thought-silencing (Kawagoe et al., 2018, 2019), where people try to empty their minds by suppressing semantic content or c) metacognitive error or failure of metamemory, where people misjudge their immediate past content (Efklides & Touroutoglou, 2010; Van Calster et al., 2017). Furthermore, it remains unclear whether MB represents a failure of access consciousness, in that there is content, but we are unable to report it, or whether there is no phenomenal experience at all (Kaufmann et al., 2024). Finally, it was recently suggested that MB might not represent a unitary experience (Andrillon et al., 2024), as it can manifest with or without meta-awareness and deliberate control (Boulakis et al., 2023).

Table 1.1: Overview of different experimental protocols and analyses of MB

Description of MB	**Task setting**	**Thought-sampling**	**Modality**	**Reference**
Awareness of no content	Prospective memory	MB Questionnaire	Behavior	Efklides & Touroutoglou (2010)
No conscious awareness Not thinking of anything	Reading comprehension	Probe-catch Self-catch	Behavior	Ward & Wegner (2013)
Not thinking of anything	SART	Probe-catch	Behavior	Stawarczyk & D'Argembeau (2016)
Not very alert	Psychomotor vigilance task	Probe-catch	Behavior	Unsworth & Robison (2016)
No reportable content Not thinking of anything Contentless No thoughts	SART	Probe-catch	Behavior Pharmacology	Van den Driessche et al. (2017)
Absence of content Thinking about nothing Lack of meta-awareness	Rest	Probe-catch	fMRI	Van Calster et al. (2017)
Thinking of nothing	Trying to think of nothing	Post-hoc report	fMRI	Kawagoe et al. (2018)
Not very alert	STROOP task Psychomotor vigilance task	Probe-catch	Pupillometry	Unsworth & Robison (2018)
Thinking of nothing	Trying to think of nothing	Probe-catch	fMRI	Kawagoe et al. (2019)
Not thinking of anything Not attending to task Zone out	SART	Probe-catch	Behavior	Robison et al. (2019)
Not attending to anything Absence of thought	Cohort	Probe-catch	Behavior	Robison et al. (2020)
No conscious awareness Thinking of nothing No recall	SART	Probe-catch	EEG Pupillometry	Andrillon et al. (2021)
Absence of content Thinking about nothing	Rest	Probe-catch	fMRI	Mortaheb et al. (2022)
Absence of content Thinking about nothing	Rest	Probe-catch	fMRI	Boulakis et al. (2023)
Reduced awareness Absence of thought Thinking about nothing No recall	Rest	Probe-catch	Pupillometry	Koroma et al. (2023)
No conscious awareness Not thinking of anything No recall Zone out	Psychometric	MB questionnaire	Behavior	Kawagoe et al. (2024)
Not thinking of anything	Rest	Probe-catch	EEG ECG EDA Respiration Pupillometry	Boulakis et al. (2025)
No conscious awareness Thinking of nothing No recall	SART	Probe-catch	EEG	Musat et al. (2024)
No conscious awareness Thinking of nothing No recall	SART	Probe-catch	ECG	Corcoran et al. (2024)

SART = sustained attention to response task; ECG = electrocardiography; EDA = electrodermal activity; EEG = electroencephalography; fMRI= functional magnetic resonance imaging; EEG = electroencephalography

1.4 Understanding MB through its behavioural and neurophysiological profile

1.4.1 MB has a unique behavioural profile

MB constitutes an experimental "blank box". We cannot know what was happening during those moments because people, by definition, cannot inform us of the phenomenon as it is taking place. Therefore, research has attempted to infer the functional and phenomenological relevance of MB by examining the behavioural and neuronal correlates of MB reports. We can look at how behaviour and brain organise during MB reports and contrast these periods to when people actually are able to report content. While inferring experience has methodological caveats, namely that MB can be created by the interaction of numerous cognitive mechanisms, such as attention, meta-cognition and perceptual encoding of sensory information, it can serve as a starting point to develop an account of what MB might be.

A first step in MB research has attempted to place MB on the mental state road-map by introducing it as a potential option in **experience sampling** paradigms (Andrillon et al., 2024). Experience sampling is a thought sampling technique where probes at random time intervals invite participants to report their immediate past thoughts (Myin-Germeys & Kuppens, 2021; Napa Scollon et al., 2009). Participants solely have to report what they were thinking at the moment preceding the probe. The immediacy of such reports minimises memory bias about recent mental states and may be more accurate in describing the dynamics of the stream of thought (Ellison et al., 2020; Mölsä et al., 2022). Probes may be presented intermittently to cognitive tasks (Andrillon et al., 2021) or during rest (Van Calster et al., 2017). So, how does MB fit into our stream of thought?

Firstly, thought probes have revealed that MB is a relatively sparse mental state, occurring roughly 0-10% of probes during spontaneous thinking at rest (Mortaheb et al., 2022; Van Calster et al., 2017) and task engagement (Andrillon et al., 2021; Robison et al., 2019). Pertinent to this, Ward & Wegner (2013) found that during self-paced reading, MB represented 15% of total experience sampling probes. While MW occurred significantly more frequently than MB during probe-catch, self-catch yielded similar frequencies of MB and MW (Ward & Wegner, 2013). The authors interpreted these results as evidence that MB might actually be frequent during ongoing thinking, but participants can detect it faster than MW (Ward & Wegner, 2013). Therefore, probe-catching techniques might underestimate the rates of MB. Interestingly, MB frequency did not correlate with task engagement or MW reports. While MW and task engagement showed anticorrelated patterns of attentional affordances, it appears that MB had a unique place in the stream of consciousness, occurring at random time points (Mortaheb et al., 2022; Ward & Wegner, 2013).

While MB manifests sparsely in neurotypical participants, another line of research has examined whether MB propensity might increase in neuroatypical populations. Van den Driessche et al. (2017) compared mental reports between ADHD, ADHD treated with methylphenidate and neurotypical children during a sustained attention to response task (SART). SART is a psychological test used to measure a person's ability to maintain focus and attention over a prolonged period. Participants are shown a sequence of stimuli, such as different faces. Participants are instructed to press a designated key in response to every stimulus (every neutral face) except for a specific target (such as a face that is showing emotion). As such, it is possible to make two types of errors: a "false alarm" error, where the participant presses a button when they are not supposed to, and a "miss" error, when the participant fails to press a button when they are supposed to. They found that non-treated ADHD children tended to report MB about twice as frequently (∼20%) as the neurotypical group, while they found no evidence for MB report frequencies between the neurotypical group and the methylphenidate-treated group. Moreover, contrasting young adults who displayed ADHD symptoms with a neurotypical group yielded similar results. The ADHD group yielded a significantly higher number of MB reports, roughly ∼15% compared to the ∼7% of the control group.

Overall, MB reports are rare within the flow of spontaneous thinking. However, people seem to be able to reach blank moments when instructed. Kawagoe et al. (2019) combined a probe-catching experience sampling approach with the instruction to "try to think of nothing". Under such a paradigm and in the absence of a task, probe-catching identified 50% MB instances Kawagoe et al. (2019).

Apart from infrequent, people also tend to report MB more slowly when given a prompt or cue, compared to when they report MW or focused on a task(Andrillon et al., 2021; Kiss &

Linnell, 2024; Koroma et al., 2023; Unsworth & Robison, 2016, 2018). A notable exception is the study of Mortaheb et al. (2022). In that study, the authors compared MB reports to stimulus-dependent thoughts, stimulus-independent thoughts and sensations, with MB apparently being the fastest. However, the protocol entailed a two-step report process, where the participants first indicated thought presence/absence and then the content. The authors interpreted these results as additional mental evaluation of the content, which required further time (Mortaheb et al., 2022). Overall, slower report times suggest greater decoupling from the environment Kam & Handy (2013) and overall reduced arousal (Włodarczyk et al., 2002; Philip et al., 2003). The idea that MB is associated with lower levels of arousal is further supported by results showing that, during MB, participants self-reported lower levels of vigilance (Andrillon et al., 2021), assessed through experience sampling reports of experience alertness, and higher scores on the Karolinska Sleepiness Scales compared to when they are on task and MW (Stawarczyk & D'Argembeau, 2016).

Finally, the effects of MB on-task performance are unique from other mental states. Andrillon et al. (2021) examined how performance during a SART task varied based on mental reports. Overall, MB was associated with a higher count of "miss" errors compared to MW and task engagement Andrillon et al. (2021); Musat et al. (2024). Furthermore, (Andrillon et al., 2021) utilised a **drift-diffusion modelling (DDM)** to understand why people make different errors between MB and MW. DDM is a statistical technique that decomposes decision processes into a set of variables describing the initial threshold for a choice, bias towards a specific choice and speed of evidence accumulation for a choice (Ratcliff & McKoon, 2008; Ratcliff et al., 2016). Andrillon et al. (2021) examined which components of the decision to indicate face or withhold a response during the SART task differ between MB and MW. MW was associated with a lowered threshold and higher decision bias compared to MB. As such, it appears that MW is tied more to impulsivity and MB more to environmental disengagement (Andrillon et al., 2021).

1.4.2 Developing a measurement of trait MB

Apart from examining the behavioural correlates of MB, another line of research attempts to uncover how trait-level factors, such as personality and age, might affect MB self-reports by developing MB experience questionnaires.

As it currently stands, there is only one validated psychometric questionnaire to examine trait-level MB, the Mind-Blanking Questionnaire (MBQ) (Kawagoe et al., 2024). The MBQ is a 5-item, Likert scale questionnaire containing items such as “There are moments that I can’t remember what I was just thinking about”, “There are moments when my mind empties out”, or “There are times when my mind goes completely blank”. The items were developed based on the theoretical construct of MB, being heavily focused on instances of “blank” moments or moments where people “space out”. As such, it still remains to be validated whether people actually describe MB this way in their everyday lives. However, factor analysis of the responses yielded one latent variable solution, highlighting that the items track similar aspects of the experience.

Preliminary results from the MBQ have yielded some interesting properties of trait MB. Firstly, MB seems to be invariant across age and assigned sex (Kawagoe et al., 2024). Furthermore, combining the MBQ with its MW counterpart, the Mind-Wandering Questionnaire (MWQ) (Mrazek et al., 2013; Kawagoe et al., 2024), favoured a two latent variable solution in factor analysis. These two questionnaires appear to track different latent structures (Kawagoe et al., 2024). This result is further corroborated by research showing that MB does not correlate with MW (Ward & Wegner, 2013), favouring an interpretation of different cognitive constructs. Finally, the authors examined how the MBQ correlated with a battery of questionnaires that track executive function, sleepiness and mindful awareness. The MBQ correlated negatively with executive and attentional scores, while results from the Epworth Sleepiness Scale (Johns, 1991) were inconclusive.

1.4.3 How does the brain blank?

How does neurophysiology broaden our perspective?

So far, the toolbox with which we further our understanding of MB has utilised behavioural properties of the phenomenon in question, such as the apparent sparseness and the reduced experienced vigilance. However, the arsenal to tackle this issue contains another correlate of experience: brain activity. Neuroimaging and electrophysiology constitute a suite of non-invasive technologies that visualise the structure and function of the brain. Techniques such as

functional magnetic resonance imaging (fMRI) and **electroencephalography (EEG)** allow researchers to observe which brain areas are more active during specific tasks, linking these regions to behaviours like decision-making, memory, and emotional regulation. On the one hand, fMRI works by detecting changes in blood flow and oxygenation levels in the brain that occur in response to neural activity (Ogawa et al., 1990; Logothetis, 2003). When neurons become active, there is an increase in local blood flow to supply the active region with more oxygen. **Blood oxygen level dependent (BOLD)** signal reflects localised changes in the ratio of oxygenated to deoxygenated haemoglobin induced by increased localised blood flow. However, this vascular response takes time to develop, typically peaking around 4-6 seconds after the onset of neural activity, and lasts for several seconds thereafter (Logothetis et al., 2001). This delay means that the fMRI signal lags behind the actual neural events and this delay is not the same across all brain regions, because of the local vasculature. The trade-off of low temporal resolution is excellent spatial localisation. fMRI allows researchers to examine spatial events at a scale of 1 to 3 millimetres. On the other hand, EEG provides us with the opposite benefits, excellent temporal precision at the cost of spatial localisation. EEG measures electrical activity in the brain through electrodes placed on the scalp. When groups of neurons fire together, the concurrent signal is strong enough for the EEG to pick up. As neural signals, such as action potentials and synaptic activity, occur on a millisecond timescale, EEG can capture these rapid changes because it measures electrical potentials in real time. At the same time, the signal recorded from an electrode is the aggregate electrical signal of multiple cortical sites, weighted by the proximity of those cortical sites to the electrode. Critically, EEG is sensitive to how electrical signals are propagated in the brain. Therefore, EEG is most sensitive to activity from radially oriented dipoles in the cortical gyri, which are perpendicular to the scalp and spread outward, and less sensitive to tangential dipoles in sulci or deeper structures. Overall, we currently possess two complementary techniques that are able to differentially tap into micro and mesoscale cortical activity. By examining cortical correlates of MB, we may uncover how the brain differs in the absence or presence of mental content, as well as similarities of MB with other states of wakefulness.

Neuronal fingerprints of MB

The first study that examined the neuronal correlates of MB asked participants to actively try to “think of nothing” (Kawagoe et al., 2019). The authors found decreased BOLD activity in the left hippocampus, the Broca’s area, the inferior frontal gyrus and the supplementary motor cortex in the moments preceding MB reports. Additionally, they found activation in the anterior cingulate cortex. Contrasting MB with MW, they found deactivations in the Broca’s area and the left anterior insula. Overall, given the role of Broca’s area and the left hippocampus in semantic production, the authors interpreted these results as reduced “internal dialogue”, as people were trying to achieve a MB state by silencing their own thoughts (Kawagoe et al., 2019). Using a similar protocol, Kawagoe et al. (2018) used functional connectivity (FC) to contrast the instruction: “think of nothing” with the instruction “let your mind wander”. The authors found decreased connectivity between the DMN and the visual, the temporal and the frontal network during “thinking of nothing”. As the DMN is considered a hub of internal cognition and predominantly appears during MW (Christoff et al., 2016; Smallwood et al., 2021), these results point to higher decoupling between spontaneous thinking hubs and networks associated with the salience of environmental stimuli.

The study of Kawagoe et al. (2018) provides a static image of FC during self-induced MB, a snapshot representing the average brain connectivity during “thinking of nothing” moments. Moving past that, Mortaheb et al. (2022) examined how brain connectivity organises over time and compared this organisation to mental state reports. The authors estimated connectivity in 100 regions of interest (ROI) at every time point in the fMRI session to get a time-varying representation of FC. Then, by means of a **clustering** approach, they extracted the most representative brain patterns. Finally, they compared how close the FC connectivity was at moments of MB to each brain pattern. First of all, the authors found that FC can be decomposed into four key patterns: a pattern of complex **fMRI anticorrelations** across short and long-range cortical areas, a pattern showing anticorrelations primarily between the visual network and the other networks, a pattern with high coherence, and a pattern of low coherence. These patterns have previously been reported in healthy and brain-injured participants (Demertzi et al., 2019), pointing to a universal mode of cortical activity organisation. Pertinently to spontaneous thinking, time-varying FC during MB was closer to the pattern of high inter-areal coherence compared to thoughts with reportable content. This brain pattern of high inter-areal coherence presents us with a connectivity profile that is significantly different in its functional and computational properties compared to brain patterns observed in typical wakefulness (Demertzi et al., 2019, 2022), and more closely resembles cortical organisation during sleep (El-Baba et al., 2019). As such, this pattern might be driven by altered cortical arousal, which is in agreement with the idea that MB is associated with reduced arousal.

Importantly, in this study, MB was also associated with higher amplitude of the **fMRI global signal** (GS) amplitude. GS represents the mean time course computed over all voxels within the brain (Zarahn et al., 1997). On the one hand, the GS has demonstrated a neuronal counterpart (Schölvinck et al., 2010; Xu et al., 2018). On the other hand, it was shown to reflect fMRI nuisance sources such as motion, scanner artefacts, respiration (Power et al., 2017), cardiac rate (Chang & Glover, 2010), and vascular activity (Colenbier et al., 2020). The diverse neuronal, physiological, and movement correlates of the GS have created a discourse on its origin and function (Liu et al., 2017), questioning whether the GS contains meaningful neuronal events or can be discarded as noise. Pertinent to MB, it appears that the GS tracks the level of cortical arousal. A concomitant fMRI-EEG showed the inverse correlation between GS and EEG markers of cortical arousal, with lower bands of the EEG frequency spectrum positively correlating to the amplitude of the global signal (Wong et al., 2013). At the same time, ingestion of arousal stimulants lowered the amplitude of the GS (Wong et al., 2013). As MB is associated with higher GS amplitude, it strengthens the claim of MB being associated with lowered cortical arousal.

Electrophysiological markers of MB

While fMRI can inform us about which cortical areas contribute during MB, another line of research examines how electrophysiological events organise preceding MB reports.

Originally, Andrillon et al. (2019) considered that attentional lapses might be attributed to intrusions of **slow-wave activity (SWA)** during wakefulness, termed "**local sleep**". Slow-wave activity is characterised by an increase in low-frequency (<4Hz) electrophysiological activity (Steriade, 2003; Davis et al., 1937), where slow, oscillatory down (hyper-polarization; period of neuronal quiescence) and up (depolarised; period of action potentials) neuronal states alternate between periods of neuronal synchronisation and neuronal silencing (Stroh et al., 2013). While SW is primarily considered a marker of NREM sleep (Massimini et al., 2004), slow-wave-like activity has been detected in animals during wakefulness (Vyazovskiy et al., 2011), leading to the formulation of the term “local sleep” (Vyazovskiy et al., 2011; Andrillon et al., 2019). These local sleeps were subsequently suggested to be the phenomenological counterpart of MB (Andrillon et al., 2019).

This hypothesis was recently validated during a SART task paired with experience sampling probes (Andrillon et al., 2021). Firstly, the authors validated the presence of slow-wave-like activity that mirrors the down-up EEG morphology present during NREM sleep. When properties of local sleeps, such as density, slope and amplitude were regressed with different mental reports, the authors found that MB could be differentiated from MW and task engagement based on the localisation of local sleeps. Specifically, MB local sleeps were found in posterior areas, while MW local sleeps were found frontally. Moreover, posterior local sleeps were associated with “misses” during the SART task, while frontal were linked to “false alarms”, concurrent with the idea that during mind-wandering, people make impulsivity mistakes, while during mind-blanking, people tend to not forgo stimuli (Andrillon et al., 2021). Coherent with an interpretation of MB as a result of lowered cortical arousal, the authors provide a mechanistic explanation as to the electrophysiological correlates of MB. At the same time, they speculated that parietal local sleeps cause the experience of MB by impeding frontoparietal network communication, a key feature of theories on conscious content emergence (Dehaene et al., 1998).

Further exploration on the same dataset examined EEG cortical markers spanning frequency, complexity and connectivity domain (Musat et al., 2024). Overall, their results provided further evidence for a double dissociation between MB and MW. While MW was associated with increased frontal power in lower EEG frequency bands (delta) and decreased frontal complexity, MB showed a posterior profile of increased amplitude in the EEG lower frequency bands (delta, theta, alpha) and reduced complexity. Interestingly, they also observed a progressive breakdown in frontal-posterior connectivity in higher EEG bands, namely in the alpha, beta and gamma bands, as they moved from task engagement to MW and MB. These results further support the idea that lower arousal moments break down frontoparietal communication, which might phenomenologically manifest as MB. Finally, the authors examined how different mental states might undercut stimulus processing by examining evoked-response potentials (ERP) to the SART stimuli. MW and task engagement showed a typical P300 component, traditionally associated with the conscious processing of stimuli. However, MB produced no clear P300 component. Furthermore, cortically averaged ERP responses for MW and task engagement had a sustained and cortically widespread response after the P300 component, something that was absent during MB. As such, the authors questioned whether a stimulus was even consciously perceived at that moment (Musat et al., 2024).

1.4.4 Interim remarks on cortical arousal and MB

Across neurophysiological studies, we can observe rare cortical states atypical to wakefulness. Currently, the most prominent state of widespread cortical synchronisation has been observed in lowered arousal states (El-Baba et al., 2019). During NREM sleep, it was observed that brain dynamics tended to transition to a cortex-wide "hyperconnected" state more frequently and remain in such a "hyperconnected" state for longer time periods compared to wakefulness (El-Baba et al., 2019; Aedo-Jury et al., 2020; Liu et al., 2015, 2018), consistent with the idea that lower cortical arousal states correlate with a progressive loss of anticorrelated brain activity and the emergence of global synchronisation (Liu et al., 2015, 2018; Lee et al., 2022). Such transitions to lowered arousal states are characterised by an increase in low-frequency electrophysiological activity with the down-up, slow-wave polarity profile (Davis et al., 1937; Steriade, 2003). Specifically, it has been observed such down-up states are linked both to a cortex-wide BOLD component (Liu et al., 2017) and to cortex-wide functional connectivity patterns (Aedo-Jury et al., 2020). Similar results have been observed in low arousal states induced by the admission of isoflurane in rats (Aedo-Jury et al., 2020; Bukhari et al., 2018). Notably, progressively lower arousal increased the intensity of slow wave activity and the strength of functional connectivity (Aedo-Jury et al., 2020), possibly by disrupting the clustering of regions into clearly demarcated and competitive networks (Bukhari et al., 2018) (Fig. 1.2).

It appears that MB presents itself at the convergence of micro- and mesoscale low cortical arousal (Mortaheb et al., 2022; Andrillon et al., 2021). However, arousal manifests not solely in the brain but also in the body. From the jitteriness of the first cup of coffee to the muscle

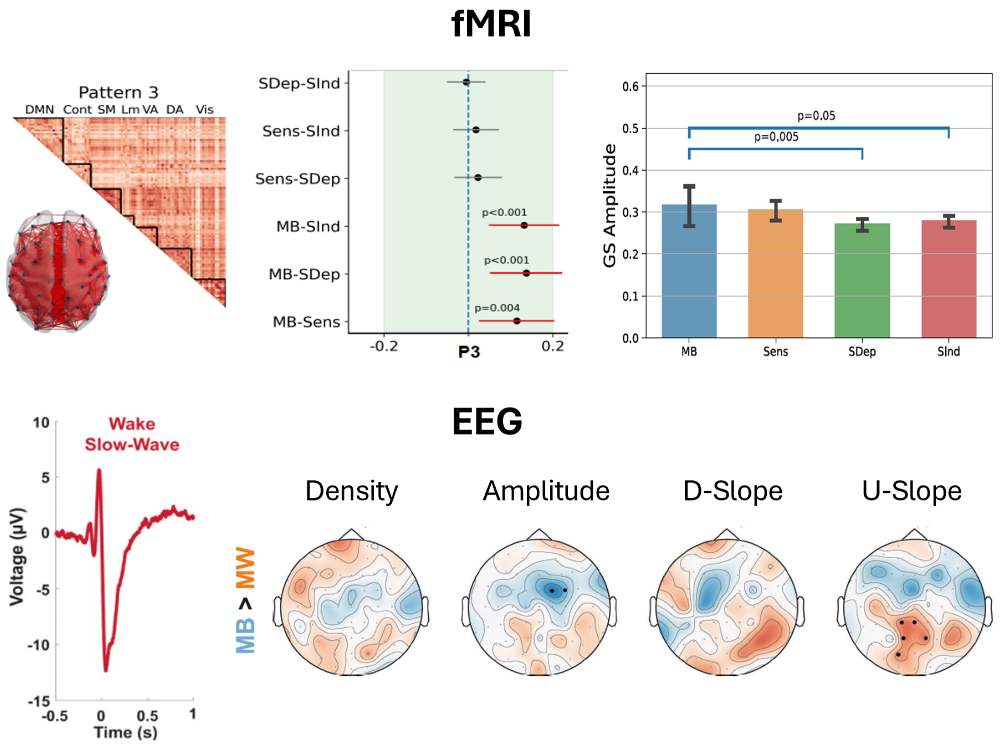

Figure 1.2: The characterisation of mind-blanking (MB) by means of neurophysiology indicates a brain mode mediated by arousal alterations. *fMRI.* Using experience sampling during spontaneous thinking at rest, a brain pattern of overall high inter-regional functional connectivity, which recurrently appeared during spontaneous thinking, had the highest similarity with the pattern estimated during MB reports, compared to thought-oriented mental states. This pattern of overall positive inter-regional connectivity was further characterised by higher amplitude of the global BOLD signal, an indirect indication of low cortical arousal (Mortaheb et al., 2022). *EEG.* Slow-wave-like activity during wakefulness, termed local sleep, preceded instances of MB, compared to mind-wandering (MW) around parietal electrodes when participants were performing a sustained attention task (Andrillon et al., 2021). DMN = Default Mode Network, Cont = Control Network, SM = Somatosensory Network, Lm = Limbic Network, DA = Dorsal Attentional Network, Vis = Visual Netowork, SDep = Stimulus-Dependent Thoughts, SInd = Stimulus-Independent Thoughts, Sens = Sensations, MB = Mind-Blanking, GS = Global Signal

relaxation of a hot bath at the end of the day, our bodies constantly alternate our capacity to think and act. When is it easier to work? After a good night's rest or after an intense workout? In the remainder of the chapter, I will investigate how MB can be integrated into the broader narrative of the brain-body relationship.

1.5 An embodied perspective on MB

1.5.1 The mind is not (only) the brain

The neurocentric approach to cognition views the mind as "embrained", that is, the cognition is the manipulation of symbolic expressions that reflect sensory information, and are geared towards adaptive behaviour. The brain, analogous to a computer, transcribes inputs (sensory information) to symbolic expressions (mental representations) and, by means of syntactic manipulations, creates outputs (mnemonic recovery, reasoning, spatial manipulation) (Dretske, 1969; Fodor, 1975; Marr, 1982). Imagine, for example, someone navigating through a familiar city. The brain receives sensory input, such as the sight of streets and sounds of traffic, and transcribes them into symbolic mental representations — a mental map of the city. These symbols are then syntactically manipulated to plan the route. The output (choosing the route) demonstrates how sensory input is transformed into symbolic representations, manipulated, and used to guide action. Cognition is brain computation, where compartmentalised cortical areas are equipped for the various manipulations of mental representations.

Embodiment seeks that challenge this notion. It begins by considering that cognition does not emerge in a vacuum. Instead, it is constricted by the effectors with which an organism acts on the world to address homeostatic demands (Varela et al., 2017). Homeostasis is the process by which living organisms maintain self-organisation despite changes in external conditions. Sensory afferents inform the organism about the state of the world and the state of the body. Motor effectors constrain the organism's capacity to alter the current world state to promote internal consistency. We can revisit the previous navigation example. Instead of relying solely on symbolic mental representations, the person's movements, bodily orientation, and interactions with the environment play a central role. For example, turning down a particular street might come from a physical sense of spatial familiarity rather than purely from an abstract mental map. In summary, embodiment posits that the body provides a physical scaffolding for ongoing mentation, one with inherent limitations, and this scaffolding eventually shapes what actions an organism is capable of taking in tackling self-preservation in complex and dynamic environments.

1.5.2 Fundamental cognitive processes have an embodied basis

The conception of the body as a constructive mechanism of cognition has generated a line of research that examines the covariate role of bodily afferents to perception and action. While a full account of this line of research extends past the scope of this thesis, I believe it is interesting to examine how the body may affect key processes that support content presence.

Converging evidence from cardiac research has highlighted the modulatory role of cardiac timing in content presence across different sensory modalities. Cardiac activity relies on the alternating phases of systole when the heart contracts to pump blood out, and diastole, when the heart relaxes to allow the chambers to fill with blood. Whether a stimulus is perceived is tied to the cardiac phase. The diastolic phase has been associated with increased reported perceivability of visual, auditory and tactile stimuli (Sandman et al., 1977; Saxon, 1970; Al et al., 2020), mnemonic recall Garfinkel et al. (2013) and pain perception (Wilkinson et al., 2013), compared to the systolic phase. Inversely, the systolic phase is more generally associated with enhanced emotional, fearful responses (Leganes-Fonteneau et al., 2021), spontaneous movement, such as saccades (Galvez-Pol et al., 2020), and self-paced exploratory actions (Palser et al., 2021). Overall, the evidence suggests that systole is associated with lower thresholds in sensory sampling, facilitating perceptual processing, while diastole is associated with action through an active sampling of environment (Skora et al., 2022).

These effects are not constricted to cardiac afferents; another dominant bodily rhythm that affects cognition is respiration (Azzalini et al., 2019). Akin to the cardiac cycle, respiration involves the alternating processes of inhalation, where the diaphragm and intercostal muscles contract to draw air into the lungs, and exhalation, where these muscles relax to expel air from the lungs. For example, Park et al. (2020) found that voluntary, but not non-voluntary action, is more frequent during the expiration phase of the breathing cycle. Moreover, during task engagement, people will gradually adjust their breathing rhythms to match trial task onsets (Grund et al., 2022). Synchronisation of task onset with the inhalation phase of the breathing cycle has been associated with increased task performance in fearful face processing Zelano et al. (2016) and visuospatial perception (Perl et al., 2019).

The examples from the cardiac and respiratory domains above, while by no means extensive, serve to show that perception and action are not uniquely guided by cortical dynamics. Instead, bodily rhythms affect what is in our mind, and how we act, a basic tenet of an embodied mind prospective. Can this tenet be applied to MB?

1.5.3 Bodily correlates of MB

The main body of research on potential bodily correlates of MB has been focused on the use of **pupillometry**. Originally, a series of studies examined whether pupil size can track trial-level fluctuations in attentional states, such as on-task thoughts or MW during task engagement (Unsworth & Robison, 2016, 2018). Overall, the authors found that MB / inattentiveness reports were associated with lower pre-trial pupil size, as well as lower task-evoked pupillary responses compared to task engagement and external distractions (Unsworth & Robison, 2016). However, the authors did not report any positive evidence for differences between MB / inattentiveness reports and MW. It appears that during attentional lapses, including MB, tonic (resting pre-trial) and phasic (task-related) locus coeruleus activity is decreased. Consistent with these results, Andrillon et al. (2021) found that MB and MW were associated with lower pupil size compared to task engagement, but they found no evidence for differences between attentional lapses. In a follow-up study, Unsworth & Robison (2018) attempted to further deconvolve the relationship between MW and MB. They found that MB was associated with lower pre-trial pupil size compared to intentional MW but not MW about external distractions. Overall, these results suggest that attentional lapses are related to discrete tonic arousal levels, as indexed by pupil size. However, this hypothesis requires further validation, as recent findings indicate that pupil size may primarily reflect overall drowsiness levels rather than specific attentional fluctuations (Stawarczyk et al., 2020).

As it stands, research on further bodily correlates is sparse. However, while pupillometry is a well-researched bodily index of arousal, it is not necessarily the only one. Recently, Corcoran et al. (2024) reanalysed a previously validated dataset that contained concomitant ECG, EEG and experience sampling reports during a SART task (Andrillon et al., 2021). Trial-by-trial fluctuations in heart rate captured dynamics of reports, with lowered heart rate associated with more frequent MB reports compared to task engagement, suggesting a dominance of the parasympathetic nervous system (Pham et al., 2021). Apart from direct cardiac measures, the authors also assessed brain-cardiac coupling by estimating heart-evoked potentials (HEP) across the different mental states. HEPs are the event-related, cortical responses time-locked to heartbeats (Coll et al., 2021). As HEP is substantially modulated by interoceptive orientation (García-Cordero et al., 2017; Mai et al., 2018; Pollatos & Schandry, 2004) and interoceptive performance (Canales-Johnson et al., 2015; Lutz et al., 2019; Schulz et al., 2015), it is hypothesised to reflect the cortical processing of cardiac activity and interoceptive orientation (Pollatos & Schandry, 2004; Coll et al., 2021). Corcoran et al. (2024) found that MB, compared to task engagement, was associated with increased HEP amplitude in central and frontal electrodes and decreased in posterior electrodes. The authors interpreted the HEP increase as enhanced processing of the cardiac signals due to an overall shift towards a mode of bodily signal processing and away from external stimuli processing. This interpretation is consistent with the idea of sensory-attentional decoupling during MB.

1.6 Thesis outline

The fundamental goal of this thesis is to elucidate the neurophysiological correlates of MB in a diverse set of brain and body rhythms, with the aim of linking MB to discrete states of altered cortical, physiological and experienced arousal.

In Chapter 2, we investigate the neuronal correlates of MB during spontaneous thinking at rest. The recency of including MB in experience sampling paradigms has left the question of which cortical areas show altered activity when report MB unanswered. By isolating BOLD activity in moments preceding MB and contrasting this with moments preceding reportable content, we aim: a) to provide novel insights into the neuronal correlates of mental reportability, b) replicate previous work on the cortical correlates of deliberate MB.

Chapter 3 explores how states of altered cortical and physiological arousal affect MB reports. In this chapter, we utilise experience sampling across three different arousal states: baseline, after sleep deprivation, and post-exercise. At the same time, we utilise concomitant EEG-physiology measurements to decode MB reports using a machine-learning approach. Therefore, the goal is two-fold: a) provide direct evidence that altered states of arousal increase the propensity to MB, and b) examine whether the brain and body carry unique MB information.

In Chapter 4, we investigate the association between time-varying FC connectivity and slow-wave-like EEG activity by combining EEG-fMRI recordings with experience sampling probes of alertness and mental states during task engagement. Since FC and electrophysiology converge at the same phenomenology of MB, we aim to a) validate the presence of a unique FC signature of MB and b) examine the generative role of electrophysiology in that signature.

Chapter 5 summarises the main findings of the studies described in chapters 2, 3, and 4 while discussing results that are contradictory to the main claims of the thesis. Finally, I discuss some outstanding questions remaining in MB and how future research may tackle them.

Chapter 2

Deactivations spanning the whole brain precede uninduced MB reports

This chapter is based on:

1. **Boulakis, P. A.**, Mortaheb, S., Calster, L. van, Majerus, S., & Demertzi, A. (2023). Whole-brain deactivations precede uninduced mind-blanking reports. *Journal of Neuroscience*, 43(40), 6807–6815.

2.1 Introduction

A notable particularity of MB studies is how MB is instructed for reports. As discussed in Chapter 1, Kawagoe et al. (2019) studied the neuronal correlates of MB by asking people to actively “empty their minds”. By analysing the fMRI BOLD signal preceding the MB reports, the authors found deactivations in Broca’s area and the left hippocampus and activations in the ventromedial prefrontal cortex (vmPFC)/subgenual region of the anterior cingulate cortex (subACC). The authors interpreted these results as reduced inner speech, elicited by the attempt of participants to silence internally generated thoughts. This possibility was considered by other authors, too, primarily in the context of mind-wandering: As our thoughts spontaneously transition across an internal-external milieu (Vanhaudenhuyse et al., 2011; Smallwood et al., 2012; Demertzi et al., 2013), the ACC serves executive functions, such as identifying attentional lapses from ongoing tasks (Christoff et al., 2009) or allowing thought transitions to be controlled (Crespo-García et al., 2022). In similar lines, deliberate MB also requires constant supervision of thoughts in the form of evaluating ongoing experience to promote thought-silencing, therefore recruiting regions such as the vmPFC/subACC, a central hub for mental state evaluative processes (Jenkins & Mitchell, 2011; Qin et al., 2020). Taken together, the use of deliberate MB in neuroimaging studies might provide a biased picture of the underlying neural mechanisms of MB that incorporate task demands of thought monitoring.

In the present study, we reasoned that the ACC activity previously observed during deliberate MB might reflect a task confound of the instruction to monitor and suppress thoughts. Instead, spontaneous MB is typically associated with failures in metacognitive monitoring of thoughts (Efklides & Touroutoglou, 2010) and appears more as interruption to the stream of thought (Ward & Wegner, 2013; Fell, 2022), rather than effortful thought silencing. Therefore, we tested the hypothesis that spontaneous MB reports are related to frontal deactivations, reflecting a failure of frontal areas to monitor the stream of thought when thoughts occur unconstrained. Using fMRI and experience sampling, we first performed a univariate analysis to test whether MB reports would indicate frontal deactivations in the periods preceding MB reports while remaining agnostic as to the contribution of the remaining cortex. To supplement our hypothesis of frontal deactivations, we performed an ROI analysis to examine the specificity of deactivations in the vmPFC-subACC and other previously identified MB-related clusters.

2.2 Methods

For an extensive overview of the methodology of this chapter, please refer to the published paper appearing in Appendix 6.1.

2.2.1 Experience sampling dataset / Experimental design

We used previously collected data (Van Calster et al., 2017) acquired during experience sampling at rest in an fMRI scanner. At random intervals, participants were probed to report what was in their mind at the moment just preceding the cue. Available options were: 1) absence, defined as MB or empty state of mind, 2) perceptions, defined as thought-free attentiveness to stimuli (Sens), and 3) stimulus-dependent thoughts (SDep; thoughts evoked from the immediate environment) and 4) stimulus-independent thoughts (SInd; thoughts irrelevant to the immediate environment) (Fig. 2.1A). The original dataset consisted of 36 participants, yet, we selected participants with at least one MB report per session, resulting in a total sample size of 31 participants. Overall, participants reported MB 6% of total reports (SD: .04, range: [1,9]) Sens 20% of trials (SD: .13, range: [1,26]) SDep 32% of total reports (SD: .14, range: [1,29]), and SInd 42% of total reports (SD: .15, range: [6,28]) (Fig. 2.1B).

2.2.2 fMRI Analysis

fMRI Preprocessing

Briefly, structural images were a) skull-stripped, b) bias-field corrected, c) segmented into white and grey matter tissues and cerebrospinal fluid, and d) normalised to the MNI space. Functional data preprocessing steps were: a) realignment, b) slice-time correction, c) co-registration, d) normalisation to MNI space, and e) spatial smoothing.

Univariate whole-brain analysis

Data were analysed using a **general linear model** (GLM). The four responses of the participants (MB, SDep, SInd, Sens) were modelled as regressors of interest. Each response instance

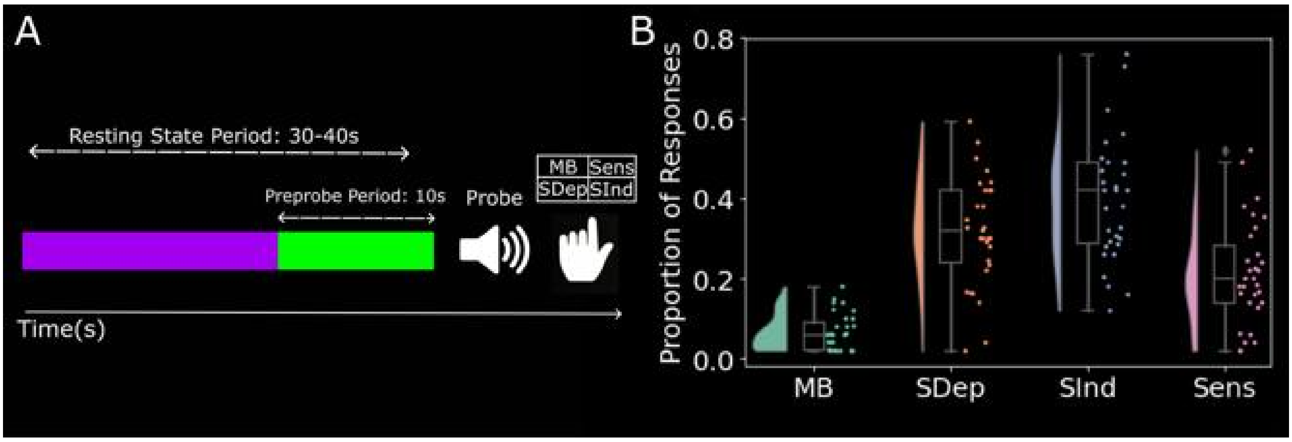

Figure 2.1: The experience sampling paradigm. A) Single trial example. During experience sampling, participants were asked to restfully lie in the scanner with their eyes open and let their minds wander without any further orientation as to the focus of their thoughts. At random intervals (30-60 s), participants are probed with an auditory cue to report the content of their thoughts at the moment preceding the probe using a button press. Four available report categories were presented as available: MB (MB), perceptions (Sens), stimulus-independent thoughts (SInd), and stimulus-dependent thoughts (SDep). For subsequent analysis, only the final 10 s of the resting period (green segment) were used. B) Raincloud plots showing MB was reported at lower rates compared to mental states with content. Density kernels show how data are distributed and where peaks where aggregated. Box plots show interquartile ranges and medians. Point plots show individual data points.

was modelled as an epoch starting five TRs before probe onset, following evidence from a “thinking aloud” paradigm that showed that mental states tend to fluctuate slowly, with one experience being reported every 10 s (Van Calster et al., 2017). Given four regressors: [MB, Sens, SDep, SInd], subject-level analysis yielded the following T contrasts of interest: (1) positive effects of MB [1 0 0 0], (2) negative effects of MB [-1 0 0 0], (3) MB > Thinking [2 0 -1 -1], (4) Thinking > MB [-2 0 1 1], (5) MB > Sens [1 -1 0 0], (6) Sens > MB [-1 1 0 0], (7) Absence > Content [3 -1 -1 -1], (8) Content > Absence [-3 1 1 1]. The resulting contrast parameter estimates were aggregated at the second level and analysed using a one-sided, one-sample t-test.

Region-of-interest (ROI) analysis

Based on the a-priori hypothesis about the role of the ACC in monitoring thought contents, we additionally performed a ROI analysis based on MNI coordinates reported in Kawagoe et al. (2019) for the ACC (MNI: 3,39,-5). To examine whether previous findings on the neuronal correlates of MB during active mental silencing can be extended to spontaneous blanking periods in ongoing mentation, we also included the left hippocampus (MNI: -27,-33,-3) and Broca’s area (MNI: -47,26,20).

Given our hypothesis for the absence of frontal engagement in MB and the reduced statistical power of traditional frequentist approaches because of multiple comparisons, we opted for

Bayesian linear modelling (McElreath, 2020). For each ROI, we fit a linear model with beta values as a dependent variable, allowing the intercept to vary freely as a function of mental state.

2.3 Results

2.3.1 fMRI univariate analysis revealed deactivations spanning the whole brain

Initially, we focused on identifying regions associated with spontaneous MB occurrence during ongoing mentation. Overall, we found deactivations in the anterior cingulate cortex, the calcarine cortex, the bilateral thalami, the right anterior insula, the precentral gyrus, the left superior parietal lobule, the inferior frontal gyrus and the right operculum (Fig. 2.2; Table 2.1). To validate these results, we examined different TRs around the probe period. Although an uncorrected voxel-level threshold of $p = .01$ recurrently showed deactivations in frontal, parietal and thalamic regions, cluster correction showed that only the thalamus was consistently deactivated across all time increments. Additionally, to control potential movement effects specific to conditions, we estimated the overall framewise displacement of each subject at each time point (Power et al., 2012). Participants did not move significantly when considering displacement values per mental state category (MB: M = -.006, SD = .182, CI = [-.022, .009], SInd: M = -.003, SD = .143, CI = [-.008, .002], SDep: M = -.004, SD = .161, CI = [-.01, .003], Sens: M = -.006, SD = .254, CI = [-.018, .007]). No significant difference was observed in terms of displacement values across mental states (F(1,4) = .146).

At an FDR cluster threshold ($p<.05$), the contrast between MB and the other mental states did not identify any significant voxels. When the threshold was lowered to the exploratory whole-brain level of $p<.001$, n voxels>50, we observed deactivations in the angular gyrus (n voxels=64, Z=3.68, x=-60, y=-58, z=32), a finding mainly driven by the MB-SInd and MB-SDep thoughts contrasts(Fig. 2.3A). An examination of the individual regressor sign of activation (positive/negative) shows that MB tended to be significantly deactivated. On the other side, the other three mental states varied around 0 (Fig. 2.3B).

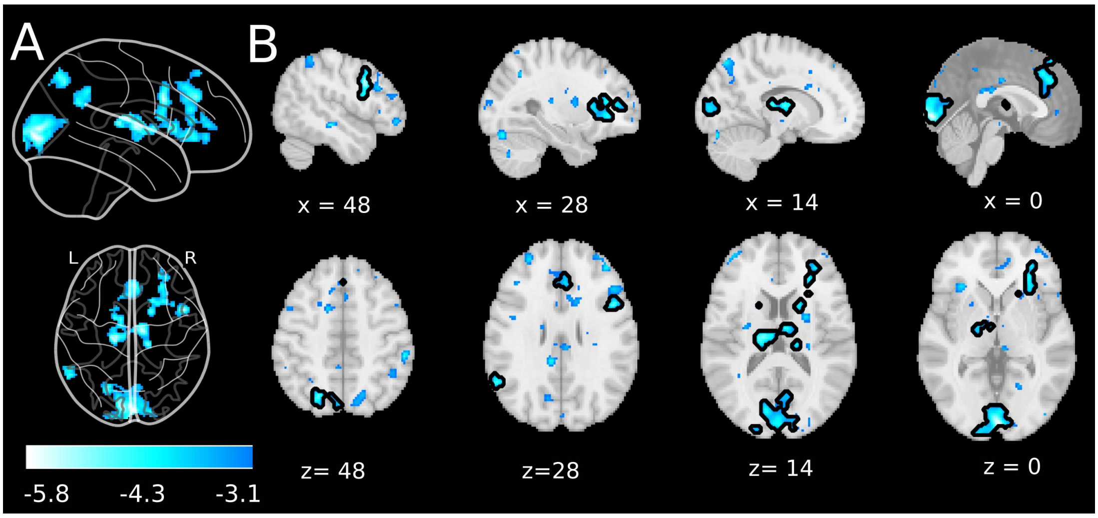

Figure 2.2: FMRI univariate analysis of MB reports reveals deactivations spanning the whole brain. Statistically significant deactivations were observed in the anterior cingulate cortex, the calcarine cortex, the bilateral thalami, the right anterior insula, the precentral gyrus, the left superior parietal lobule, the inferior frontal gyrus and the right operculum. A) Glass brain projection (view: top=sagittal, bottom=axial) at voxel-level $p_{\text{uncorrected}}<.001$, and cluster level $p_{\text{FDR}}<.05$. Color-bar indicates t-statistic. B) Activation maps of negative MB effects projected on the MNI152 cortical template (sagittal and axial views). Maps are calculated on 10 s preceding MB reports. The deactivated map projection is performed at voxel-level $p_{\text{uncorrected}}<.001$. Black contours signify the clusters that were significance at $p_{\text{FDR}}<.05$.

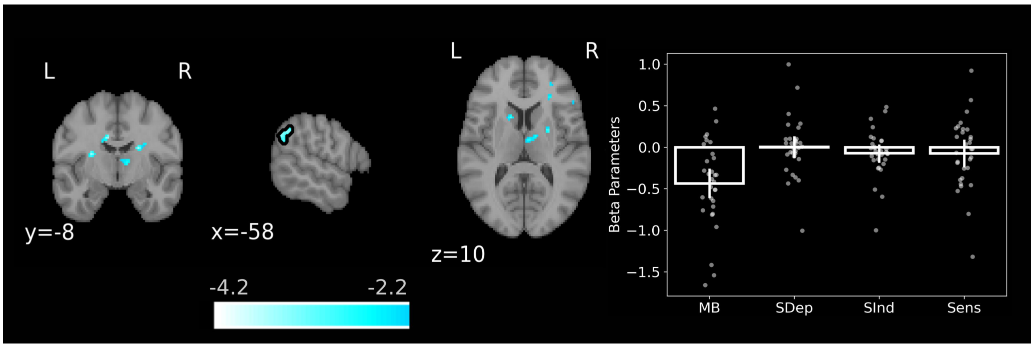

Figure 2.3: fMRI contrast analysis between content-oriented reports and MB at a lower exploratory threshold reveals deactivations in the left angular gyrus. A) Activation map of presence versus absence of content contrast, projected on the MNI152 cortical template (voxel-level $p_{\text{uncorrected}}<.001$). Black contours signify the significant clusters at a cluster-extent threshold > 50 voxels. The colorbar indicates t-statistic. B) Box plots representing the beta parameters of each mental state in the left angular gyrus cluster. Error bars indicate 95% confidence intervals. Data points show single-subject parameter values. MB: mind-blanking, SDep: stimulus-dependent thoughts, SInd: stimulus-independent thoughts, Sens: sensations.

2.3.2 fMRI Bayesian ROI analysis provided evidence of deactivations in the vmPFC/subACC

Based on our a-priori assumptions about the role of vmPFC/subACC in thought monitoring, we examined activations in the clusters reported in Kawagoe et al. (2019), namely, the vmPFC/subACC, Broca's area and the left hippocampus (Fig. 2.4A). Descriptive statistics of the posterior distributions for each ROI and mental state are presented in Table 2.2.

Table 2.1: fMRI univariate analysis reveals deactivations during 5 TRs preceding MB reports.

Region	**No. of voxels**	**Z peak**	***x***	***y***	***z***
Right calcarine cortex	1491	4.68	2	-92	0
Left calcarine cortex		4.54	-8	-88	6
Inferior frontal gyrus	243	4.51	48	10	32
Right operculum		3.76	48	10	22
Right thalamus	617	4.49	12	-12	8
Left thalamus		4.49	-18	-18	16
Superior frontomedial gyrus	472	4.21	2	36	34
Right anterior cingulate cortex		4.00	5	34	22
Left anterior cingulate cortex		3.55	-1	31	21
Left superior parietal lobule	187	4.14	-22	-68	46
Left precuneus		3.56	-4	-76	50
Right anterior insula	510	4.09	30	17	8
Right caudate		4.09	18	8	16
Left supramarginal gyrus	164	3.99	-58	-56	28

Voxel-level puncorr=.01, cluster-level pFDR <.05. X, Y, and Z coordinates refer to the AAL map.
HDI = highest density intervals.

Overall, the three ROIs' MB intercepts did not include 0 in their 95% credibility intervals (vmPFC/subACC = median: -.242, SD: .119, HDI: [-.471, -.01], Broca's area = median: -.245, SD: .091, HDI: [-.429, -.07], left hippocampus = median: -.113, SD: .056, HDI: [-.219, -.001]; Fig. 2.4D,F,H), suggestive of functional deactivations in these clusters. To examine whether the clusters showed specificity in MB compared with the other mental states, pairwise comparisons between the MB beta parameters and the betas of each other mental state were calculated, as well as an overall MB versus rest contrast. Pairwise comparison inference was performed by subtracting the MB posterior of each ROI from the posterior of the other mental states (Table 2.2). We found evidence only for the vmPFC/subACC cluster, namely MB reports were associated with reliably lower beta values compared with the other mental states (median = -.298, SD: .119, HDI: [-.527, -.054]). Additionally, we found significant effects for the contrast MB-SInd (median = -.366, SD: .167, HDI: [-.693, -.064]; Fig. 2.4E,G,I). Compared with the other mental states, MB was the only report category that was systematically deactivated, while the rest varied around. These results were consistent across the choices of different priors. No other ROI showed specificity for MB. To further validate whether the fitted models performed better against null models with only one intercept, for each fitted ROI we estimated the Watanabe–Akaike information criterion (WAIC) of the fitted and null model, as well as the expected log pointwise predictive density using leave-one-out cross-validation. Only for betas in

Table 2.2: Descriptive statistics for the posterior distributions of the beta parameters for each ROI and mental state.

Region of interest	Contrast	Median	SD	HDI (.025)	HDI (.975)
vmPFC-ACC	MB	-.242	.119	-.471	-.01
	SDep	.072	.118	-.158	.306
	SInd	.123	.118	-.114	.35
	Sens	-.027	.119	-.262	.204
	MB-All	-.298	.119	-.527	-.064
	MB-SDep	-.314	.167	-.64	.013
	MB-SInd	-.366	.167	-.693	-.04
	MB-Sens	-.214	.168	-.547	.111
Broca's area	MB	-.245	.091	-.429	-.072
	SDep	-.064	.091	-.242	.112
	SInd	-.205	.09	-.384	-.031
	Sens	-.202	.091	-.378	-.021
	MB-All	-.088	.091	-.272	.085
	MB-SDep	-.18	.129	-.434	.069
	MB-SInd	-.041	.129	-.287	.216
	MB-Sens	-.043	.128	-.289	.21
Left hippocampus	MB	-.113	.056	-.219	-.001
	SDep	-.119	.056	-.229	-.009
	SInd	-.069	.055	-.178	.041
	Sens	-.177	.056	-.287	-.068
	MB-All	.009	.056	-.098	.121
	MB-SDep	.007	.079	-.15	.162
	MB-SInd	-.044	.079	-.198	.111
	MB-Sens	.064	.079	-.094	.217

SD=standard deviation, HDI=highest density interval, vmPFC=ventromedial prefrontal cortex, ACC=anterior cingulate cortex

Table 2.3: Model comparison of fitted models.

Region of interest	Model	WAIC	ELPD
vmPFC-ACC	Fitted	-129.687	-129.868
	Null	-129.833	-129.908
Broca's area	Fitted	-93.934	-93.972
	Null	-91.857	-91.877
Left hippocampus	Fitted	-32.831	-32.856
	Null	-30.82	-30.847

WAIC = Watanabe–Akaike information criterion;
ELPD = expected log pointwise predictive density.

the vmPFC/subACC did the model containing multiple intercepts perform better than the null model (Fitted WAIC -129.687 < Null WAIC: -129.833, Fitted ELPD: -129.868 < Null ELPD: -129.908; Table 2.3). The validity of the model fit, as well as the specificity of the vmPFC/ACC cluster in MB was replicated across all examined prior distributions for every model.

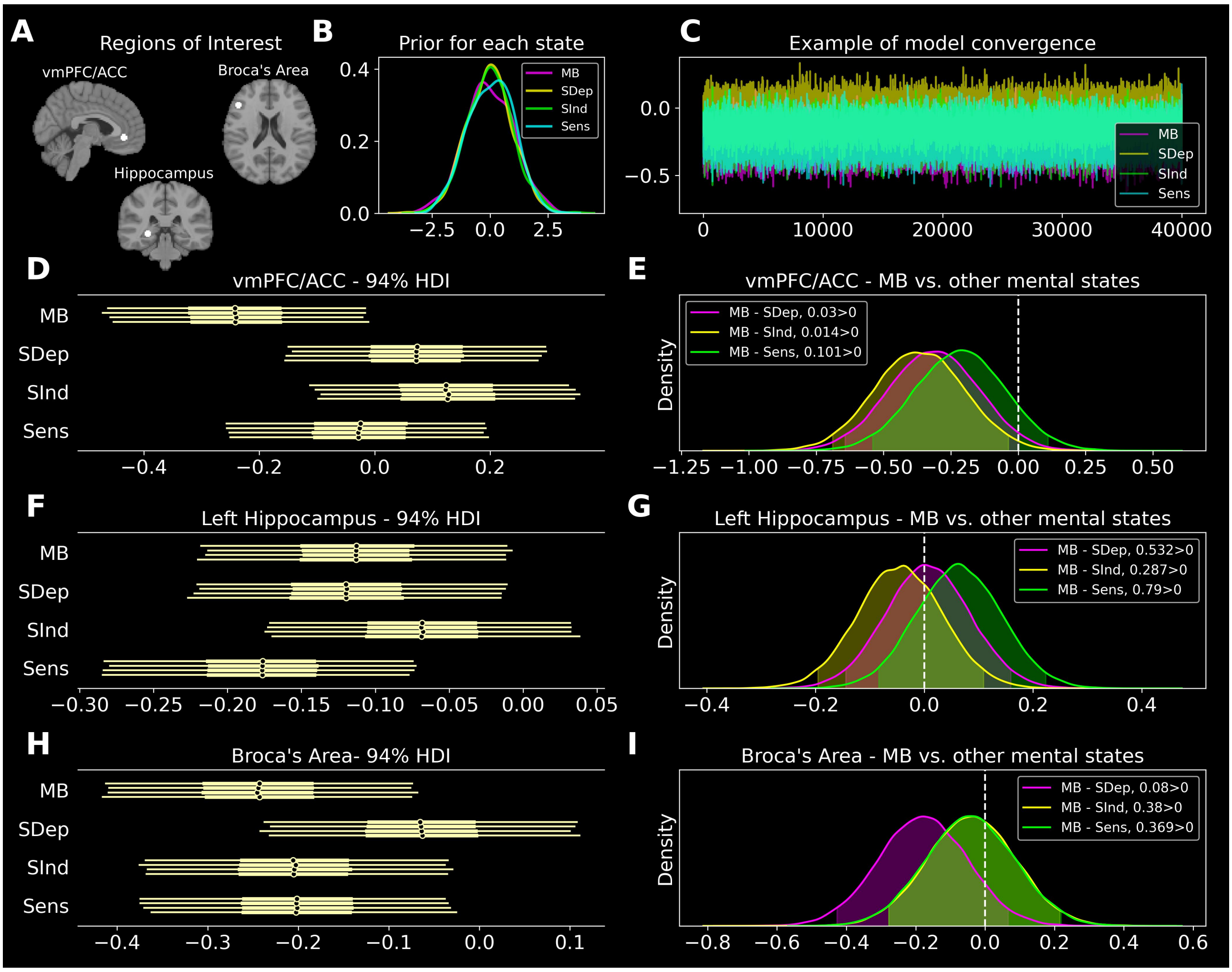

Figure 2.4: Bayesian analysis of the beta parameters in the vmPFC/ACC ROI reveals MB-related deactivations in this cluster. A) Regions of interest based on coordinates reported in Kawagoe et al. (2019) in the vmPFC/ACC, Broca's area, and the left hippocampus. B) Null model prior expectations, modelling each prior as $N(0, 1)$. C) Example traceplot of the model fit. Visual inspection of the random walk indicates that models converged, as the chains sampled the whole posterior space without autocorrelated data and sequential sampling of the same posterior space. D) Forest plot of each of the four sampled chains of the posterior distribution indicate that vmPFC/ACC contains significant evidence for MB deactivations, as the beta values did not contain 0 in the 94% highest density interval (HDI). Each line represents 94% highest HDIs. This was not the case for the rest of the mental states. E) Posterior differences between MB and the other mental states. We observed that the contrast MB-SInd did not contain 0 in the 94% HDI (shaded area), providing evidence that frontal deactivations differentiated between MB and SInd. F) Forest plot of each of the four sampled chains of the posterior distribution indicate that the left hippocampus is deactivated only in MB. This was also the case for SDep and Sens. G) Posterior differences between MB and the rest of the mental states at the left hippocampus. We observed that no contrast indicated any specificity of the ROI in MB. H) Forest plot of each of the four sampled chains of the posterior distribution indicate that the Broca's area contains evidence for MB contributions, as it does not contain 0 in the HDI. This was also the case for SInd and Sens. I) Posterior differences between MB and the rest of the mental states the Broca's area. We observed that no significant contrast indicating no specificity of the ROI in MB. MB=mind-blanking, SDep=stimulus-dependent thoughts, SInd=stimulus-independent thoughts, Sens=sensations.

2.4 Discussion

We re-analysed an fMRI experience sampling dataset to study the neural correlates of MB (MB) during unconstrained thinking and explore how instructions affect these correlates. Compared with mental states with reportable content, our findings indicate that spontaneous MB is linked to widespread deactivations in thalamocortical networks, which deviate from previous results.

We first show that deactivations spanning thalamocortical areas precede MB reports. The fMRI univariate analysis, examining positive and negative effects of MB, yielded deactivations in the anterior cingulate and calcarine cortex, the bilateral thalami, the right anterior insula, the precentral gyrus and the left parietal lobule. Such cortical deactivations have been previously associated with reduced neuronal resource allocation (Hester et al., 2004), task demands (Hairston et al., 2008), and impaired cognitive performance (Ji et al., 2010). Overall, we consider that the identified deactivations might represent brief periods of neuronal disengagement, during which the brain cannot support attentional and mental-reporting processes.

This is further supported by the finding that two key subclusters were further deactivated: the primary visual cortex and multiple cortical nodes of the salience network (Seeley et al., 2007). In previous work, thoughts unrelated to the immediate environment correlated with the decoupling of sensory areas from regions contributing to stimulus salience (Mittner et al., 2016). Indeed, instructing participants to think of nothing results in decreased connectivity between the DMN and the sensory cortices, potentially reflecting this decoupling of the sensory system and a system of internal thoughts (Kawagoe et al., 2018). The disengagement explanation is also supported by the deactivation of the thalamus, a recurrent node in saliency and engagement in mental state reportability (Kucyi et al., 2013). Thalamic activity covaries with executive control and attentional demands (Jansma et al., 2000; Antonucci et al., 2021). Potentially, the integrative nature of the thalamus (Hwang et al., 2017) is necessary to cast a mental spotlight and selectively allocate resources to bring a specific thought into conscious awareness. Overall, the rich profile of deactivations preceding MB reports highlights the important role of cortical nodes, traditionally associated with the salience of information.

On our quest to better understand the neuronal significance of such deactivations, we could resort to recent findings that analysed the same dataset but examined functional connectivity.

In that work, we show that MB reports are associated with a hypersynchronized fMRI cortical connectivity profile, further characterised by high global signal amplitude, which we interpreted as neuronal down-states (Mortaheb et al., 2022). Although it would be tempting to hypothesize a similarly low neural activation mediating the identified deactivations, we recognize that a one-to-one comparison between the two analyses is difficult to make, as different aspects of the BOLD signal are examined. Indeed, while task-based BOLD activations can be considered as proxies of neuronal firing (Logothetis et al., 2001), changes in resting-state activity can result from complex interactions among neural, vascular, and metabolic factors (Liu, 2013). As a result, it is not clear whether there is a direct mapping between BOLD activations and functional connectivity analyses.

Moving to report-specific effects by contrasting the presence versus absence of content, we also found that MB is characterised by deactivations in the left angular gyrus. Supporting variant mnemonic (Ciaramelli et al., 2008), attentional (Cattaneo et al., 2009), and semantic processes (Kuhnke et al., 2022), the angular gyrus is recurrently present in content-oriented mental states. Indeed, angular activations have been correlated with both MW during ongoing mentation (Christoff et al., 2004; Maillet et al., 2019) and external orientation of thought during task engagement across demanding and non-demanding tasks (Turnbull et al., 2019). Therefore, the idea of generalised contributions of the angular gyrus to content-oriented mental states is further supported by our finding of the inability to report mental content during deactivation of this region. Our results also are in line with previous electrophysiological results, where MB attentional lapses during task were predicted by posterior EEG slow-wave activity (Andrillon et al., 2021). The authors emphasised the role of parietal cortices in the emergence of conscious reports, where slow-wave activity might inhibit parietal-frontal communication and lead to the MB experience. We supplement this explanation by providing more granular structural information, introducing the angular gyrus as an important parietal node.

By performing an ROI analysis to examine previously reported MB-specific cortical areas, we found MB deactivations in the ACC/vmPFC. In the context of thought content, frontal activations were observed during MW with no meta-awareness compared with periods of MW with meta-awareness. The authors interpreted these larger activations as the ACC signalling a mismatch between the expected thought stream and actual, wandering thoughts, eliciting a higher degree of surprise to the participant (Christoff et al., 2009). Additionally, vmPFC activation is correlated with episodic and social self-generated thought (Konu et al., 2020). However, given the multiple partitions of the ACC, treating it as a unimodal region that collectively contributes to one specific cognitive process might be misleading. In our study, the cluster originated close to the borders between ACC and vmPFC, denoting that the previous activation might include multiple processes (a detailed account can be found in `https://neurosynth.org/locations/?x=4&%20y=40&z=-4`). Indeed, the vmPFC-ACC cluster is systematically implicated in evaluative (D'Argembeau, 2013) and metacognitive processes (Vaccaro & Fleming, 2018), which are facilitatory to the internal stream of thought (Smallwood et al., 2012). Given the self-evaluative aspect of ACC-vmPFC, we here interpret these deactivations as failures to recurrently examine the content of a thought, which can be formulated as self-referential questions ("Am I thinking of anything?"; D'Argembeau et al. 2007).

A series of studies have explored ongoing thought using multidimensional experience sampling questionnaires, aiming to decompose it into a low-dimensional space where all content types can be represented (Konu et al., 2020, 2021; Mulholland et al., 2023). Interestingly, this approach has revealed an overlap in the low-dimensional space of ongoing thought content between everyday life and in-lab task engagement, with consistent clusters related to social cognition, intrusive, unpleasant thoughts, and task focus (Konu et al., 2021; Mulholland et al., 2023). In this space, where each dimension represents different content, we suggest that MB could represent the origin point, devoid of specific thought engagement while moving away from this point would result in clearer content. Conversely, thoughts closer to the origin would exhibit less clearly reportable content. The activation patterns observed in the ventromedial prefrontal cortex (vmPFC) for thoughts along the social-episodic axis (Konu et al., 2020) and in the parietal lobule for thoughts along the task-focus axis (Turnbull et al., 2019) support this idea, as both these regions are deactivated during MB reports.

So far, only one study has examined the fMRI neural correlates of MB from a univariate perspective (Kawagoe et al., 2019). In that protocol, participants were instructed to "think of nothing" resulting in deactivations in Broca's area and the left hippocampus, and activations in ACC. Similar frontal activations have been observed in clinical settings, where patients with depressive symptoms were guided to suppress their thoughts (Carew et al., 2015). By bridging the current literature together, we suggest that the discrepancy between uninduced and self-induced MB may reflect the existence of different forms of MB, similar to mind-wandering, for which intentional and unintentional forms have been proposed (Seli et al., 2016). Intentional MB may originate from top-down monitoring to exclude thoughts, such as during meditation, while unintentional MB may arise from spontaneous lapses in frontal-parietal-sensory-thalamic systems that monitor the stream of consciousness and guide the ability to attribute semantic content to mental life. While this interpretation is still speculative, and the clear presence of different MB forms cannot be extrapolated from our dataset, it paves a promising avenue for future research contrasting different forms of "thought absence".

Several limitations pertain to our study. The duration and sampling rate of mental states, including MB, in fMRI experience sampling studies, may lead to under-sampling of infrequent and transient states (Mortaheb et al., 2022). Complementary methods, such as EEG, which allow for subsecond-level estimation of brain dynamics, could provide valuable insights into momentary markers of MB. Additionally, the standard GLM-summary statistics approach may be suboptimal because of the fundamentally unbalanced count of different mental states, resulting in reduced statistical power. In that sense, although the here identified effects remain safeguarded, we might nevertheless have missed others because of underpowered statistics. Finally, multivariable decoding approaches varying the duration of mental states could overcome the assumption of uniformity of mental state duration.

2.5 Conclusions

In conclusion, we investigated the neural correlates of uninduced MB during free-thinking conditions and found widespread thalamocortical deactivations, which may not allow the formulation of an efficient neural substrate to serve content reporting. We think these results provide mechanistic insights into the phenomenology of MB and point to the possibility of MB being expressed in different forms. As MB holds experimental, philosophical, and potential clinical implications for understanding the thought-oriented and stimulus-driven mind, we believe future research would benefit by incorporating MB in the investigation of unconstrained thinking.

Chapter 3

Variations of autonomic arousal mediate the reportability of MB occurrences

This chapter is based on:

1. **Boulakis, P. A.**, Simos, S. N., Zoi, S., Mortaheb, S., Schmidt, C., Raimondo, F., & Demertzi, A. (2025). Variations of autonomic arousal mediate the reportability of mind-blanking occurrences. *Scientific Reports*, 15(1), 4956.

3.1 Introduction

Cortical indices of low cortical arousal, such as the global signal amplitude or the presence of slow-wave activity, have previously been implicated during moments of MB (For an overview, please refer to Chapter 1). Much as it may have been done regarding cortical arousal, the current chapter focuses on how autonomic arousal influences MB reportability, which is widely understudied.

The study of autonomic implications in MB is motivated by the fact that arousal is a multidimensional term generally referring to the behavioural state of being awake and alert, supporting wakefulness, responsiveness to environmental stimuli, and attentiveness (Ogilvie, 2001). Early on, Lacey viewed arousal in terms of behavioural arousal (indicated by a responding organism, like restlessness and crying), cortical arousal (evidenced by desynchronised fast oscillatory activity), and autonomic arousal (indicated by changes in bodily functions) (Lacey, 1967). Anatomically, arousal is supported by the ascending arousal system, the autonomic nervous system, and the endocrine system. Therefore, different arousal pathways shape cortical excitability, and isolating cortical arousal does not capture the multiplicity of such pathways. For example, lower levels of arousal indexed by pupil size have been correlated with a higher probability of MB reports in sustained attention tasks (Andrillon et al., 2021; Stawarczyk et al., 2020; Unsworth & Robison, 2018). Finally, alterations in autonomic arousal were also found to influence brain activity in that fMRI volumes characterised by lower arousal levels (indexed by decreased pupil size) showed reduced in-between network integration and inter-subject variability in comparison to scans characterised by high arousal levels (indexed by increased pupil size) (Lee et al., 2022), a pattern of cortical integration-segregation that reflects the connectome brain properties in moments around MB reports (Mortaheb et al., 2022).

The current study examined whether different arousal states affect the propensity to report MB. Firstly, we examined how MB report distribution shifted across different autonomic arousal conditions, namely *baseline arousal*, *high arousal* elicited by intense exercise, and *low arousal* elicited by sleep deprivation. We expected deviations from baseline arousal levels to promote more frequent MB reports. Secondly, we opted to identify specific brain-body interaction patterns that would promote MB reportability. To this end, we utilised multimodal neurophysiological recordings and a machine-learning approach to decode MB reports from brain-body signals.

3.2 Methods

For an extensive overview of the methodology of this Chapter, please refer to the accepted paper appearing in Appendix 6.1.

3.2.1 Design

Experience sampling was utilised in a within-participants, repeated-measures design. During the experience sampling session, participants rested comfortably without specific instructions on where to direct their thoughts. Auditory probes (total n=40, inter-probe interval = ∼110 s) invited participants to report what they were thinking at the moment just preceding the probe, selecting from blank (MB), mind-wander (MW), perceptual sensations (SENS), or sleep (SLEEP).

We repeated the experience sampling task on three distinct days, under three conditions: a) experience sampling under spontaneous thinking without any arousal modulation (*Baseline*), b) experience sampling elicited through short, high-intensity interval training (*High Arousal*), c) experience sampling after total sleep deprivation (*Low Arousal*)(Fig. 3.1). Both arousal manipulations aimed to promote distinct changes in physiological and cortical markers associated with arousal mechanisms (Supplementary Table S6.2-2).

3.2.2 Brain-based measures

EEG was acquired using a 64-channel active electrode array, sampled at 500 Hz. Preprocessing included band-pass filtering (0.1 Hz–45 Hz, FIR filter), notch filtering (50 Hz), and epoch definition (t_{start} = 110 s preceding the probe, $t_{\max}$ = probe). We then used **independent component analysis** (ICA) decomposition to remove non-neuronal components such as blinks, heartbeats, muscle artefacts, etc. Finally, channels removed due to rejection were interpolated using neighbouring channels, and all channels were re-referenced to the average.

Based on EEG recordings, we estimated three classes of measures: 1) measures estimating

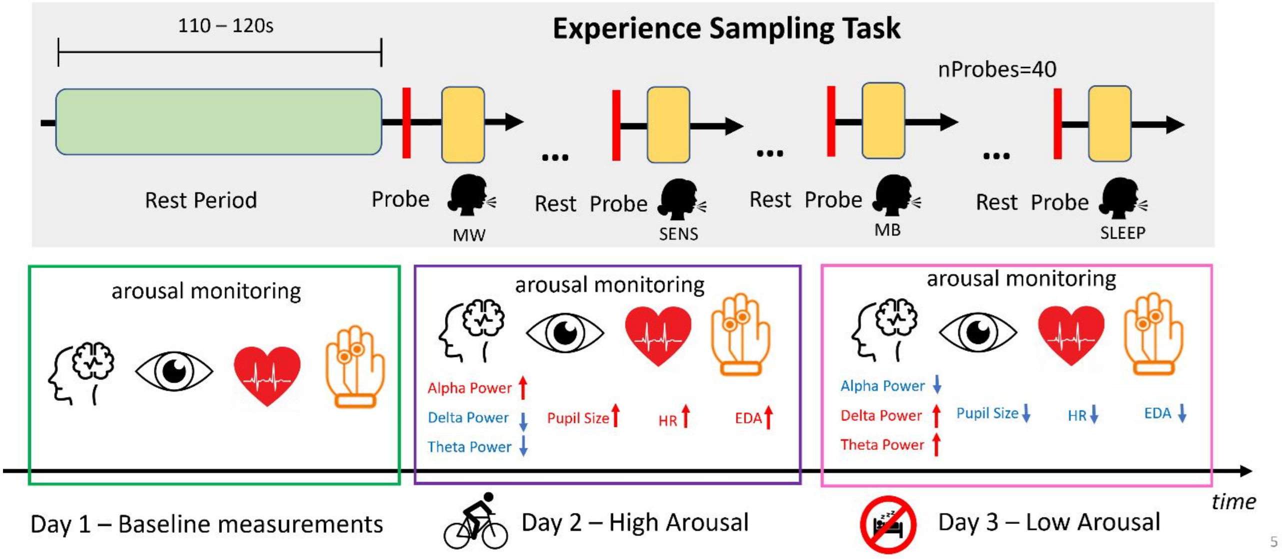

Figure 3.1: Experimental protocol. *Top.* The experience sampling task invited participants to sit idly and relax, letting their minds wander. Every 110-120 s, a 500 Hz auditory cue probed participants to report what they were thinking at that moment. Participants were able to choose from 4 presented responses: mind-blanking (MB), mind-wandering (MW), sensations (SENS), and sleep (SLEEP). *Bottom.* Repeated-measures autonomic arousal recordings. To test how spontaneous thoughts unfold over time across different arousal conditions, we first invited people for baseline assessments on Day 1 (*Baseline* condition). On Day 2, participants underwent a 15-minute high-intensity exercise routine (*High Arousal* condition), and on Day 3, they participated in a total sleep deprivation protocol (*Low Arousal* condition). The *High* and *Low Arousal* conditions were counter-balanced across participants. Multimodal physiological recordings were used to monitor arousal manipulations. The dataset was constituted of EEG, pupillometry, ECG, EDA, and respiratory data; the arrows indicate the hypothesised directions of the derived metrics. EEG=electroencephalography, ECG=electrocardiography, EDA=electrodermal activity

spectral power - raw and normalised power spectra, Median Spectral Frequency (MSF), spectral edge 90 (SEF90), and spectral edge 95 (SEF95), 2) measures estimating information content – spectral **entropy**, Kolmogorov-Chaitin complexity (K) and Permutation Entropy, and 3) measures estimating functional connectivity – Symbolic Mutual Information and weighted Symbolic Mutual Information. Power spectrum density (PSD) was computed over the delta (1-4 Hz), theta (4-8 Hz), alpha (8-12 Hz), beta (12-30 Hz), and gamma (30-45 Hz) spectral bands.

Regarding peripheral physiology, we acquired **Electrocardiography (ECG)**, respiration, pupillometry and **Electrodermal activity (EDA)**, sampled at 2 kHz. Body features were extracted from time, frequency, spectral and information domains.

3.2.3 Pattern recognition

To examine the physiological counterpart of the behavioural shifts in MB reports, we employed a supervised decoding approach. Using the multimodal neurophysiological measurements during the three experience sampling sessions, we trained multiple classifiers to discriminate across

MB, MW, and SENS reports and identify whether a unique brain-body interaction pattern supports MB. This approach allowed us to extract meaningful brain-body profiles from the proposed arousal metrics without being conservative about the nature of the multiple comparisons between the various body metrics. As learning algorithms, we tested parametric and non-parametric models, such as Support Vector Machines (Cortes & Vapnik, 1995), Random Forests (Breiman, 2001), and Extremely Randomized Trees (Geurts et al., 2006). Adopting a benchmarking approach, we analysed only the classifier with the highest classification performance. The classification was evaluated based on the balanced accuracy metric. Balanced accuracy is an evaluation metric suitable for imbalanced datasets, where one class appears at significantly different frequencies than the others. Balanced accuracy is useful because it is estimated as the average of specificity and sensitivity, simultaneously controlling for very high precision due to classifying nothing as the infrequent class and very high recall due to classifying everything as the infrequent class.

We adopted two classification schemes. In the first, we pooled reports across participants and each test/train split could contain reports from the same subject. This scheme creates meaningful brain-body profiles that can predict MB reports in participants it has already been trained in (“known”). In the second classification scheme, each participants could only be present either in the train or the test sample of the cross validation fold. The second scheme creates brain-profiles that can generalize to novel or “unknown” participants.

3.3 Results

3.3.1 Participants

To achieve a power of 0.95 at an alpha threshold of 0.05, we acquired three sessions of 40 trials per session from 26 participants (mean age=26.38, std=4.53, min=20, max=40; female=11). As a post-registration note, in case participants could not adhere to the strict 3-week protocol (30% total sessions), they were rescheduled to a later date that respected their sleep schedules to avoid time windows with potential extreme slow-wave activity (Lazar et al., 2015). Due to data corruption, one participant had 30 trials in one of the three sessions, and one participant had 33 trials in one of the three sessions. Both participants completed the remaining two sessions.

3.3.2 Behavioural Data

Occurrences of mental state reports altered across arousal conditions.

We found a main effect for mental states, with MB being reported at significantly lower rates (Mean proportions ±SD: MW=.56±.21, SENS=.2±.14, MB=.12±.13; Kruskal H=124.07, p=1.2e-27, eta2=.53) compared to MW (Dunn's test=-10.75, p_{FDR}=1.8e-26) and to SENS (Dunn's test=-2.85, p_{FDR}=4.3e-03). Additionally, MW was reported significantly more frequently compared to SENS (Dunn's test=7.9, p_{FDR}=4.3e-15; Fig. 3.2). As the study was focused on wakeful mental states, "SLEEP" reports were not included in the analysis (Mean proportions ±SD: *Baseline*=.03±.05, *High Arousal*=.05±.07, *Low Arousal*=.26±.21, Total =.1±.17).

We found that a model including all conditions outperformed a null model with only an intercept ($\text{Full}_{\text{LogLik}}$=-1021, $\text{Null}_{\text{LogLik}}$=-1046.83, chi^2=51.57, df=2, p_{Bonf}=6.1e-12): MB was reported significantly more frequently in *Low Arousal* compared to *Baseline* (MeanMarginal Mean=-.79, SE=.14, CL=[-1.16,-.43], p_{FDR} = 1.8e-08) and to *High Arousal* (Marginal Mean=-.97, SE=.15, CL=[-1.35,-.59], p_{FDR}=7.9e-11) (Fig. 3.3a). However, MB reports during *Baseline* and *High Arousal* were comparable (Marginal Mean=.17, SE =.15, CL=[-.21,.56], p_{FDR}=2.4e-01). A visual inspection of the individual marginal means showed that this effect was consistent across participants and was not driven by extreme cases (Fig. 3.3b-d). For a full list of mental state probabilities across arousal levels, please see Table 3.1

Additionally, generalised estimating equations (GEE) showed a significant interaction for MW between *Low Arousal* - *Baseline* (beta=6, SE=1.5, CL=[3.06, 8.94], p_{FDR}=6.4e-05) and *Low* - *High Arousal* (beta=8.23, SE=1.6, CL=[5.1, 11.36], p_{FDR}=2.6e-07). We also found significant interactions in SENS reports, such that SENS tended to be higher in *Baseline* compared to *High* (SENS *Baseline* - SENS High: beta=2.54, SE=.81, CL=[.96, 4.12], p_{FDR}=1.7e-3) and *Low Arousal* (SENS *Baseline* - SENS *Low*: beta=2.46, SE=.77, CL=[.96, 3.97], p_{FDR}=1.3e-3). It is of note that this analysis yielded no significant results for MB, but the overall trend of the beta estimates was consistent with our positive results of the logit model above (Supplementary Fig. S6.2-3). On a first glance, this result contradicts our registered analysis. However,

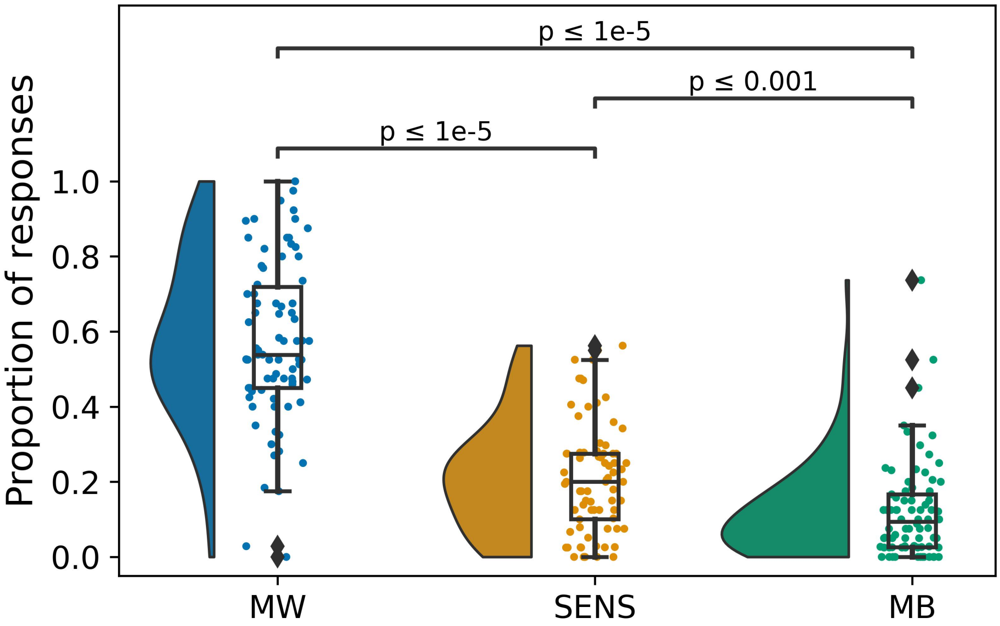

Figure 3.2: Mind-blanking (MB) was reported significantly less frequently compared to mind-wandering (MW) and Sensations (SENS) across all arousal conditions. Density kernels show overall data dispersion and clustering trends. Point plots are individual subject estimates. Box plots show medians and interquartile ranges, while whiskers indicate extreme values and diamonds indicate outliers.

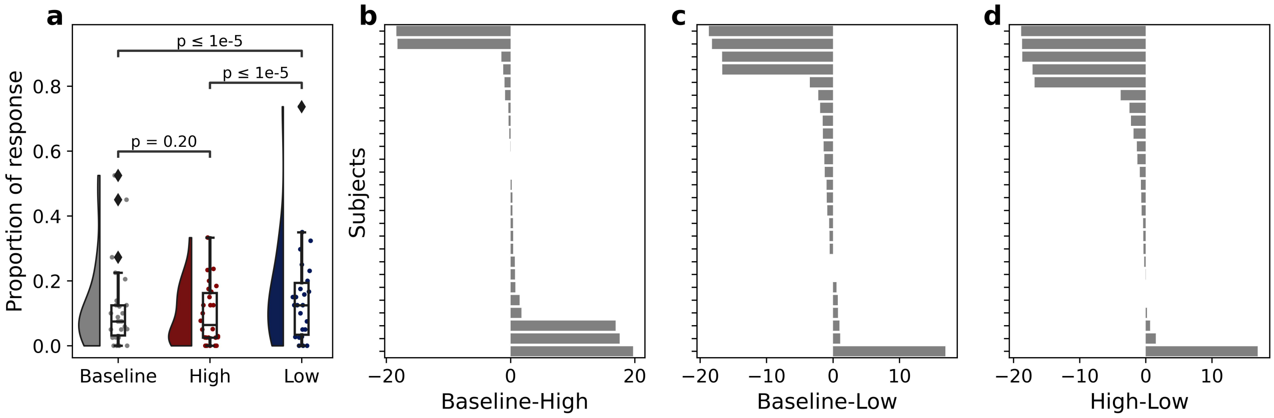

Figure 3.3: The frequency MB reports altered across the three arousal conditions. a) Mind-blanking (MB) report probability increased in *Low Arousal* (after sleep deprivation) compared to *High Arousal* (after intense exercise) and *Baseline*. Density kernels indicate overall data dispersion and clustering trends. Point plots represent participants' MB report probabilities. Box plots indicate medians and interquartile ranges, whiskers indicate extreme values, and diamonds indicate data outliers. b-d) Bar plots denote single-subject marginal means, comparing MB reports across arousal conditions. Compared to *Baseline*, there was no significant change during *High Arousal* (b). However, there was a visible trend favouring an increased probability of MB reports in the *Low Arousal* condition compared to *Baseline* and *High Arousal*, signifying that the effect was present in most participants (c-d).

considering that the directionality of the parameters remained the same and this protocol was not powered for a GEE analysis and the subsequent multiple contrasts, it is more likely that the present GEE analysis was underpowered to uncover significant results.

Table 3.1: Mental state report frequencies alter across arousal levels

Arousal Level	Mental State	Mean	SD
Baseline	MW	0.62	0.17
	SENS	0.26	0.15
	MB	0.13	0.14
Low	MW	0.53	0.23
	SENS	0.23	0.16
	MB	0.24	0.23
High	MW	0.69	0.17
	SENS	0.2	0.15
	MB	0.11	0.14

SD=standard deviation, MW=mind-wandering,
MB=mind-blanking, SENS=sensation

MB was characterised by higher reaction times.

There was a main effect of arousal conditions, with reports during *Baseline* being reported the fastest and during *Low Arousal* the slowest (Fig. 3.4a). Also, there was a main effect of mental states, with MW reports being reported the fastest and MB reports the slowest (Fig. 3.4b). A significant interaction between MW and arousal showed that MW was reported the slowest in *Low Arousal* (Fig. 3.4c). A significant interaction between MB and arousal condition showed that MB was reported the slowest in *High Arousal* and *Low Arousal* (Fig. 3.4e). A model including both arousal and reaction times outperformed simplified models including only null or main effect terms ($\mathrm{Full}_{\mathrm{LogLik}}$=2889.76, chi^2=47.1, df=4, p_{Bonf}=1.5e-09; Fig. 4c). For a detailed overview of main effects and interactions, see Supplementary Table SS6.2-3.

Transition probabilities showed reduced probability to transition to MW in Low arousal.

Markov transition probabilities indicated significant differences only between *High* and *Low Arousal* conditions (Fig. 3.5), such that MW was more likely to be followed by MB (t=3.26, CI=[.03,.15], p_{FDR}=9.7e-03, Cohen's D=.74). Also in *Low Arousal*, both MW (t=-3.79,CI=[-.31, -.9], p_{FDR}=7.6e-03, Cohen's D=-.86) and SENS (t=-3.43, CI=[.37, -. 09], p_{FDR}=9.5e-03, Cohen's D=-.77) were less likely to be followed by MW (Fig. 3.5; Supplementary Fig. S6.2-4).

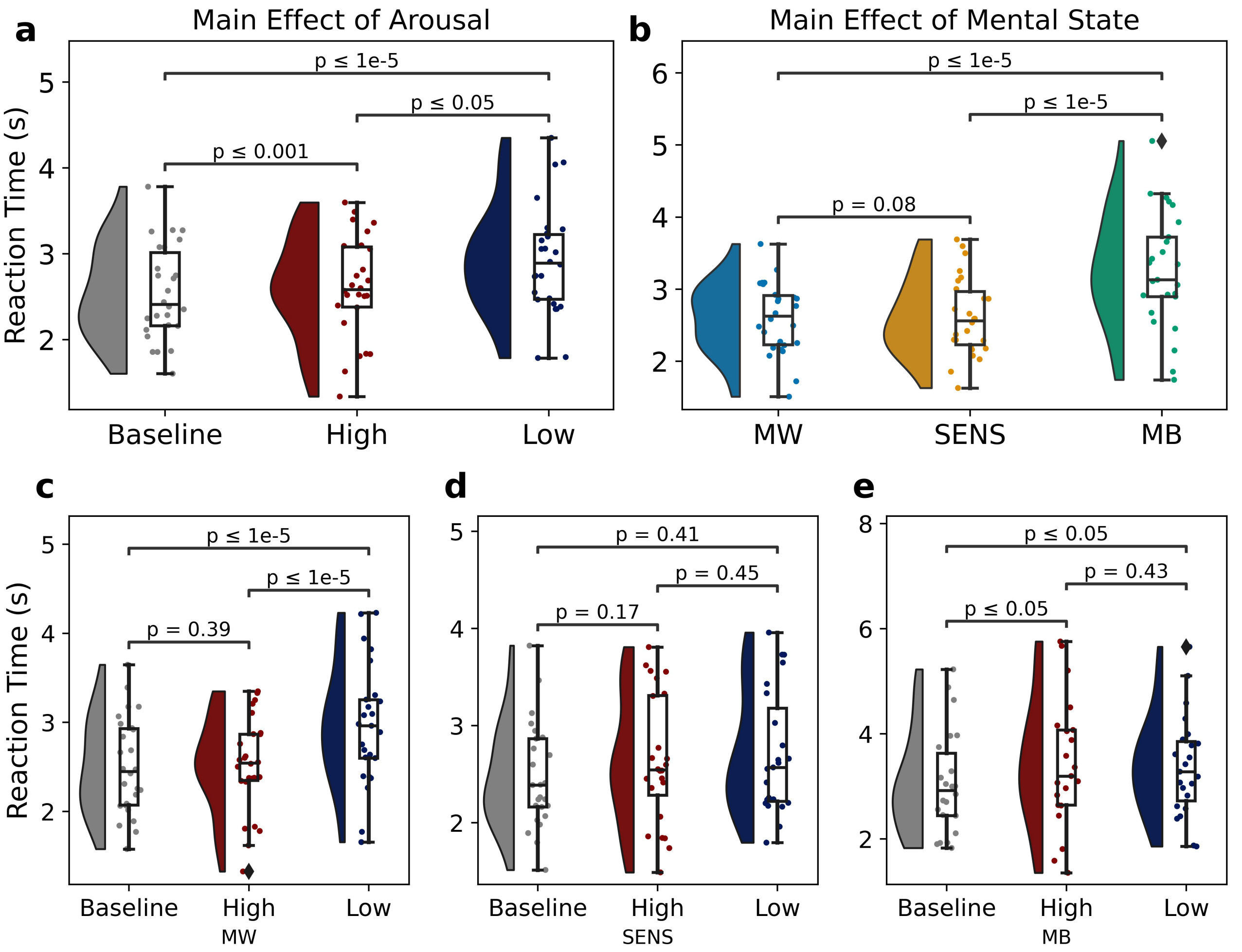

Figure 3.4: Mental states had different report times depending on arousal conditions. a) Reaction times, defined as the time difference between the auditory response probe and the mental state reports, were reported the fastest at *Baseline Arousal*, followed by *High* (after exercise) and *Low Arousal* (after sleep deprivation), collapsed across all mental states. Point plots show individual subject estimates. Box plots show medians and interquartile ranges, while whiskers show extreme values. b) Mind-wandering (MW) was reported the fastest, followed by Sensations (SENS) and mind-blanking (MB), collapsed across all arousal conditions. Point plots show individual subject estimates. Box plots show medians and interquartile ranges, while whiskers show extreme values. c-e) Interaction between arousal condition and mental state report times: MW was reported the slowest in *Low Arousal* compared to *Baseline* and *High Arousal*. In contrast, MB was reported the slowest in the *Low Arousal* and *High Arousal* conditions compared to *Baseline*.

Exploratory Analysis 1: MB frequency did not correlate with SLEEP frequency.

As we wanted to avoid participants confounding MB and SLEEP reports, we opted for a paradigm that allowed participants to report both. Spearman correlations on each condition examined whether these two states were correlated. Across all arousal states, there was no evidence of a correlation between MB and sleep report frequencies (*Baseline*: r=.13, p=5.3e-01, *High Arousal*: r=.31, p=1.3e-01, *Low Arousal*: r=-.05, p=8.2e-01) (Supplementary Fig. S6.2-5). To strengthen the claim that MB and SLEEP reports do not covary, we additionally ran separate equivalence tests on each correlation. No test was able to reject an equivalence claim

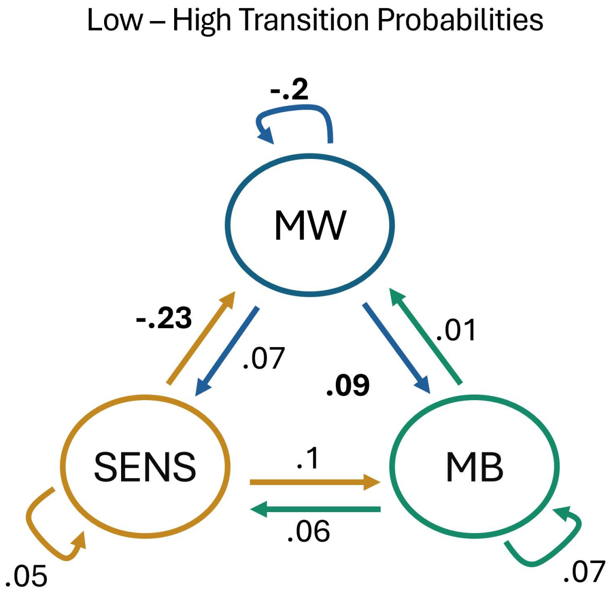

Figure 3.5: Sleep deprivation leads to more frequent mind-blanking (MB) and less frequent mind-wandering (MW). After sleep deprivation (*Low Arousal*), participants were more likely to transition from MW to mind-blanking MB compared to the condition of physical exercise (*High Arousal*). Additionally, participants were less likely to transition to MW. Arrows indicate the direction of the mental state transition. Bold font indicates statistical significance (FDR corrected).

(*Baseline*: z=-.34, p=3.7e-01, *High Arousal*: z=.54, p=7e-01, *Low Arousal*: z=.72, p=2.3e-01). Therefore, these results remain indeterminate.

Exploratory Analysis 2: High Arousal MB reports increased at the start, but not the end, of the experience sampling session.

While we found that MB reports were more frequent in *Low Arousal*, we did not find any significant effect of *High Arousal*. In our original hypothesis (Supplementary Table S6.2-1), we registered as a potential alternative explanation for the absence of an effect that high arousal, as elicited by high-intensity exercise, might not last for the full session, and our session would represent a gradual return to *baseline Arousal*. To test for potential effects of more frequent MB reports only at the start of the experience sampling we split the *High Arousal* session in two parts and compared the count of MB reports across the start and the end of the experiment. Using a chi-squared test we found a significant effect, with MB reports being more frequent (divergence=4.08, p=3.2e-02) during the first half of the *High Arousal* condition compared to the second half (MB_{start}=93, MB_{end}=66). We additionally attempted to validate this hypothesis by splitting the session into 4 and 6 discrete segments of 10 and 7 trials each and replicated the same analysis. However, this analysis did not reach significance. Finally, to provide further evidence for reduced occurrences of MB across time, we considered only the first and last 10 trials. We found a significant effect of more frequent MB occurrences (divergence=7.39, p=6.6e-03), with the first 10 trials of the *High Arousal* condition inducing more MB compared to the second half ($\mathrm{MB}_{\mathrm{start}}$=51, $\mathrm{MB}_{\mathrm{end}}$=27).

3.3.3 Brain-Body decoding

Classification of MB reports was outperformed by classification containing both BRAIN-BODY markers.

We evaluated the capacity to classify MB reports from mental states with content (MW, SENS) based on 26 BRAIN (EEG) and 31 BODY features (12 ECG, 4 EDA, 8 RSP, 7 EYE), spanning time, frequency, information, and connectivity domains for each mental state report. In our original report, we registered that these features would be estimated across the 110 s pre-probe window, with bad epochs being dropped. However, across an 110s epoch, even a nonlinearity of 1 s would result in epoch removal, leaving a total clean sample of 25 / 78 sessions (29.4%), and a total of 1060/3120 (33.3%) clean epochs. Therefore, to preserve data points and data quality, and minimize data discarding due to brief non-linearities, we opted for an extra step in bad epoch removal. After the initial epoch definition of 110 s, we followed it up by partitioning that epoch into 5 s sub-epochs, resulting in 22 sub-epochs per epoch. We then proceeded to do bad epoch removal and EEG marker estimation on those sub-epochs. If an epoch consisted of more than 50% bad sub-epochs, it was discarded. Then, we averaged across within each epoch, resulting in no lost sessions, and a total of 2734 / 3120 (87.6%) total sample size.

Having a final 2734 reports x 57 features matrix per report, we trained multiple classifiers on the total dataset, to examine whether a specific brain-body profile would outperform chance level classification of MB reports (Table 3.2).

Due to the unbalanced nature of our dataset, we evaluated classifier performance based on balanced accuracy, as it avoids inflated performance on unbalanced datasets. Overall, we found that a balanced random forest (a random forest that undersamples the majority class in each bootstrap to equate class count) has above-chance performance and outperforms all other examined classifiers (Fig. 3.6a). We additionally examined whether we could predict unknown subjects, by leaving a subset of subjects out on each iteration. Due to the high degree of per-

Table 3.2: A balanced random forest classifier outperformed all classifiers when compared across balanced accuracy. Cells indicate mean and 95% CI.

Examined	Classifier	Recall	Precision	F1	ROC AUC	Balanced Accuracy
Known Subjects	Balanced RF	.62, [.6, .64]	.26, [.26, .27]	.37, [.36, .37]	.71, [.7, .72]	.66, [.65, .67]
	SVM	.29, [.28, .31]	.28, [.27, .29]	.29, [.27, .3]	.62, [.61, .63]	.58, [.58, .59]
	ET	.16, [.15, .17]	.61, [.58, .64]	.25, [.23, .26]	.73, [.72, .74]	.57, [.56, .58]
	RF	.14, [.13, .15]	.57, [.53, .6]	.22, [.21, .23]	.71, [.7, .72]	.56, [.56, .56]
	IF	.14, [.13, .16]	.2, [.19, .22]	.17, [.15, .18]	.52, [.52, .53]	.52, [.52, .53]
	OC SVM	.89, [.86, .92]	.15, [.14, .15]	.25, [.25, .25]	.51, [.5, .51]	.51, [.5, .51]
	DUMMY	.14, [.13, .15]	.14, [.13, .15]	.14, [.13, .15]	.5, [.49, .5]	.5, [.49, .5]
Unknown Subjects	Balanced RF	.46, [.41, .51]	.18, [.16, .2]	.25, [.23, .27]	.55, [.53, .57]	.54, [.53, .56]
	IF	.23, [.19, .27]	.18, [.16, .2]	.19, [.17, .22]	.53, [.51, .54]	.53, [.51, .54]
	RF	.05, [.04, .06]	.36, [.29, .44]	.08, [.06, .09]	.54, [.52, .55]	.51, [.51, .52]
	OC SVM	.87, [.82, .92]	.14, [.13, .15]	.24, [.22, .26]	.51, [.5, .52]	.51, [.5, .52]
	ET	.03, [.02, .03]	.36, [.26, .45]	.05, [.04, .06]	.53, [.52, .55]	.51, [.5, .51]
	DUMMY	.15, [.14, .16]	.15, [.13, .17]	.14, [.13, .16]	.5, [.49, .51]	.5, [.5, .51]
	SVM	.2, [.17, .22]	.16, [.14, .17]	.16, [.15, .17]	.49, [.47, .5]	.5, [.49, .51]

RF = Random Forest; SVM = Support Vector Machine; ET = Extreme Trees; IF = Isolation Forest;
OC SVM = One-Class Support Vector Machine

Table 3.3: A classifier trained on both BRAIN and BODY features outperformed classifiers trained solely on BRAIN or BODY features when evaluated with balanced accuracy. Cells indicate mean and 95% CI.

Classifier	**Recall**	**Precision**	**F1**	**ROC AUC**	**Balanced Accuracy**
BRAIN + BODY	.62, [.6, .64]	.26, [.26, .27]	.37, [.36, .37]	.71, [.7, .72]	.66, [.65, .67]
BRAIN	.61, [.59, .62]	.24, [.24, .25]	.35, [.34, .36]	.7, [.69, .71]	.65, [.64, .65]
BODY	.59, [.58, .6]	.22, [.21, .22]	.32, [.31, .32]	.66, [.66, .67]	.61, [.61, .62]
EYE	.57, [.55, .59]	.21, [.21, .22]	.31, [.3, .32]	.64, [.63, .65]	.61, [.6, .62]
ECG	.55, [.54, .57]	.18, [.17, .18]	.27, [.26, .27]	.58, [.57, .59]	.56, [.55, .57]
EDA	.6, [.57, .63]	.17, [.17, .17]	.26, [.26, .27]	.57, [.56, .58]	.55, [.54, .56]
RSP	.52, [.5, .54]	.15, [.15, .16]	.24, [.23, .24]	.53, [.52, .54]	.52, [.51, .53]

fold variance, we do not consider any classifier as meaningfully performing above chance level (Fig. 3.6b). Importantly, these results were replicated when we trained the classifiers in the 1 Hz filtered data (Supplementary Fig. S6.2-66a,b; Supplementary Table S6.2-4).

Having established that MB reports can be predicted from known subjects, we then examined whether a brain-body data pattern would outperform classifiers trained solely on either BRAIN or BODY features. To this end, we fit and optimized a separate balanced random forest classifier on discrete feature combinations of our dataset. For a full report of the performance on different features, see Table 3.3 and Supplementary Table S6.2-5.

Overall, we found that a classifier trained on both BRAIN and BODY markers marginally outperformed classifiers trained solely on BRAIN or BODY features across all our performance metrics (Fig. 3.7a,c; Supplementary Fig. S6.2-7a,c; Table 3.3; Supplementary Table S6.2-5). To evaluate the impact of the number of features on the capacity of the learning algorithm to

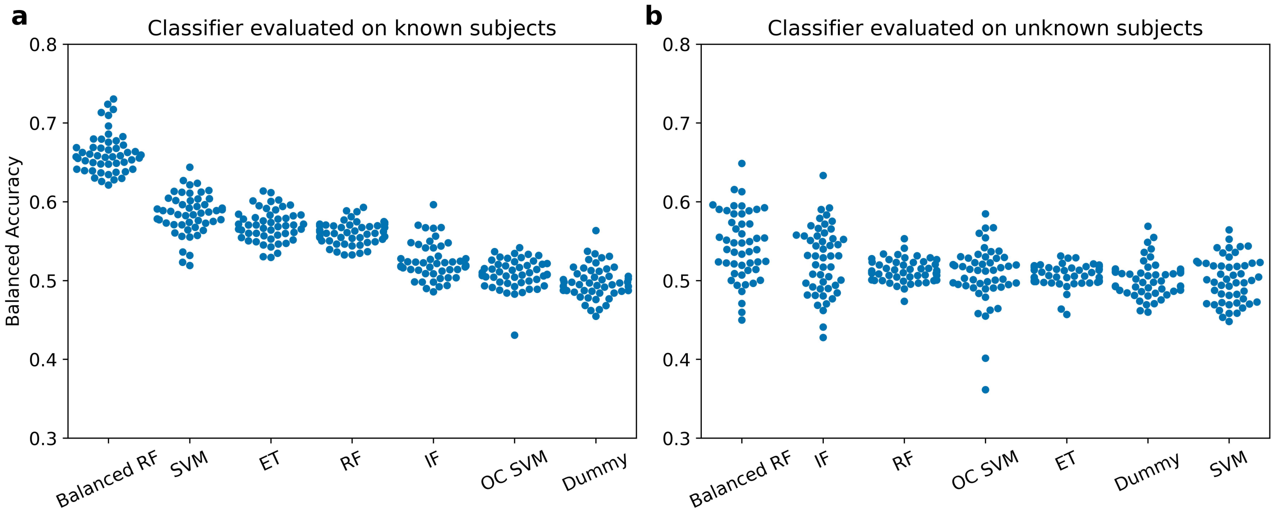

Figure 3.6: Classification performance was above chance level when mind-blanking (MB) reports were pooled across subjects, but not after training on a subset of participants and classifying the remaining subset. a) A balanced random forest classifier provided the highest classification performance across all examined classifiers including known subjects. b) An isolation forest classifier provided the highest classification performance across all examined classifiers on unknown samples. However, due to the high variance, we could not consider it meaningful. Individual points indicate performance on the folds of the repeated cross-validation. Results are ordered based on descending order of performance. Chance level performance is indicated by the Dummy classifier. RF = random forest; SVM = support vector machine; ET = extreme trees; IF = isolation forest; OC SVM = one-class support vector machine.

extract relevant information, we also trained the balanced random forest model using randomly shuffled bodily features. EEG features were not altered. The model with the shuffled values showed a decline in classification performance, providing evidence that, when classifying mental states, a model trained on both brain and body data learns unique information from both domains (Fig. 3.7d; Supplementary Fig. S6.2-7d). For feature importance, we calculated **Shapley Additive Explanations (SHAP)** (SHAP) values for each feature in our dataset. SHAP values estimate the marginal contribution of each feature, averaged across every potential feature combination. In this manner, each value represents how much this feature contributes to the classification, after controlling for the impact of other features on this feature's importance. We found that the model relied mostly on EEG and EYE openness features to discriminate MB reports when pooling MB occurrences across all three conditions. (Fig. 3.7b; For an extensive list of all SHAP values, see Supplementary Fig. S6.2-8). Importantly, feature importance did not substantially change when filtering the data with a 1 Hz filter (Supplementary Fig. S6.2-7b; For an extensive list of all SHAP values, see Supplementary Fig. S6.2-9). Overall, the comparable performance of the models, and the high degree of overlap in the ranking of the feature importance point to the robustness of the models.

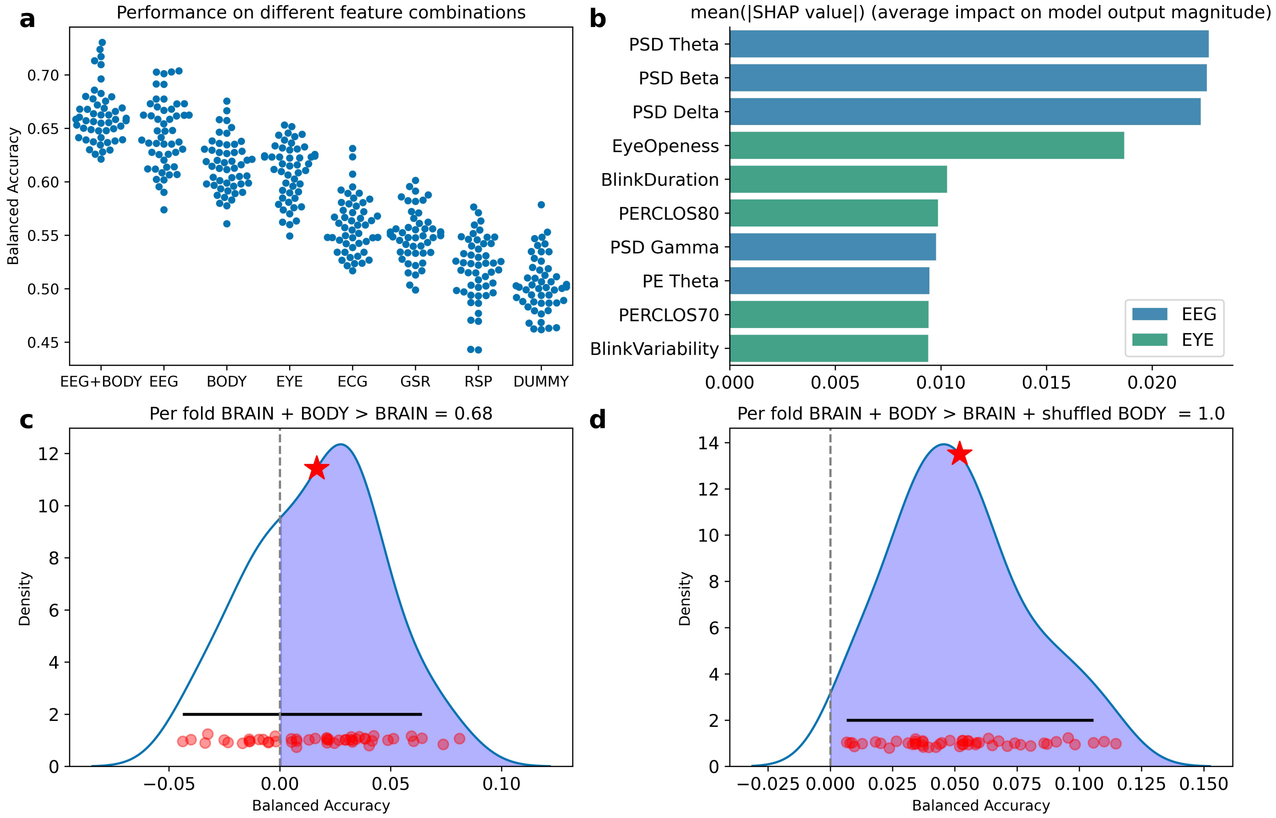

Figure 3.7: Combining information from both BRAIN and BODY markers leads to optimal classification performance. a) A balanced random forest classifier trained on a combination of BRAIN and BODY features outperformed classifiers trained solely on BRAIN or BODY features when evaluated with balanced accuracy. Individual points indicate performance on the folds of the repeated cross-validation. b) Subset of the 10 features with the highest mean of the absolute SHAP values obtained from the balanced random forest classifier. c) The per-fold differences between the classifier trained on both BRAIN and BODY features and the one trained only on BRAIN data suggest that incorporating both feature domains provides a slight performance improvement over using BRAIN data alone. The shaded region indicates better performance for the classifier trained on both feature domains. The star indicates the mean difference. The solid, horizontal line represents the 95% highest-density intervals of the distribution. Red dots indicate per-fold differences. d) The per-fold differences between the classifier trained on both BRAIN and BODY features and the one trained on BRAIN and shuffled BODY data suggest that the model with both BRAIN and BODY data does not consider the body markers as noise.

Exploratory analysis 3: Feature importance altered across arousal conditions.

The decoding analysis in known samples showed we could predict MB instances from the combination of brain-body markers with adequate accuracy when MB instances were aggregated across different arousal conditions. We were further interested in whether this classification was achieved based on a universal mechanism or whether we could detect arousal-dependent brain-body configurations that predict MB. To this end, we trained a balanced random forest classifier solely on data acquired from *Baseline*, from *High*, and from *Low Arousal*. We found that *Baseline* had the best performance (.67, [.65, .68]), followed by *Low Arousal* (.64, [.63, .65]), and finally *High Arousal* (.61, [.6, .63]). We retained comparable performance when examining the arousal partitions of the 1 Hz filtered dataset (Supplementary Table S6.2-6). We examined the SHAP values for each arousal state and found that the models relied on distinct feature domains. During *Baseline*, the model relied on markers from the frequency domain of EEG (Fig. 3.8a). During *Low Arousal*, MB classification was obtained using the delta band power, by far the most dominant marker (Fig. 3.8b). Finally, in *High Arousal*, the model did not rely on a single feature but rather on a combination of eye openness, EDA, and the frequency domain of EEG (Fig. 3.8c). Similar feature importances were observed in the 1 Hz filtered dataset (Supplementary Fig. S6.2-10). However, in the 1 Hz filtered dataset, we observed that ECG features tended to rank higher (Supplementary Fig. S6.2-11 to 6.2-16).

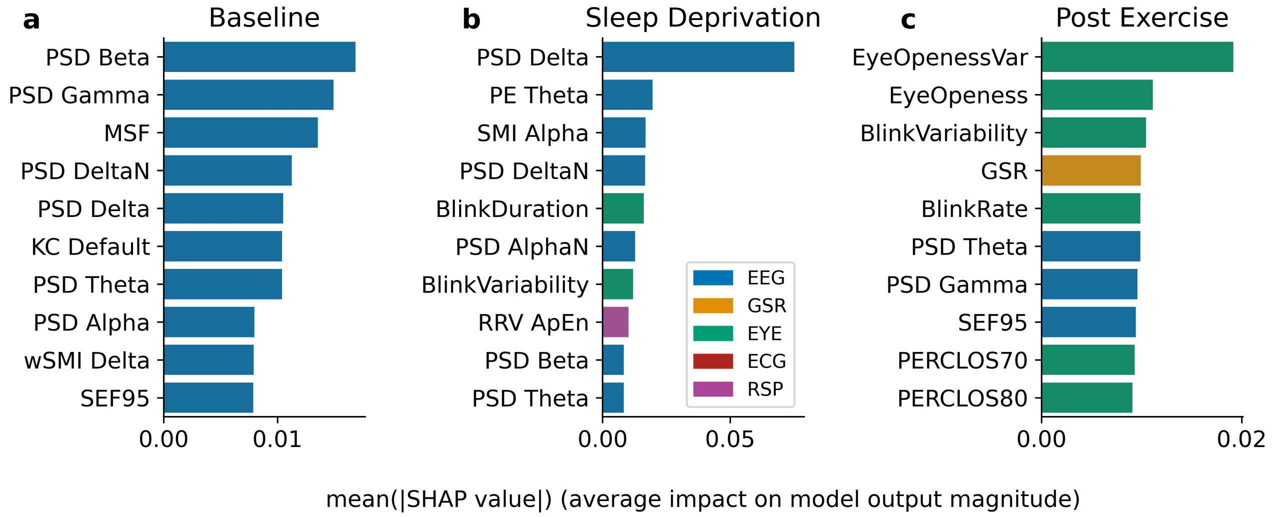

Figure 3.8: Ranking of features by mean absolute SHAP value extracted from the balanced random forest classifier varied across different arousal conditions. a) Magnitude of SHAP values for a balanced random forest classifier trained on MB reports collected during the *baseline Arousal* condition. The model relied mostly on features from the EEG frequency domain. b) Magnitude for SHAP values for a classifier trained on MB reports collected during the *Low Arousal* condition (after sleep deprivation). The model mostly used spectral power in the EEG delta band. c) Magnitude for SHAP values for a classifier trained on MB reports collected during the *High Arousal* condition (after intense exercise). The model relied mostly on features from eye openness, EDA, and the EEG frequency domain.

Exploratory analysis 4: Feature importance altered based on the pre-probe analysis window.

A potential caveat of utilising the entire pre-probe period of 110 s before a report is that we might capture multiple mental states, and the actual statistical regularities might be weakened when averaged across. With this consideration, we examined whether we could improve classification performance when classifying MB from the last 10 s before a report. We defined a secondary brain-body data matrix, with body features that could be estimated from 10 s of body activity. Across both 0.1 and 1 Hz filters we retained comparable performance in the classifiers trained on both EEG and bodily markers, as well as solely EEG or body markers (Supplementary Fig. S6.2-17 to 6.2-20; Supplementary Table S6.2-7 and 6.2-8). However, we observed decreased performance in the classifier trained solely in the eye openness data (Supplementary Table S6.2-7 and 6.2-8). An examination of feature importance showed that the beta, delta, and theta bands of the EEG frequency domains remained the most important EEG features, but there was a reduction in the importance of the EYE features and an increase in the importance of EDA (Supplementary Fig. S6.2-17b,6.2-18,6.2-19b,6.2-20). Importantly, our results were not affected by the choice of filtering parameters, indicating robustness of our results to preprocessing parameters.

3.4 Discussion

We used experience sampling combined with EEG and peripheral physiological recordings under different autonomic arousal conditions to determine whether MB reports in neurotypical individuals were supported by distinct brain-body configurations compared to mental states with reportable content. Overall, our results show that MB is a mental state that becomes more prevalent in low and partially high arousal states and is correlated both with brain and body processes, providing evidence for an embodied account of MB.

Behaviourally, we found that MB was reported at significantly lower rates compared to sensory experiences or MW, irrespective of the arousal condition. This finding is in line with past research showing that MB rates vary between 5-10% of total probe instances across both uninterrupted thinking (Mortaheb et al., 2022) and task engagement (Andrillon et al., 2021). We also show that sleep deprivation significantly increases the frequency of MB occurrences. Sleep deprivation induces a low arousal state during which cognitive performance declines (Hudson et al., 2020), metabolic and physiological processes change (Csipo et al., 2021), and unique neuronal markers, such as slow-wave activity, emerge (Krause et al., 2017). After sleep deprivation, participants also tend to perform worse in sustained attention tasks (Qi et al., 2010), with results suggesting a true effect of sleep deprivation on more “misses” (no response when necessary) compared to “false alarms” (response when unnecessary)(Gosselin et al., 2019), a finding that was recently shown as a behavioural correlate of MB. Additionally, sleep deprivation and mounting sleep pressure were positively correlated with more MW instances (Poh et al., 2016; Carciofo et al., 2014), suggesting an overall mode shift from task engagement to MW (Jubera-Garcia et al., 2021). Our results challenge these past findings by showing that participants were more likely to blank than mind wander after sleep deprivation. We also show that MW was, in fact, more likely to decrease after sleep deprivation. This is further supported by the results of the transition matrix analysis, where MW reports were less likely to be followed by another MW report and more likely to be followed by MB. Such discrepancies in the reportability of MW after sleep deprivation could be explained by the explicit inclusion of MB and sleep as available mental states for report. In other words, the previously observed increase in the frequency of MW after sleep deprivation could be accounted for by MB and sleep reports, once participants could opt between these mental states in a more fine-grained way.

In terms of high arousal induced by high-intensity exercise, our analysis did not reveal any significant effects on MB occurrences. As per the provided registered protocol alternative explanation (Supplementary Table S6.2-1), we hypothesised that this arousal manipulation might not have been overall effective as it could not produce effects that would last across the whole experience sampling session. We split the dataset into two parts to test whether MB frequency reports would differ between the beginning and the end of the session. When split, we found a significant difference between the frequency of MB reports. This result was replicated when considering only the first and last 10 trials per subject, which maximised the distance between initial and final physiological arousal within the session. However, we were not able to find any differences when the data were split into smaller bins. Together, we consider that these results provide partial evidence for our registered hypothesis, showing that residual high arousal effects after intense exercise can increase the frequency of MB reports.

In addition to the frequency of mental states across arousal conditions, we also examined whether report times differ across arousal conditions and mental states. In general, reports in low arousal tended to be the slowest, consistent with a wide range of attention tasks that show slower report times in sleep deprivation compared to baseline arousal (Lim & Dinges, 2008). We consider these findings as additional evidence that the arousal manipulation was effective in that it lowered overall vigilance levels. We also observed a main effect of mental states, such that MB tended to be reported significantly slower compared to MW and SENS. Contrary to our current results, we recently found that MB was reported faster when compared to other mental states when content had to be evaluated (Mortaheb et al., 2022). This apparent mismatch in results can be explained when considering that MB can be a state devoid of content, and therefore, there is the binary consideration of "yes/no" when evaluating thought content, which might be a relatively fast decision. This can be different, for example, from the evaluation of contentful mental states, which demand a sequential evaluation of both content presence ("yes/no") and content evaluation ("what is the content about?"). This way, the difference in results can be explained by the imposition of an additional cognitive evaluation. Overall, we suggest that these results might reflect a gradient of vigilance, with participants being the most alert at baseline arousal and progressively declining during high and low arousal conditions, as well as more vigilant when reporting mental states with content compared to MB. An alternative explanation is that slower reaction times might reflect longer introspection periods, where people need more time to recover and evaluate their mental content. When they fail to recover content, they report MB. Of note, we observed two interesting interactions between mental states and arousal conditions. MW tended to be reported slower in low arousal than baseline and high, consistent with our interpretation of reaction times as marking vigilant states. However, as we also observed that MB reports tended to be reported the slowest in both High and Low arousal conditions, we speculate that this might be preliminary evidence that arousal modulates how engaged participants are with their current mental states. In this sense, exercise fatigue can lead to a MB state that takes longer to recover from when probed for a report.

A final explanatory analysis revolved around the relationship between sleep and MB. We recently posited that MB is a distinct mental state characterised by a unique phenomenological profile of no content (Boulakis et al., 2023) and unique neuronal markers, characterised by high cortical integration and low cortical segregation (Mortaheb et al., 2022). This neuronal configuration is atypical of wakefulness (Demertzi et al., 2019) and is more closely reminiscent of brain configurations during deep sleep (El-Baba et al., 2019). In conjunction with the presence of slow wave intrusions during wakefulness as a marker of MB reports, a classic marker of NREM sleep, an emerging issue is whether MB is a misrepresented instance of sleep. This issue is further complicated by the postulation that in MB, there is no content (Boulakis et al., 2023), and thus does not functionally represent a wakeful state where people can recover content. To avoid this pitfall, we introduced Sleep as a potential response during experience sampling. We found that people discretely reported MB and sleep, providing evidence that when provided with such options, people can differentiate between these two experiences. Additionally, we did not find that MB and sleep tended to covary. To strengthen this claim, we ran equivalence tests for each correlation across arousal conditions. However, no test showed a positive result for equivalence. Therefore, these results remain indeterminate, with a trend for no relationship between MB and sleep.

Having established that MB occurrence varied across different physiological arousal conditions, we examined whether MB could be decoded by brain and body markers. To show single trial prediction, we trained different models on EEG and physiological signal markers from time, spectral, complexity, and connectivity domains. Overall, we were able to achieve above-chance-level classification, showing that there exist unique brain-body patterns that can discriminate MB reports from mental states with content. However, we were not able to show above-chance-level classification when training classifiers on unknown subjects. Therefore, our results are not generalisable to novel populations due to the high variance between subjects. Of importance is the result that a combination of EEG and physiological markers marginally but consistently outperformed both EEG and physiological markers. Overall, we observed an improvement of 2–5% in classification performance in balanced accuracy. This improvement can be attributed to unique information inherent in body signals, as evidenced by comparing the classifier trained on both brain and body data to classifiers trained solely on brain data or brain and shuffled body data. The classifier trained on both brain and body data does not consider body features as noise or redundant. Overall, while our results suggest a high degree of overlap between brain and body information in MB, they indicate that information about MB extracted from the body is partially independent of the EEG features. Feature importance ranking derived from the decoding model suggests that the low and mid frequencies of the EEG power spectrum and metrics of eye openness are useful predictors of MB. This finding was consistent across analysis windows and preprocessing parameters. Importantly, all classifiers trained on body markers had above chance performance with variant degrees of variability, with the highest performing being the EYE (eye openness) and the ECG (heart-rate variability), providing evidence that MB can be decoded solely from bodily signals.

To further validate our protocol, we ran two exploratory analyses, intending to examine whether classification performance varies based on the analysed pre-probe window and whether feature importance alters across arousal conditions (For a complete Discussion, see Supplementary Discussion on Methodology in Appendix 6.2). Overall, when examining a classifier trained on a brief 10 s window before MB reports, we found comparable performance compared to the complete 110 s classifier. Interestingly, while EEG performance remained the same, performance on classifiers trained solely on body features decreased. As brain-physiology coupling occurs at varying time delays across cardiac (Lin et al., 2016) and respiratory domains (Bartsch et al., 2014), we interpret these results as evidence that bodily contributions on MB are based on slow, oscillatory processes that might not be captured from examining short pre-probe periods. At the same time, our classification analysis on separate arousal conditions showed distinct brain-body configurations that can predict MB reports. As our decoding approach does not permit any inference of the directionality effect or decomposing interactions within and across physiology modalities, at this stage, we claim that our results point to discrete physiological pathways that elicit MB reports. Overall, we show that our enhanced classification is retained across different analysis windows and different arousal conditions.

Similarly, enhanced classification when considering a brain-heart matrix compared to solely brain markers was also shown for patients with disorders of consciousness, where the inclusion of cardiac features outperformed classification based solely on EEG markers (Raimondo et al., 2017). To our knowledge, our results are the first to extend multivariate decoding past the brain-heart axis and consider the inclusion of multiple unique bodily afferent sources in classifying mental states. The overall success of the brain-body decoding paradigm in classifying consciousness levels and mental states provides evidence that bodily information is not redundant and is not necessarily fully represented within brain dynamics. Instead, an embodied approach, stressing bidirectional information routes between brain and body, can provide better predictive power and assist in more comprehensive generative, computational models of experience Allen et al. (2022); Candia-Rivera et al. (2022).

A neurobiological explanation of our results comes from an integrative model about content, task engagement, and arousal, which suggests that the relationship between thought and arousal can be conceptualised as an inverted u-curve. This means that an optimal arousal level modelled by LC-NE firings is necessary to actively engage and control our thoughts, either during task engagement or MW (Mittner et al., 2016). This stance treats thought as an active task, where engagement is necessary for clear content and control of thought dynamics. As arousal tapers off to non-optimal levels of the inverted u-curve, we experience concurrent, opposing thoughts that serve exploratory purposes for optimal performance, such as exploring different strategies. This necessitates flexibility and malleability of content. Here, we suggest that our results supplement this model by providing an account of the extremities of the optimal u-curve. As the model suggests degradation of thought clarity when we move closer to arousal extremities, we consider MB reports as instances where no content can be clear or present, extending this unifying framework to the entire arousal u-curve. Neurophysiologically, this model has translated to investigations of pupil dilation, an index of LC-NE firing, as a function of mental state and task engagement with pupil size yielding both positive (Chang et al., 2016; Unsworth & Robison, 2016) and null results (Andrillon et al., 2021) in discriminating on-task vs off-task mental states, as well as contrasting MB and MW. Part of the ascending arousal network, the LC modulates cardiac, galvanic, respiratory, and pupillary activity (Wang et al., 2018; Iwamoto et al., 2023). In addition, the LC innervates projections responsible for eyelid openness (Dauvergne et al., 2008). The combinatorial high performance of different body markers in classifying MB reports and the evidence that altered levels of arousal increase MB occurrences provide further support for the modulatory role of the ascending arousal system in mental states and thought reportability.

From a theoretic perspective, our study challenges the conception that brain information is uniquely suitable to understand thought reportability and provides support for an embodied account of the mind. Embodiment moves the seat of mental events away from the brain and reformulates cognition resulting from brain-body interactions. An extensive literature has shown how catalogued cardiac, respiratory, gut, and pupillary effects on perception (Park et al., 2014), action (Park et al., 2020), metacognition (Garfinkel et al., 2013) and consciousness (Raimondo et al., 2017), while the collective interplay of peripheral systems has discriminatory power for clinical evaluation (Tian et al., 2023) and consciousness classification (Bashan et al., 2012). We show here that within embodiment, the body is not only facilitatory but might impede access to our mental lives. Under specific brain-body configurations, we cannot formulate mental content.

Some limitations pertain to our study. First, the nature of experience sampling discretises the continuous nature of ongoing thinking. As there is no consensus on how long a mental state might last or whether all mental states last the same length, results might average across different mental states. While we attempted to circumvent this problem by analysing different pre-probe windows, it remains unclear whether all mental states last the same and what their actual duration is. Secondly, the post-exercise setup might be suboptimal in examining the effects of high arousal on ongoing cognition. Neuronal and electrophysiological recordings have shown that the duration of the impact of exercise on ongoing brain and physiological activity is highly variant (Gourine & Ackland, 2019; Lin et al., 2021; Basso & Suzuki, 2017). In addition, it is unclear whether brain and body recover to baseline states at the same rates, potentially confounding the post-exercise importance of cortical and physiological markers in cognition. Experience sampling with online probes during exercise could overcome this challenge. Finally, by adding the option of sleep report, we aimed to circumvent the possible caveat that MB is a misreported sleep incident. Our exploratory correlation analysis showed no significant evidence for correlations between MB and sleep reports. However, it is worth noting that our sample size was too small to reliably estimate correlation coefficients (Schönbrodt & Perugini, 2013).

3.5 Conclusions

In conclusion, our study suggests that MB is an arousal-modulated mental state with a unique cortical and physiological profile. We think our results pave a new paradigm for an embodied account of mental states, where the phenomenology of our mental lives is expressed based on both our body and brain state. At the same time, our results challenge the neurocentric approach to mental state research, emphasising the constant brain-body interactions that shape our cognition. As MB research continues to evolve, we consider our findings elaborative for clinical and experimental accounts of the mind, where we move towards a complex and dynamic conception of our mind.

Chapter 4

Time-varying connectivity differentiates mental states and experienced alertness during task engagement

This chapter is based on:

1. **Boulakis, P. A.**, Kusztor , A., Andrillon, T. & Demertzi, A. (In prep). Time-varying connectivity differentiates mental states and experienced alertness during task engagement.

4.1 Introduction

Thought is inherently a dynamic process. Therefore, an approach that describes how thoughts evolve (Christoff et al., 2016) might be better positioned to understand the interplay of MB with contentful mental states and the differences in their underlying neuronal mechanisms. The biological and theoretical motivation behind this dynamics-based approach is that time-varying functional connectivity organises itself across consistent and robust connectivity patterns, characterised by varied degrees of integration (functional communication) and segregation (functional specialisation) (Demertzi et al., 2019). These patterns show generalisability between species (Uhrig et al., 2018; Hudetz et al., 2015; Barttfeld et al., 2015), suggesting that they represent a fundamental mode of cortical organisation (Demertzi et al., 2019).

The repertoire of connectivity patterns the brain explores appears to describe conscious experience (Castro et al., 2024; Demertzi et al., 2019; Türker et al., 2024), providing a time-resolved approach to mapping subjective phenomenology to cortical activity (Mortaheb et al., 2022, 2024). Leveraging this approach, Mortaheb et al. (2022) found that MB is associated with a brain pattern of high inter-areal connectivity and absence of functional cortical segregation during experience sampling at rest. The role of this "hyperconnected" brain pattern is unclear. Typically, cognitive processes and task demands prompt the brain to switch between local segregation and global integration, optimising cognitive performance and computational efficiency (Ekman et al., 2012). However, in a "hyperconnected" state, the brain's connectivity profile differs from typical wakefulness, with minimal segregation and maximal integration (Demertzi et al., 2019). This results in low modularity and high global efficiency, where information is highly accessible across the network. Although this configuration maximises connectivity, it is not optimal for daily functioning, as the brain needs both segregation and integration to maintain a coherent sense of self (Di Plinio et al., 2020), support conscious awareness (Singh et al., 2024) and perform specialised cognitive tasks (Wang et al., 2021; Cohen & D'Esposito, 2016). This raises the question of the functional relevance of this "hyperconnected" brain pattern.

Mechanistically, when the "hyperconnected" pattern is accompanied by a high amplitude of the fMRI BOLD global signal, a proxy of low cortical arousal, it is typically associated with MB experiences (Mortaheb et al., 2022). Inversely, when accompanied by a low global signal amplitude during psychedelic intake, it is behaviourally associated with psychedelic experiences, such as oceanic boundlessness and altered sensations (Mortaheb et al., 2024). An increase in whole-cortex functional connectivity was previously observed during NREM sleep (El-Baba et al., 2019). Consistent with this, MB reports, which correlate with "hyperconnectivity", are preceded by the presence of slow wave-like (SW-like) activity during wakefulness, termed "local sleep" (Andrillon et al., 2021). Previously, SW activity following isoflurane administration in rodents generated a cortex-wide increased connectivity BOLD pattern (Aedo-Jury et al., 2020; Schwalm et al., 2017), providing evidence to the hypothesis that "hyperconnectivity" is a function of cortical synchronisation elicited by the presence of slow-waves (Mortaheb et al., 2022; Andrillon et al., 2024). Overall, SW-like activity and "hyperconnectivity" appear to converge at the same phenomenology: MB. However, this hypothesis has not been directly tested during wakefulness.

In the present study, our aim was to address the hypothesis that the "hyperconnected" pattern reflects reduced arousal (in the form of SW-like activity) during wakefulness by utilizing concomitant fMRI-EEG recordings during an experience sampling task. Specifically, we hypothesised that a) the propensity to report MB would increase as people progressively become less alert, replicating work from Andrillon et al. (2021), b) fMRI BOLD scans around MB and sleepiness reports would be characterized by higher levels of global signal amplitude, following results from Mortaheb et al. (2022), c) FC around MB and sleepiness reports would be associated with a brain pattern characterised by "hyperconnectivity", as indicated by Mortaheb et al. (2022) and d) "hyperconnectivity" would correlate with the presence of SW-like activity.

4.2 Methods

4.2.1 Participants

Thirty-nine participants were recruited for the study (mean age = 26.38, sd = 4.53, range = [18,32]; N female = 24). All participants reported normal or corrected-to-normal vision and no neurological or psychiatric disorders. One participant was excluded because of subsequent changes in the experimental paradigm, leading to a total sample size of n=38. Participants received monetary compensation for their participation. The project was approved by the

Monash University Human Resources Ethics Committee (Project ID 17674).

4.2.2 Experimental design and stimuli

The experimental design consisted of a SART task (Robertson et al., 1997), where participants were requested to pay attention to a series of pictures of human faces (Fig. 4.1). In each trial, face stimuli (one male face or eight different female faces) were presented for 500 ms, followed by a blank screen. The trial duration was between 1000–1500 ms (random uniform jitter). Participants were instructed to indicate the presence of a female face (GO trials) by pressing a button using a keypad placed under their dominant hand, and withhold button presses (NOGO trials) for male faces. The order of the face stimuli was randomised before the onset of each session. Participants completed four blocks of the task with self-paced breaks in between, each block lasting approximately 12-15 minutes. Each experimental session lasted approximately 50 minutes (Fig. 4.1). Face stimuli were extracted from the Radboud Face Database (Langner et al., 2010).

Intermittently to the SART task, we utilised experience sampling to probe reports of participants' mental states and alertness levels throughout the session. Specifically, every 30-70 s (uniformly jittered), we interrupted the SART task with a probe sound and displayed the word "STOP" on the screen. Following the probe, participants were asked: *"Just before the interruption: Where was your attention focused?"*. Possible responses were a) On-Task (defined as fully focused on the task), b) Off-Task (defined as thinking about something other than the task), Blank (defined as not thinking of anything), and d) I cannot recall. If participants selected the Off-Task option, they were additionally presented with the following question: *"Just before the interruption: What distracted your attention from the task?"*. Available options were: b1) Something in the room, b2) Something personal, and b3) Something about the task. After reporting their mental states, participants were asked: *"Over the past few trials: How alert have you been?"*. Available levels were: a) Extremely Alert, b) Alert, c) Sleepy, and Extremely Sleepy (Fig. 4.1). The mental state options were explained to participants orally and in writing before the experiment. Each block included 10 sets of probes. Each participant responded to 40 probes across 4 blocks. As these two reports point to the same phenomenology of no available content, for the current study, we aggregated "Blank" and "No recall" reports to improve the

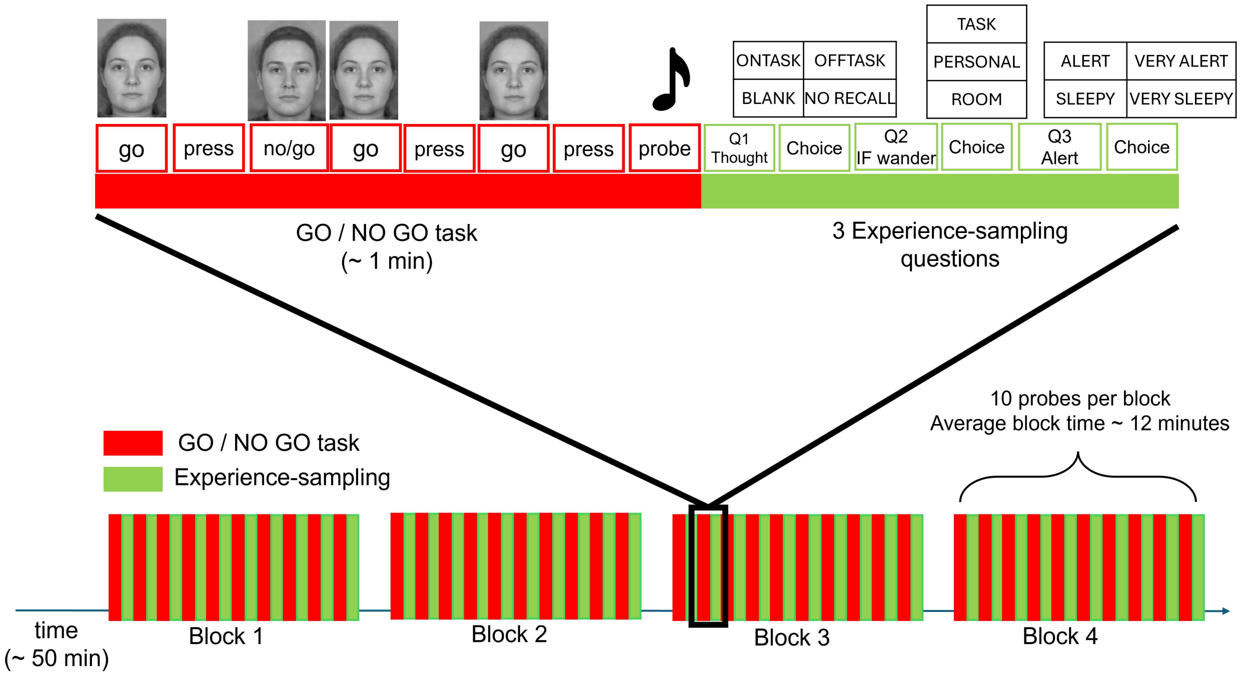

Figure 4.1: Experimental design of sustained attention to task (SART) combined with experience sampling probes of mental states and attentional levels. Across four experimental blocks, each lasting ∼12 minutes, participants were presented with a sequence of female or male faces. Participants were instructed to press a button when a female face was presented (GO stimulus) and avoid pressing a button when male faces were presented (NOGO stimulus). At random intervals within each block, participants were presented with auditory probes inviting them to report their mental content and alertness level. Firstly, participants indicated their mental content by choosing amongst a) ONTASK thoughts, b) OFFTASK thoughts, c) BLANK, or d) I cannot recall my thoughts. If participants selected the OFFTASK thought option, they were further probed to report whether the OFFTASK thought revolved around the task, the experimental room or personal content. Finally, participants indicated their alertness levels by choosing amongst a) Very Alert, b) Alert, c) Sleepy or d) Very Sleepy. In every block, we presented 10 probes, for a total of 40 probes per participant.

study's statistical power, following our previous analysis protocol (Andrillon et al., 2021).

4.2.3 Behavioural Analysis

Mental state reports and alertness levels were aggregated across the whole experience sampling session and contrasted across different runs to examine whether later runs altered the propensity of responses. Similarly, report times, defined as the difference between probe and button press, were contrasted across mental states and alertness levels. Reaction times larger than 6 seconds were discarded as reflecting moments when participants forgot to respond, following our previous analysis protocol (Boulakis et al., 2025). Overall, we removed <2% of the total probes. Finally, each mental report was binarised, and we contrasted whether we could predict mental states from alertness levels.

4.2.4 EEG analysis

EEG acquisition parameters

The EEG data were acquired using the BrainAmp MR plus system (Brain Products, Munich, Germany), designed for simultaneous EEG and fMRI recordings. The BrainAmp MR plus system is equipped with 64 channels EEG Cap (64Ch Standard BrainCap-MR with multitrodes). Electrode placement followed the international 10-20 system. The ground electrode was positioned in the location of AFz, and the reference was in the location of FCz. The electrodes were prepared with conductive gel to reduce impedance levels below 5 kΩ. The data were recorded with the BrainAmp MR plus DC and bipolar BrainAmp ExG MR amplifiers and the BrainVision Recorder (Version 2.2) software (BrainProducts, Munich, Germany) with a resolution of 0.5 μV/bit at 5000 Hz and with a low cut-off hardware filter with a time constant of 10 s and high cut-off at 250 Hz. We synchronised the EEG and fMRI data acquisition using the Brain Products SyncBox.

EEG preprocessing

Gradient artefact removal was done via subtraction of a mean template in each channel, according to the average artefact subtraction (AAS) methodology, utilising the software Brain Vision Analyzer 2 (Version 2.2, Brain Products GmbH, Gilching, Germany). A sliding moving-average window implementation of 21 epochs of a full gradient artefact (1.56 s time window) was used to construct the average artefact template. The reason for using 21 epochs was based on the default settings of the Brain Vision Analyzer. After this step, data was downsampled to 500 Hz. Cardioballistic artefacts were also removed using the AAS methodology. The R peaks were identified via a semi-automated pipeline but then were visually inspected and corrected when necessary. Further preprocessing was done using the EEGLAB MATLAB toolbox (v2021.1). Data were split into 25 s pre-probe epochs and filtered using a 100 Hz high cut-off hamming filter. Next, data were visually inspected for bad electrodes and epochs. Eye- and cardiac-related artefacts were detected and removed using ICA. At that stage, we noticed that residual cardioballistic artefacts were still present in the frontal and temporal channels, so we applied denoising source separation (DSS) on heartbeat-evoked potentials and removed the time-locked activity from every channel (de Cheveigné & Simon, 2008).

SW marker extraction

To detect SW activity during wakefulness, we followed a previously validated procedure described by Andrillon et al. (2021). First, data were re-referenced to the average of mastoid electrodes and band-pass filtered within a [1,10] Hz range. Then, SWs were located in each electrode separately based on the negative peaks in the signal. Waves with extreme amplitudes ($> 75\,\mu$V positive peak and $> 150\,\mu$V peak-to-peak differences) and with duration corresponding to larger than 7 Hz activity were excluded. Finally, we selected the top 10% largest waves in each electrode and extracted their timings, amplitudes and downward and upward slopes. We have extracted SWs from a 10 s window before each probe. Overall, we successfully extracted markers from 22 participants.

4.2.5 fMRI analysis

fMRI acquisition parameters

Participants were instructed to lie still in the MRI scanner. Data were collected using a Siemens Skyra 3T MRI system equipped with a Siemens 20-channel Head/Neck coil, allowing for simultaneous EEG and ECG recordings. The participants' heads were stabilised with foam pillows placed between the cap and the MR coil. Anatomical images were acquired using a T1-weighted MPRAGE sequence with a voxel size of 1.00 mm^3, TR = 2.3 s, TE = 2.07 s, and a slice thickness = 1.00 mm. Functional images were obtained using an Echo Planar Imaging (EPI) sequence with the following parameters: TR = 1.56 s, TE = 0.03 s, slice thickness = 3 mm, flip angle = 70°.

fMRI preprocessing

Results included in this manuscript come from preprocessing performed using *fMRIPrep* 23.2.1 (Esteban et al. (2019); Esteban et al. (2018); RRID:SCR_016216), which is based on *Nipype* 1.8.6 (Gorgolewski et al. (2011); Gorgolewski et al. (2018); RRID:SCR_002502), and the AFNI software 24.3.00 (Cox & Hyde, 1997). For a full description of the pipeline, please refer to the Supplementary Methodology appendix 6.3.

Briefly, T1-weighted images were skull-stripped and bias-field corrected. We extracted grey matter, white matter and cerebrospinal fluid masks. Both the mask and the skull-stripped image were normalised to MNI space. T2-weighted image preprocessing included realignment to account for head motion, slice-time correction, co-registration to the T1-weighted image, and normalisation to MNI space. Apart from the *fMRIPrep* pipeline, we additionally applied a Gaussian kernel of 6 mm full width at half-maximum using the `3dmerge` function from *AFNI*. Following smoothing, denoising was performed using a locally developed *Nipype* pipeline. We fitted a generalised linear model (GLM) to each fMRI BOLD voxel time series in this pipeline. The GLM modelled the effect of six movement parameters (translation in x, y, and z directions, and rotation in yaw, roll, and pitch directions) and their first derivative, constant, and linear trends using zero-order and first-order Legendre polynomials, principal components of signals in the WM and CSF masks, and outlier data points. Then, a bandpass filter in the range of 0.008 - 0.09 Hz was applied to the model's residuals to extract low-frequency fluctuations of the BOLD signal. Finally, we utilised the Schafer 100 ROI parcellation (Schaefer et al., 2018) and 19 subcortical ROI to extract the averaged BOLD signals inside each ROI. As previously indicated (Luppi et al., 2024; Botvinik-Nezer et al., 0 06), different fMRI preprocessing steps can greatly affect subsequent statistical inferencing. To mitigate this issue and ensure the robustness of our pipeline, we varied the following steps: regression of the global signal, previously shown to create different connectivity patterns (Mortaheb et al., 2022), regression of task events, as the brain explores different connectivity patterns during task engagement (Gonzalez-Castillo & Bandettini, 2018) and re-analysing our data using the Schafer 400 ROI parcellation, to ensure our results are not confounded by the precision of our parcellation nodes.

Global signal amplitude analysis

We extracted the instantaneous global signal amplitude by applying the Hilbert transform at each ROI time point and extracting the real component of the signal. Then, we extracted the GS of the last 6 TR ($\sim$10 s) preceding probes for each mental report and alertness level. To account for the potential lag of the BOLD response, we also re-analyzed the shifted global signal amplitude time series by 1 and 2 TR, similarly to the protocol of Mortaheb et al. (2022).

Functional connectivity pattern estimation

Following the approach of Demertzi et al. (2019) and (Mortaheb et al., 2022), we used **phase-based coherence** analysis to calculate ROI-ROI connectivity patterns at each TR of the scanning session.

For every participant i, we z-scored each of the ROI r time series and applied a band-pass filter of 0.1-0.4 Hz to isolate the low, BOLD oscillatory signal of interest. Then, we calculated the Hilbert transform as:

$$\hat{x}_{i,r}(t) = \left(\frac{1}{\pi t}\right) * x_{i,r}(t)$$

where $*$ indicates a convolution operator. Using this transformation, we produced an analytical signal for each regional time series as:

$$x^a_{i,r}(t) = x_{i,r}(t) + j\hat{x}_{i,r}(t)$$

where $j = \sqrt{-1}$. From this analytical signal, the instantaneous phase of each time series can be estimated as:

$$\phi_{i,r}(t) = \tan^{-1}\left(\frac{\hat{x}_{i,r}(t)}{x_{i,r}(t)}\right)$$

.

To ensure that the phase time series were accurately represented and free from artefacts, we applied Empirical Mode Decomposition (EMD) to each voxel phase time series. EMD is a signal processing technique that decomposes a signal into underlying frequency components called intrinsic mode functions (IMF). At each iteration of the algorithm, EMD identifies the local extrema of the original signal, from which upper and lower envelopes are constructed using spline interpolation. The mean of these envelopes is calculated and subtracted from the original signal to extract the first IMF. This procedure is iterated until the extracted signal meets the criteria for being an IMF. Therefore, at each iteration, the algorithm produces an IMF and the residual trend of the signal after the IMF is subtracted. The resulting IMFs represent various oscillation scales within the signal, where the first IMF corresponds to the highest-frequency oscillations, and the last IMF corresponds to the lowest-frequency oscillations. As such, we kept the first IMF.

Then, we warped the denoised phase signal $\phi_{i,r}(t)$ to the $[-\pi, \pi]$ interval and, naming the obtained signal as $\theta_{i,r}(t)$, we calculated a connectivity measure for each pair of regions as the cosine of their phase difference. For example, the connectivity measure between regions r and s in subject i was defined as:

$$\mathrm{conn}_{i,r,s}(t) \triangleq \cos\left(\theta_{i,r}(t) - \theta_{i,s}(t)\right).$$

By this definition, completely synchronised time series lead to a connectivity value of 1, completely desynchronised time series produce a connectivity value of zero, and anticorrelated time series produce a connectivity measure of -1. Using this approach, we created a connectivity matrix of N+19 × N+19, where N = number of Schaefer atlas parcels, in addition to the 19 subcortical ROI, at each time point t for each subject $i$that we called $C_i(t)$:

$$C_i(t) \triangleq \left[\mathrm{conn}_{i,r,s}(t)\right]_{r,s}.$$

K-means clustering

A clustering approach was utilized across all connectivity matrices to estimate distinct patterns of signal configurations (brain patterns).

First, given that the connectivity matrices described above are symmetrical, we extracted the triangular lower parts of the matrix for every participant at every TR. By aggregating all connectivity vectors, we created a new matrix where each row represents a participant's connectivity at a single time point (TR), and each column represents the phase-based connectivity values at that TR.

Second, we applied K-means clustering to the resulting connectivity matrix, using the Manhattan distance as the distance metric. To assess the robustness of the brain configurations to the algorithm choice, we also clustered the data using cosine and Euclidean distance. Clustering produced k distinct centroids that represented brain connectivity matrices, along with the occurrence frequency of each configuration for every participant. To ensure the centroids' robustness and replicability, we varied the number of centroids from $k = 3$ to $k = 8$. We initialised clusters using the "K-means++" algorithm (Arthur & Vassilvitskii, 2007). Finally, we ordered the patterns by their standard deviation and estimated the frequency of each centroid by counting the number of matrices assigned to each centroid for each participant.

Third, following the approach of Demertzi et al. (2019), we estimated the optimal amount of centroids by calculating the inter-pattern correlation variance across all k. We further tested the stability and robustness of the centroids by estimating the correlations of all patterns with the first and last centroid of $k= 5$. If centroids were stable, we would expect that across all k, the first and the last centroid would be the highest correlated, meaning that across k, the clustering algorithm identifies similar centroids.

Coupling between brain patterns and experience sampling

We used the approach described in Mortaheb et al. (2022) to examine the brain patterns related to each mental state and alertness level. Initially, we extracted the upper triangular parts of the connectivity matrices 6 TR (∼10 s) preceding each report. As the goal of this study is to eventually link electrophysiology with FC, the choice of the window was motivated by previous results in EEG showing that mental states can be decoded from this window (Andrillon et al., 2021). To account for a potential effect of the hemodynamic response, additional analyses were performed on the shifted versions of the connectivity matrices with time lags ranging from zero to two TR. For every distance metric used during K-means clustering (Euclidean, Manhattan or cosine), we estimated the distance of the extracted connectivity vectors with each of the k centroids. In the main text, we present results originating from a k=5.

Coupling between brain patterns and SW-like activity

To understand how SW activity correlates with brain patterns, we used Canonical Correlation Analysis (CCA). CCA is a multivariate statistical technique used to identify and measure the relationships between two sets of variables. In our dataset, these sets map to the SW-like markers per EEG channel and the distances of every connectivity matrix to the underlying patterns. Considering a set of variables X_M^N, where M represents SW-like activity at every EEG channel averaged at 10 s preceding probes and N represents the sum of reports across every subject and every run, and a set of variables Y_P^N, where P represents the average distance of a connectivity matrix from each of the k identified patterns and N represents the sum of reports across every subject and every run, the goal of CCA to find linear combinations (canonical components) between the variables in$X$ and Y that maximise the correlation between the canonical components. A regularisation penalty $L1$ and $L2$ was added to each set of variables to ensure numerical stability and avoid multicollinearities. We adopted a permutation approach to assess the significance of each canonical component. We permuted the Y variable 5000 times and fit the CCA model again, extracting an empirical null distribution for the correlations. The resulting empirical p values were Bonferroni-corrected for the number of centroids tested per model. Finally, to assess how much every variable contributes to the canonical component, we estimated the correlations between canonical components with each variable. This way, we can examine whether a component was predominantly driven by distance to a specific pattern or slow-wave activity in specific EEG electrodes.

4.2.6 Statistical analysis

Statistical analysis was performed using generalised mixed-effect models. The modelling of the dependent variable varied depending on the distribution the dependent variable was following. In the case of binary variables, data were modelled using a binomial distribution with a logit link function. In the case of positive variables, data were modelled using a gamma distribution with an inverse link function. Finally, the rest of the tests were conducted using a Gaussian distribution with an identity function. When data were analysed using a hierarchical, mixed effect structure, we allowed intercepts to vary freely, using subject and run ID as random effects. All models were contrasted to null models containing only intercepts. If multiple models were tested, they were corrected using Bonferroni correction. Pairwise multiple contrasts of significant models were performed using FDR correction. In the case of singular fit, we iteratively removed the random effect intercepts of run ID and subject ID.

4.3 Results

4.3.1 MB increased with lower levels of experience alertness

Participants reported being primarily engaged with the task (ONTASK = .49±.25, OFFTASK = .39±.21, BLANK = .1±.11; NO RECALL=.0±.04, Mean proportions±SD) and being Alert (ExAlert =. 08±.02, Alert = .48±.11, Sleepy = .28±.07, ExSleepy = .14±.07) (Fig. 4.2a,b). MB was reported significantly less frequently compared to other mental states (MB-ONTASK:

Contrast Estimate = -.36, SE = .03, CL = [-.43, .29], p_{FDR} = 5e-29, MB-OFFTASK: Contrast Estimate = -.26, SE = .03, CL = [-.34, -.19], t = -8.89, p_{FDR} = 2.8e-17)(Fig. 4.2a). To examine whether these probabilities altered with time spent on task, we further checked where mental reports and arousal levels remained constant across scanner runs by fitting a linear mixed-effects model (formula = proportion of responses $\sim$ state*run + 1|subject): FDR-corrected contrasts showed that OFFTASK thoughts increased from the 1st to the 2nd run (OFFTASK Run1 - Run2: Contrast Estimate = -.11, SE = .04, CL = [-.22, -.001], t = -2.71, p_{FDR} = 4.7e-2). On the opposite side, ONTASK reports decreased (ONTASK Run1 - Run2: Contrast Estimate = .17, SE = .04, CL = [.06, .29], t = 4.13, p_{FDR} = 2.4e-4, ONTASK Run1 - Run3: Contrast Estimate = .17, SE = .04, CL = [.06, .28], t = 4.10, p_{FDR} = 2.4e-4, ONTASK Run1 - Run4: Contrast Estimate = .12, SE = .04, CL = [.01, .23], t = 2.88, p_{FDR} = 9.6e-3). We found no positive evidence for MB frequency alterations across runs. To assess evidence for a null relationship between MB reports and runs, we performed an equivalence test, yet the results failed to accept practical equivalence (Fig. 4.2c). Finally, as expected, subsequent runs were associated with a marked and significant decrease in alertness and an increase in sleepiness (Fig. 4.2d).

To examine whether mental reports were associated with alertness levels, we estimated the proportion of each mental state, stratified by alertness level. Specifically, ONTASK and OFFTASK reports showed an inverted U-curve pattern in which sleepiness and alertness showed a higher proportion of responses compared to arousal extremities (OFFTASK Alert - ExAlert: Contrast Estimate = 1.98, SE = .37, CL = [1.01, 2.95], p_{FDR} = 1.4e-7, OFFTASK Alert - ExSleepy: Contrast Estimate = -.71, SE = .22, CL = [-1.29, -.12], p_{FDR} = 1.6e-3, OFFTASK Alert - Sleepy: Contrast Estimate = -.80, SE = .16, CL = [-1.22, -.39], p_{FDR} = 6.2e-7, OFFTASK ExAlert - ExSleepy: Contrast Estimate = -2.68, SE = .41, CL = [-3.77, -1.60], p_{FDR} = 2.0e-10, OFFTASK ExAlert - Sleepy: Contrast Estimate = -2.78, SE = .38, CL = [-3.78, -1.78], p_{FDR} = 1.4e-12, ONTASK Alert - ExAlert: Contrast Estimate = -2.07, SE = .36, CL = [-3.01, -1.13],p_{FDR} = 7.7e-9, ONTASK Alert - ExSleepy: Contrast Estimate = 2.60, SE = .30, CL = [1.82, 3.39], p_{FDR} = 3.9e-18, ONTASK Alert - Sleepy: Contrast Estimate = 1.49, SE = .17, CL = [1.05, 1.94], p_{FDR} = 2.0e-18, ONTASK ExAlert - ExSleepy: Contrast Estimate = 4.67, SE = .45, CL = [3.48, 5.86], p_{FDR} = 2.0e-2, ONTASK ExAlert - Sleepy: Contrast Estimate = 3.56, SE = .38, CL = [2.57, 4.55], p_{FDR} = 9.0e-21, ONTASK ExSleepy - Sleepy: Contrast Estimate

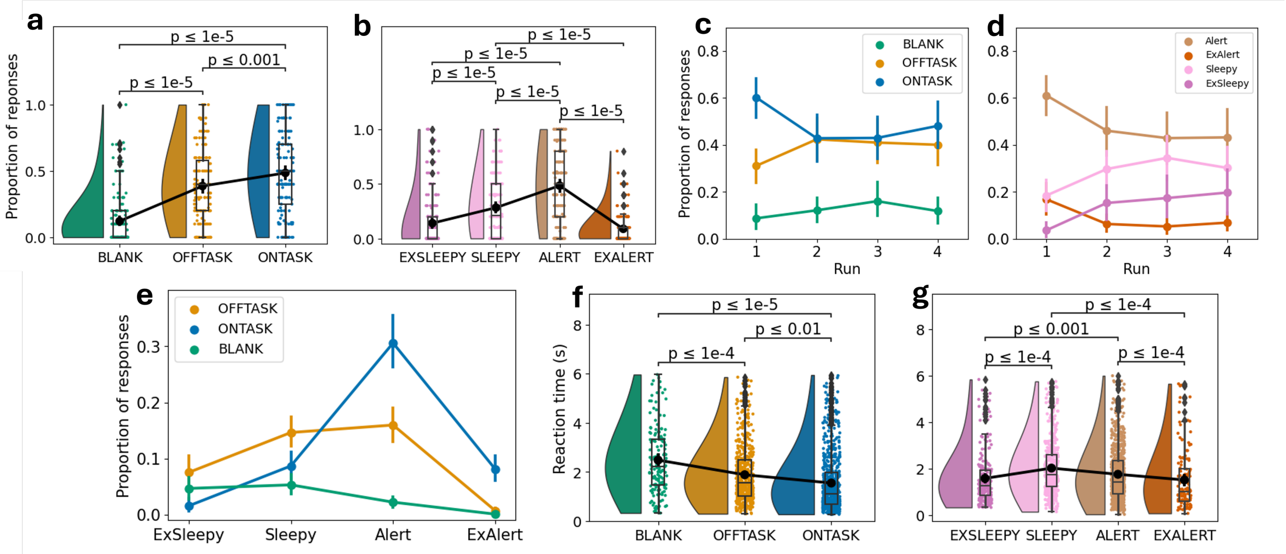

Figure 4.2: Behavioral results. a) MB is reported more sparsely than ONTASK and OFFTASK mental reports. Raincloud density plots indicate data dispersion. Box plots indicate medians and inter-quantile ranges. Point plots indicate the proportion of reports per trial and run. Line plots indicate means. b) Participants tended to report being Alert during the sustained attention to the Sustained Attention to Response Task (SART). c) Across runs, ONTASK reports tended to decrease, while OFFTASK thoughts tended to increase. Importantly, BLANK reports remained constant. Line plots indicate the mean proportion of response times. Error bars indicate 95% confidence intervals. d) Across runs, overall alertness levels tended to decrease. e) Alertness reports altered the propensity to report mental states. Specifically, BLANK reports tended to decrease as alertness increased, while ONTASK frequency tended to increase with higher alertness levels. f) Reaction times differed across mental reports. BLANK was reported the slowest, followed by OFFTASK and ONTASK. g) Lower alertness levels were associated with slower reaction times. All contrasts were FDR-corrected for multiple comparisons. All statistical models included a run and subject ID as random effects intercept. All statistical models were compared with null models containing only random intercepts.

= -1.11, SE = .29, CL = [-1.88, -.34], p_{FDR} = 1.4e-4). However, MB reports showed a constant decrease moving from low to high levels of arousal (BLANK Alert - ExSleepy: Contrast Estimate = -2.65, SE = .31, CL = [-3.48, -1.82], p_{FDR} = 2.0e-16, BLANK Alert - Sleepy: Contrast Estimate = -1.71, SE = .27, CL = [-2.41, -1.00], p_{FDR} = 4.8e-10, BLANK ExAlert - ExSleepy: Contrast Estimate = -4.29, SE = 1.01, CL = [-6.95, -1.63], p_{FDR} = 4.3e-5, BLANK ExAlert - Sleepy: Contrast Estimate = -3.35, SE = .99, CL = [-5.97, -.72], p_{FDR} = 9.3e-4, BLANK ExSleepy - Sleepy: Contrast Estimate = .94, SE = .24, CL = [.30, 1.59], p_{FDR} = 1.7e-4) (Fig. 4.2e).

Finally, we examined pairwise differences between mental reports, alertness levels and report times. We fit a generalised mixed-effects model for both mental and alert reports (formula = proportion of responses ∼ state*run + 1|subject + 1|run, family=Gamma). Regarding mental states, MB was the slowest, followed by OFFTASK thoughts and then ONTASK (BLANK - OFFTASK: Contrast Estimate = -0.10, SE = .02, CL = [-0.16, -0.04], p_{FDR} = 3.7e-5, BLANK - BLANK: Contrast Estimate = -0.17, SE = .03, CL = [-0.23, -0.11], p_{FDR} = 1.8e-10, OFFTASK

- BLANK: Contrast Estimate = -0.07, SE = .02, CL = [-0.12, -0.02], p_{FDR} = 1.3e-3) (Fig. 4.2f). Moreover, as expected, sleepiness was associated with longer report times compared to alertness (Alert - ExAlert: Contrast Estimate = -0.15, SE = .03, CL = [-0.24, -0.06], p_{FDR} = 4.5e-5, Alert - ExSleepy: Contrast Estimate = -0.12, SE = .03, CL = [-0.21, -0.04], p_{FDR} = 1.4e-4, ExAlert - Sleepy: Contrast Estimate = 0.16, SE = .04, CL = [0.06, 0.26], p_{FDR} = 4.5e-5, ExSleepy - Sleepy: Contrast Estimate = 0.14, SE = .03, CL = [0.06, 0.21], p_{FDR} = 2.0e-5) (Fig. 4.2g).

4.3.2 Sleepiness was associated with higher GS amplitude

Previous work suggested that the increased global signal amplitude is associated with lowered cortical arousal (Wong et al., 2013) and MB (Mortaheb et al., 2022). We estimated the global signal amplitude as the real part of the Hilbert transform of the BOLD global signal (mean ROI time course). Then, we fitted a generalised mixed-effects model containing the main effects and interaction terms of alertness levels and mental reports (formula = amplitude $\sim$ state*alert + 1|subject, family=Gamma). FDR-corrected contrasts showed that lower levels of alertness were associated with a progressive increase in global signal amplitude (Alert - Sleepy: Contrast mean = 0.61, SE = 0.12, CL = [0.26, 0.97], p_{FDR} = 3.51e-6, Alert - ExSleepy: Contrast mean = 0.71, SE = 0.17, CL = [0.19, 1.23], p_{FDR} = 3.14e-4) (Fig. 4.3). We did not find any significant main effects of MB (Fig. 4.3). No significant interactions were observed (Supplementary Fig. S6.3-1). These results were replicated across analysis lags and parcellations schemes and did not change based on whether we regressed out task events (Supplementary Fig. S6.3-4 and 6.3-5). At BOLD lag = 2, we additionally observed an increase in global signal amplitude moving from sleepiness to high sleepiness (Supplementary Fig. S6.3-4 and 6.3-5). Critically, global signal regression removed this effect (Supplementary Fig. S6.3-2 and 6.3-3).

4.3.3 FC organised in distinct and replicable brain patterns

We estimated how FC organises across different connectivity patterns during task engagement. Specifically, we estimated phase-based connectivity matrices using coherence as the connectivity measure. We then aggregated the instantaneous-phase connectivity matrices at every TR and every subject. We applied K-means clustering to generate k representative patterns that can

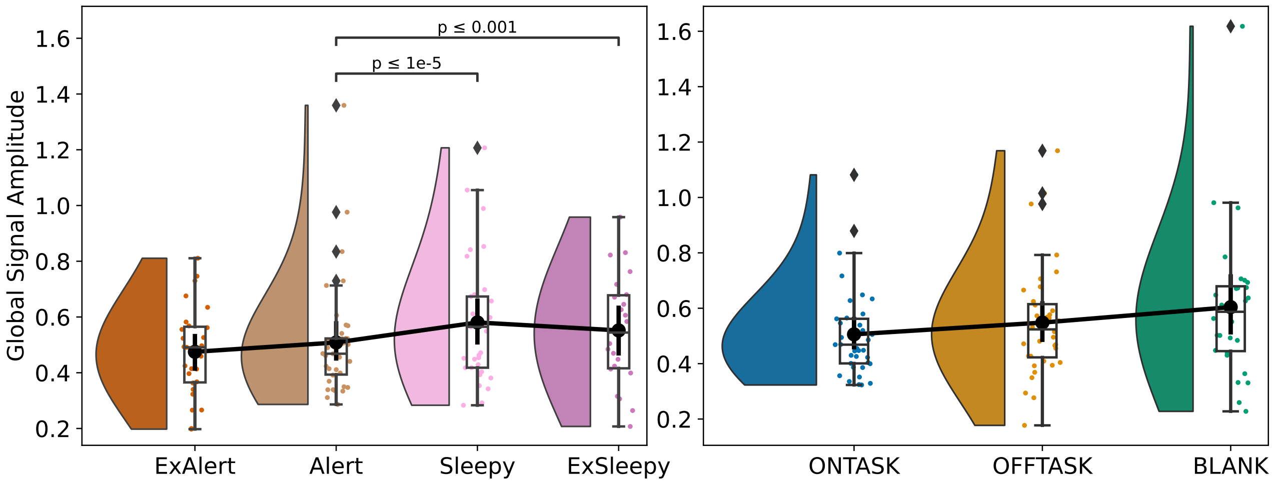

Figure 4.3: Global signal amplitude is progressively increased in lower alertness levels but does not differ across mental states. Raincloud density plots indicate data dispersion. Box plots indicate medians and inter-quantile ranges. Point plots indicate the proportion of reports per trial and run. Line plots indicate means.

explain the variation in the connectivity matrices using Manhattan distance as the distance metric. The number of k centroids was varied from 3 to 8. Here, we will discuss $k = 5$, as fewer clusters showed reduced inter-pattern correlation variance, indicating that patterns were not as clearly defined. Inversely, higher levels of k only marginally increased inter-pattern correlation variance (Supplementary Fig. S6.3-7 to 6.3-18).

Overall, we found that FC during task decomposed into a) a pattern of complex inter-areal interactions, containing positive and negative phase coherence values, with higher coherence between the DMN and the limbic network (P1), b) a pattern of anticorrelations primarily between the visual network and the other networks (P2), c) a pattern of complex inter-areal interactions, containing positive and negative phase coherence values, with higher coherence between the DMN and the visual and limbic networks (P3), d) a pattern of overall low-coherence, and high coherence between the visual and the somatosensory networks (P4), and e) a pattern of overall high inter-areal coherence (P5) (Fig. 4.4). Critically, patterns 1,2 and 5 were reproduced irrespective of clustering algorithm or denoising parameters (Supplementary Fig. S6.3-7 to 6.3-18). A visual inspection of the pattern profiles across different clustering parameters showed that global signal regression had the largest effect, resulting in pattern 5 becoming the most infrequent (Supplementary Fig. S6.3-7 to 6.3-18).

To examine pattern frequency, we fitted a linear model (formula: proportion $\sim$ pattern). FDR-corrected contrasts showed that the pattern of high inter-areal coherence (P5) was the most frequent (Fig. 4.4), followed by the complex, anticorrelations patterns (P1, P3) (Pattern1

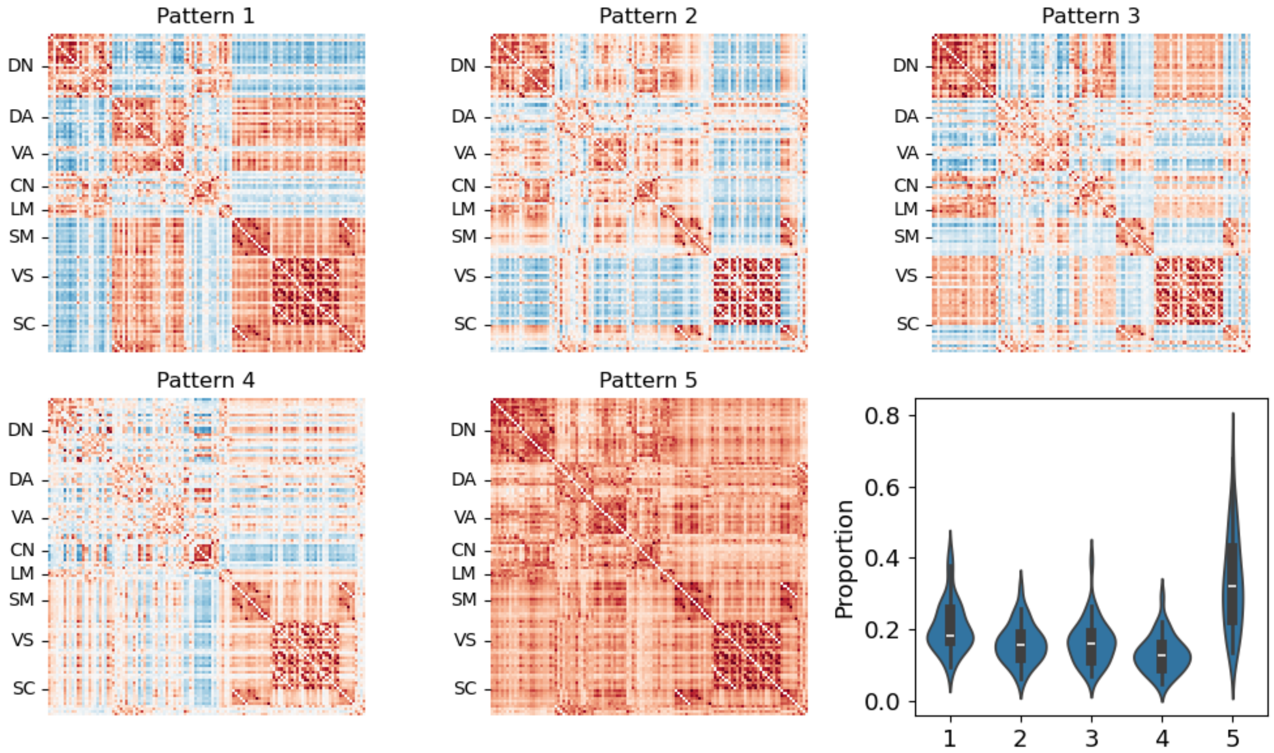

Figure 4.4: Functional connectivity during task engagement can be summarised into five brain patterns. These patterns display different connectivity profiles. Specifically, we found a pattern dominated by anticorrelations, with higher coherence between the DMN and the limbic network (Pattern 1), a visual network anticorrelations pattern (Pattern 2), a pattern dominated by anticorrelations, with higher coherence between the DMN and the visual and limbic networks (Pattern 3), a lowered overall coherence pattern (Pattern 4), and a cortex-wide high coherence pattern (Pattern 5). Patterns are ordered in terms of decreasing metastability, defined here as the standard deviation of the pattern. All specified coherence patterns had similar occurrence rates, except P5, which recurrently appeared more often across participants. DN = default network, DA = dorsal attentional network, VA = ventral attentional network, CN = control network, LM = limbic network, SM = somatosensory network, VS = visual network, SC = subcortical network.

- Pattern2: Contrast Estimate = 0.04, SE = .01, CL = [0.01, 0.08], p_{FDR} = 6.4e-4, Pattern1 - Pattern3: Contrast Estimate = 0.04, SE = .01, CL = [0.00, 0.07], p_{FDR} = 1.9e-3, Pattern1 - Pattern4: Contrast Estimate = 0.07, SE = .01, CL = [0.04, 0.11], p_{FDR} = 4.2e-9, Pattern1 - Pattern5: Contrast Estimate = -0.13, SE = .01, CL = [-0.16, -0.09], p_{FDR} = 1.6e-24, Pattern2 - Pattern4: Contrast Estimate = -0.17, SE = .01, CL = [-0.21, -0.13], p_{FDR} = 3.2e-40, Pattern2 - Pattern3: Contrast Estimate = 0.03, SE = .01, CL = [0.00, 0.07], p_{FDR} = 5.8e-3, Pattern3 - Pattern5: Contrast Estimate = -0.20, SE = .01, CL = [-0.24, -0.17], p_{FDR} = 8.3e-53). We did not find any significant changes in pattern frequency across runs (Supplementary Fig. S6.3-6).

4.3.4 Neurobehavioural coupling associated sleepiness reports with distinct brain patterns

To link mental states and alertness levels to the underlying brain patterns, we followed the approach described in Mortaheb et al. (2022). First, we extracted the last 10 s (6 TR) of connectivity matrices preceding each probe. We estimated the Manhattan distance of each connectivity matrix with each of the five brain patterns produced by the clustering approach. Then, we fit a generalised linear model (formula = distance from pattern $k \sim$ state*run, family=Gamma). Model significance was corrected for the total number of k clusters examined.

Firstly, FDR-corrected contrasts showed that lower levels of alertness are associated with connectivity that is closer to the pattern of overall high-coherence (ExAlert - Alert: Contrast Estimate = -1.46e-5, SE = 5.20e-6, CL = [-3.04e-5, 1.21e-6], p_{FDR} = 3.39e-2, ExAlert - Sleepy: Contrast Estimate = -1.51e-5, SE = 5.18e-6, CL = [-3.08e-5, 6.21e-7], p_{FDR} = 1.73e-3, ExAlert - ExSleepy: Contrast Estimate = -1.54e-5, SE = 5.31e-6, CL = [-3.15e-5, 7.11e-7], p_{FDR} = 2.15e-8) (Fig. 4.5a, Distance from Pattern 5). Moreover, we found that Alert levels were closer to the complex anticorrelations pattern P1, characterised by higher coherence between the DMN and the limbic network P1 (Alert - Sleepy: Contrast Estimate = 3.54e-6, SE = 9.64e-7, CL = [6.13e-7, 6.47e-6], p_{FDR} = 1.48e-2, Alert - ExSleepy: Contrast Estimate = 5.44e-6, SE = 1.31e-6, CL = [1.45e-6, 9.42e-6], p_{FDR} = 1.89e-4) and closer to the complex anticorrelations pattern P3, characterised by higher coherence between the DMN and the visual and limbic networks (Alert - Sleepy: Contrast Estimate = 3.54e-6, SE = 9.64e-7, CL = [6.13e-7, 6.47e-6], p_{FDR} = 1.48e-2, Alert - ExSleepy: Contrast Estimate = 5.44e-6, SE = 1.31e-6, CL = [1.45e-6, 9.42e-6], p_{FDR} = 1.89e-4) (Fig. 4.5a, Distance from Pattern 1, Distance from Pattern 3).

When we examined the main effects of mental states, we failed to replicate the results of Mortaheb et al. (2022), showing that MB is closest to the high-coherence pattern. Counter-intuitively, we showed that ONTASK reports were closest to the high coherence pattern compared to OFFTASK thoughts (OFFTASK - ONTASK: Contrast Estimate = -6.56e-6, SE = 2.17e-6, CL = [-1.32e-5, 3.20e-8], p_{FDR} = 2.15e-8) (Fig. 4.5b, Distance from Pattern 5).

Interaction contrasts are summarised in the Supplementary Table S6.3-1. Overall, we found that conditional on Alert levels, MB was associated with connectivity matrices closer to P1 and P3, characterised by complex inter-areal anticorrelations.

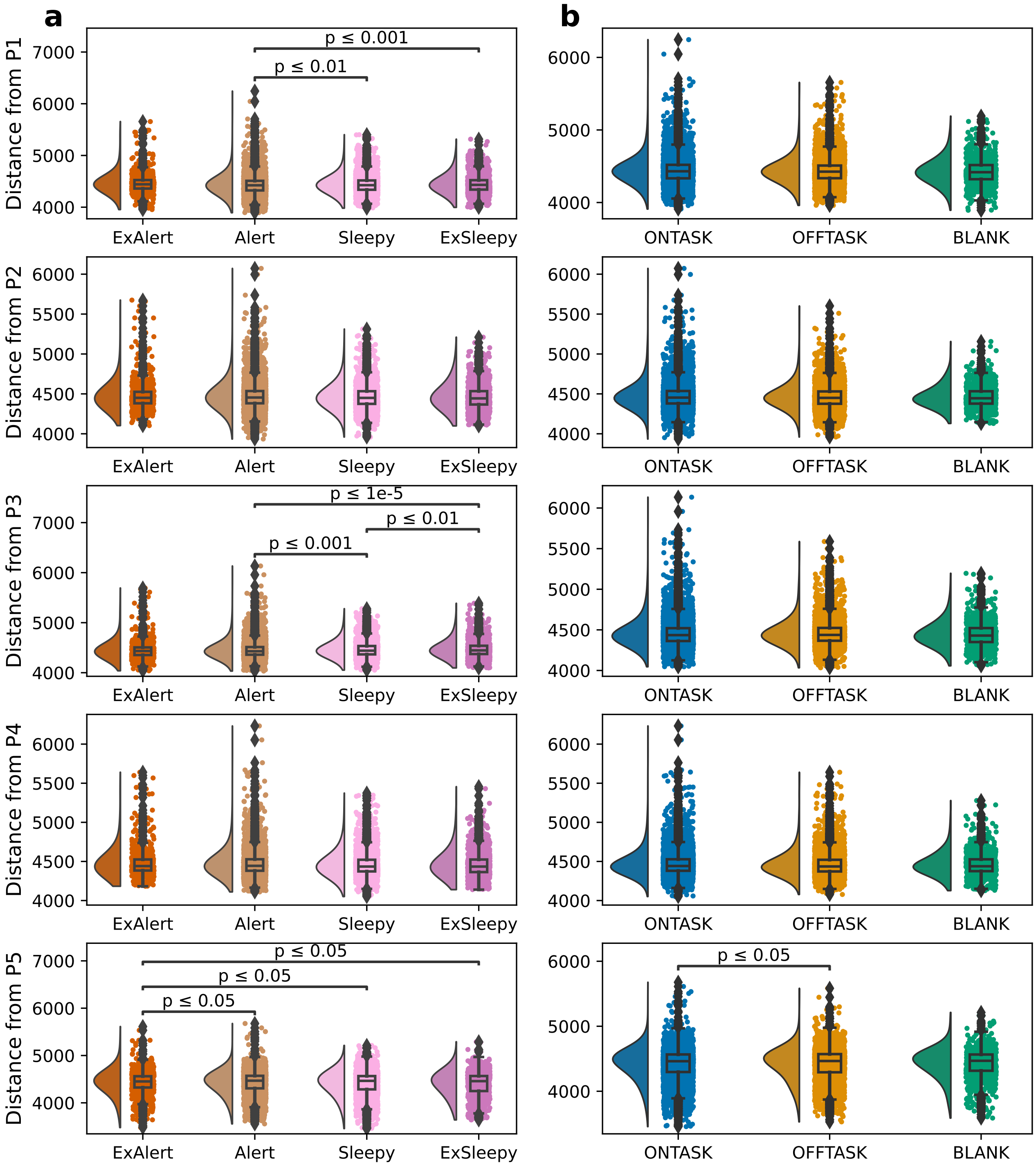

Figure 4.5: Brain pattern distance can differentiate alertness levels but minimally differentiate mental states. a) For every brain pattern ($k = 5$), we fit a generalised linear model (family = Gamma) containing alertness levels, mental states and their interaction terms. The main effects of alertness show that Alert levels have the smallest distance from the complex anticorrelations patterns P1 and P3, characterised by connectivity between the DMN, the limbic and the visual networks. Inversely, Sleepy levels were closest to a brain pattern of high inter-areal coherence (P5). b) Main effects of mental states show that ONTASK reports were closest to the high inter-areal coherence pattern. Density plots and point plots show data dispersion and clustering trends. Box plots indicate medians and inter-quantile ranges.

4.3.5 Distance from the high-coherence brain pattern increased as SW-like activity decreases

We analysed the relationship between brain patterns and SW-like activity using Regularized Canonical Correlation Analysis (rCCA). Specifically, we examined the distance of connectivity matrices from each of the five brain patterns in relation to per-channel SW activity during the 10 seconds preceding the presentation of a reported probe. rCCA is a multivariate statistical method that maximises the correlation between latent components derived from two sets of variables. Our analysis yielded five canonical components. To assess the significance of each component, we conducted permutation testing by running the rCCA model 5000 times with a randomised fMRI variable set. This generated an empirical null distribution of correlations for the dataset. The results were Bonferroni-corrected to account for the number of clusters examined.

First, permutation tests of dimensionality for the canonical correlation analysis (Fig. 4.6, histograms) indicate that SW amplitude, SW upslope and SW downslope produced small but statistically significant canonical correlations. To estimate how each variable affects the canonical components, we estimate the canonical loadings of each component. For SW amplitude, we found that the fMRI component was positively correlated with distance with high coherence, while the EEG component was negatively correlated with SW amplitude. These results suggest that as SW amplitude decreases, FC moves further away from the high-coherence brain pattern (P5). Similarly, for SW downslope, we found that as frontal and temporal SW downslope increases, connectivity matrices come closer to P5. Moreover, occipital and frontal increases in SW downslope activity are associated with connectivity that is closer to the brain pattern of anticorrelations to the visual network (P2), while occipital increases and frontotemporal decreases in SW downslope are associated with connectivity closer to the brain pattern of correlations between the DMN and the limbic and visual network (P3). Finally, regarding SW upslope, the first EEG component was correlated with frontocentrotemporal decreases in SW activity and the first fMRI component was associated with a higher distance from P5, again pointing to the role of SW presence in proximity to high coherence. Finally, occipital SW activity was associated with decreased distance to P1 and increased distance to P3 (Fig. 4.6).

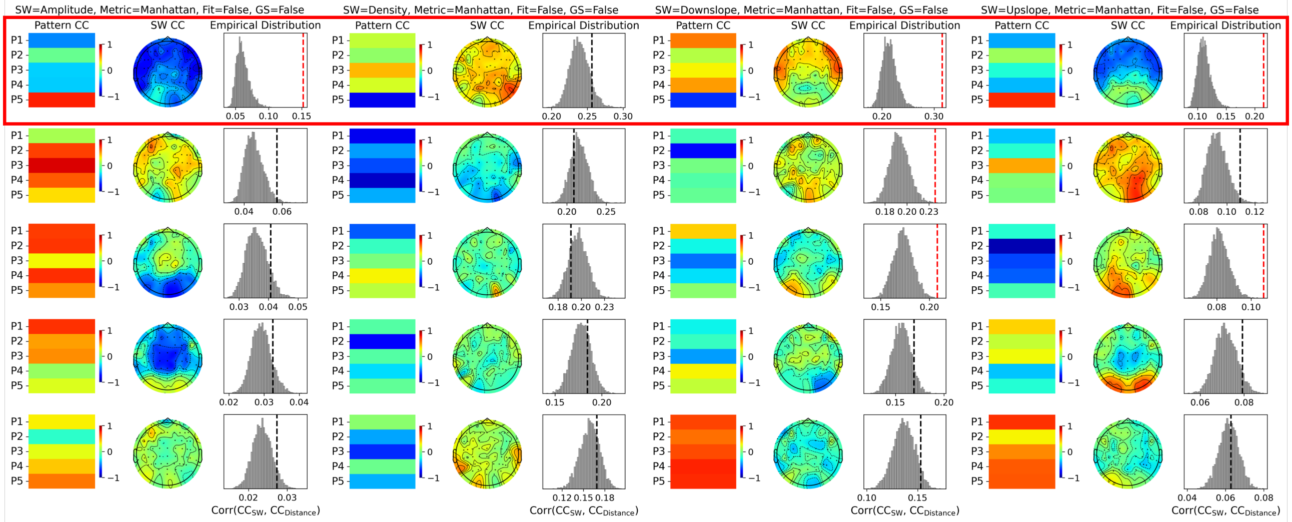

Figure 4.6: A decrease in slow-wave (SW) activity was associated with increased distance between the connectivity matrices and the brain pattern characterised by high coherence. We fit a regularised Canonical Correlation Analysis (rCCA) model to examine the relationship between SW activity and the distance from brain patterns. Across all SW markers examined, we found that the proximity of dynamic functional connectivity to a brain configuration of "hyperconnectivity" was associated with the presence of SW activity (red box). Specifically, an increase in distance from the high-coherence pattern (P5) corresponded to a decrease in SW amplitude across the whole brain. For SW downslope activity, we found that increased anterior-temporal SW activity was associated with smaller distances from the high-coherence pattern (P5). Increased posterior-frontal SW downslope activity was associated with smaller distances from the visual anticorrelations pattern (P2). Additionally, reduced frontal SW downslope activity and increased parietal SW downslope activity were linked to complex cortical interactions characterised by higher coherence between the default mode network (DMN), the visual network, and the limbic networks (P3). Finally, decreased frontocentral SW upslope activity was associated with increased distances to the high-coherence pattern (P5). In contrast, increases in posterior SW upslope activity corresponded to larger distances from both the DMN-limbic coherence pattern (P1) and the visual anticorrelations pattern (P2). Heatmaps illustrated the correlation between the fMRI canonical components and the Manhattan distance of the dynamical connectivity matrices from brain patterns (P1–P5). EEG topo maps depicted the correlation between the EEG canonical components and SW activity in each brain channel. The colour bars represented correlation values. A histoplot displayed the empirical null distribution of correlations in the rCCA model, with vertical lines marking model correlations and red lines indicating significant components. Each column was ordered by the strength of the canonical component correlations. (CC = Canonical Component, Corr = Correlation, SW = Slow Wave)

4.4 Discussion

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In the present study, we combined fMRI-EEG during a SART with experience sampling to understand how different brain configurations lead to discrete self-reported alertness levels and mental states and whether these brain configurations originate from discrete patterns of SW-like activity. Overall, our findings differentiate MB from its alertness contributions, providing a more precise characterisation of their neuronal correlates.

Behaviourally, we first validated that MB is reported less frequently compared to mental states with reportable content, namely on-task and off-task thoughts, in line with previous results (Andrillon, 2021; Boulakis et al., 2025; Mortaheb et al., 2022). Importantly, we did not find evidence for significant modulation of MB frequency in later runs of the SART task. This result is consistent with previous findings suggesting that MB falls outside the typical on-off attention antagonistic dipole (Ward & Wegner, 2013). While periods of on- and off-task engagement fluctuate during a trial, and off-task engagement becomes more prevalent as attentional resources diminish, MB occurs uniformly during the stream of thought (Mortaheb et al., 2022). We can currently only speculate as to the reason, but a potential explanation is that MB functions more like a failure to transition state between thought content (Boulakis & Demertzi, 2025). In this sense, MB would be expected more frequently in states where global brain modes of activity impair content to emerge in the first place. Aligning with this hypothesis, we previously showed that MB frequency increases after sleep deprivation (Boulakis et al., 2025). This hypothesis is further substantiated by the fact that MB had the slowest reaction times compared to on and off-task thoughts, a behavioural proxy of lowered alertness. Together, our behavioural results suggest that MB is modulated more by global states of experienced alertness rather than attentional affordances based on time spent on a task.

Given the link between experienced alertness and MB, we set out to examine whether alertness levels and mental states are dissociable at the cerebral level. We first attempted to replicate previous results showing that MB is linked to the higher amplitude of the global signal (Mortaheb et al., 2022) while accounting for potential alertness confounds. Overall, we found no significant evidence that MB is characterised by increased global signal amplitude once we account for the contributions of alertness. Instead, we showed that global signal amplitude increases as participants become sleepier. The functional role of the global signal is heavily contested (Liu et al., 2017). From one perspective, GS is typically assumed to represent a mixture of physiological, motion and scanner artefacts (Colenbier et al., 2020; Power et al., 2012). This idea is motivated by results showing that the variance introduced by the global signal can be explained away by artefactual regressors, such as motion and physiology (Bolt et al., 2024; Wong et al., 2013). At the same time, GS covaries with electrophysiological (Schölvinck et al., 2010) and metabolic markers (Turchi et al., 2018) of ongoing neuronal activity, suggesting a neuronal component. This neuronal component seems to track cortical and peripheral arousal fluctuations (Bolt et al., 2024). Indeed, arousal fluctuations during wakefulness Bolt et al. (2024); Wong et al. (2013); Zhang & Northoff (2022) and sleep (Bolt et al., 2024; Özbay et al., 2019) modulate global signal amplitude, leading to the formulation that arousal propagation across the cortex elicits cortical synchronisation and subsequent global signal amplitude increase (Raut et al., 2021). Our results build upon past the present literature and show that fluctuations in global signal amplitude not only track cortical and physiological arousal but translate to alertness, showing that GS has an experiential counterpart.

Having found that the global signal amplitude during task engagement is linked to lower arousal levels, we set out to replicate results from Mortaheb et al. (2022). In that study, we previously showed that a brain pattern of cortex-wide high inter-areal coherence supports MB. First, we found that FC can optimally be described across five brain patterns, ranging from complex inter-areal anticorrelations to global synchronised modes. The patterns elicited during the task bear a resemblance to patterns previously reported during rest (Mortaheb et al., 2022; Türker et al., 2024) and different levels of consciousness (Demertzi et al., 2019), suggesting that across different consciousness states and cognitive demands, the brain explores a similar space. We consistently replicated three previously observed patterns: a complex anticorrelations pattern, a pattern driven by anticorrelations with the visual network and a high coherence pattern. A significant deviation from previous works was that we failed to replicate the low-coherence pattern marked by reduced functional connectivity (Demertzi et al., 2019). During rest though, this pattern seems to dominate the clustering space as it occurs more frequently. Yet, we did not manage to reproduce it during the SART. Instead, the high coherence pattern was the most frequent. These results can be accounted for by the fact we directly estimated brain patterns from task connectivity instead of estimating brain patterns from resting state data and then relating these patterns to task connectivity. While rest and task connectivity produce similar whole-brain network structures (Cole et al., 2014), task engagement produces weaker connectivity to rest and less variable neuronal dynamics (Cole & Kvavilashvili, 2021; Ito et al., 2020). Despite similar network organisation, task connectivity shows altered within (Betti et al., 2013) and between network connectivity (Shine et al., 2016; Spadone et al., 2015) compared to rest, with connectivity increases across task-relevant cortical sites (Shine et al., 2016; Spadone et al., 2015). Our results show that although some brain patterns are shared between tasks and rest, the brain's time-varying functional connectivity patterns are shaped by the specific neuronal space it explores to meet task demands.

To relate the brain patterns produced by the clustering approach to ongoing cognition, we estimated the distance of all connectivity matrices to each brain pattern produced, as per the approach described in Mortaheb et al. (2022). An interaction model containing both mental reports and alertness levels failed to show any relationship between MB and the high coherence pattern. Instead, when stratified by alertness, MB was closer to the anticorrelation-dominated patterns (P1, P2, P3). These results appear contrary to our original hypothesis. Anticorrelation patterns, characterised by balanced levels of cortical integration and segregation, are typical in wakefulness (Demertzi et al., 2019), allowing for flexible cortical communication that promotes differential computations and promoting subjective experience (Demertzi et al., 2022). Similar anticorrelation patterns were previously associated with enhanced stimulus perception at threshold levels (Türker et al., 2024). This does not fit with the narrative of MB being a low arousal state characterised by no reportable content (Andrillon et al., 2024; Boulakis & Demertzi, 2025). We recently proposed that probes during MB might be capturing moments of transition between different content, and this phenomenologically translates as "no thought", as content is not yet established (Boulakis & Demertzi, 2025). A potential interpretation of our results is that the predominantly anticorrelated brain pattern might reflect moments of brain reconfiguration in response to ongoing task demands. This interpretation is supported by the fact spontaneous thought initiation is accompanied by increased connectivity between the DMN, the limbic and the control network, regions with positive correlations in both pattern 1 and 3 (Kim et al., 2022; Bartoli et al., 2024; Girn et al., 2017). However, since the brain patterns in the study are generated from task data, pre-probe periods contain a mixture of overlapping cognitive processes associated with SART tasks, such as perceptual discrimination, inhibition and motor processing. Therefore, the hypothesis remains to be further explored.

When we examined the experiential correlates of the "hyperconnected" brain pattern, we found that it was linked to lower alertness levels, consistent with previous results (El-Baba et al., 2019; Li et al., 2020). We recently hypothesised that global synchronisation may result due to the presence of SW-like activity during wakefulness (Andrillon et al., 2024; Mortaheb et al., 2022), based on results showing that the presence of SWs is linked to a cortex-wide BOLD activation pattern (Schwalm et al., 2017) and a cortex-wide increase in FC (Schwalm et al., 2017; Aedo-Jury et al., 2020) in anaesthetize rats, and cortex-wide BOLD activation pattern during NREM sleep in humans (Ilhan-Bayrakcı et al., 2022). The altered BOLD and connectivity profile disappeared when SW activity was regressed out (Schwalm et al., 2017; Aedo-Jury et al., 2020). Following these results, we show that most SW markers during wakefulness (amplitude, downslope, upslope) promote FC characterised by increased inter-areal connectivity and decreased anticorrelated and segregated connectivity. Interestingly, we observed that the topology of SW activity was associated with proximity to different brain configurations. Global and fronto-central SW-like activity was linked to increased proximity to the "hyperconnected" brain pattern. Instead, frontal, parietal and occipital SW-like activity was associated with proximity to patterns dominated by anticorrelated activity. Mechanistically, SW activity originates through rhythmic and alternating patterns of neuronal firing (Up states) and neuronal silencing silence (Down states) at an infra-slow scale (<1Hz). As SW activity emerges when the cortex is disconnected from the environment (Steriade et al., 1993) and in conditions of cortical isolation (Timofeev et al., 2000), it was recently posited that SW activity serves as a fundamental mode of cortical activity (Sanchez-Vives et al., 2017; Sanchez-Vives & Mattia, 2014). This raises the question of whether the "hyperconnected" brain pattern elicited during the presence of SW-like activity is a fundamental brain pattern.

The joint consideration of alertness levels and mental states showed that the previously reported neurophysiological correlates of MB (Mortaheb et al., 2022) could be better accounted for by the overall alertness levels of participants. Specifically, global signal amplitude and "hyperconnectivity" were linked to sleepiness, not MB. These results mirror previous physiological investigations in mind-wandering. Stawarczyk et al. (2020) showed that daytime sleepiness fully accounted for the variance of pupillometry that was explained by mind-wandering. These results suggest that physiological variations are driven by arousal fluctuations and not attentional state (Mittner et al., 2016). Similarly, our results align with the idea that physiology follows global arousal levels, not mental states.

Our study is not without limitations. A major caveat of our research is that brain patterns were estimated using task data. This approach runs the risk of utilising contaminated data from task demands. Therefore, it is not easy to disentangle the neuronal correlates of MB from those of the SART responses. Another major caveat of MB research with experience sampling probes is the infrequency of MB events. As such, to increase statistical power, researchers typically group different reports that indicate no experience (in our case, no recall and thinking of nothing). Although this practice increases the power of the study, these different blank reports indicate different cognitive mechanisms and different levels of awareness of the past mental state. Further research is needed to elaborate on whether a unitary neuronal background supports different blank reports. Moreover, discrete experience sampling methodologies, such as the one utilised here, give variant estimates of mental state frequency dependent on the number of available report options (Robison et al., 2019). Finally, our experience sampling approach can only detect a mental state's end, not the start. As such, we can never be sure that the 10 s of activity analysed here contain neuronal activity associated with solely one report. This issue is further confounded by the fact that mental state duration is not constant over time. As such, model-free approaches may be more suited to uncovering the dynamics of mental states.

4.5 Conclusions

In conclusion, our results show that MB is a mental state that becomes more prevalent in lower alertness levels. Neuronally, we show that MB and lower levels of alertness are mediated by dissociable cortical correlates. Specifically, we link lower levels of alertness to increased amplitude of the global signal and brain configurations characterised by high inter-areal connectivity. Finally, we link macro-scale (fMRI) and mesoscale (EEG) physiology to show that high coherence is tied to slow-wave activity. Overall, our work expands on the neurophysiological correlates of ongoing experience, providing insights into its underlying neural mechanisms.

Chapter 5

General Discussion

This chapter is based on:

1. **Boulakis, P. A.,** & Demertzi, A. (2025). Relating mind-blanking to the content and dynamics of spontaneous thinking. *Current Opinion in Behavioral Sciences*, 61, 101481.

5.1 Thesis summary

The work presented in this thesis has made advancements toward understanding MB by viewing human experience (or the lack thereof) as grounded in a complex brain-body communication system and providing a neurophysiological classification of MB across various brain and body rhythms.

In Chapter 2, we examined whether it is possible to localise the cortical areas involved in the occurrence of MB. We utilised a previously validated dataset containing experience sampling reports during rest in an MRI scanner (Van Calster et al., 2017). We used an activation approach and found that MB is preceded by a deactivation profile spanning the whole brain. In order to isolate blank-specific deactivations, we compared BOLD activity between MB and the mental states of reportable content. Overall, we showed that MB was associated with more pronounced deactivations in the angular gyrus. Finally, we attempted to replicate cortical areas previously associated with self-induced MB (Kawagoe et al., 2019). We show that BOLD deactivations appeared in ventromedial frontal areas (for which previous work pointed to activations), and we provide no evidence for a contribution of the hippocampus or the Broca's area. In general, our results expand the literature on cortical correlates of MB by isolating cortical areas during spontaneous thinking involved in MB occurrences.

In Chapter 3, we tested the hypotheses that a) MB is an arousal-dependent mental state and b) MB has unique bodily correlates that cannot be tracked in brain activity. To answer these questions, we collected mental reports under three different arousal conditions (baseline, after sleep deprivation, and after exercise). In each session, we monitored arousal by tracking brain-body signals, namely EEG, ECG, EDA, pupillometry, and respiration. Our results confirmed that MB became more frequent after low-arousal manipulations, and there was a tendency for MB to increase after high-arousal manipulations. Then, using a machine-learning approach, we showed that mental states could be classified solely on brain or body mechanisms. As predicted, a classifier trained on both brain and body signals showed consistent, yet marginal, improved classification performance.

In Chapter 4, we examined how FC, guided by SW-like activity, organises across different alertness levels and mental reports during task engagement. We estimated phase-based connectivity matrices based on the approach described by Mortaheb et al. (2022). Then, employing clustering, we produced a set of representative brain patterns that occur recurrently across the acquisition time. We showed that MB was associated with a pattern of anticorrelations, while sleepiness was associated with a pattern of "hyperconnectivity". Sleepiness was also associated with higher amplitude of the BOLD global signal. Finally, we employed a canonical correlations analysis to bridge FC with the underlying electrophysiology. We showed that the "hyperconnectivity" brain pattern was linked to SW-like activity.

We can summarise the main findings of the present thesis as follows: a) MB during rest is associated with a pattern of global deactivations, b) MB is an arousal-dependent state, and c) both brain and body carry information about MB, d) FC, correlating with SW-like activity, differentiates mental states and alertness levels. In the remainder of this chapter, I will discuss these findings. At the same time, I will discuss contradictory or difficult-to-reconcile results with the overarching idea that MB is associated with a distinct neurophysiological state of altered arousal.

5.1.1 fMRI deactivations and ongoing cognition

Chapter 2 provides insights into the role of cortical deactivations during the stream of consciousness. BOLD activations in response to cortical stimulation correlate with increased metabolic demands and synaptic activity. Therefore, a potential interpretation of negative BOLD responses is neuronal resource re-allocation in the presence of localised increased metabolic demands elsewhere in the brain. This interpretation is consistent with animal (Shmuel et al., 2006; Harel et al., 2002) and human (Reddy et al., 2000; Shmuel et al., 2006; Smith et al., 2000; Stefanovic et al., 2004) studies showing that contra-lateral cortical stimulation is concomitant with BOLD negative responses in the ispilateral cortex. Similarly, fMRI studies involving cross-modal stimuli have revealed that visual stimulation leads to deactivation of the auditory cortices, while auditory stimulation leads to deactivation of the visual cortices (Laurienti et al., 2002; Lewis et al., 2000; Mozolic et al., 2008).

Critically, in the case of MB, we found such deactivations in occipital, parietal, frontal and thalamic areas, without a clear indication of where such resources may be reallocated. Such deactivations spanning the whole brain have been previously associated with altered states of consciousness in absence seizures (Groulx-Boivin et al., 2024). Absence seizures, characterised by brief lapses in consciousness, are primarily associated with synchronous oscillatory activity in thalamocortical circuits, leading to a distinctive spike-and-wave EEG pattern at 2-4 Hz. Such cortical synchronisation translates into extensive cortical deactivations in frontal, occipital, parietal and subcortical areas, and thalamic activations (Guo et al., 2016; Bai et al., 2010). Inversely, recovery from absence seizures was accompanied by a recovery in the posterior cingulate cortex BOLD amplitude (Bai et al., 2010). The involvement of posterior cingulate cortex deactivations in consciousness levels is further supported by research mediators showing that posterior cingulate cortex deactivations are linked to decreases in subjective experience during meditation (Garrison et al., 2013). While these examples do not suggest that MB is similar to a pathological state, such as seizures, or meditation, they serve to demonstrate that cortical deactivations might promote an overall detachment of ongoing experience from awareness.

When we attempted to isolate MB-specific effects by contrasting MB with mental states where people report content, we found two key areas that showed decreased BOLD activity: the angular gyrus and the vPFC-ACC. However, we found no evidence for regional effects in the MB-SENS contrast. Likewise, explorations of time-varying connectivity differences in the same dataset did not yield differences between MB and sensations. In the original dataset of Van Calster et al. (2017), sensations referred to perceptions without any thoughts. While people seem to experientially differentiate between MB and sensations, the absence of neuronal differences weakens the strength of the claim that MB represents a state of no reportable content. If MB is discrete from states with content, we should expect differences when people report perceptual experiences. Following this, the deactivations observed in the angular gyrus potentially suggest the absence of thought in the propositional form “I am thinking of X”, rather than awareness of content. Overall, the experiential and neuronal differences between MB and sensations remain to be elaborated.

5.1.2 Tracking arousal to track MB

In Chapter 3, we incorporated MB as an option within an experience sampling paradigm during rest under varying arousal conditions and showed that MB increases following sleep deprivation and exercise.

Behaviourally, it was previously shown that MB reports covary with higher levels of self-reported sleepiness (Stawarczyk & D'Argembeau, 2016; Stawarczyk et al., 2020; Madiouni et al., 2020) and lower levels of self-reported alertness (Andrillon et al., 2021) during task engagement. Extending these results, we show that MB propensity increases after sleep deprivation while MW propensity decreases. Previously, both bad sleep quality (Carciofo et al., 2014) and sleep deprivation (Poh et al., 2016) were associated with more frequent task-unrelated thoughts and reduced awareness of MW. A key improvement of our study was the explicit option to report MB occurrences. Since mental state reporting in experience sampling is a zero-sum game — where selecting one option inherently excludes others - adding more available states to report will alter the distribution of reported mental states and influence their observed propensities (Robison et al., 2019). As such, we can acquire better insights into the stream of thoughts when we explicitly model a large cohort of mental states (Turnbull et al., 2019; Mulholland et al., 2023). Therefore, our results suggest that, while both MW and MB are associated with lower arousal states, progressing to arousal extremities, such as sleep deprivation, results in more frequent MB.

While transitions toward low arousal states have garnered a substantial theoretical mapping (Goupil & Bekinschtein, 2012; Tanaka et al., 2013; Cimenser et al., 2011), the other end of the arousal spectrum still remains unrefined (Ciria et al., 2021). High arousal states are heterogeneous (post-aerobic exercise, post-stimulant consumption, post-emotional stimulation), and creating an experimental setting with steady-state high arousal is challenging. In this thesis, we utilised a high-intensity exercise to promote high arousal. The choice of this manipulation rested on research showing unique cortical, electrophysiological, metabolic and cognitive alterations after fatigue-induced aerobic exercise (Ciria et al., 2021; Erickson et al., 2015; Kenney et al., 2015). When considering the whole post-exercise experience sampling period, we failed to find evidence of MB frequency increase. However, partitioning the experience sampling period into two halves (first 20 probes and second 20 probes), we observed increased frequency in MB reports in the first half. Our results suggest that high-arousal effects on mental state reportability might be brief, where there is an increase in MB propensity at the extremity of high arousal and a decrease as we transition from high to medium levels. This idea is consistent with an optimal arousal account of ongoing cognition, where moderate-to-high intensity exercise leads to a selective enhancement of mental state reportability while arousal extremities hinder it. However, this idea remains to be further validated. At the same time, our experience sampling resting intervals were relatively large (∼2 minutes). Given that physiologic arousal returns to baseline levels faster (Javorka et al., 2002; Kannankeril et al., 2004) compared to cortical arousal (Basso & Suzuki, 2017), shorter experience sampling resting intervals might be better suited to capture MB frequency increases following exercise-induced high arousal.

Across all arousal sessions, we found that low arousal, compared to high, involved a trade-off between MW and MB. Importantly, we did not find significant differences when comparing baseline to high or low arousal. One possible explanation is that the drop in MB reports during the second half of the high arousal experience sampling sessions skewed the contrast between high and low arousal. This suggests that the reduction in MB during the second half of the post-exercise experience sampling session is substantial enough to distort the overall comparison. As a result, the relationship between baseline, high, and low arousal levels of MB remains unclear.

5.1.3 Brain-body decoding

In Chapter 3, we further demonstrated that MB could be predicted solely from bodily rhythms such as ECG, EDA, eye openness, and respiration. Additionally, combining EEG brain markers with bodily markers yielded the highest classification performance, marginally but significantly outperforming classification when only considering EEG markers.

Critically, our brain-body model showed negligible improvements. More substantial evidence for our hypothesis would be demonstrated by consistent improvements in classification across all testing folds. An alternative explanation for these results is that the model's performance might be unstable or coincidental, offering weak support for the hypothesis. However, this is unlikely, as the model learned unique information from body features that contribute to classification and did not consider bodily features as noise. Additionally, the marginal improvement in classification was retained across different pre-processing parameters and feature extraction windows.

These results aligned with recent evidence that information from the body could track consciousness states (Raimondo et al., 2017), such as neurotypical wakefulness compared to disorders of consciousness. Contrary to previous results, we only found marginal classification improvement. This discrepancy can be accounted for when considering the length over which brain-body markers are estimated. In previous research, the classified states (disorders of consciousness vs wakefulness) were stable and uniform over time and brain-body measurements are estimated over large time windows (>5 minutes). Moving to shorter time windows, the estimation of bodily features could become more variant and unstable (Nussinovitch et al., 2011; McNames & Aboy, 2006). Moreover, the classified state in question (MB vs other mental states) was not stationary, like a consciousness state, but dynamic and spanning brief periods (Van Calster et al., 2017). This raises the issue that our analysis window (110 s) spanned multiple mental states. Therefore, the analysis of Chapter 3 faced a detrimental trade-off. Either consider large time periods (110 s) spanning multiple mental states, which would reduce interpretability of what the classifier is actually classifying but would create more robust brain-body classification maps, or consider brief periods before mental reports (10 s), which would limit how descriptive the brain-body maps can be.

5.1.4 Mental reportability during cortical “hyperconnectivity”

In Chapter 4, we showed that experientially, MB overlapped with reports of increased sleepiness. On a neuronal level, the previously reported “hyperconnectivity” pattern was linked to sleepiness rather than directly to MB. Directly, this does not invalidate that moments of MB characterised by “hyperconnectivity”; rather than that, overall ‘hyperconnectivity” is better described by altered arousal, which subsequently leads to MB. Therefore, this pattern might be more sensitive to overall sleepiness than the concomitant presence of MB events. At the same time, these results were consistent with the view that a brain pattern of overall reduced arousal would give rise to thoughts with less reportable content (Mittner et al., 2016). Yet, it remains unresolved why this pattern manifests both at moments of less reportable content (Mortaheb et al., 2022) and altered consciousness states (Mortaheb et al., 2024).

The role of “hyperconnectivity” during altered arousal can be contextualised within the broader discussion regarding conscious content and consciousness states (Koch et al., 2016). Typically, conscious content (what we are conscious of) refers to the phenomenal character of our experience (Seth et al., 2008). Research on content-specific properties aims to separate how distinct items of experience are differentially represented neurally, like delineating the role of the fusiform gyrus during face processing (Kanwisher & Yovel, 2006). At the same time, consciousness states refer to “global” states or “modes” of consciousness that provide specific background conditions for any content to appear (Koch et al., 2016). These states are content-invariant and describe how brain anatomy, functional connectivity, or cortical arousal create the background conditions for content to manifest. As “hyperconnectivity” is heavily driven by cortical and bodily arousal, it may be more akin to a conscious state, similar to that of NREM sleep or absence seizures, instead of leading to specific content. It is important to mention that state and content as presented are not necessarily orthogonal; to be conscious is to be conscious of something. However, this distinction raises the issue of whether the neuronal correlates of “hyperconnectivity” can support content or not (Andrillon et al., 2024).

5.2 Putting the blank in the mind

5.2.1 How to naturalise MB in the stream of thought?

In the following section, I will provide some speculatory notes on how I believe MB can be conceptualized as a component in the stream of thought (Boulakis & Demertzi, 2025). As the investigation of MB has been heavily approached with the methodologies of ongoing thinking, it is worth seeing how it relates to key aspects of ongoing thinking, namely thought content and thought dynamics.

Regarding thought content, Smallwood et al. (2021) suggested that content should not be viewed in isolation. Instead, we should examine along which axis different contents co-evolve, creating a multi-dimensional space where the axes represent the key sources of co-variation. The utility of the multidimensional space is the robust organisation of how thoughts covary, allowing us to map similarities across all thought content. We recently speculated that, in such a multi-dimensional coordinate space, in which various content types can be represented as distant points, MB could be placed at the origin point. This would imply that MB is of undifferentiated content, and, as we move away from the origin point, it dissolves, and content becomes more representative of the axis on which it varies (Fig. 5.1). Starting from the deactivations profile of MB, at the origin point, thoughts along a specific axis would neuronally translate to neuronal activations exclusive to that thought content. At the same time, content closer to the origin access would be related to mental states where content is progressively less clear and reportable. In support of this hypothesis, Mulholland et al. (2023) found that thoughts during mundane automated tasks, such as eating and chores, are closer to the origin axis. Taken together, in the dimensional space representing content types, MB is reported as such because it does not seem to relate to any type of content.

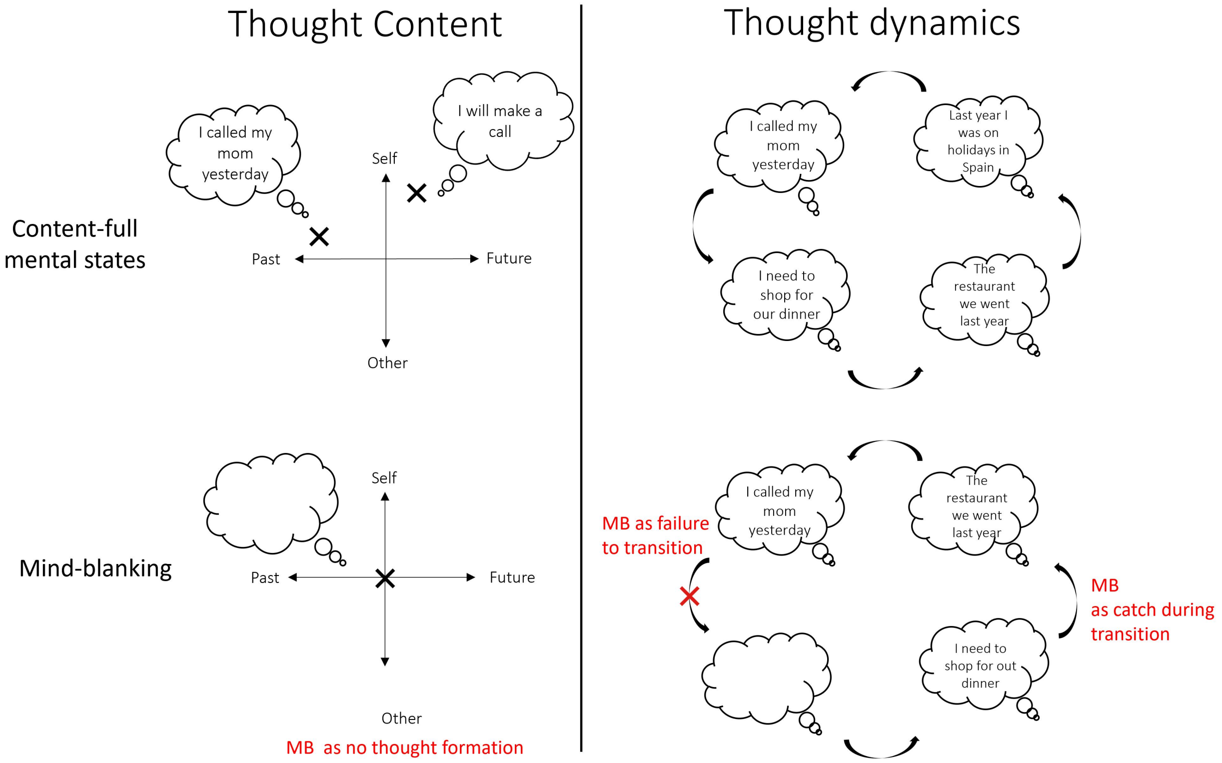

Figure 5.1: On the way to understanding mind-blanking (MB), we can conceptualise it in terms of key aspects of spontaneous thinking, namely thought content and thought dynamics. Left column: Specific thoughts can be represented as points in a multidimensional space, where each dimension reflects key patterns of variation (thought components) in thought content. MB can be considered as resting at the origin point of each dimension to indicate that it does not relate to any other content. Right column: Thought dynamics can be represented as transitions from one content to another. An individual can report a train of thoughts because they can navigate across variant content. In that respect, MB can be considered as the instances happening during content transitions or as the inability to transition.

Accounting for the dynamic aspect of thinking, we observe that thoughts with reportable content can lead toward other contentful mental states thanks to semantic associations, hence creating the perception of a stream of thought (Fig. 5.1). Since MB is not semantically associated with any particular thought content, we previously considered that MB might represent the moments during which we transition across different contents, which get to be phenomenologically translated as MB (Mortaheb et al., 2022). This view is supported by behavioural findings showing that MB has a low chance of being reported when reporting a content-oriented state before and that re-reporting MB is also of low likelihood (Mortaheb et al., 2022). It can also be that transitions happen too fast, like in certain cognitive phenotypes, such as ADHD, which are characterised by mental restlessness and fast thought pacing. In that scenario, MB events are also reported more frequently (Van den Driessche et al., 2017), potentially due to more frequent thought transitions. Another scenario stresses that MB might result from unsuccessful transitions across states in the first place. Evidence for this explanation comes from activation studies showing reduced activity in the hippocampus (Kawagoe et al., 2019) and ventromedial prefrontal areas (Boulakis et al., 2023), potentially reflecting a failure in generating and binding sequential thought content altogether (Fig. 5.1).

5.2.2 Using MB to uncover the neural correlates supporting ongoing thinking

As MB represents a rough dissociative line between reportable and non-reportable moments, it can be of value in uncovering the neural correlates of spontaneous thinking more comprehensively. Current research in spontaneous thinking examines how neural activity correlates with content and does not examine content-invariant mechanisms that facilitate thought content presence and thought dynamics (Smallwood et al., 2021; Stawarczyk & D'Argembeau, 2015; Axelrod et al., 2017). Based on this, we suggest that the neural correlates of thinking can be defined as the minimal neural mechanisms jointly necessary for thought to be manifest. To elaborate on this, we can draw a parallel from the research on the minimal neural prerequisites of consciousness: the neural mechanisms that are prerequisites for conscious experience are discrete from the content of the experience (Koch et al., 2016). For example, the neural correlates of a visual experience differ from mechanistic prerequisites, such as global brain states of desynchronised activity. The isolation of mechanisms that support specific conscious experience can then be uncovered in two ways: a) with a conjunctive approach, where neural correlates of different clusters of content are taken as a union, and b) with a contrastive approach, where neural correlates during the absence of consciousness are subtracted from the neural correlates during consciousness presence. Using the conjunctive approach, we can sample multiple thought content clusters and examine the neural overall, isolating common content-supporting mechanisms. On the other end, using the contrastive approach, we can subtract neural activity of MB reports from moments of reportable content or moments where thought transitions are successful, isolating mechanisms that support these specific phenomena (Fig. 5.2). Overall, MB reports can serve as a point of self-reported no thought during wakefulness and provide an adequate contrast for eliminating brain activity unrelated to thought.

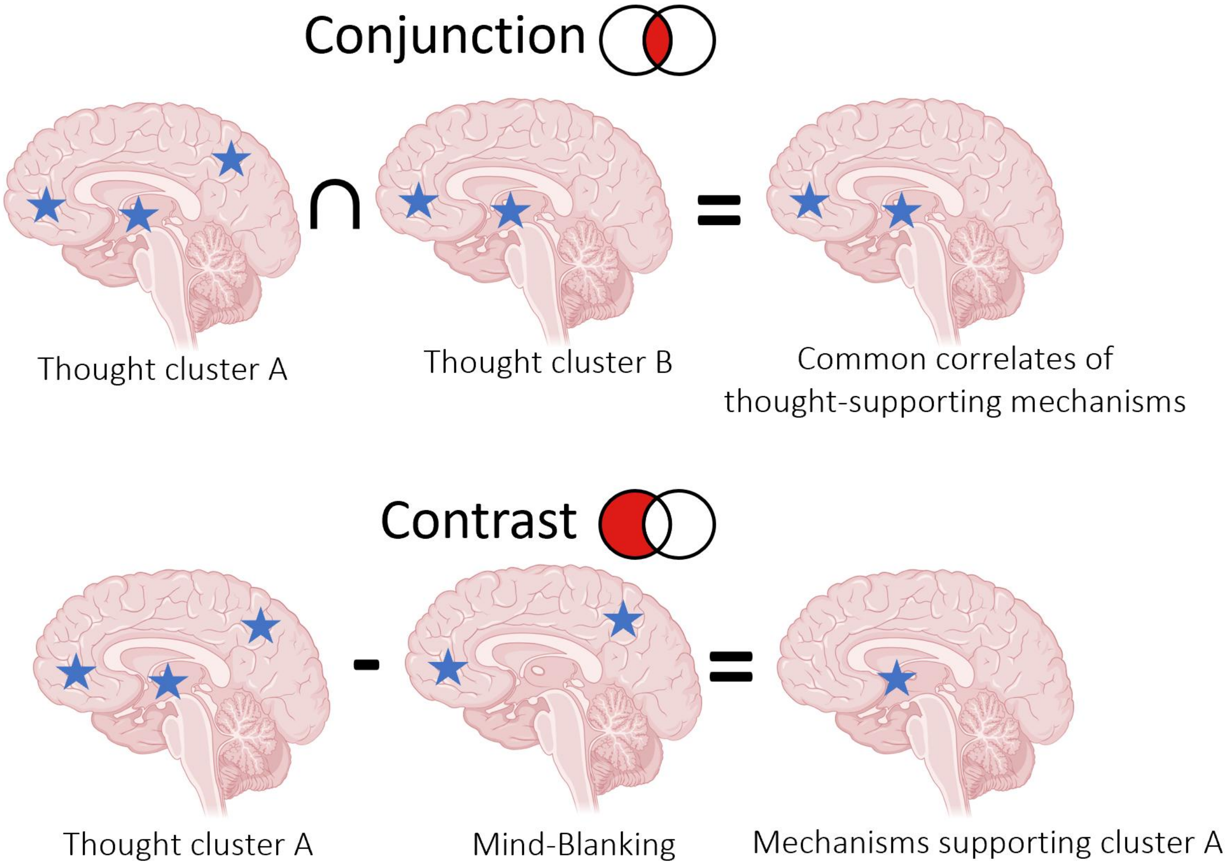

Figure 5.2: Mind-blanking (MB) can help to isolate the neuronal correlates of thinking. The isolation of the neural correlates of thinking can be approached via the conjunction of brain activity, which supports common content clusters, or by contrasting the activity of brain areas, which support specific clusters of thought and no-thought. The conjunction approach can be used by identifying brain areas, the activity of which supports different content and by examining the neuronal overlap between them, leading to a common mechanism that supports thought content. The contrast approach can be achieved by subtracting the neuronal correlates of mind-blanking (MB) from brain activity supporting states with reportable content, leading to the neural correlates of that specific content. Note: the stars represent brain activity associated with different thought clusters and MB.

5.2.3 Towards a standardised definition of MB

Moving forward, a key issue in the study of MB is the standardisation of how MB is defined in experimental settings. We here propose to define MB as a “mental state where people have nothing to report or are unable to report anything about their immediate experience". We find that this definition respects the phenomenological experience of "having no content" without being rigid about whether MB reflects no content or no access to content. Furthermore, this definition remains agnostic as to the psychological underpinnings of MB, i.e., whether people fail to attend to something or forget what they were thinking. Critically, it can function as an **operational definition** for exploring MB. First, this definition respects the phenomenological experience of "having no content" without being rigid about the nature of the content lost (perceptual experiences, thoughts, emotions, sensations). Additionally, this operational definition is a clear, precise, and measurable definition of MB under current experience sampling paradigms. An operational definition specifies the exact procedures or operations used to measure or manipulate a concept or variable in a study (Stevens, 1935). It translates an abstract concept into a concrete, measurable form that researchers can consistently and reliably observe or assess. In such a definition, MB is translated from the experience of "our mind went away" to discrete moments in our stream of consciousness that can be communicated to participants. At the same time, as an umbrella term, it does impose a prior assumption about how MB might manifest, such as deliberate, effortful thought absence (Kawagoe et al., 2018, 2019) or momentary lapses of mental content (Andrillon et al., 2021; Mortaheb et al., 2022; Ward & Wegner, 2013). Critically though, it remains unresolved whether "having no content" and "being unable to report any content" share any neurophysiological overlap or just represent similar experiences during spontaneous thinking. To this end, a future research avenue can focus on the commonalities and differences of blank reports.

Overall, MB is a recent psychological concept, and focusing solely on instances of having no thoughts or content might oversimplify how this phenomenon indeed occurs. Therefore, MB might constitute a heterogeneous construct (Andrillon et al., 2024), but the present **family-resemblance definition** focuses on the absence of reportable content. Therefore, this does not negate the presence of distinct MB subtypes. For example, a distinction may be made between deliberate or spontaneous MB. In the first case, a person enacts cognitive control on their thoughts until reaching a period where they have nothing to report, and the second is more akin to a lapse in attention. Finally, this definition purposefully remains agnostic about the cognitive mechanisms that generate MB experiences. It remains inconclusive whether MB is a bottom-up process where nothing may be encoded (Andrillon et al., 2021; Mortaheb et al., 2022; Musat et al., 2024) or a top-down meta-cognitive failure in evaluating content presence (Efklides, 2014).

Finally, this definition can tell us what does *not* constitute a MB event. Contemplative and meditative practices have been described as distinct states of consciousness, separate from wakefulness and sleep, characterised by a lack of object-oriented awareness (Metzinger, 2020; Costines et al., 2021). During these contemplative states, individuals report an absence of thoughts, perceptual content, or even a sense of self (Boly et al., 2024). However, there is remnant content, described as "pure presence", a sense of awareness of the present, irrespective of the absence of any other content. Therefore, these states do not fulfil the requirement of no reportable content. Similarly, minimal forms of consciousness observed during sleep, such as "lucid dreamless sleep", do not constitute MB. For example, "white dreams" lack object-oriented content, as people report awareness of dreams, yet no content in the dream (Windt et al., 2016; Windt, 2016). However, such experiences are accompanied by a **meta-awareness** that the dreamer is in fact dreaming, and awareness that there is nothing to dream about (Alcaraz-Sánchez, 2021; Alcaraz-Sánchez et al., 2022).

5.3 Future Prospects

5.3.1 Microphenomenology

Advances in the neuroscientific study of MB have begun to elucidate how the brain and body contribute to the MB experience by mapping its neurophysiological correlates. However, a more fundamental question still remains unresolved: When people say, *I am thinking of nothing*, what do they actually mean? Therefore, whether this absence of thought refers to no experience, experiences of no immediate past memory, or raw perceptions without propositional attitudes remains unresolved. The phenomenal heterogeneity of how MB might manifest and the nature of the traditional experience sampling task that probes for content categories (such as MW, on-task engagement, or MB) provide unsubstantial evidence about the effective phenomenology of mental states.

To this end, a microphenomenological approach might be better suited to studying struc-

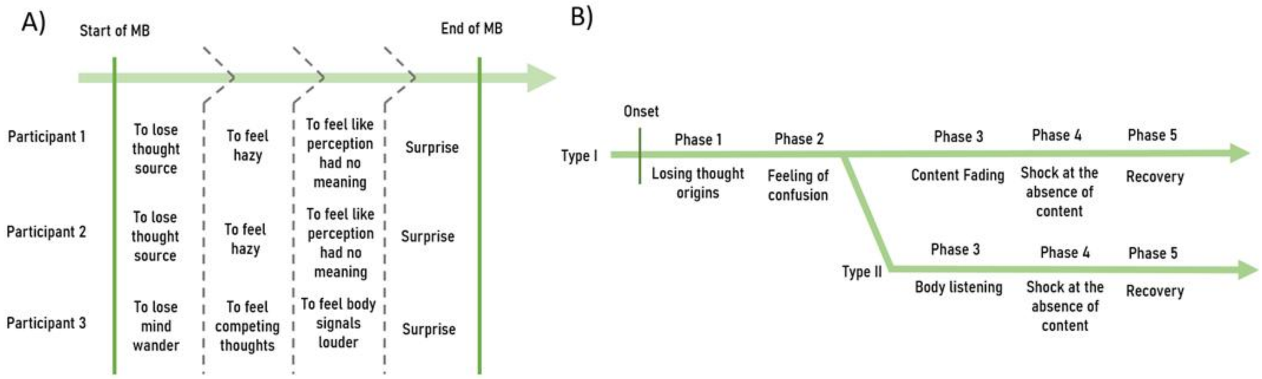

Figure 5.3: Example of potential MB experience structure of microphenomenological analysis. a) In microphenomenological analysis, the aim is to isolate key components of how experience unfolds over time. The mock example sketches descriptions elicited at three different interviews. The contents of each time structure represent the label of the grouped reports the subject gave about that precise time of his experience. The green arrow indicates time. Each column represents a stage. b) Example of potential intersubjective structures based on the individual reports from mock example A. While participants showed coherence during the start and the end of the experience, reflecting in a general trend to lose monitoring of thought origin and the surprise associated with recovery from MB, the most common flow of experience included a fading phase, where there was detachment between perceptual content and semantic processing. Another type of MB experience involved a transition from thoughts to bodily sensations. The different types of MB structures indicate their frequency, with Type I being the most frequent and Type II being the least.

tures of experience. **Microphenomenology** signifies a departure from the traditional third-person study of the mind (Dennett, 2003), as a principled, irreducible study of conscious experience (Varela, 1996). As such, microphenomenology aims to uncover pre-reflective aspects of our experience, mental activity that is implicit and usually unnoticed (Petitmengin, 2007; Petitmengin et al., 2019; Bitbol & Petitmengin, 2017) and that displays coherence or “intersubjectivity” across the population (Valenzuela-Moguillansky & Vásquez-Rosati, 2019). The final goal is to create a formal, invariant structure of human experience, as that is elicited from a first-hand perspective, and guide exploration of neuronal events through such structures (Lutz & Thompson, 2003; Petitmengin & Lachaux, 2013) (For a mock example of intersubjectivity, please refer to Fig. 5.3). To this extent, microphenomenological studies have uncovered regular experience structures in clinical (Petitmengin et al., 2007; Valenzuela-Moguillansky, 2013; Depraz et al., 2017) and cognitive settings (Valenzuela Moguillansky et al., 2013; Gould et al., 2014). Such structures have had translational value in guiding neuroimaging studies. For example, Lutz & Thompson (2003) was able to explain trial-by-trial variability in neuronal dynamics based on first-person, subjective reports. Pertinently to MB research, microphenomenological approaches have uncovered structure and content in other “blank” states (Alcaraz-Sánchez, 2021; Alcaraz-Sánchez et al., 2022). Alcaraz-Sánchez (2021) conducted phenomenological interviews to uncover the structure of objectless conscious sleep, a type of lucid dreaming where participants experience no content. The decomposition of these experiences revealed both consistent themes across time ("how the experience unfolded") and the content of the experience (Alcaraz-Sánchez, 2021; Alcaraz-Sánchez et al., 2022).

Overall, an avenue of future research rests on examining how truly blank is the mind-blank. By using phenomenological interviews instead of thought categories and allowing participants to describe their experience, we can map commonalities and differences between individual MB experiences and whether MB represents absence of content or absence of thought.

5.3.2 Causal models of MB

As highlighted in the Introduction, different overlapping psychological models have been proposed to explain MB, spanning memory, attention, metacognition, semantic production and arousal. These accounts provide univariate explanations of MB, such that MB can result from a failure of attentional affordances (I was not attending to something) or failures in metamemory (I know that I forgot something) (Boulakis & Demertzi, 2025). However, they fail to account for the complex multivariate relationships between different cognitive domains in promoting MB experiences. A better alternative to creating a psychological theory of MB is to eschew the notion of a single causal pathway towards MB and describing the multifaceted and interconnected nature of cognitive domains in creating MB events. In this context, a network perspective might be more appropriate (Borsboom et al., 2021; Borsboom, 2017; Briganti et al., 2024).

The network perspective treats all cognitive domains as interacting nodes of a complex network. Connections ("edges") between the nodes represent directed or undirected relationships between the different cognitive domains. As such, cognition is not attributed to individual nodes but rather emerges from the interaction of the entire network. Applied already to psychopathology (Briganti et al., 2021; Curtiss et al., 2019), personality (Curran & Bauer, 2011) and intelligence (Van Der Maas et al., 2006), this approach has provided a more integrative and systems-based understanding of mental processes. In turn, we can combine MB reports with large-scale neuropsychological assessments of cognitive capacities to isolate which nodes directly relate to MB.

This approach presents an attractive alternative in creating a causal, psychological model

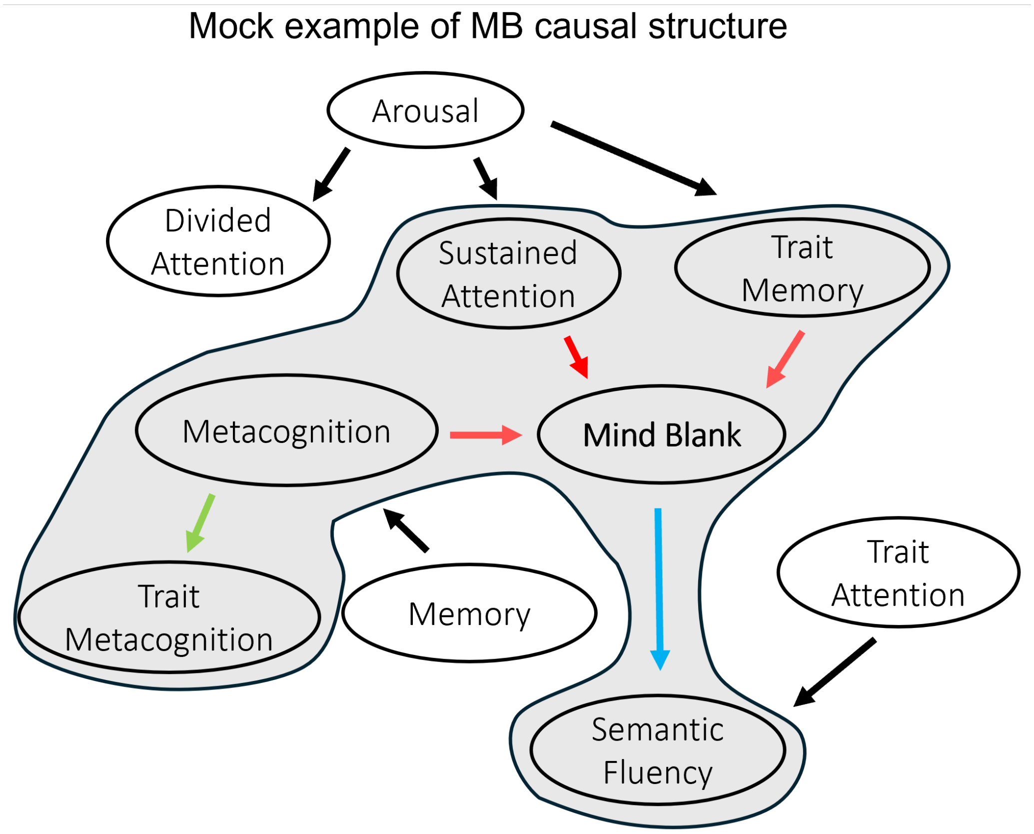

Figure 5.4: A Bayesian network can uncover the causal structure of mind-blanking (MB). In network theory, each cognitive domain can considered a node, and edges represent how strongly the nodes interact. Bayesian networks can uncover the causal structure of a cognitive phenomenon in a data-driven way. For example, the Markov blanket of MB (shaded region) can describe all the parent domains that cause MB (red arrows), all the spouse domains that share variance with MB (green arrows) and all the children domains that are causally affected by MB (blue arrows). This way, we can uncover a cause-and-effect MB structure in a data-driven way, examining which cognitive domains directly relate to MB and which ones affect MB through other intermediating nodes. In the current model, trait-level behaviours model people's beliefs and attitudes towards their own cognitive capacity (e.g. trait attention = beliefs about attentional capacities, sustained attention = performance in sustained attention task).

of MB. Firstly, this approach can map causal relationships. In a Bayesian networks, the edges represent conditional independence, meaning that we can isolate which cognitive domains create a cause-and-effect relationship with MB once accounting for all possible interactions in a model. Secondly, networks infer relationships between cognitive domains directly from the data rather than requiring prior specification of those relationships. As there are currently multiple competing explanations, it allows us to remain agnostic as to the actual underlying cognitive mechanisms that lead to MB. Finally, the network structure mapping cause-and-effect relationships of MB can function as a preliminary psychological theory of MB. We can examine the sum of nodes that show conditional independence with MB (i.e. the Markov Blanket of MB) and make causal inferences about which cognitive domains lead to MB, and which cognitive domains are affected by MB (For a mock example, please refer to Fig. 5.4).

The definitional ambiguity of MB has led to a plethora of psychological explanations of MB. A network approach to MB can help us alleviate this issue. Instead of examining isolated cognitive domains, we can pit them against each other and examine the whole spectrum of human cognition in relationship to MB

5.4 Thesis Conclusions

How does the mind blank? This was the original motivation for my thesis. Across three studies, I attempted to show that MB occurs at the convergence of altered experiential, physiological and cortical arousal. Overall, MB is a fascinating topic, raising a critical issue: can we be conscious but not conscious *of* something? This question challenges our current understanding of our own consciousness. As the study of MB is still in its infancy, I believe that the inclusion of MB as an additional mental state can benefit future spontaneous thinking protocols such that the multiplicity of conscious experiences can be fully represented.

Appendix

6.1 Publications

Available online at www.sciencedirect.com

ScienceDirect

Current Opinion in Behavioral Sciences

Review

Relating mind-blanking to the content and dynamics of spontaneous thinking

Paradeisios Alexandros Boulakis[1,2,3] and Athena Demertzi[1,2,3]

During wakefulness, the stream of thought is occasionally interrupted by moments when we cannot report any content, termed 'mind-blanking' (MB). As MB is a relatively unexplored mental state, we here examine how it relates to spontaneous thinking, namely, thought content and thought dynamics. By reviewing empirical studies on the neural correlates of MB, we first indicate that MB reports are mediated by variations in cortical and physiological arousal levels. In terms of thought content, we propose to view MB on a dimensional space representing content types, where MB is unrelated to any type of content. In terms of thought dynamics, we suggest conceptualizing MB as a moment during content transitioning or as a failure to transition across contents. Taken together, we suggest that MB has a unique place in the study of spontaneous thinking, and its inclusion can facilitate the isolation of the neural correlates of ongoing cognition.

Addresses
[1] Physiology of Cognition Lab, GIGA Research, CRC Human Imaging Unit, Allée du 6 Août 8 (B30), University of Liège, 4000, Belgium
[2] Fund for Scientific Research FNRS, Rue d'Egmont 5, B-1000, Brussels, Belgium
[3] Psychology and Neuroscience of Cognition Research Unit, University of Liège, Place des Orateurs 3 (B33), 4000, Belgium

Corresponding author: Demertzi, Athena (a.demertzi@uliege.be)

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Mind-blanking is an ontologically unclear mental state

During wakefulness, we spend approximately half of the time delving into random thoughts that are unrelated to present engagement, highlighting the centrality of spontaneous thoughts [1,2]. The thought-centric approach to cognition suggests that spontaneous thinking can be described as a sequence of discrete cognitive and emotional states that can be decomposed in terms of 'content' (what the state is about) and 'dynamics' (how states transition across each other) [3]. Recently, the study of spontaneous thinking has expanded to account for brief and infrequent moments when people cannot report content, termed mind-blanking (MB) [4].

While the inclusion of 'blank' or 'empty' reports has increased in recent thought-sampling studies, there is no agreement as to what MB refers to. For example, MB has been referred to as 'blank mind' [5], 'not thinking of anything' [6••], 'awareness of absence' [7], or 'no conscious awareness' [8••]. From the diversity of these definitions, we notice a lack of consensus in the phenomenology of MB [9•,10••], which is further evident in the way that MB is described to participants (Table 1).

Importantly, this phenomenological heterogeneity can translate to different psychological interpretations of MB. This means that MB could be the result of (a) attentional lapses [8••], suggesting that there is mental content, but we miss it by not attending to it; (b) thought-silencing [11], where people try to empty their minds by suppressing semantic content; and (c) metacognitive error or failure of metamemory, where people misjudge their immediate past content [7]. Furthermore, it remains unclear whether MB represents a failure of access consciousness, in that there is content, but we are unable to report it, or whether there is no phenomenal experience at all [12•]. Finally, we recently suggested that MB might not represent a unitary experience [10••], as it can manifest with or without meta-awareness and deliberate control [13•].

Here, we aimed at shedding light on the heterogeneity posed by MB by developing an intuition about the relation of MB with spontaneous thinking. The goal is to locate where MB and spontaneous thinking intersect in terms of thought content and thought dynamics. We think that by answering this question we will not only have a better understanding of MB's psychological profile, but also, we will be able to determine the neuronal correlates of thinking in a more precise way. To that end, delineating the neural correlates of MB first is needed.

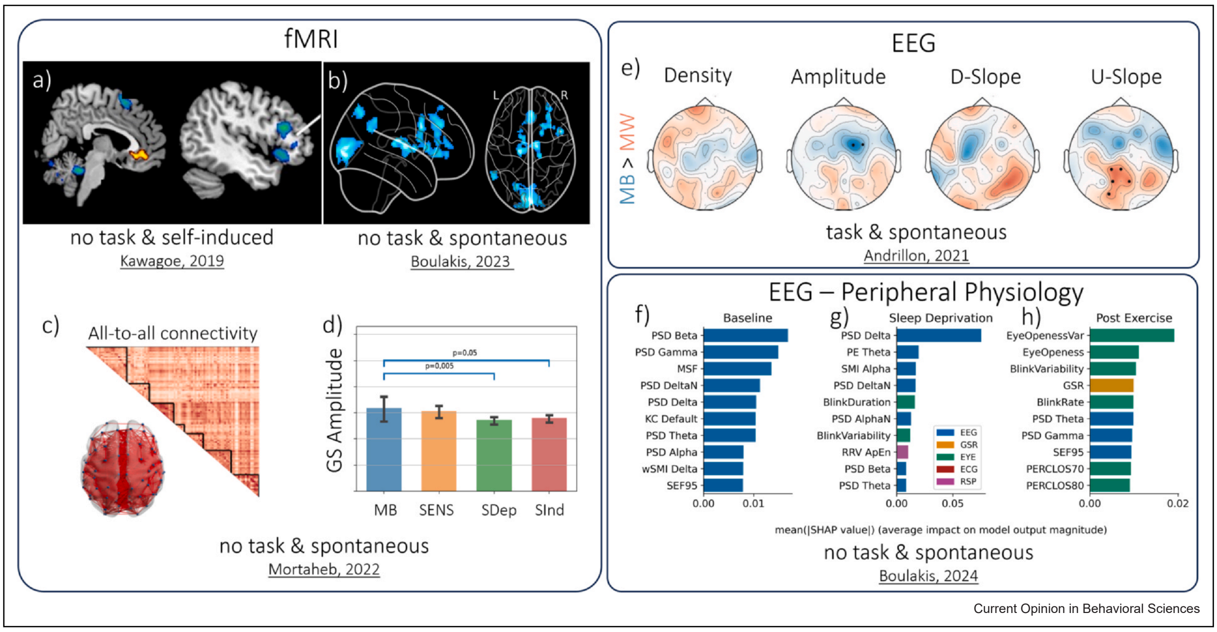
Table 1

Overview of different experimental protocols and analyses of MB.

Descriptions of MB	Task setting	Thought sampling	Modality	Reference
Awareness of no content	Prospective memory	MB questionnaire	Behavior	Efklides & Touroutoglou, 2010 [7]
No conscious awareness Not thinking of anything	Reading comprehension	Probe-catch Self-catch	Behavior	Ward & Wegner, 2013 [4]
Not thinking of anything	SART	Probe-catch	Behavior	Stawarczyk & D'Argembeau, 2016 [14]
Not very alert	Psychomotor vigilance task	Probe-catch	Behavior	Unsworth & Robison, 2016 [15]
No reportable content Not thinking of anything Contentless No thoughts	SART	Probe-catch	Behavior Pharmacology	Van den Driessche et al., 2017 [5]
Absence of content Thinking about nothing Lack of meta-awareness	Rest	Probe-catch	fMRI	Van Calster et al., 2017 [16]
Thinking of nothing	Trying to think of nothing	Post hoc report	fMRI	Kawagoe et al., 2018 [17]
Not very alert	STROOP task Psychomotor vigilance task	Probe-catch	Pupillometry	Unsworth & Robison, 2018 [18]
Thinking of nothing	Trying to think of nothing	Probe-catch	fMRI	Kawagoe et al., 2019 [11]
Not thinking of anything Not attending to task Zone out	SART	Probe-catch	Behavior	Robison et al., 2019 [19]
Not attending to anything Absence of thought	Cohort	Probe-catch	Behavior	Robison et al., 2020 [20]
No conscious awareness Thinking of nothing No recall	SART	Probe-catch	EEG Pupillometry	Andrillon et al., 2021 [8••]
Absence of content Thinking about nothing	Rest	Probe-catch	fMRI	Mortaheb et al., 2022 [6••]
Absence of content Thinking about nothing	Rest	Probe-catch	fMRI	Boulakis et al., 2023 [13•]
Reduced conscious awareness Absence of thought Thinking about nothing No recall	Rest	Probe-catch	Pupillometry	Koroma et al., 2023 [21]
No conscious awareness Not thinking of anything No recall Zone out	Psychometric	MB questionnaire	Behavior	Kawagoe et al., 2024 [22]
Not thinking of anything	Rest	Probe-catch	EEG ECG EDA Respiration Pupillometry	Boulakis et al., 2024 [23••]
No conscious awareness Thinking of nothing No recall	SART	Probe-catch	EEG	Musat et al., 2024 [24]
No conscious awareness Thinking of nothing No recall	SART	Probe-catch	ECG	Corcoran et al., 2024 [25]

ECG = electrocardiography; EDA = electrodermal activity.

Figure 1



Current Opinion in Behavioral Sciences

The neurophysiological correlates of mind-blanking (MB) indicate a mediation by altered arousal levels. *fMRI.* **(a)** Deliberate MB is linked to cortical deactivations in areas associated with thought-silencing [11]. **(b)** Spontaneous MB is linked to cortical deactivations spanning frontal, parietal, occipital, and thalamic areas, including medial frontal regions [13•]. **(c)** Dynamic functional connectivity around MB reports is characterized by an all-to-all connectivity brain profile [6••]. **(d)** MB is characterized by higher amplitude of the fMRI global signal (GS), an indirect indication of low cortical arousal, compared to reports about direct sensory perceptions (SENS), stimulus-dependent (SDep) and stimulus-independent (SInd) thoughts [6••]. *EEG.* **(e)** MB is preceded by posterior slow-wave-like activity, compared to mind-wandering (MW) [8••]. *EEG-peripheral physiology*. **(f)** During baseline arousal, the most informative features for decoding MB originate from the brain. **(g)** During lowered arousal induced by sleep deprivation, the most informative feature for decoding MB was the power spectrum of the delta EEG band. **(h)** During increased arousal induced by high-intensity exercise, the most informative features for decoding MB originate from eye openness (EYE), electrodermal activity (GSR), and EEG. A SHapley Additive exPlanations (SHAP) analysis indicated that the model relied mostly on features from EEG, electrocardiogram (ECG), and eye openness (EYE) to accurately classify MB reports [23••]. GSR: galvanic skin response, RESP: respiration.

Neurophysiological correlates of mind-blanking

So far, electrophysiological and neuroimaging studies point to the possibility that the brain during MB reports is characterized by reduced activity indicative of reduced arousal levels (Figure 1). One of the first neuroimaging studies using functional magnetic resonance imaging (fMRI) showed that when participants were instructed to actively attempt to empty their minds, MB reports were associated with BOLD deactivations in Broca's area, the left hippocampus, and the supramarginal gyrus and activation of the anterior cingulate cortex [11] (Figure 1a/fMRI). At the time, these deactivations were considered representative of thought silencing. Although this might be the case, the finding that the parallel activation of anterior cingulate areas was not following the general deactivation pattern led to the assumption that the instruction 'to empty the mind' might have indicated task-related activity, where participants were following the instruction to monitor and suppress their thoughts [9•]. Using fMRI with experience sampling where MB was not deliberate, we showed that MB reports correlated with widespread deactivations in frontal, parietal, occipital, and thalamic regions [13•]. Importantly, when contrasting MB with mental states about stimulus-dependent and stimulus-independent thoughts, the deactivations spanned the angular gyrus and medial anterior regions [13•] (Figure 1b/fMRI). In another analysis of the same data set [6••], we showed a brain mode, in which MB was linked to a brain pattern where all regions were covarying in activity the same way (Figure 1c/fMRI). Additionally, this pattern was linked to low amplitude of the fMRI global signal (Figure 1d/fMRI), which was previously linked to reflect vigilance levels [26]. In combination with other studies showing that all-to-all fMRI connectivity patterns are observed also during sleep [27], it is collectively inferred that MB is closely linked to low arousal levels.

Using electroencephalography (EEG), the implication of arousal in MB reports became clearer. When EEG was combined with experience sampling during a sustained attention to response task (SART), attentional lapses (MB and mind-wandering [MW]) were associated with the presence of slow-wave-like activity. The localization of the slow waves further differentiated the two mental reports: slow-wave-like activity in posterior electrodes was associated with MB reports, while slow-wave-like activity in frontal electrodes was associated with MW [8••] (Figure 1e/EEG). A re-analysis of the same data set aiming to characterize the spectral and complexity profile of attentional lapses revealed that MB was associated with higher power in delta and alpha bands, lower power in beta and gamma, and reduced parietal complexity, indicative of a reduced cortical arousal mode [24].

More recently, we tested the hypothesis that MB is mediated by arousal levels more directly by quantifying MB frequency not only when arousal was reduced (after sleep deprivation) but also when it was increased (after intense physical exercise) [23••]. Using experience sampling and multimodal brain–body physiology recordings, we showed that MB occurred more frequently in low and high arousal, compared to baseline levels. Additionally, a decoder trained on both brain and physiological features outperformed chance-level classification, as well as the classification performance of decoders trained solely on brain or body features. Critically, classification was arousal dependent, as different levels of arousal were associated with different patterns of brain–body feature importance (Figure 1f–h/EEG-peripheral physiology).

Collectively, these results show that fluctuations of arousal are a critical mediator in MB, such that optimal cortical and physiological arousal leads to reportable content [10••]. Apart from this neurophysiological substrate, how can MB be further accounted in the context of spontaneous thinking?

Mind-blanking as an origin point in the multidimensional content space

Research on spontaneous thinking has proposed to view thought content as having two main clusters: one where thoughts are guided by external demands and one where thoughts are episodic and self-generated [28•]. In the absence of strong deliberate external constraints, self-referential or autobiographical content acts as an attractor, pulling related thoughts and memories into a tendency to generate spontaneous thoughts about the self. As thoughts flow, content tends to settle into these autobiographical attractors, guiding spontaneous thinking toward reflections on personal history, self-identity, and related emotions [29•]. This internal–external dipole is further supported by neuroimaging evidence pointing to antagonistic cortical network activity: an intrinsic or 'default mode' network (DMN) [30–33], and an extrinsic or 'task-positive' network [34–36]. The DMN includes the medial prefrontal cortex (mPFC), the posterior cingulate cortex, the hippocampus, the medial temporal lobules, and the angular gyrus and has been associated with ongoing thinking [37], internal dialog [38], daydreaming [39], rumination [40], and unrelated thoughts from ongoing task activity [39]. The 'task-positive' network includes primarily lateral frontoparietal areas [36,37], and it is theorized to support the perception of the environment. By considering the underlying neural mechanism (neural inhibition), which supports anticorrelations to rise, this antagonistic activity was proposed to account not only for spontaneous thinking but also to provide the necessary substrate for conscious experience in general to happen [41].

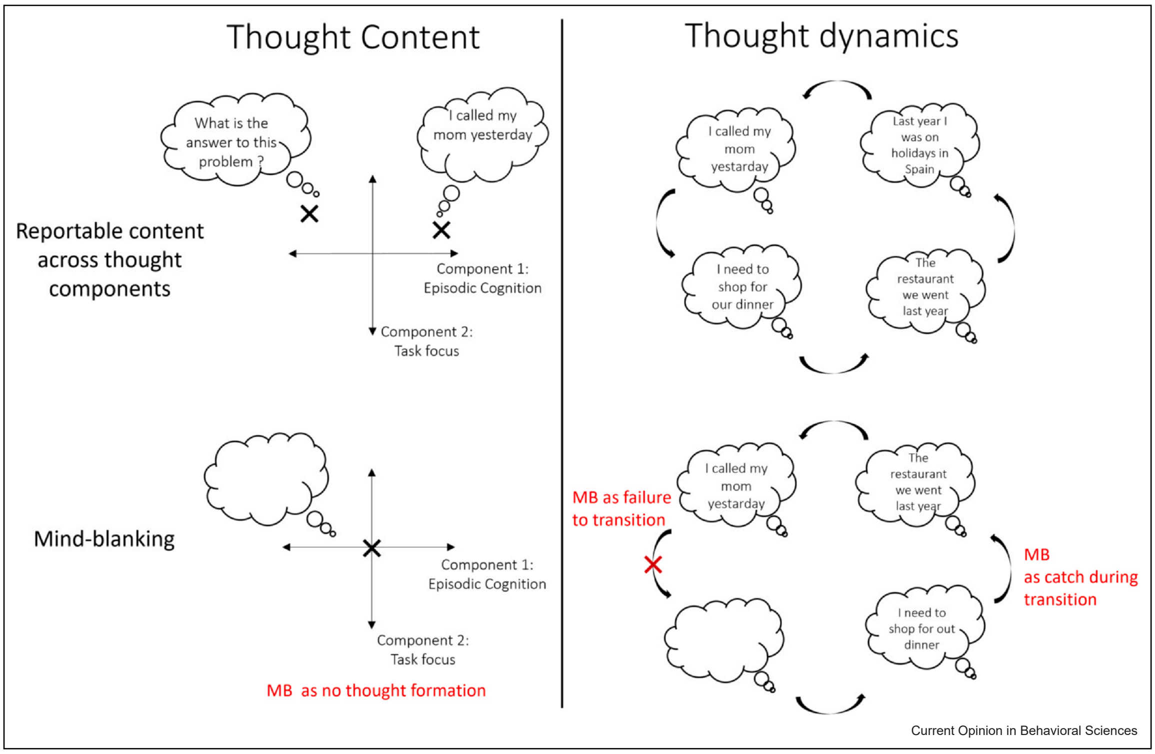
To account for all potential content (beyond the external–internal dipole), a novel approach attempted to uncover how different types of content may appear together. This approach has utilized extensive questionnaires to group covarying content into representative clusters through dimensionality reduction techniques. Identified patterns include self-related processing, episodic social cognition, and task relatedness [42–44*], both during task and naturalistic settings [45,46]. The utility of the multidimensional space is the robust organization of how thoughts covary, allowing us to map similarities across all thought content. What is of interest is that these patterns seem to appear consistently across data sets and experimental settings, which points to their universality [28*]. Neuronally, these thought patterns translate to discrete neuronal substrates. Task-related patterns link to frontal and parietal regions [42,47], and patterns related to the self to the ventromedial prefrontal cortex [43].

We recently speculated that, in such a multidimensional coordinate space, in which various content types can be represented as distant points, MB could be placed at the origin point. This would imply that MB is of undifferentiated content, and as we move away from the origin point, it dissolves, and content becomes more representative of the axis on which it varies (Figure 2). Starting from the deactivations profile of MB, at the origin point, thoughts along a specific axis would neuronally translate to neuronal activations exclusive to that thought content. At the same time, content closer to the origin access would be related to mental states where content is progressively less clear and reportable. In support of this hypothesis, Mullholand et al. [44*] found that thoughts during mundane automated tasks, such as eating and chores, are closer to the origin axis. Taken together, in the dimensional space representing content types, MB is reported as such because it does not seem to relate to any type of content.

Mind-blanking as the result of transition catch or failure

The dynamic components of thinking emphasize the presence of bottom-up automatic constraints (such as

Figure 2



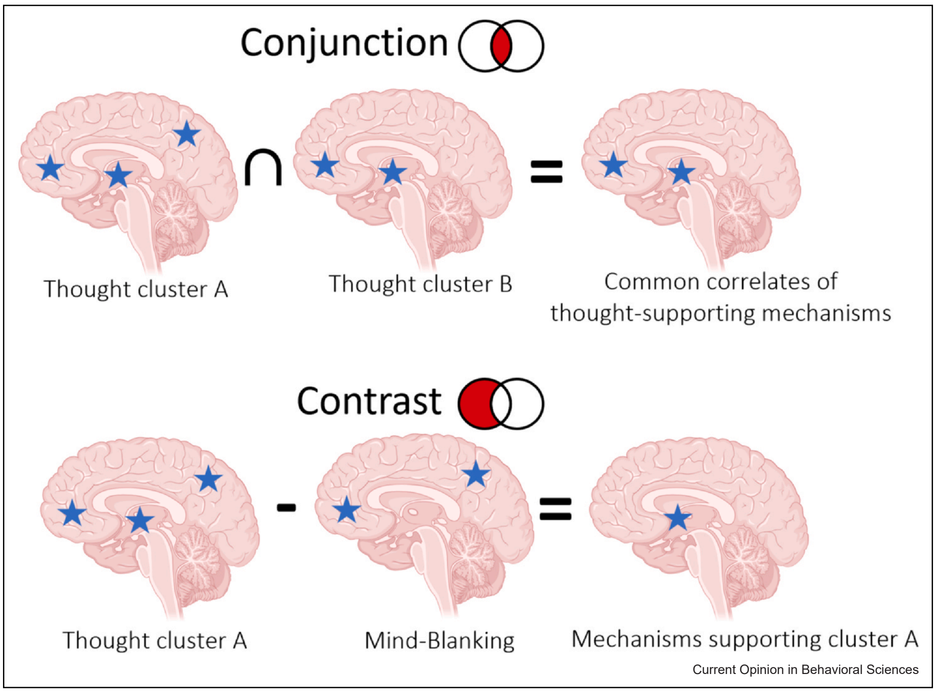
Current Opinion in Behavioral Sciences

On the way to understand mind-blanking (MB), we can conceptualize it in terms of key aspects of spontaneous thinking, namely thought content and thought dynamics. *Left column*: Specific thoughts can be represented as points in a multidimensional space, where each dimension reflects key patterns of variation (thought components) in thought content. MB can be considered as resting at the origin point of each dimension to indicate that it does not relate to any other content. *Right column*: Thought dynamics can be represented as transitions from one content to another. An individual can report a train of thoughts because they can navigate across variant content. In that respect, MB can be considered as the instances happening during content transitions or as the inability to transition at all.

sensory salience), as well as top-down cognitive control constraints of thought (such as motivational factors) [3]. This approach stresses that there are mechanisms that generate and propagate thoughts and indicate how these mechanisms alternate based on the presence of such constraints. For instance, generative accounts of thought initiation and propagation have focused on the role of subcomponents of the DMN, specifically the mPFC [48], the medial temporal lobe (MTL) [49] and the hippocampus [50]. The mPFC was postulated to bind semantically adjacent concepts to propagate the stream of consciousness [51,52] by appropriately retrieving associated concepts [51,53]. The hippocampus was shown to assist in the propagation of ongoing thought by memory retrieval functions that reactivate memory traces relevant to ongoing experiences [54], potentially binding content under context similarity [3]. Finally, the MTL has been implicated both in thought initiation and in associative processes that bind sequential thoughts: ongoing MTL BOLD activity has been observed preceding ongoing thoughts [55], while MTL lesions have been associated with reduced variability of content during MW [56]. This decrease was explained as reduced conceptual variability due to impaired associative processing [57].

Accounting for the dynamic aspect of thinking, we observe that thoughts with reportable content can lead toward other content-full mental states thanks to semantic associations, hence creating the perception of a stream of thought (Figure 2). Since MB is not semantically associated with any particular thought content, we previously considered that MB might represent the moments during which we transition across different contents, which get to be phenomenologically translated as MB [6**]. This view is supported by behavioral findings showing that MB has a low chance of being reported when reporting a content-oriented state before and that rereporting MB is also of low likelihood [6**]. It can also be that transitions happen too fast, like in certain cognitive phenotypes, such as ADHD, which are characterized by mental restlessness and fast thought pacing. In that scenario, MB events are also reported more frequently [5], potentially due to more frequent

Figure 3



Mind-blanking can help to isolate the neural correlates of thinking. The isolation of the neural correlates of thinking can be approached via the conjunction of brain activity, which supports common content clusters, or by contrasting the activity of brain areas, which support specific clusters of thought and no-thought. The *conjunction* approach can be used by identifying brain areas, the activity of which supports different content and by examining their neural overlap between them, leading to a common mechanism that supports thought content. The *contrast* approach can be achieved by subtracting the neural correlates of MB from brain activity supporting states with reportable content, leading to the neural correlates of that specific content. *Note*: the stars represent brain activity associated with different thought clusters and MB.

thought transitions. Another scenario stresses that MB might be the result of unsuccessful transitions across states in the first place. Evidence for this explanation comes from activation studies showing reduced activity in the hippocampus [11] and ventromedial prefrontal areas [13*], potentially reflecting a failure in generating and binding sequential thought content altogether (Figure 2).

Using mind-blanking to uncover the neural correlates supporting spontaneous thinking

Having examined how the neuronal substrate of MB can be incorporated into the study of spontaneous thinking, we can examine how we can leverage it to uncover the neuronal correlates of thought. As MB represents a rough dissociative line between reportable and non-reportable moments, it can be of value in uncovering the neural correlates of spontaneous thinking more comprehensively. Current research in spontaneous thinking examines how neural activity correlates with content and does not examine content-invariant mechanisms that facilitate thought content presence and thought dynamics [28*,58,59]. Based on this, we suggest that the neural correlates of thinking can be defined as the minimal neural mechanisms jointly necessary for thought to be manifest. To elaborate on this, we can draw a parallel from the research on the minimal neural prerequisites of consciousness: the neural mechanisms that are prerequisites for conscious experience are discrete from the content of the experience. For example, the neural correlates of a visual experience differ from mechanistic prerequisites, such as global brain states of desynchronized activity. The isolation of mechanisms that support specific conscious experience can then be uncovered in two ways: (a) with a *conjunctive* approach, where neural correlates of different clusters of content are taken as a union and (b) with a *contrastive* approach, where neural correlates during the absence of consciousness are subtracted from the neural correlates during consciousness presence. Using the *conjunctive* approach, we can sample multiple thought content clusters and examine the neural overall, isolating common content-supporting mechanisms. On the other end, using the *contrastive* approach, we can subtract neural activity of MB reports from moments of reportable content or moments where thought transitions are successful, isolating mechanisms that support these specific phenomena (Figure 3). Overall, MB reports can serve as a point of self-reported no thought during wakefulness and provide an adequate contrast for eliminating brain activity that is not associated with thought.

Discussion and conclusions

We here attempted to get insights into the current heterogeneity of MB by developing a proposal about the relation between MB and spontaneous thinking. We first notice that MB is associated with altered arousal, raising the issue of whether something can be reported under such a neuronal background [10**].

The role of arousal in MB can be contextualized within the broader discussion regarding conscious content and consciousness states [60]. Typically, conscious content (what we are conscious of) refers to the phenomenal character of our experience [61]. Research on content-specific properties aims to separate how distinct items of experience are differentially represented neurally, like delineating the role of the fusiform gyrus during face processing [62]. At the same time, consciousness states refer to 'global' states or 'modes' of consciousness that provide specific background conditions for any content to appear [60]. These states are content invariant and describe how brain anatomy, functional connectivity, or cortical arousal creates the background conditions for content to manifest. As MB is heavily driven by cortical and bodily arousal, it may hence be more akin to a conscious state, similar to that of NREM sleep or absence seizures, rather than to a specific content. It is important to mention that state and content as presented are not necessarily orthogonal; to be conscious is to be conscious of something. However, this distinction raises the issue of whether the neuronal correlates of MB can support content or not [10**].

Jumping off that point, we attempted to position MB within the context of spontaneous thinking by connecting it to two key aspects: content and dynamics. In both cases, MB can represent the absence of key components necessary for uninterrupted spontaneous thinking. Subsequently, by contrasting MB to thoughts with reportable content, we can get further insights into the neuronal mechanisms that make content reportable.

Moving forward, a key issue in the study of MB is the standardization of how MB is defined in experimental settings. We here propose to define MB as a "mental state where people have nothing to report or are unable to report anything about their immediate experience". We find that this definition respects the phenomenological experience of 'having no content' without being rigid about whether MB reflects no content or no access to content. Furthermore, this definition remains agnostic as to the psychological underpinnings of MB, that is, whether people fail to attend to something or forget what they were thinking.

Overall, we aimed to examine how MB relates to current conceptions of spontaneous thinking. As the study of MB is regaining attetion and current research on MB has utilized heterogeneous definitions, we advocate for the inclusion of MB as an additional mental state in empirical future protocols, such that the multiplicity of conscious experience can be fully represented.

CRediT authorship contribution statement

PAB: Conceptualization, Writing – original draft, Visualization. **AD**: Conceptualization**,** Writing – original draft, Visualization, Supervision.

Data Availability

No data were used for the research described in the article.

Declaration of Competing Interest

Regarding our manuscript "What's the blank about? Relating mind-blanking to aspects of ongoing thinking", we would like to declare we hold no competing interests.

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Spontaneous thoughts and experiences across wakefulness and sleep

Paradeisios Boulakis[1,2], Athena Demertzi[1,2], Jacobo Diego Sitt[3], Thomas Andrillon[3,4*]

[1] GIGA-CRC Human Imaging Unit, Allée du 6 Août, 8 (B30), 4000 Sart Tilman, GIGA Institute, University of Liège, Belgium

[2] Psychology & Neuroscience of Cognition Unit (PsyNCog), Place des Orateurs, 1 (B33), 4000 Sart Tilman, University of Liège, Belgium

[3] Paris Brain Institute, Sorbonne Université, Inserm-CNRS, Paris 75013, France

[4] Monash Centre for Consciousness & Contemplative Studies, Monash University, Melbourne, VIC 3800, Australia

*Corresponding author

Thomas Andrillon
thomas.andrillon@icm-institute
Paris Brain Institute
Hôpital de la Pitié-Salpêtrière
47 Boulevard de l'Hôpital
75013 Paris France

Abstract

Consciousness research can be divided into two main areas: the study of states of consciousness and the study of contents of consciousness. States of consciousness can include normal states of the brain associated with the presence or absence of consciousness, such as wakefulness and sleep, but can also refer to states caused by brain lesions or external interventions. Contents of consciousness refer to what we experience and what we are conscious *of*. Within a given conscious state, conscious contents constantly change, ranging from content-full to content-less experiences. In this chapter, we emphasize the similarities across experiences reported in wakefulness and sleep. We further discuss how the possibility of having conscious experiences without specific content challenges the idea that being conscious necessarily involves being conscious *of* something. Finally, by reviewing the literature on the neural correlates of consciousness, we propose a potential convergence in the study of conscious states and contents.

1. Consciousness is a dynamic phenomenon

1.1 Being conscious and being conscious *of*

Consciousness can be described both as a state of being (being conscious), but also in terms of the contents that are being experienced (being conscious *of* something). The study of consciousness as a state stems from the presupposition that different levels of consciousness exist, ranging from wakefulness to dreamless sleep and dreaming, but also coma and anesthesia. At the same time, consciousness as subjective experience refers to being conscious *of* something (Figure 1a). Studying consciousness in its intransitive sense (awake/asleep) means exploring the global "states" or "modes" that allow the formation of various experiences (e.g. dreaming). Studying consciousness in its transitive sense (i.e., being conscious *of*) means describing particular contents of consciousness, that is the phenomenal properties of specific experiences.

Similarly, in clinical neurology, the bedside examination of comatose patients stresses the distinction between arousal (the ability to be awake) and awareness (evidenced by cognitive and affective responses to commands and the patient's surroundings) (Figure 1b). This dichotomy is not only useful to categorize and diagnose different types of patients but can also generalize to other conscious states like the transition from wakefulness to deep sleep (Laureys, 2005; Posner et al., 2007). It also suggests a relationship between states and contents: the less aroused we get, the less aware we become of our surroundings. This model, though, can be restrictive in that it cannot accommodate more nuanced states of consciousness. Therefore, multi-dimensional models have been introduced to emphasize that not all conscious experiences might fit into a simple bi-dimensional model; rather, consciousness can be described as a continuum space that unfolds along many different dimensions, like sensory, temporal, emotional or cognitive, which, when taken together, they shape the type of subjective experiences an individual can have (Bayne et al., 2016; Walter, 2021).

The state and content approaches are not orthogonal. Being conscious and being conscious *of something* are often presented as two sides of the same coin, in that, if you are conscious of something then you are by definition conscious. Accordingly, in cognitive neuroscience the mind is usually described as a content-oriented operator. Conscious states, though, can give rise to very different types of experiences and recent research on altered or non-standard states of consciousness (such as psychedelic-induced states, dreaming, etc) has stressed the importance of considering not only the type of content that is being experienced (synchronic aspect) but also the dynamic of these contents (diachronic aspect) (Petitmengin, 2006). At the same time, it can be that one can be conscious without being aware of any specific content. These so-called "contentless" states include certain type of meditative practices or low-arousal states that are described by individuals as having a "blank mind" (Andrillon et al., 2024).

1.2 Conscious contents as a stream

Consciousness is a highly dynamic phenomenon. Throughout our days and nights, we cycle across many different types of states and contents (Figure 1c). Conscious states can be influenced by the levels of arousal, as mentioned above. Large fluctuations in arousal can determine large changes in the overall conscious state, such as transitions between wakefulness and dreamless sleep (Tononi et al., 2024). These shifts between arousal states further lead to drastic changes in brain function.

At the same time, within a given conscious state, there can be nested fluctuations in the conscious contents that individuals experience. For example, during wakefulness, individuals often fluctuate between contents oriented to a specific goal or task, and self-generated, task-unrelated contents such as those occurring during mind wandering (Smallwood & Schooler, 2015). Likewise, during sleep, individuals can alternate between dreaming and dreamless sleep, even within physiological states that are considered fairly homogenous such as Non Rapid Eye-Movement (NREM) sleep stage 2 (Siclari et al., 2013; Wong et al., 2023) (Figure 1c). The fluctuations in conscious states and contents are, thus highly dynamic, a feature captured by William James' metaphor of "the stream of consciousness" (James, 1890).

The relationship between conscious states and conscious contents is naturally tight. Wakefulness is typically associated with rich conscious experiences whereas sleep is more often associated with no or oneiric contents (e.g., (Siclari et al., 2013)). However, the wide palette of dreams, which can have vivid features or minimal contents (Windt, 2015), showcases the variability of content within a given state. Besides, there is also some continuity between the contents belonging to different states. For example, the transition between wakefulness and sleep cannot be summarized to a specific tipping point (Lacaux et al., 2023) and individuals themselves frequently fail to notice that they have fallen asleep. This implies that individuals can move from one conscious state to another without necessarily having experienced a break in their stream of thoughts, further stressing the importance of examining states and contents of consciousness jointly.

1.3 Arousal and attention shape the dynamics of consciousness

What we are conscious *of* is determined by our current brain state and its interaction with our bodies and our environment. Specific brain states are necessary for any content to be made conscious, providing background conditions that constrain conscious contents and their reportability. These background conditions include brain anatomy, function and dynamics, but also the general arousal level of an individual (Koch et al., 2016). We here define arousal as the physiological processes determining an individual's level of alertness, wakefulness and responsiveness. However, arousal is not restricted to changes in brain activity (Sabat et al., 2024). Controlled by the autonomic system, autonomic arousal also refers to alterations in bodily functions, like cardiac or respiratory activity, to maintain homeostasis and respond to environmental changes. These peripheral changes are further integrated at the level of the brain and can impact both the state and content of consciousness (Park & Tallon-Baudry, 2014).

On top of these background conditions, sensory inputs available to the brain as well as cognitive functions, such as attention, memory, language, meta-cognition can also shape the contents of consciousness. These different conditions are considered as content-invariant or domain-general mechanisms of consciousness and do not contribute directly to the content of experience (Koch et al., 2016). Attention, which refers to the neural mechanisms allowing an individual to select (top-down attention) or leading to the selection (bottom-up attention) of specific information and ignore others, shapes the stream of consciousness within a specific arousal state by influencing which exogenous or endogenous inputs are integrated to conscious experience.

Neuronally, both arousal and attentional mechanisms can be identified as changes in cortical excitability, which refers to the strength of the response of cortical neurons to a given stimulation. Arousal changes can indeed shift cortical dynamics toward different levels of synchronization which can be more or less favorable for conscious states (Koch et al., 2016). Additionally, attentional orientation can modulate the encoding of specific sensory inputs in specific neural networks through changes in neuronal gain (Harris & Thiele, 2011). Consequently, global changes in cortical excitability can determine the overall state of consciousness, accounting for the transition from wakefulness to sleep. At the same time, local neuronal changes can shape the content of experience within a state by facilitating or suppressing the process of certain internal or external inputs.

Consciousness is thus a multidimensional phenomenon characterized by variant richness of contents which are strongly affined to the dynamic changes in global states mediated by arousal and attention. Consequently, our mental lives are also of a dynamic character which, during waking periods, take the form of spontaneous thinking. In the next section, we will see how spontaneous thinking unfolds during wakefulness and sleep in terms of behavior and neuro-physiological states.

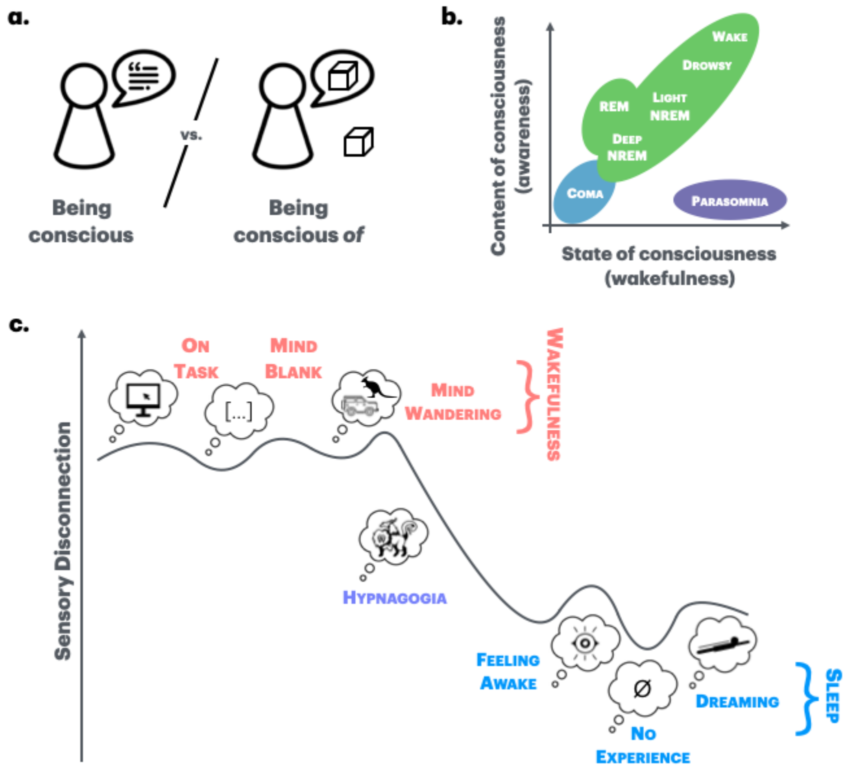

Figure 1. Consciousness as a dynamic phenomenon.

a: Consciousness can be investigated as a state (being conscious) or through its contents (being conscious of something). b: Standard 2D model of consciousness used in disorders of consciousness (DoC) that distinguished states and contents of consciousness (from (Laureys, 2005)). c: We rather propose that, within a given conscious state, there can be nested fluctuations in the conscious contents that an individual can experience. For example, during wakefulness, consciousness often fluctuates between contents oriented to a specific task, task-unrelated contents (such as those occurring during mind wandering) or mind blanks. Likewise, during sleep individuals can alternate between dreaming and dreamless sleep, with the ability to later report on the dream content or not.

2. Spontaneous thoughts and experiences during wakefulness

2.1 Emergence of the concept of mind wandering

During wakefulness, we typically engage with a variety of tasks. Frequently, though, our minds stray away from the here and now of the tasks we perform and we spend a big part of our mental lives delving into spontaneous thoughts that do not necessarily reflect our current environment (Killingsworth & Gilbert, 2010; Seli et al., 2018a). These spontaneous thoughts and experiences are largely freewheeling, in that they are elicited by the absence of constraints. Two types of constraints have been proposed: deliberate constraints which describe how the exertion of cognitive control regulates mental flow in a goal-directed fashion, and automatic constraints which reflect the fact that the stream of experiences can be driven by the salience of mental representations or by physiological needs (Christoff et al., 2016).

Among different types of spontaneous thinking, mind-wandering has seen extensively studied over the past two decades (Smallwood & Schooler, 2015). Mind wandering is operationalized as thoughts unrelated to the task at hand (task-unrelated thoughts) or being decoupled from the current environmental stimuli (stimulus-irrelevant thoughts) (Stawarczyk et al., 2011). Mind-wandering spans multiple cognitive and emotional domains, intertwining with processes like attention, mood, and memory, often playing a dual role in daily life by either disrupting focus or facilitating creative thinking (Smallwood & Schooler, 2015). However, there are ongoing debates about the nature of mind-wandering as to whether it refers to a unitary phenomenon or a family of phenomena with overlapping and non-overlapping features (Christoff et al., 2018; Seli et al., 2018b). Yet, all the different models of mind wandering tend to agree on its core dynamic features, its centrality for wakeful cognition and consciousness, and, at the mechanistic level, its association with activations of the default mode network (DMN).

2.2 The Default Mode Network and its implication in mind wandering and consciousness

This DMN refers to a set of brain regions comprising the posterior cingulate cortex and adjacent precuneus, the medial prefrontal cortex, the inferior parietal lobule, the angular gyrus, the temporal poles, the hippocampus, the parahippocampal gyrus and the retrosplenial cortex (Raichle et al., 2001) (Figure 2). The DMN is widely known, among others, thanks to its paradoxical discovery: using functional neuroimaging (PET) studies which compared task activations to resting periods revealed that the abovementioned regions showed systematic deactivations (Shulman et al., 1997). Using fMRI later on, these regions were found to be active by default during rest only, and hence they were named as default mode network[1]. Convergent evidence suggests that DMN might be directly implicated in self-referential or internally focused thought processes, such as prospective or autobiographical thinking, mental simulations, self-referential reflection, and emotional appraisal (Andrews-Hanna et al., 2014). Accordingly, shifts from the external environment towards "internal" events are associated with increased activity in DMN nodes (Vanhaudenhuyse et al., 2011).

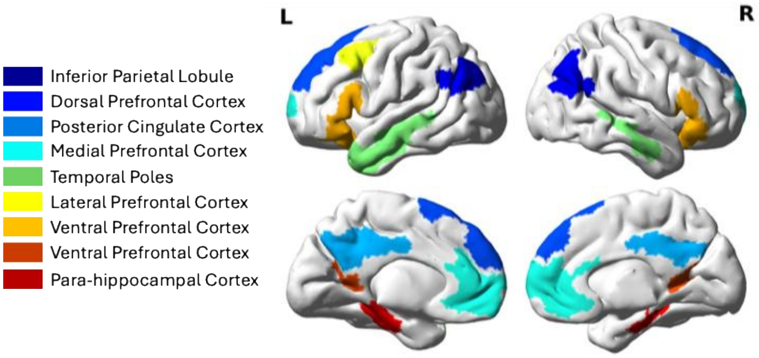

Figure 2. Topology of the DMN

Representations of the main brain regions of the Default Mode Network based on the Schaefer atlas (Schaefer et al., 2018).

The DMN shows anticorrelated function with the so-called "task-positive" or "external" networks, such as the dorsal attentional network (Fox et al., 2005). On a broader scope, it appears that brain activity during wakefulness organizes itself across an "internal-external" dipole, mapped by distinct functional networks. Given that the presence of such anticorrelations decreases across states of lower arousal, such as sleep (Chow et al., 2013), sedation (Luppi et al., 2019) and disorders of consciousness (Demertzi et al., 2015), it was recently proposed that such anticorrelations might be a central organizational feature of wakeful experiences without which consciousness cannot be supported (Demertzi et al., 2022).

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[1] It is important to note that since these early observations the DMN has been shown to also recruit different sets of brain regions when engaging in task performance, therefore it is not merely a resting state network.

Importantly, mind wandering is associated with the activation of a medio-temporal cluster of the MDN, spanning the hippocampus and the parahippocampal cortex (Fox et al., 2015). These medio-temporal regions have been long associated with episodic, associative and contextual memory, as well as pattern recognition and mental simulations. Crucially, the hippocampus can spontaneously replay sequences of neural activity that resemble those originally experienced during learning or encoding, a process known as "memory replay" (Pfeiffer, 2020). Such reactivations of associated memory networks enable the retrieval of related memories, contexts, or details that were not consciously accessed during the initial experience. These results have generated the hypothesis that the hippocampus might serve as a source of “thought variability”, providing a stream of cue-irrelevant, but contextually appropriate thoughts (Christoff et al., 2016; Mildner & Tamir, 2019).

The “thought variability” provided by the hippocampus might be utilized by medial subdivisions of the DMN to construct a coherent stream of thought (Christoff et al., 2016). Hippocampal ripples, a specific pattern of brain activity associated with memory replays, have been proposed as a brain mechanisms triggering instances of mind wandering (Iwata et al., 2024; O’Callaghan et al., 2021). Interestingly, hippocampal ripples are also observed during sleep (Girardeau & Zugaro, 2011) and the DMN is also activated during dreaming, suggesting some continuity between mind wandering and dreaming (Domhoff & Fox, 2015; Fox et al., 2013).

In conclusion, spontaneous thinking and states of consciousness seem to be mediated by similar neural underpinnings. What happens in the brain, though, when the spontaneous stream of thought is experienced as interrupted, empty, or void while we are still wakeful?

2.3 Mind blanking and seemingly “contentless” states

Our mind does not always move from thought to thought. Occasionally, we cannot or have nothing to report about our immediate past experiences (Ward & Wegner, 2013), a phenomenon called mind-blanking. This experience is accompanied by a metacognitive feeling that something went missing from our stream of thought (Efklides & Touroutoglou, 2010).

What does mind blanking actually reflect? Is it about the absence of available content, akin to a moment of unconsciousness during wakefulness, or does it concern a failure to introspect and evaluate mental content, akin to failure of meta-awareness and memory? As it currently stands, there is no consensus to define or capture the variant properties of mind-blanking episodes (Fell, 2022). Indeed, mind blanking has been described as inattention to anything (Andrillon et al., 2021), as the absence of reportable content (Boulakis et al., 2024; Mortaheb et al., 2022), or the voluntary act of thinking of nothing (Kawagoe et al., 2019). However, by examining how brain, body and behavior organize during mind blanking periods we can come closer to acquire insights into what the blank in mind blanking may be.

During studies that probe participants to report their thoughts, mind blanking is typically reported 10-15% of the time (Andrillon et al., 2021; Mortaheb et al., 2022; Ward & Wegner, 2013). Periods of mind-blanking are associated with reduced vigilance (Andrillon et al., 2021) and reduced physiological arousal (Unsworth & Robison, 2018). At the behavioral level, mind blanking differs from other types of attentional lapses like mind wandering, because it has a unique impact on task performance. Indeed, during mind blanking people fail to respond to stimuli, suggesting a tendency for sluggishness; whereas during mind wandering, people show signs of impulsivity (Andrillon et al., 2021).

Brain-wise, mind blanking was first examined by instructing people to actively try to think of nothing. This way, mind blanking was associated with reduced fMRI BOLD activity in the left hippocampus, Broca’s area, the inferior frontal gyrus and the supplementary motor cortex, and activations in the anterior cingulate cortex (Kawagoe et al., 2019). This atypical activation in the anterior cingulate cortex was interpreted as the neuronal counterpart of the effort to silence thoughts. A later study combining fMRI and experience-sampling focused this time on reports of mind blanking that were not voluntarily induced (Boulakis et al., 2023). Mind blanking was associated here with widespread deactivations in parietal, occipital, and thalamic areas as well as in the anterior cingulate cortex. Contrasting mind-blanking reports with content-oriented mental states revealed deactivations in the left angular gyrus as well, potentially representing periods of reduced neuronal resource allocation to mental faculties associated with mental state reportability, namely attentional and semantic processes (Boulakis et al., 2023).

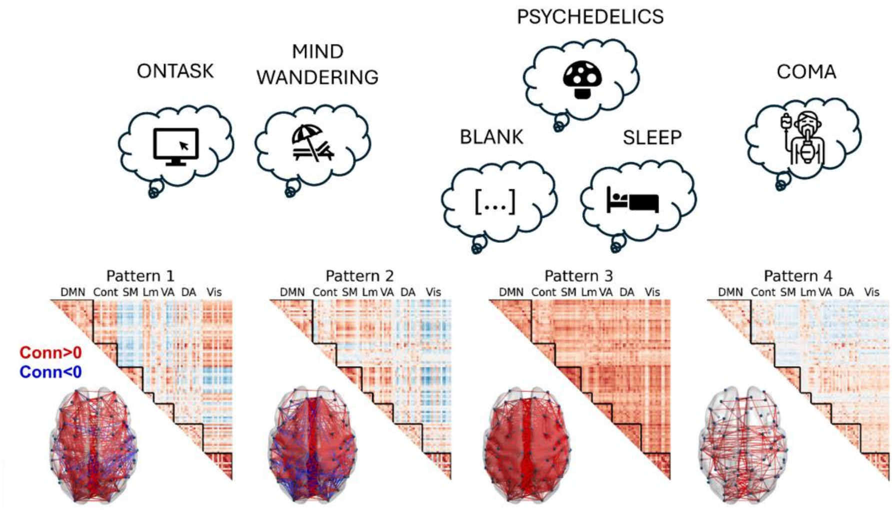

Figure 3. Brain connectivity patterns and subjective experience

Across wakefulness and sleep, the brain explores connectivity patterns of different integration (cortical communication) and segregation (cortical specialization). These patterns (bottom) could help describe consciousness states and contents (top). Content-oriented experiences, task-related or not, are typically associated with a balance between segregation and integration (Patterns 1 and 2). However, states of decoupling from the environment, such as mind-blanking, sleep, and psychedelics are characterized by high inter-areal connectivity, and hence low of functional segregation (Pattern 3). Finally, patients with disorders of consciousness show more frequent exploration of a pattern characterized by reduced integration and segregation, which mostly reflects the underlying anatomy (Pattern 4). Modified from (Mortaheb et al., 2022).

What could these deactivations represent? This question was partially answered by another analysis of the same dataset which identified that, during mind blanking reports, there were brain alterations linked to low arousal levels (Figure 3). In particular, mind blanking was associated to a brain pattern where all brain regions were functionally connected to one another (Mortaheb et al., 2022), a pattern previously found during sleep (El-Baba et al., 2019). At the same time, it was shown that the amplitude of the fMRI BOLD global signal[2] was higher during mind blanking reports compared to content-oriented reports, which had also been previously linked to reduced arousal levels (Wong et al., 2013).

Complementary results from electroencephalography (EEG) corroborate the link between low arousal and mind blanking. Sleep-like slow waves, akin to those observed in sleep, have been observed prior to attentional lapses, including before reports of mind blanking (Andrillon et al., 2021). Moreover, parietal alterations in EEG activity

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[2] The fMRI BOLD (Blood Oxygen Level Dependent) global signal is a measure representing the average BOLD signal across all brain voxels at a given time, reflecting widespread, synchronized fluctuations in neural and physiological activity. It captures global changes in blood oxygenation levels that may arise from neural processes as well as non-neuronal sources such as respiration, heart rate, and other systemic physiological factors.

typically associated with states of low arousal, such as reduced brain complexity, were also present preceding mind blanking compared to both task-focused and mind-wandering reports (Musat et al., 2024).

Together, these results could shed light on the mechanisms leading to mind blanking. For example, an increase in sleep-like dynamics over parietal areas might impede frontoparietal communication, a key neuronal substrate of conscious processing (Dehaene et al., 2006). At the same time, they could also reflect the de-activation of a posterior "hot spot", which also appears central for consciousness (Boly et al., 2017) resulting in mind blanking reports. Finally, modulations of general arousal through intense physical activity and after sleep deprivation can also increase the probability of mind blanking (Boulakis et al., 2024).

3. Consciousness during sleep

3.1 Sleep as a natural modulation of consciousness

Sleep is usually characterized by a period of immobility or rest, a typical posture, and a decreased responsiveness to external stimuli (Andrillon & Oudiette, 2023). Contrary to death or coma, sleep is easily reversed, and we can quickly regain our ability to react and respond to environmental demands. These behavioral signs reflect physiological changes orchestrated by the brain, to such an extent that sleep has been described as "of the brain, for the brain, by the brain" (Hobson, 2005).

Yet, sleep is not a monolith. In humans, there are two forms of sleep: Rapid Eye-Movement (REM) sleep (also called Paradoxical Sleep) and Non Rapid Eye-Movement (NREM) sleep (Carskadon & Dement, 2005). In terms of cortical activity, NREM sleep is characterized by an increase in neural synchronization, evidenced by the presence of large-amplitude slow waves (1-4Hz, delta range) across the entire cortex. This contrasts with the small-amplitude desynchronized activity typically observed in wakefulness but also in REM sleep.

Sleep does not only affect behavior and physiology. It also impacts subjective experience (Andrillon & Oudiette, 2023). During REM sleep, individuals can report conscious experiences following ~85% of forced awakenings (Siclari et al., 2013; Wong et al., 2023). Yet, if REM sleep is associated with a form of consciousness (dreams), these conscious experiences differ from wakeful experiences: they are largely dissociated from the environment and are characterized by a reduced if not absent meta-awareness and sense of agency (Nir & Tononi, 2010; Windt, 2015). Even in NREM sleep, which has been often associated with a state of unconsciousness, ~35% of forced awakenings are associated with reports of conscious experiences (Siclari et al., 2013; Wong et al., 2023).

Sleep can also be associated with a feeling of being awake while individuals show clear physiological signs of sleep. These discrepancies between the subjective experience and the current electrophysiological signature of sleep are commonplace (Valko et al., 2021), particularly in insomnia (Bastien et al., 2014). Part of these discrepancies can be attributed to the common misconceptions that consciousness disappears at sleep onset and that subjective experiences during sleep are all dream-like (e.g., bizarre, fantastic storylines) (Andrillon, 2021). However, consciousness does not always fade after the first electrophysiological signs of sleep. Rather, it can transform into specific experiences called hypnagogia (Lacaux et al., 2023), which can share features with dreams but also with mind-wandering, potentially making them hard to distinguish from wakeful experiences (Figure 1). Furthermore, sleep onset is a gradual process that does not occur synchronously in all the brain at once (Magnin et al., 2010). Cortical regions (e.g., the hippocampus) transition to sleep before other subcortical regions (e.g., the thalamus), leading to very specific dissociated states that individuals themselves do not necessarily associate with sleep.

Finally, there are also dissociations between the physiological state of sleep and behavior. If responsiveness drastically reduces following sleep onset, it is not completely abolished (Strauss et al., 2022) and sleepers can process sensory inputs overtly or covertly in a surprisingly complex way (Andrillon & Kouider, 2020; Lacaux et al., 2023). These cognitive processes include lexical or semantic integration, rule violation, the identification and amplification of salient stimuli and even the learning of basic associations. Importantly here, the relationship between endogenous conscious contents and external processing remains largely unexplored (Andrillon & Kouider, 2020; Koroma et al., 2020) and reported estimates of the integration of sensory inputs into dreams vary between 0 and 95% (Salvesen et al., 2023).

3.2 Neural dynamics associated with conscious and unconscious reports during sleep

Because sleep jointly alters behavior, brain activity and subjective experience, it has been recognized as a unique opportunity to explore the neural correlates of conscious and unconscious states and to identify the background conditions necessary for consciousness (Revonsuo, 2009; Wong et al., 2020). Normal individuals can report having no conscious experience following a forced or spontaneous awakening from NREM sleep. These reports of unconsciousness are associated with the apparition of cortical slow waves and an increase in local synchrony (Tononi & Massimini, 2008). Interventional studies relying on TMS[3] or electrical stimulation showed that these slow waves lead to a breakdown of cortico-cortical connectivity (Massimini et al., 2005; Pigorini et al., 2015). This is because these slow waves reflect a phenomenon of cortical bistability, which represents an alternance between periods of neuronal activity (ON) and silence (OFF) (Vyazovskiy & Harris, 2013) (Figure 4). Neuronal silencing especially seems to prevent the kind of sustained activity and integration of information that appear so central to consciousness (Koch et al., 2016; Mashour et al., 2020). The fact that reports of dreams and conscious experiences are so prevalent in REM sleep, a state deprived of the sort of global slow waves observed in NREM sleep, support the notion that a desynchronized brain is required for the formation of conscious experiences. Yet, the presence of slow waves does not always predict an absence of consciousness. In some pathological conditions (Frohlich et al., 2020) or pharmacologically-induced states (Blackburne et al., 2024; Bréant et al., 2022), slow waves can be observed along faster activity in association with reports of conscious experiences, or behaviors suggesting that a form of consciousness is preserved (Frohlich et al., 2021).

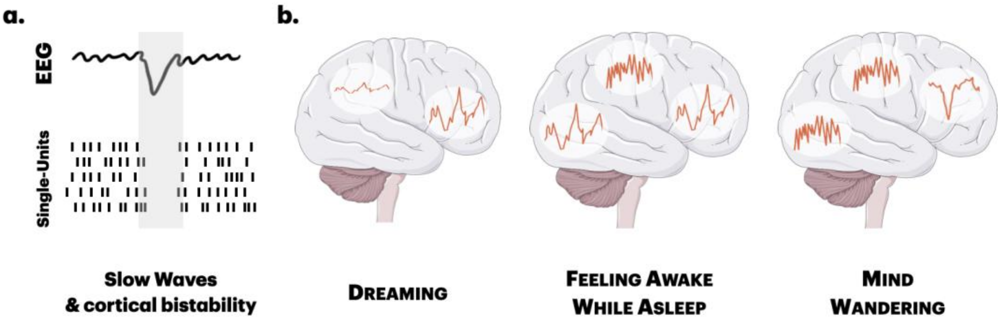

Figure 4. Local aspects of sleep and conscious experiences.

(a) Slow waves are high-amplitude low-frequency patterns of EEG activity and a hallmark of NREM sleep. Slow waves result from the synchronization of neuronal activity with a period of silence (OFF) followed by a period of neuronal activity (ON). b: Local and global modulations of slow/fast activity can predict fluctuations in subjective experience. A decrease of slow waves over parietal cortices predicts dreaming. An increase in fast activity over widespread cortical networks are associated with the feeling of being awake while sleep. In wakefulness, the presence of sleep-like slow waves can predict lapses of attention like mind wandering.

Beyond the coarse division between wakefulness, NREM and REM sleep, a subdivision of NREM sleep called stage 2 (NREM2) represents an exceptional opportunity to study how subtle changes in brain activity can support the formation of conscious experiences. NREM2 is a rather homogenous and stable physiological state, which represents half of an adult's night and is characterized by intermittent sleep slow waves (Carskadon & Dement, 2005). However,

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[3] Transcranial Magnetic Stimulation (TMS) is a non-invasive neuromodulation technique that uses magnetic fields to stimulate specific areas of the brain, altering neural activity in targeted regions.

when awoken from NREM2, individuals can report drastically different experiences: no conscious experience, conscious experience or even conscious experience without recall of the content itself (Siclari et al., 2013). Contrasting these different types of reports revealed that consciousness can be predicted by a decrease in slow wave activity (1-4Hz) over a "hot spot" of cortical brain regions and an increase of fast activity (25-50Hz) over cortical areas more centrally distributed (Siclari et al., 2017). This approach could allow the identification of chore nodes necessary for the formation of any conscious experience. Going into further detail, this approach also revealed that specific contents of the conscious experience are associated with a decrease in slow wave power in the same networks that are activated by experiencing these contents while awake (Siclari et al., 2017).

When awoken from NREM2, sleepers can also report they had the impression to have been awake. This feeling of being awake while asleep is associated with diffuse signs of wakefulness (increased in fast activity or signal complexity) (Stephan et al., 2021). Conversely, during NREM parasomnias, participants can show complex behaviors (screaming, laughing, walking) despite brain dynamics showing a mixture of wakefulness and sleep (Castelnovo et al., 2018). This highlights the complexity of sleep dynamics and the importance of local regulations of sleep/wake activity to understand fluctuations of subjective experience.

Collectively, classically sleep and wakefulness have been described as a set of all-or-nothing phenomena with clear boundaries. Yet, recent findings show that sleep and wakefulness can be best conceptualized as a continuum with a superposition of both global and local changes which jointly determined the overall states of consciousness, but also the kind of contents that are experienced (Andrillon & Oudiette, 2023) (Figure 4). Considering these new findings, new avenues in sleep and dream research can be envisaged.

3.3 The new frontiers of sleep and dreaming research

Although we have now a better understanding of how local and global cortical changes can alter the state and contents of consciousness, how specific contents come about is still unclear. An influential hypothesis posits that the contents of dreams could be triggered by subcortical volleys of activations (Hobson & Pace-Schott, 2002). Indeed, in REM sleep, invasive electrophysiological recordings in animals revealed the existence of so-called Ponto-Geniculo-Occipital (PGO) waves which originates in the Pons and propagate via the Thalamus toward the cortex (Gott et al., 2017; Jouvet & Michel, 1959). These PGO waves can trigger Rapid Eye Movements (REMs) in REM sleep. Given the relative relationship between REMs and dream contents (Arnulf, 2011) and the fact that REMs are followed by functional activations in networks involved in perception, imagination and memory (Andrillon et al., 2015), it is possible that PGO waves could trigger specific snippets of subjective experience. The fact that LSD administration in cats trigger an increase in PGO waves in wakefulness (Brooks, 1975) represents another argument in favor of a role of PGO waves in the generation of endogenous conscious experiences: dreams in sleep, hallucinations in wakefulness. Dreaming could, thus, require a combination of subcortical activations and a pattern of cortical activity supportive of consciousness. Although this hypothesis is tantalizing, the deep source of PGO waves make it particularly challenging to test it in humans.

Another critical challenge of dream research is the private nature of dreams. Dreams are identified with post-hoc subjective reports which require trusting individuals and their ability to remember and report truthfully their experience (Windt, 2013). This is because sleepers are immobile during sleep, and even paralyzed in REM sleep (muscular atonia). However, in patients with REM sleep Behavior Disorder this muscular atonia is partially lifted, allowing the behavioral expression of certain dream contents (Arnulf, 2012). REM sleep Behavior Disorder patients thus provide a unique opportunity to witness the dream unfold in real-time. Other parasomnias include sleep-talking, which can similarly provide evidence of the dream content independently of dream reports (Idir et al., 2022).

Finally, dreams are typically passive and uncontrolled experiences, making them hard to study in the laboratory. However, in the case of lucid dreaming, sleepers become aware that they are dreaming while dreaming (Van Eeden, 1913). During lucid dreams, individuals may also recover a sense of agency and control on the dream scenario and environment. For example, lucid dreamers can control their eye movements and signal to the outside world that they are lucid (La Berge et al., 1981). These signal-verified lucid dreams have been leveraged to identify the correlates of lucid dreaming and it has been proposed that an increase in pre-frontal activity could underlie lucidity (Voss et al., 2009), although this result is debated (Baird et al., 2022). Lucid dreamers can also accomplish tasks within their sleep providing a unique opportunity to test consciousness and responsiveness in real-time during dreams (Konkoly et al., 2021). Studying lucid dreaming is however extremely challenging and there are ongoing efforts to make the generation of lucid dreaming more reliable (Zerr et al., 2024).

4. Markers and mechanisms of spontaneous experiences

4.1 The search for the Neural Correlates of Consciousness

Consciousness is obvious from a first person perspective as Descartes stressed with the famous "Cogito ergo sum" (Descartes, 1637). Yet, the scientific study of consciousness necessitates tools to objectively assess someone's else conscious state or content of experience. Markers of consciousness can be verbal as humans have most of the time the ability to directly communicate about the content of their subjective experience. These markers can also be behavioral since the way individuals behave can allow us to make inferences about the presence or absence of consciousness. For example, complex goal-directed behavior is usually associated with conscious experience. Pattern of eye movements can also indicate the content of visual perception in the absence of explicit reports (Frässle et al., 2014). There are obviously many exceptions that can make verbal or behavioral correlates of consciousness debatable. Conversely, consciousness can be sometimes present in the absence of the ability to immediately report on this experience or without any behavior associated with this experience (e.g., dreaming or anesthesia). This situation can become a relevant clinical challenge in patients with disorders of consciousness who suffer of a cognitive motor dissociation (Bodien et al., 2024).

A complementary approach is, thus, to examine brain activity associated with specific states or contents of consciousness. This search for Neural Correlates of Consciousness (NCCs) represents a foundational challenge for the science of consciousness (Crick & Koch, 1990; Koch et al., 2016). NCCs are classically defined as the "*minimal neuronal mechanisms jointly sufficient for any one specific conscious percept*" (Crick & Koch, 2003). In practice, the concept of NCCs can be understood in varied ways. NCCs can be specific to a given subjective experience, or the phenomenal dimension of that experience such as the redness of an apple (content-specific NCC). But NCCs can also refer to the mechanisms or brain structures that are directly conducive of conscious experiences in general (full NCC). NCCs and the investigation of spontaneous conscious experiences in wakefulness and sleep are tightly associated for two reasons: (1) NCCs can help track fluctuations in subjective experience without requiring participants to report on these fluctuations, (2) in return, these fluctuations can help understand the strengths and limits of NCCs.

4.2 State and content-specific the Neural Correlates of Consciousness

Contrasting different states of consciousness, such as wakefulness or dreaming on the one hand and dreamless sleep or anesthesia on the other hand has allowed to identify several "full NCCs". For example, activated and desynchronized patterns of activity are characteristic of wakefulness, but also states in which individuals might be unresponsive but conscious, such as REM sleep or certain types of anesthesia (e.g., after ketamine intake) (Koch et al., 2016). On the contrary, the presence of large-amplitude slow waves is typically associated with unconscious states (Tononi et al., 2024) although the presence of slow waves is not always a reliable indicator that consciousness is absent (Frohlich et al., 2021) as mentioned above. It is likely that the anatomical location of activated or deactivated patterns of neural activity provide key information about their association with consciousness. Accordingly, specific cortical and subcortical networks appear central for the maintenance of a stable state of consciousness, although there is still some debate about which networks are necessary and/or sufficient for consciousness (Mashour et al., 2020; Tononi et al., 2016).

Content-specific NCCs target contents or phenomenal dimensions of conscious experience. For example, the conscious processing of a new image or sound is typically associated with a widespread and sustained pattern of activation in cortical areas (Dehaene et al., 2006). There are intense debates to better specify the minimal set of neuronal mechanisms necessary and sufficient for the formation of a content-specific conscious experience (Mashour et al., 2020; Tononi et al., 2016). It is worth noting that content-specific NCCs can reflect prerequisites or cognitive functions associated with conscious processing rather than the conscious representation itself. Strategies have been proposed to distill the neural correlates of the conscious representation from its prerequisites and consequences (Aru et al., 2012) but even when conflating these different types of correlates, NCCs can prove extremely useful to detect the presence of consciousness. For example, the sensitivity to the violation of simple or complex auditory rules as in the Oddball or Local/Global paradigms[4] allowed the identification of specific EEG signatures including the Mismatch Negativity (MMN) or P300. These signatures can provide invaluable information about the (un)conscious state of an individual and its (un)connectedness to the environment even when the said individual is not responsive, such as in sleep (Strauss et al., 2015), anesthesia (Uhrig et al., 2016), or in disorders of consciousness (Bekinschtein et al., 2009).

Koch and colleagues stress nonetheless the importance of establishing NCCs that are “directly” associated with conscious experience to distinguish NCCs from background conditions necessary for consciousness, such as arousal (Koch et al., 2016). Accordingly, structures promoting arousal, like as the Ascending Reticular Activating System would not be considered a NCC because it is mainly associated with the regulation of arousal, which is itself a background condition for consciousness. Some NCCs used in basic or clinical research (e.g., slow waves, alpha oscillations, etc.) (Sitt et al., 2014) could thus reflect changes in arousal rather than direct changes in conscious states or contents, although clinical categories such as Minimally Conscious State (MCS) and Unconscious Wakefulness Syndrome (UWS) partially account for this confounding factor since they are similar in terms of arousal. Second, NCCs can also reflect consequences of conscious processing. Content-specific NCCs such as the P300 could at least partially reflect report (including self-report) rather than the formation of a conscious mental representation per se (Sergent et al., 2021). Examining how these NCCs are impacted in states in which individuals are conscious but not necessarily in a reflective way (such as during dreaming) can provide a unique window to dissociate the neural processes associated with the formation of a conscious mental representation and its cognitive consequences (Tsuchiya et al., 2015). Third, NCCs can also target putative mechanisms of consciousness, sometimes by being inspired or derived from theoretical accounts of consciousness. Ignition-like mechanisms (which can be captured by the P300 and the temporal generalization method (King & Dehaene, 2014)) have been proposed to represent the mechanisms by which a mental representation becomes conscious (Dehaene et al., 2006). Likewise, consciousness has been defined as the integration of information at the level of a system (Tononi et al., 2016) and therefore tracking a brain’s ability to maintain both distributed and integrated patterns of activity has been proposed as a way to quantify consciousness in neural recordings (Casali et al., 2013).

4.3 State and contents of consciousness, reunited at last?

Searching for the NCCs has long been structured along the level/content dichotomy of consciousness science. Yet, there are recent attempts at operating a convergence between the level and state approach of consciousness through the NCCs. First, content-specific NCCs can help address questions about states of consciousness because being conscious of something logically implies being conscious. Accordingly, as mentioned earlier, markers of conscious processing of sensory information provide interesting tools to identify consciousness in sleep (Strauss et al., 2015; Türker et al., 2023) or disorders of consciousness[5] (Rohaut et al., 2024). These tools typically have a good specificity but a more limited selectivity (King et al., 2013; Sitt et al., 2014) as states of consciousness disconnected of the environment can exist (Sanders et al., 2012). Conversely, NCCs of states can also inform on the types of conscious contents than an individual can experience. For example, the presence of sleep-like slow waves (a marker that is

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[4] The Local/Global Paradigm is an experimental framework used to study how individuals process hierarchical stimuli by focusing on either the local details or the overarching global shape, therefore providing insights into selective attention and conscious processing.

[5] Disorders of consciousness are medical conditions characterized by impaired awareness and responsiveness, ranging from coma to minimally conscious states, where patients have limited or no interaction with their environment.

usually associated with unconsciousness when observed globally) or patterns of high inter-areal functional connectivity can help predict the occurrence of specific experiences such as mind wandering and mind blanking (Andrillon et al., 2021; Mortaheb et al., 2022).

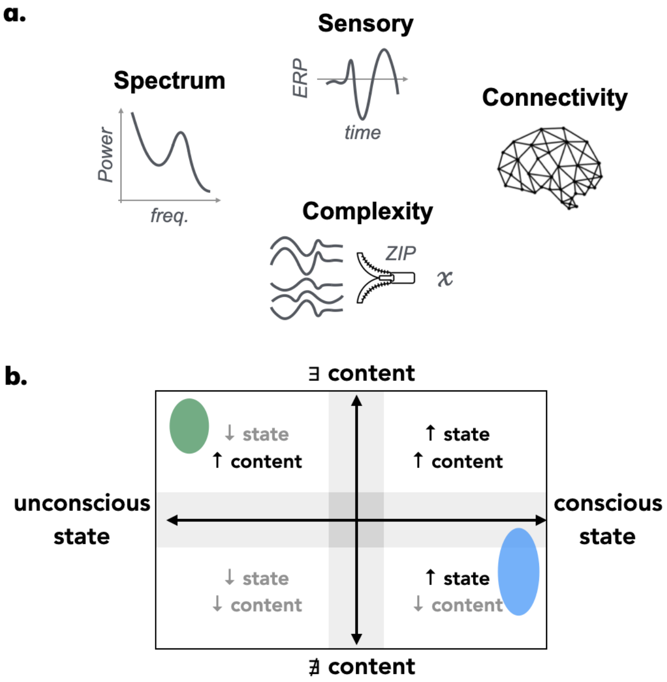

Figure 4: Neural correlates of consciousness across states and contents

a: Neural correlates of consciousness include markers of sensory processing (event-related potentials, ERPs), signal complexity, connectivity, or spectral features. They are derived from neural recordings. b: Neural correlates of consciousness can be compared regarding their sensitivity to conscious states and contents. Circles show the area in which most of the known correlates have been found. From (Pérez et al., 2024).

Two influential classes of markers of consciousness regards complexity (Lempel-Ziv, Kolmogorov, Perturbational Complexity Index etc.) and connectivity (weighed Symbolic Mutual Information, Phase Lag Index, etc.) measures (Sitt et al., 2014). These metrics try to estimate the richness of neural activity. Their relationship with consciousness is still debated, but is motivated by the notion that consciousness depends on a balance between integration and segregation, order and chaos (Bassett & Gazzaniga, 2011; Carhart-Harris et al., 2014). The entropic brain hypothesis suggests that the entropy of brain activity could directly determine the content of conscious experience (Carhart-Harris et al., 2014). Interestingly, some complexity and connectivity measures can differentiate between different states of consciousness (Sitt et al., 2014) and, in some cases, are even sensitive to changes in consciousness that are pharmacologically induced or associated with neuro-psychiatric disorders (Fernández et al., 2013; Scott & Carhart-Harris, 2019).

Yet, a more systematic investigation of the sensitivity of NCCs to both states and contents of consciousness indicates that these relationships are complex (Pérez et al., 2024). Pérez and colleagues found that many NCCs, such as EEG alpha and beta power, complexity or entropy were found to positively correlate with conscious states (e.g., larger in wakefulness than in NREM2) but were eventually negatively correlated with conscious contents (larger for unseen stimuli than for seen stimuli). This reversal is striking although it is mitigated by the fact that “content” effects are typically much smaller that “state” effects. This means that if a variable X is positively associated with a state of consciousness but negatively associated with conscious access of a specific content, the value of X will still be higher for a participant experiencing a content than the same participant when unconscious. Yet, it could be argued that an ideal NCC should be sensitive to both state and contents with the same directionality. A more systematic mapping of how NCCs behave in different contexts, especially during fluctuations of consciousness throughout wakefulness and sleep, could help understand what these NCCs are indexing (e.g., pre-requisites, mechanisms, consequences, or functions of consciousness).

Conclusions

The dichotomy between states and levels of consciousness profoundly shaped the way consciousness is studied. However recent investigation focusing on the fine-grained fluctuations in conscious contents in wakefulness and sleep, particularly relative to the phenomenal properties and temporal dynamics of conscious experiences, draw interesting parallels between these states. These findings stress the continuity between wakeful and sleep experiences, blurring the distinction between states and contents of consciousness. This movement is reinforced by the examination of neural correlates and mechanisms of consciousness, which show a convergence of general principles regarding the kind of neural dynamics that are conducive or unfavorable for the formation of conscious experiences. For example, markers of cortical (de)synchronization can be extracted at the whole-brain or network level, allowing a finer prediction of consciousness. This reunion of the state and content approach of consciousness might have important implications for our conceptualization of the conscious experiences that constitute our days and nights but also for our understanding of consciousness in clinical populations.

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Behavioral/Cognitive

Whole-Brain Deactivations Precede Uninduced Mind-Blanking Reports

Paradeisios Alexandros Boulakis,[1,2] **Sepehr Mortaheb,**[1,2] **Laurens van Calster,**[2,3,4,5] **Steve Majerus,**[2,3,4] and **Athena Demertzi**[1,2,3]

[1]Physiology of Cognition Lab, GIGA-Cyclotron Research Center In Vivo Imaging, University of Liège, Liège 4000, Belgium, [2]National Fund for Scientific Research (FNRS), Brussels 1000, Belgium, [3]Psychology and Neuroscience of Cognition Research Unit, University of Liège, Liège 4000, Belgium, [4]GIGA-Cyclotron Research Center In Vivo Imaging, University of Liège, Liège 4000, Belgium, and [5]Department of Neurology, Cliniques Universitaires Saint-Luc, Brussels 1200, Belgium

Mind-blanking (MB) is termed as the inability to report our immediate-past mental content. In contrast to mental states with reportable content, such as mind-wandering or sensory perceptions, the neural correlates of MB started getting elucidated only recently. A notable particularity that pertains to MB studies is the way MB is instructed for reporting, like by deliberately asking participants to "empty their minds." Such instructions were shown to induce fMRI activations in frontal brain regions, typically associated with metacognition and self-evaluative processes, suggesting that MB may be a result of intentional mental content suppression. Here, we aim at examining this hypothesis by determining the neural correlates of MB without induction. Using fMRI combined with experience-sampling in 31 participants (22 female), univariate analysis of MB reports revealed deactivations in occipital, frontal, parietal, and thalamic areas, but no activations in prefrontal regions. These findings were confirmed using Bayesian region-of-interest analysis on areas previously shown to be implicated in induced MB, where we report evidence for frontal deactivations during MB reports compared with other mental states. Contrast analysis between reports of MB and content-oriented mental states also revealed deactivations in the left angular gyrus. We propose that these effects characterize a neuronal profile of MB, where key thalamocortical nodes are unable to communicate and formulate reportable content. Collectively, we show that study instructions for MB lead to differential neural activation. These results provide mechanistic insights linked to the phenomenology of MB and point to the possibility of MB being expressed in different forms.

Key words: angular gyrus; anterior cingulate cortex; fMRI; experience-sampling; mental content; mind-blanking; spontaneous thinking

Significance Statement

This study explores how brain activity changes when individuals report unidentifiable thoughts, a phenomenon known as mind-blanking (MB). It aims to detect changes in brain activations and deactivations when MB is reported spontaneously, as opposed to the neural responses that have been previously reported when MB is induced. By means of brain imaging and experience-sampling, the study points to reduced brain activity in a wide number of regions, including those mesio-frontally which were previously detected as activated during induced MB. These results enhance our understanding of the complexity of spontaneous thinking and contribute to broader discussions on consciousness and reportable experience.

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Correspondence should be addressed to Athena Demertzi at a.demertzi@uliege.be.

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Introduction

During spontaneous thinking mental content appears continuous and seamless (Christoff et al., 2009). Probing people to report what they think yields various mental states with distinct contents and attitudes toward those contents, such as daydreaming, task engagement, and mind wandering (Van Calster et al., 2017; Smallwood et al., 2021). A critical component of these states is the presence of content. Recently, however, the study of unconstrained cognition has begun to focus on the experience of the inability to report on immediate mental content, termed mind-blanking (MB; Ward and Wegner, 2013).

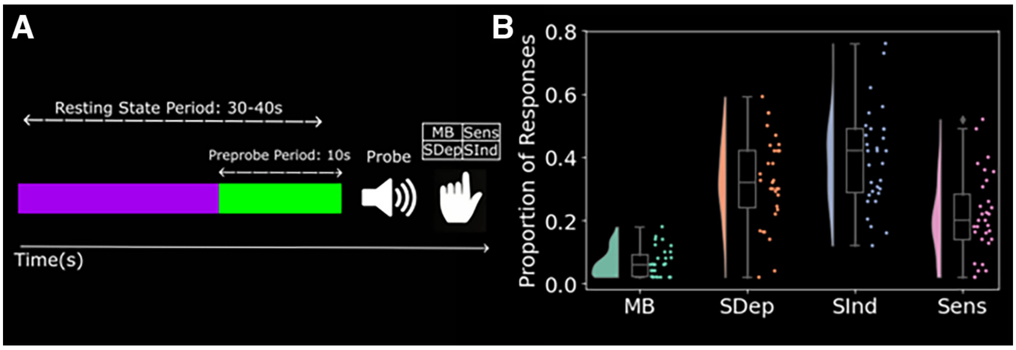

Figure 1. The experience-sampling paradigm. ***A***, Single trial example. During experience-sampling participants are asked to restfully lay in the scanner with eyes open and let their mind wander without any further orientation as to the focus of their thoughts. At random intervals (30–60 s), participants are probed with an auditory cue to report the content of their thoughts at the moment preceding the probe using button press. Four available report categories were presented as available: mind-blanking (MB), perceptions (Sens), stimulus-independent thoughts (SInd), and stimulus-dependent thoughts (SDep). For subsequent analysis, only the final 10 s of the resting period (green segment) were used. ***B***, Raincloud plots showing MB was reported at lower rates compared with mental states with content. Density kernels show how data are distributed and where peaks where aggregated. Boxplots show interquartiles ranges and medians. Pointplots show individual datapoints.

Recent research into the neural correlates of MB using fMRI experience-sampling (i.e., asking people at random times to report their immediate mental state; Smallwood and Schooler, 2015; Weinstein, 2018) showed that spontaneous MB reports were close to a cerebral configuration characterized by a positive all-to-all connectivity profile (Mortaheb et al., 2022). Such a pattern of overall positive statistical dependencies implies that all cortical regions communicate in the same way when MB is reported. It is of interest that similar functional organization is observed in NREM sleep (El-Baba et al., 2019), suggesting that MB might be the result of overall low cortical arousal. Similar evidence was found on shorter timescales using EEG, where localized slow-wave activity was linked with MB reports, leading to the possibility of cerebral "local sleeps" during MB (Andrillon et al., 2019). Indeed, posterior electrode slow-wave activity during a go/no-go task was predictive of MB reports, in contrast to frontal electrode slow-waves, which were linked to mind-wandering (Andrillon et al., 2021). Collectively, these studies propose that MB events are tied to neuronal profiles which do not permit efficient cortical communication, therefore hindering people from reporting clear mental content (Mortaheb et al., 2022).

A notable particularity of MB studies is the way MB is instructed for report. For example, Kawagoe et al. (2019) studied MB by asking people to actively "empty their minds" until they experience no thoughts, upon when they reported they had achieved this state. By analyzing the fMRI BOLD signal preceding these reports, the authors found deactivations in Broca's area and the left hippocampus, and activations in the ventromedial prefrontal cortex (vmPFC)/subgenual region of the anterior cingulate cortex (subACC). The authors interpreted these results as reduced inner speech, elicited by the attempt of participants to silence internally generated thoughts. This possibility was considered by other authors, too, primarily in the context of mind wandering: As our thoughts spontaneously transition across an internal-external milieu (Vanhaudenhuyse et al., 2011; Smallwood et al., 2012; Demertzi et al., 2013), the ACC serves executive functions, such as identifying attentional lapses from ongoing tasks (Christoff et al., 2009) or allowing thought transitions to be controlled (Crespo-García et al., 2022). In similar lines, self-induced MB also requires constant supervision of thoughts in the form of evaluating ongoing experience to promote thought-silencing, therefore recruiting regions such as the vmPFC/subACC, a central hub for mental state evaluative processes (Jenkins and Mitchell, 2011; Qin et al., 2020). However, a hyperexperienced meditator showed decreases in fMRI connectivity between the posterior cingulate cortex and mesio-frontal regions when he was practicing content-free versus content-related meditation (Winter et al., 2020). Taken together, the use of MB induction in neuroimaging studies might provide a biased picture about the underlying neural mechanisms of MB that incorporates task demands of thought monitoring.

In the present work, we test the hypothesis that uninduced MB reports are linked to frontal deactivations, inverting the pattern observed in self-induced MB. By means of fMRI and experience-sampling, we first performed a univariate analysis to test whether MB reports would indicate frontal deactivations in the periods preceding MB reports, while remaining agnostic as to the contribution of the remaining cortex. To supplement our hypothesis of frontal deactivations, we performed ROI analysis to examine the specificity of deactivations in the vmPFC-subACC and other previously identified MB-related clusters.

Materials and Methods

Experience-sampling dataset/experimental design

We used previously collected data (Van Calster et al., 2017) acquired during resting-state with eyes open in a 3T head-only scanner (Magnetom Allegra, Siemens Medical Solutions). At random intervals ranging from 30 to 60 s, participants were probed with an auditory cue to report via button press what was in their mind at the moment just preceding the cue. Each probe started with the appearance of an exclamation mark lasting for 1000 ms inviting the participants to review and characterize the cognitive event(s) they just experienced. After this period, participants were presented with four options, classifying their mental content as: (1) absence, defined as MB or empty state of mind; (2) perceptions, defined as thought-free attentiveness to stimuli via the senses; and (3) thoughts (Fig. 1*A*). In the case of a "thought" report, participants were asked to report if the content was stimulus-dependent (SDep; thoughts evoked from the immediate environment) or stimulus-independent (SInd; thoughts irrelevant from the immediate environment). Depending on the probes' trigger times and participants' reaction times, the duration of the recording session was variable (48–58 min). To minimize misclassification rates, participants had a training session outside of the scanner at least 24 h before the actual session.

The dataset contains structural and functional MRI volumes for 36 healthy, right-handed participants (27 female, mean = 23, SD = 3, range = [18,30]). Five participants were excluded as they did not report each mental state option at least once (total participants = 31, 22 female). Overall, participants reported MB 6% of total reports (SD: 0.04, range: [1,9]) Sens 20% of trials (SD: 0.13, range: [1,26]) SDep 32% of total reports (SD: 0.14, range: [1,29]), and SInd 42% of total reports (SD: 0.15, range: [6,28]) (Fig. 1*B*). All participants gave their written informed consent to take part in the experiment. The study was approved by the ethics committee of the University Hospital of Liège.

FMRI acquisition parameters

FMRI data were acquired with standard transmit–receive quadrature head coil using a T2*-weighted gradient-echo EPI sequence with the following parameters: repetition time (TR) = 2040 ms, echo time (TE) = 30 ms, field of view (FOV) = 192 × 192 mm2, 64 × 64 matrix, 34 axial slices with 3-mm thickness and 25% interslice gap to cover most of the brain. A high-resolution T1-weighted MP-RAGE image was acquired for anatomic reference (TR = 1960 ms, TE = 4.4 ms, inversion time = 1100 ms, FOV = 230 × 173 mm, matrix size = 256 × 192 × 176, voxel size = 0.9 × 0.9 × 0.9 mm). The participant's head was restrained using a vacuum cushion to minimize head movement. Stimuli were displayed on a screen positioned at the rear of the scanner, which the participant could comfortably see using a head coil-mounted mirror.

Statistical analysis

Preprocessing

Structural and functional images were preprocessed using a locally developed pipeline written in the Nipype module (v1.8.2; https://nipype.readthedocs.io/) in Python (v3.8), combining functions from Statistical Parametric Mapping software (SPM12; https://www.fil.ion.ucl.ac.uk/spm/), the FMRIB Software Library v6.0 (FSL; https://fsl.fmrib.ox.ac.uk/fsl/fslwiki), and the Artifact Detections Tools (ART; https://www.nitrc.org/projects/artifact_detect). For each node of the pipeline, we have specified the respective module and function used. Structural images were skull stripped (fsl.Bet), bias-field corrected, and segmented into white matter, gray matter, and cerebrospinal fluid (spm.Segment). Finally, the restored, bias-corrected structural image was normalized into the standard stereotaxic Montreal Neurologic Institute (MNI) space (spm.Normalize). The first four volumes (8.16 s) of the functional data were removed to avoid T1 saturation effects (fsl.ExtractROI). The volumes were slice-scan time corrected to account for the accumulation of offset delays between the first slice and the remaining slices (fsl.SliceTimer). Then, the scans were realigned to the mean functional volume (spm.Realign) using a second B-spline interpolation with least-squares alignment. We used the realignment parameters to estimate motion outlier scans. An image was defined as an outlier or artifact image if the head displacement in the *x*, *y*, or *z* direction was >3 mm from the previous frame, if the rotational displacement was >0.05 rad from the previous frame, or if the global mean intensity in the image was >3 SDs from the mean image intensity for the entire scans. The realignment parameters were also saved so that these variables can be used as regressors when modeling subject-level BOLD activity. Then, the images were coregistered to the participant space using the bias-corrected structural image as the target and a normalized mutual information function (spm.Coregister) and then normalized to MNI space (spm.Normalize). Finally, the normalized images were smoothed using a Gaussian kernel of 8 mm full width at half-maximum. For comparability purposes, the preprocessing pipeline followed the approach as in previous works with this dataset (Van Calster et al., 2017) with MB analysis (Kawagoe et al., 2019).

Univariate whole-brain analysis

Data were analyzed using a univariate linear general linear model (GLM). The four responses of the participants (MB, SDep, SInd, Sens) were modeled and convolved with the canonical hemodynamic response function (HRF) as regressors of interest for each participant in the first-level analysis. Each response instance was modeled as an epoch starting five TRs before probe onset, following evidence from a "thinking aloud" paradigm that showed that mental states tend to fluctuate slowly, with one experience being reported every 10 s (Van Calster et al., 2017). Each participant's six motion parameters (three rigid body translations and three rotations from the realignment procedure) were included to regress out effects related to head movement-related variability. We used a high-pass filter cutoff of 1/128 Hz to remove the slow signal drifts with a longer period, and a first-order autoregressive model [AR (1)] was used for serial correlations with the classical restricted maximum likelihood (REML) parameter. Regionally specific condition effects were tested using linear contrasts for each key event relative to the baseline and each participant. Contrasts for "Perception" and "Thinking" regressors have been reported elsewhere (Van Calster et al., 2017). Therefore, we tested for contrasts specific to MB. Given four regressors: [MB, Sens, SDep, SInd], subject-level analysis yielded the following T contrasts of interest: (1) positive effects of MB [1 0 0 0], (2) negative effects of MB [−1 0 0 0], (3) MB > Thinking [2 0 −1 −1], (4) Thinking > MB [−2 0 1 1], (5) MB > Sens [1 −1 0 0], (6) Sens > MB [−1 1 0 0], (7) Absence > Content [3 −1 −1 −1], (8) Content > Absence [−3 1 1 1]. The resulting contrast parameter estimates from the individual subject-level were entered into a random effects model for a second level analysis, using a one-sided, one-sample *t* test. Regarding result reporting and visualization, we have opted for a "don't hide/highlight" approach (Taylor et al., 2023), effectively presenting all relevant maps at $p_{\text{uncorrected}} < .001$ and by annotating the contours of statistically significant clusters at $p\text{FDR} < 0.05$. Exploratory analysis will be conducted at clusters with voxel size >50. Interactive 3D surface projections of the contrasts presented in results are available on https://gitlab.uliege.be/Paradeisios.Boulakis/mb_activation/-/tree/main/plotting. The unthresholded maps are publicaly available at Neurovault: https://identifiers.org/neurovault.collection:14761.

Region-of-interest (ROI) analysis

Based on the a-priori hypothesis about the role of the ACC in monitoring thought contents, we additionally performed a ROI analysis based on MNI coordinates reported in Kawagoe et al. (2019) for the ACC (MNI: 3,39,−5). To examine whether previous findings on the neuronal correlates of MB during active mental silencing can be extended to spontaneous blanking periods in ongoing mentation, we also included the left hippocampus (MNI: −27,−33,−3) and Broca's area (MNI: −47,26,20). To extract single-participant β parameters for each regressor of interest, 5-mm radius binary spheres were created for each ROI using the flsmaths function of the FSL software, which were then used to mask first-level subject-specific β parameter maps, and extract the signal of interest. Localization of the ROIs was performed based on the MNI coordinates reported in Kawagoe et al. (2019).

Given our hypothesis for the absence of frontal engagement in MB and the reduced statistical power of traditional frequentist approaches because of multiple comparisons, we opted for Bayesian linear modeling (McElreath, 2020), allowing us to make inferences on potential null results while not being overly conservative. For each ROI, we fit a linear model with β values as a dependent variable, allowing the intercept to freely vary as a function of mental state:

$$Beta \sim a[mental\,state] + error.$$

As prior for the intercept we chose a normal distribution as it is the maximum entropy distribution (or "least surprising") for any random variable with an unknown mean and unknown, finite variance. Effectively, a maximum entropy distribution is the most probable distribution for a random variable, given the potential constraints placed on its parameters. We chose to model the intercepts as $N(0, 1)$, as we expected small effects. To examine the robustness of our choice of priors, we constructed two variants of normal distributions, one skeptical distribution that reduces effect sizes close to 0 by having high precision, marked as low variance $N(0, .5)$, and one lax prior, marked by low precision, permitting extreme effects $N(0, 3)$. Prior predicative simulation for the skeptical prior places the mass of effect sizes of each state within half a standard deviation from the mean. Likewise, the lax prior places the mass of effect sizes within three standard deviations. Additionally, we also fit a model using a uniform prior $U(-2, 2)$, giving equal probability to effect sizes within two standard deviations from the mean. To further validate that our priors

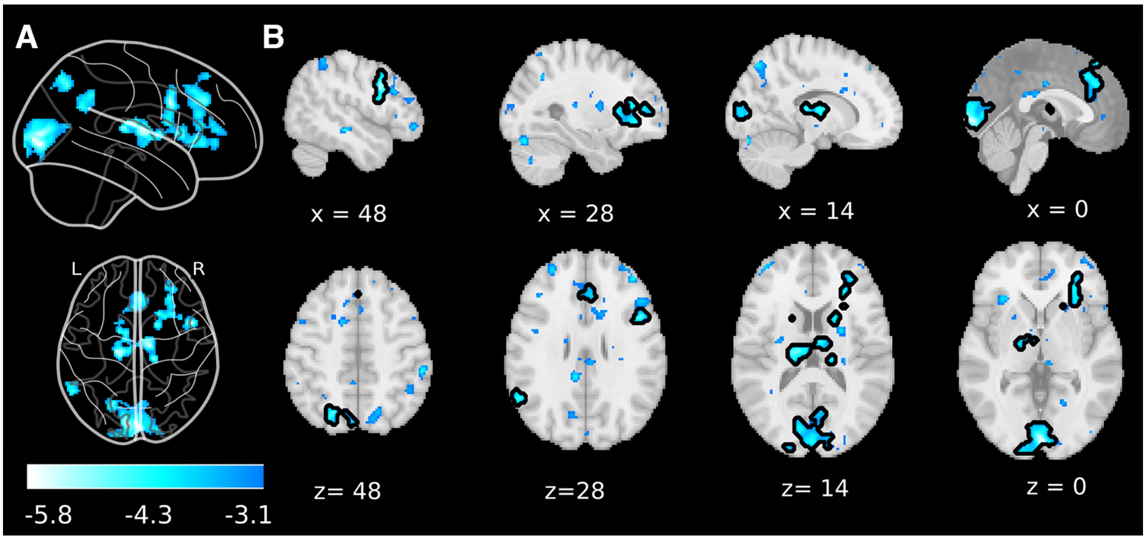

Figure 2. FMRI univariate analysis of MB reports reveals whole-brain deactivations. Statistically significant deactivations were observed in the anterior cingulate cortex, the calcarine cortex, the bilateral thalami, the right anterior insula, the precentral gyrus, the left superior parietal lobule, the inferior frontal gyrus and the right operculum. ***A***, Glass brain projection (sagittal and axial views) at voxel-level $p_{\text{uncorrected}} < 001$, and cluster level $p_{\text{FDR}} < .05$. Color-bar indicates *t* statistic. ***B***, Activation maps of negative MB effects projected on the MNI152 cortical template (sagittal and axial views). Maps are calculated on 10 s preceding MB reports. The deactivated map projection is performed at voxel-level $p_{\text{uncorrected}} < .001$. Black contours signify the clusters that were significance at $p_{\text{FDR}} < .05$.

generated the desired ranges of parameters, we sampled from the prior distribution to perform a prior predictive visual check.

We estimated one posterior distribution for each one of the intercepts of the four mental states. Difference posterior was estimated by the pairwise subtraction of the mental state intercepts. Posterior distributions are summarized by their median, their standard deviation, and the 95% highest density intervals (HDIs), representing the 95% probability that the true parameter lies within that range. To validate that the posterior accurately represented a generative model of the data, we also performed posterior predictive simulations, to examine whether the ranges of our model can encompass the different β values.

To fit the models, we used a Markov Chain Monte-Carlo No U-Turn Sampler (MCMC-NUTS). MCMC is a class of algorithms for sampling from an unknown posterior distribution. The sampler uses a stochastic, random-walk procedure to draw samples from a random variable, and then approximates the desired distribution by integrating across the sum of the drawn samples (Harrison, 2010). The NUTS sampler is the mechanism of effective sample generation. As MCMC is sensitive to its tuning parameters, NUTS facilitates the sampling process by providing good candidate points in the distribution for the algorithm to sample (Hoffman and Gelman, 2014). To examine the convergence of the models, we sampled the posterior from four different chains, and both visually inspected the traceplot for points in the sampling procedure where the sampler stuck and accepted a model only if its scale reduction factor was at 1.00 (Fig. 4*B*). The stability of estimates was evaluated using an effect sample size (ESS) > 10,000. We sampled 5000 samples from the posterior, with 2000 samples as burn-in.

Each model was compared with a null model:

$$\mathit{Beta} \sim a + \mathit{error},$$

where the intercept does not differentiate between the mental states, effectively representing the mean of the mental states. Model fitting was performed using the PYMC3 (https://docs.pymc.io/en/v3/index.html) Python package Salvatier et al. (2016).

Code accessibility

All codes to replicate the analysis is available on https://gitlab.uliege.be/Paradeisios.Boulakis/mb_activation (Boulakis, 2023). The code is based on existing Python libraries and custom functions. The provided repository contains all the necessary information to install an environment and reproduce the analysis on the experience-sampling dataset. We used an existing experience-sampling dataset, during which participants had the option to report the absence of thoughts (Van Calster et al., 2017). Previous research on this dataset, examining has replicated consistent fMRI findings in other mental states (MW: DMN and executive cortical areas). The raw data are also freely available in BIDS format from: https://openneuro.org/datasets/ds004134/versions/1.0.0. The unthresholded maps present in this paper can be found at https://identifiers.org/neurovault.collection:14761.

Table 1. FMRI Univariate analysis reveals deactivations during five TRs preceding MB reports

Region	No. of voxels	Z peak	*x*	*y*	*z*
Right calcarine cortex	1491	4.68	2	−92	0
Left calcarine cortex		4.54	−8	−88	6
Inferior frontal gyrus	243	4.51	48	10	32
Right operculum		3.76	48	10	22
Right thalamus	617	4.49	12	−12	8
Left thalamus		4.49	−18	−18	16
Superior frontomedial gyrus	472	4.21	2	36	34
Right anterior cingulate cortex		4.00	5	34	22
Left anterior cingulate cortex		3.55	−1	31	21
Left superior parietal lobule	187	4.14	−22	−68	46
Left precuneus		3.56	−4	−76	50
Right anterior insula	510	4.09	30	17	8
Right caudate		4.09	18	8	16
Left supramarginal gyrus	164	3.99	−58	−56	28

An uncorrected voxel-level threshold of $p = 0.01$ was set and FDR-corrected at the cluster level $p < 0.05$. The *x*-, *y*-, and *z*-coordinates refer to the AAL anatomic labeling map.

Results

fMRI univariate analysis reveals whole-brain deactivations

Initially, we focused on identifying regions associated with spontaneous MB occurrence during ongoing mentation. Overall, we found deactivations in the anterior cingulate cortex, the calcarine cortex, the bilateral thalami, the right anterior insula, the precentral gyrus, the left superior parietal lobule, the inferior frontal gyrus and the right operculum (Fig. 2; Table 1). To validate these results, we examined different TRs around the probe period. Although an uncorrected voxel-level threshold of $p = 0.01$

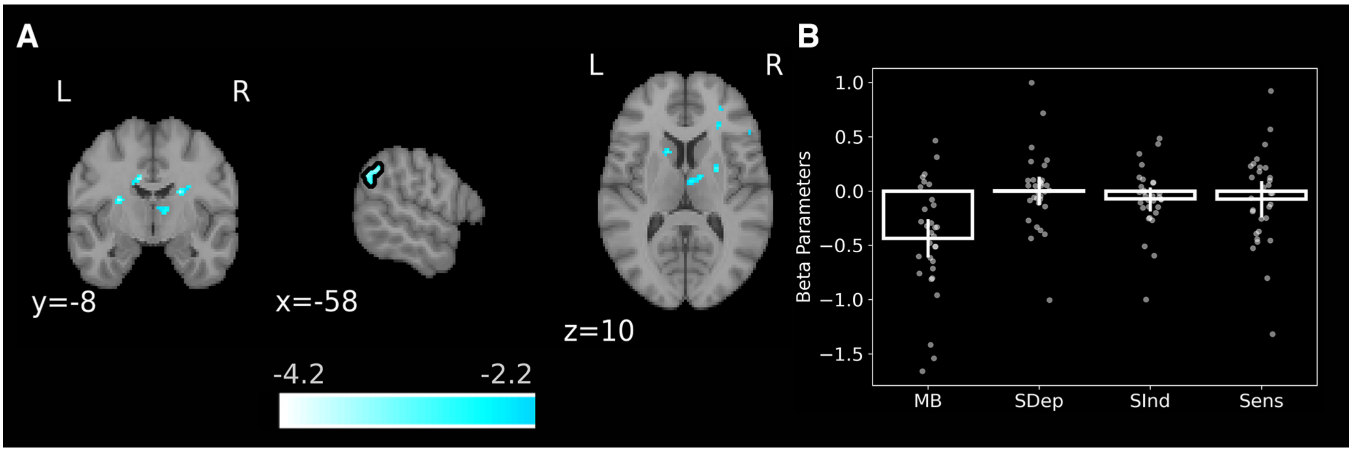

Figure 3. FMRI contrast analysis between content-oriented reports and MB at a lower exploratory threshold reveals deactivations in the left angular gyrus. ***A***, Activation map of presence versus absence of content contrast, projected on the MNI152 cortical template. The deactivated map projection is performed at voxel-level $p_{\text{uncorrected}} < 001$. Black contours signify the clusters that were significance at a cluster-extent threshold >50 voxels. Color-bar indicates *t* statistic. ***B***, Boxplots representing the β parameters of each mental state in left angular gyrus cluster. Error bars indicate 95% confidence intervals. Datapoints show single-subject parameter values. MB: mind-blanking, SDep: stimulus-dependent thoughts, SInd: stimulus-independent thoughts, Sens: perceptions.

recurrently showed deactivations in frontal, parietal and thalamical regions, cluster correction showed that only the thalamus was consistently deactivated across all time increments. Additionally, to control potential movement effects specific to conditions we estimated the overall framewise displacement of each subject at each time point (Power et al., 2012). Participants did not move significantly when considering displacement values per mental state category (mean: M; standard deviation: SD, confidence interval: CI) (MB: M = −0.006, SD = 0.182, CI = [−0.022, 0.009], SInd: M = −0.003, SD = 0.143, CI = [−0.008, 0.002], SDep: M = −0.004, SD = 0.161, CI = [−0.01, 0.003], Sens: M = −0.006, SD = 0.254, CI = [−0.018, 0.007]). Also, no significant difference was observed in terms of displacement values across mental states ($F_{(1,4)} = 0.146$).

At the FDR cluster threshold ($p<0.05$), the contrast between MB and the other mental states did not identify significant number of voxels. When the threshold was lowered to the exploratory level of whole-brain $p<0.001$, voxels >50, deactivations were observed in the angular gyrus (*n* voxels: 64, Z = 3.68, $x = -60$, $y = -58$, $z = 32$), a finding mainly driven by consistent deactivation of MB reports compared with stimulus dependent and stimulus independent thoughts (Fig. 3). An examination of the individual regressor sign of activation (positive/negative) shows that MB tended to be significantly deactivated. On the other side, the other three mental states varied around 0, and as their confidence intervals included 0, we cannot clearly estimate the direction of their activation.

fMRI bayesian ROI analysis provides evidence of deactivations in the vmPFC/subACC

Based on our a-priori assumptions about the role of vmPFC/subACC in thought monitoring, we examined the activation effects in the clusters reported in Kawagoe et al. (2019), namely, the vmPFC/subACC, Broca's area and the left hippocampus. Extensive descriptive statistics of the posterior distributions for each ROI and mental state are presented in Table 2. Overall, the three ROIs' MB intercepts did not include 0 in their 95% credibility intervals (vmPFC/subACC = median: −0.242, SD: 0.119, HDI: [−0.471, −0.01], Broca's area = median: −0.245, SD: 0.091, HDI: [−0.429, −0.07], left hippocampus = median: −0.113, SD: 0.056, HDI: [−0.219, −0.001]; Fig. 4C), suggestive of functional deactivations in these clusters.

Table 2. Descriptive statistics for the posterior distributions of the β parameters for each ROI and mental state

Region of interest	Contrast	Median	SD	HDI (0.025)	HDI (0.975)
vmPFC-ACC	MB	−0.242	0.119	−0.471	−0.01
	SDep	0.072	0.118	−0.158	0.306
	SInd	0.123	0.118	−0.114	0.35
	Sens	−0.027	0.119	−0.262	0.204
	MB-All	−0.298	0.119	−0.527	−0.064
	MB-SDep	−0.314	0.167	−0.64	0.013
	MB-SInd	−0.366	0.167	−0.693	−0.04
	MB-Sens	−0.214	0.168	−0.547	0.111
Broca's area	MB	−0.245	0.091	−0.429	−0.072
	SDep	−0.064	0.091	−0.242	0.112
	SInd	−0.205	0.09	−0.384	−0.031
	Sens	−0.202	0.091	−0.378	−0.021
	MB-All	−0.088	0.091	−0.272	0.085
	MB-SDep	−0.18	0.129	−0.434	0.069
	MB-SInd	−0.041	0.129	−0.287	0.216
	MB-Sens	−0.043	0.128	−0.289	0.21
Left hippocampus	MB	−0.113	0.056	−0.219	−0.001
	SDep	−0.119	0.056	−0.229	−0.009
	SInd	−0.069	0.055	−0.178	0.041
	Sens	−0.177	0.056	−0.287	−0.068
	MB-All	0.009	0.056	−0.098	0.121
	MB-SDep	0.007	0.079	−0.15	0.162
	MB-SInd	−0.044	0.079	−0.198	0.111
	MB-Sens	0.064	0.079	−0.094	0.217

HDI = highest density interval.

To examine whether the clusters showed specificity in MB compared with the other mental states, pairwise comparisons between the MB β parameters and the betas of each other mental state were calculated, as well as an overall MB versus rest contrast. Pairwise comparison inference was performed by subtracting the MB posterior of each ROI from the posterior of the other mental states (Table 2). We found evidence only for the vmPFC/subACC cluster, namely MB reports were associated with reliably lower β values compared with the other mental states (median = −0.298, SD: 0.119, HDI: [−0.527, −0.054]). Additionally, we found significant effects for the contrast MB-SInd (median = −0.366, SD: 0.167, HDI: [−0.693, −0.064]; Fig. 4*E*,*G*,*I*). Compared with the other mental states, MB was the only report category that was

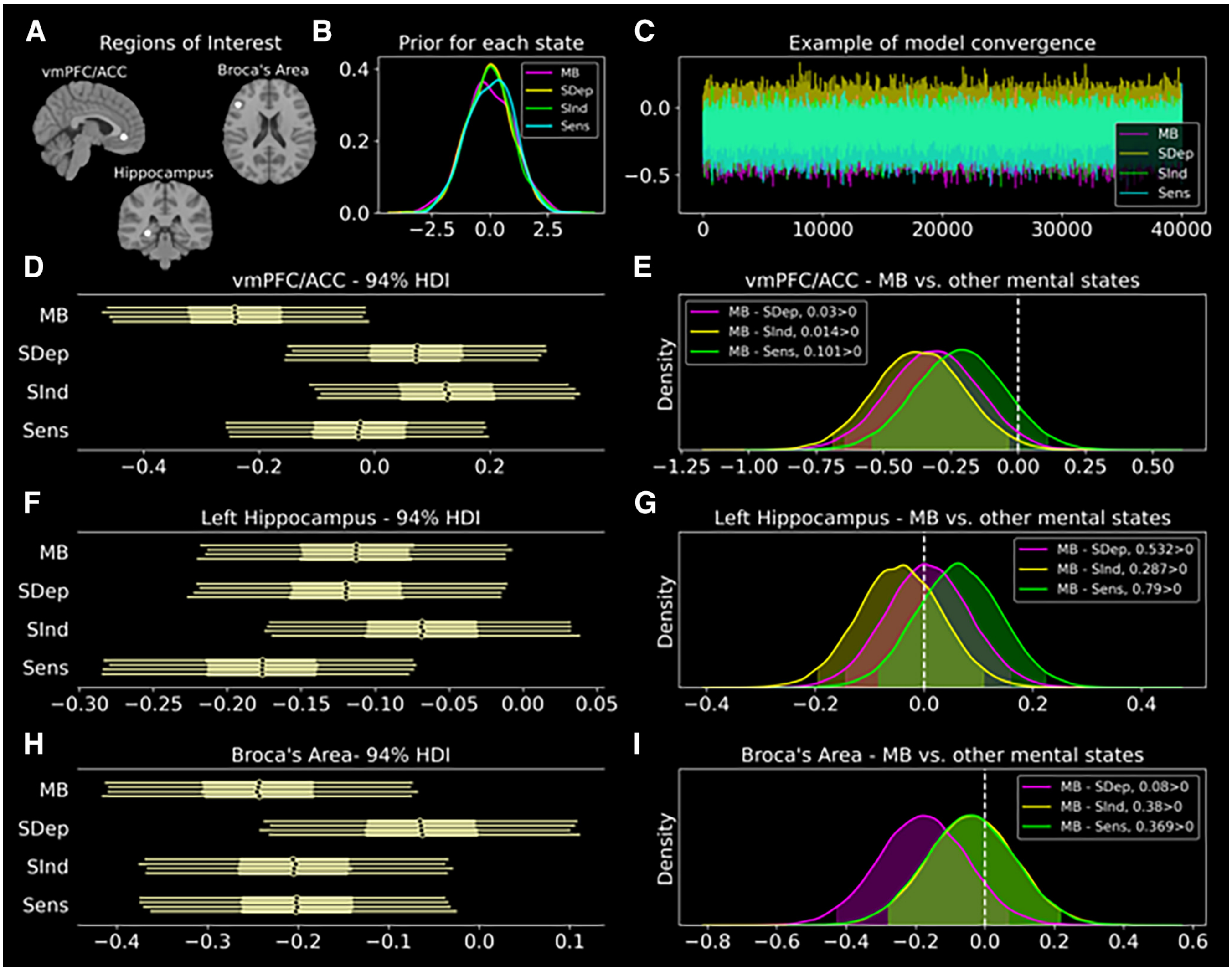

Figure 4. Bayesian analysis of the β parameters in the vmPFC/ACC ROI reveals MB-related deactivations in this cluster. ***A***, Regions of interest based on coordinates reported in Kawagoe et al. (2019) in the vmPFC/ACC, Broca's area, and the left hippocampus. ***B***, Null model prior expectations, modeling each prior as $N(0,1)$. ***C***, Example traceplot of the model fit. Visual inspection of the random walk indicates that models converged, as the chains sampled the whole posterior space without autocorrelated data and sequential sampling of the same posterior space. ***D***, Forest plot of each of the four sampled chains of the posterior distribution indicate that vmPFC/ACC contains significant evidence for MB deactivations, as the β values did not contain 0 in the 94% highest density interval (HDI). Each line represents 94% highest HDIs. This was not the case for the rest of the mental states. ***E***, Posterior differences between MB and the other mental states. We observed that the contrast MB-SInd did not contain 0 in the 94% HDI (shaded area), providing evidence that frontal deactivations differentiated between MB and SInd. ***F***, Forest plot of each of the four sampled chains of the posterior distribution indicate that the left hippocampus is deactivated only in MB. This was also the case for SDep and Sens. ***G***, Posterior differences between MB and the rest of the mental states at the left hippocampus. We observed that no contrast indicated any specificity of the ROI in MB. ***H***, Forest plot of each of the four sampled chains of the posterior distribution indicate that the Broca's area contains evidence for MB contributions, as it does not contain 0 in the HDI. This was also the case for SInd and Sens. ***I***, Posterior differences between MB and the rest of the mental states the Broca's area. We observed that no significant contrast indicating no specificity of the ROI in MB. MB: mind-blanking, SDep: stimulus-dependent thoughts, SInd: stimulus-independent thoughts, Sens: perceptions.

systematically deactivated, while the rest varied around 0. These results were consistent across the choices of different priors. No other ROI showed specificity for MB. To further validate whether the fitted models performed better against null models with only one intercept, for each fitted ROI we estimated the Watanabe–Akaike information criterion (WAIC) of the fitted and null model, as well as the expected log pointwise predictive density using leave-one-out cross-validation. Only for betas in the vmPFC/subACC did the model containing multiple intercepts perform better than the null model ($\text{Fitted}_{\text{WAIC}}$ $-129.687 <$ $\text{Null}_{\text{WAIC}}$: -129.833, $\text{Fitted}_{\text{ELPD}}$: $-129.868 <$ $\text{Null}_{\text{ELPD}}$: -129.908; Table 3). The validity of the model fit, as well as the specificity of the vmPFC/ACC cluster in MB was replicated across all examined prior distributions for every model.

Discussion

We re-analyzed an fMRI experience-sampling dataset to study the neural correlates of mind-blanking (MB) during unconstrained thinking and explore how instructions affect these correlates. Compared with mental states with reportable content, our findings indicate that spontaneous MB is linked to widespread deactivations in thalamo-cortical networks, which deviate from previous results.

Widespread thalamo-cortical deactivations are linked to MB reports

We first show that whole-brain, thalamo-cortical deactivations precede MB reports. The fMRI univariate analysis, examining positive and negative effects of MB, yielded deactivations in the anterior cingulate and calcarine cortex, the bilateral thalami, the

Table 3. Model comparison of fitted models

Region of interest	Model	WAIC	ELPD
vmPFC-ACC	Fitted	−129.687	−129.868
	Null	−129.833	−129.908
Broca's area	Fitted	−93.934	−93.972
	Null	−91.857	−91.877
Left hippocampus	Fitted	−32.831	−32.856
	Null	−30.82	−30.847

WAIC = Watanabe–Akaike information criterion; ELPD = expected log pointwise predictive density.

right anterior insula, the precentral gyrus and the left parietal lobule. Such cortical deactivations have been previously associated with reduced neuronal resource allocation (Hester et al., 2004), task demands (Hairston et al., 2008), and impaired cognitive performance (Ji et al., 2010). Overall, we consider that the identified whole-brain deactivations might represent brief periods of neuronal disengagement, during which the brain cannot support attentional and mental-reporting processes.

This is further supported by the finding that two key subclusters were further deactivated: the primary visual cortex and multiple cortical nodes of the salience network (Seeley et al., 2007). In previous work, thoughts unrelated to the immediate environment correlated with the decoupling of sensory areas from regions contributing to stimulus salience (Mittner et al., 2016). Indeed, instructing participants to think of nothing results in decreased connectivity between the DMN and the sensory cortices, potentially reflecting this decoupling of the sensory system and a system of internal thoughts (Kawagoe et al., 2018). The whole-brain disengagement explanation is also supported by the deactivation of the thalamus, a recurrent node in saliency and engagement in mental state reportability (Kucyi et al., 2013). Thalamic activity covaries with executive control and attentional demands (Jansma et al., 2000; Antonucci et al., 2021). Potentially, the integrative nature of the thalamus (Hwang et al., 2017) is necessary to cast a mental spotlight and selectively allocate resources to bring a specific thought into conscious awareness. Overall, the rich profile of deactivations preceding MB reports highlights the important role of cortical nodes, traditionally associated with the salience of information.

On our quest to better understand the neuronal significance of such deactivations, we could resort to recent findings that analyzed the same dataset but examined functional connectivity. In that work, we show that MB reports are associated with a hypersynchronized fMRI cortical connectivity profile, further characterized by high global signal amplitude, which we interpreted as neuronal down-states (Mortaheb et al., 2022). Although it would be tempting to hypothesize a similarly low neural activation mediating the identified deactivations, we recognize that a one-to-one comparison between the two analyses is difficult to make, as different aspects of the BOLD signal are examined. Indeed, while task-based BOLD activations can be considered as proxies of neuronal firing (Logothetis et al., 2001), changes in resting-state activity can result from complex interactions among neural, vascular, and metabolic factors (Liu, 2013). As a result, it is not clear whether there is a direct mapping between BOLD activations and functional connectivity analyses.

MB-specific deactivations are linked to parietal and frontal regions

Moving to report-specific effects by contrasting presence versus absence of content we also found that MB is characterized by deactivations in the left angular gyrus. Supporting variant mnemonic (Ciaramelli et al., 2008), attentional (Cattaneo et al., 2009), and semantic processes (Kuhnke et al., 2023), the angular gyrus is recurrently present in content-oriented mental states. Indeed, angular activations have been correlated with both mind-wandering during ongoing mentation (Christoff et al., 2004; Maillet et al., 2019) and external orientation of thought during task engagement across demanding and nondemanding tasks (Turnbull et al., 2019). Therefore, the idea of generalized contributions of the angular gyrus to content-oriented mental states is further supported by our finding of inability to report mental content during deactivation of this region. Our results also are in line with previous electrophysiological results, where MB attentional lapses during task were predicted by posterior EEG slow-wave activity (Andrillon et al., 2021). The authors emphasized the role of parietal cortices in the emergence of conscious reports, where slow-wave activity might inhibit parietal-frontal communication and lead to the MB experience. We supplement this explanation by proving more granular structural information, introducing the angular gyrus as an important parietal node.

By performing an ROI analysis to examine previously reported MB-specific cortical areas, we found MB deactivations in the ACC/vmPFC. In the context of thought-content, frontal activations were observed during mind-wandering with no meta-awareness compared with periods of mind-wandering with meta-awareness. The authors interpreted these larger activations as the ACC signaling a mismatch between expected thought stream and actual, wandering thoughts, eliciting a higher degree of surprise to the participant (Christoff et al., 2009). Additionally, vmPFC activation is correlated with episodic and social self-generated thought (Konu et al., 2020). However, given the multiple partitions of the ACC, treating it as a unimodal region that collectively contributes to one specific cognitive process might be misleading. In our study, the cluster originated close to the borders between ACC and vmPFC, denoting that the previous activation might include multiple processes (a detailed account can be found in https://neurosynth.org/locations/?x=4&%20y=40&z=-4). Indeed, the vmPFC-ACC cluster is systematically implicated in evaluative (D'Argembeau, 2013) and metacognitive processes (Vaccaro and Fleming, 2018), which are facilitatory to the internal stream of thought (Smallwood et al., 2012). Given the self-evaluative aspect of ACC-vmPFC, we here interpret these deactivations as failures to recurrently examine the content of a thought, which can be formulated as self-referential questions ("Am I thinking of anything?"; D'Argembeau et al., 2007).

MB as the mental state of "no thought"

A series of studies has explored ongoing thought using multidimensional experience sampling questionnaires, aiming to decompose it into a low-dimensional space where all content types can be represented (Konu et al., 2020, 2021; Mulholland et al., 2022). Interestingly, this approach has revealed an overlap in the low-dimensional space of ongoing thought-content between everyday life and in-lab task engagement, with consistent clusters related to social cognition, intrusive unpleasant thoughts, and task focus (Konu et al., 2021; Mulholland et al., 2022). In this space, where each dimension represents different content, we suggest that MB could represent the origin point, devoid of specific thought engagement, while moving away from this point would result in clearer content. Conversely, thoughts closer to the origin would exhibit less clearly reportable content.

The activation patterns observed in the ventromedial prefrontal cortex (vmPFC) for thoughts along the social-episodic axis (Konu et al., 2020) and in the parietal lobule for thoughts along the task-focus axis (Turnbull et al., 2019) support this idea, as both these regions are deactivated during MB reports.

Intentional and unintenional MB

So far, only one study has examined the fMRI neural correlates of MB from a univariate perspective (Kawagoe et al., 2019). In that protocol, participants were instructed to "think of nothing" resulting in deactivations in Broca's area and the left hippocampus, and activations in ACC. Similar frontal activations have been observed in clinical settings, where patients with depressive symptoms were guided to suppress their thoughts (Carew et al., 2015). By bridging the current literature together, we suggest that the discrepancy between uninduced and self-induced MB may reflect the existence of different forms of MB, similar to mind-wandering, for which intentional and unintentional forms have been proposed (Seli et al., 2016). Intentional MB may originate from top-down monitoring to exclude thoughts, such as during meditation, while unintentional MB may arise from spontaneous lapses in frontal-parietal-sensory-thalamic systems that monitor the stream of consciousness and guide the ability to attribute semantic content to mental life. While this interpretation is still speculative and the clear presence of different MB forms cannot be extrapolated from our dataset, it paves a promising avenue for future research contrasting different forms of "thought absence".

Limitations and conclusions

Several limitations pertain our study. The duration and sampling rate of mental states, including MB, in fMRI experience-sampling studies may lead to under-sampling of infrequent and transient states (Mortaheb et al., 2022). Complementary methods, such as EEG, which allow for subsecond level estimation of brain dynamics, could provide valuable insights into momentary markers of MB. Additionally, the standard GLM-summary statistics approach may be suboptimal because of the fundamental unbalanced count of different mental states, resulting in reduced statistical power. In that sense, although the here identified effects remain safeguarded, we might nevertheless have missed others because of underpowered statistics. Finally, multivariable decoding approaches varying the duration of mental states could overcome the assumption of uniformity of mental state duration.

In conclusion, we investigated the neural correlates of uninduced MB during free-thinking conditions and found wide-spread thalamo-cortical deactivations, which may not allow the formulation of an efficient neural substrate to serve content reporting. We think that these results provide mechanistic insights on the phenomenology of MB and point to the possibility of MB being expressed in different forms. As MB holds experimental, philosophical, and potential clinical implications for understanding the thought-oriented and stimulus-driven mind, we believe future research would benefit by incorporating MB in the investigation of unconstrained thinking.

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REGISTERED REPORT

Variations of autonomic arousal mediate the reportability of mind blanking occurrences

Paradeisios Alexandros Boulakis[1,2], Nicholas John Simos[1], Stefania Zoi[1], Sepehr Mortaheb[1,2], Christina Schmidt[2,3], Federico Raimondo[4,5,7] & Athena Demertzi[1,2,6,7]✉

Mind blanking (MB) is the inability to report mental events during unconstraint thinking. Previous work shows that MB is linked to decreased levels of cortical arousal, indicating dominance of cerebral mechanisms when reporting mental states. What remains inconclusive is whether MB can also ensue from autonomic arousal manipulations, pointing to the implication of peripheral physiology to mental events. Using experience sampling, neural, and physiological measurements in 26 participants, we first show that MB was reported more frequently in low arousal conditions, elicited by sleep deprivation. Also, there was partial evidence for a higher occurence of MB reports in high arousal conditions, elicited by intense physical exercise. Transition probabilities revealed that, after sleep deprivation, mind wandering was more likely to be followed by MB and less likely to be followed by more mind wandering reports. Using classification schemes, we found higher performance of a balanced random forest classifier trained on both neural and physiological markers in comparison to performance when solely neural or physiological were used. Collectively, we show that both cortical and autonomic arousal affect MB report occurrences. Our results establish that MB is supported by combined brain-body configurations, and, by linking mental and physiological states, they pave the way for novel embodied accounts of spontaneous thinking.

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Keywords Mind blanking, Experience sampling, Brain-body interactions, Machine learning, Spontaneous thinking

During ongoing mentation, our mind constantly shifts across different mental states. These mental states typically bear some content ("what we think about") and indicate a relationship towards that content (i.e., perceiving, fearing, hoping, remembering)[1]. As we move through the environment, our thoughts fluctuate between the external and internal milieu[2,3], resulting in a fluid stream of consciousness[4]. External content is tightly coupled to the processing of environmental stimuli and task-demanding conditions. Internal content is more associated with self-referential processing and internal dialogue, widely referred to as "mind wandering" (MW)[4]. Inclusive as this external-internal dipole may seem, it does not capture the full scope of the "aboutness" of mental content. Recent work has highlighted another mental state, where people report that they are "thinking of nothing" or "their mind just went away", a phenomenological experience termed "mind blanking" (MB)[5]. As MB is relatively new in the landscape of ongoing cognition, the extent of MB episodes in daily and clinical settings remains widely uncharacterized. For example, a recent study found that MB might be miscategorized as MW in ADHD symptom evaluation[6]. Therefore, the experience of MB occurrences poses a challenge to our everyday functioning and our understanding of the continuous nature of the stream of consciousness.

[1]Physiology of Cognition Lab, GIGA-CRC Human Imaging Unit, GIGA Research, University of Liège, Liège, Belgium. [2]Fund for Scientific Research FNRS, Brussels, Belgium. [3]Sleep & Chronobiology Lab, GIGA-CRC Human Imaging Unit, GIGA Research, University of Liège, Liège, Belgium. [4]Institute of Neuroscience and Medicine, Research Centre Jülich, Brain & Behaviour (INM-7), Jülich, Germany. [5]Institute of Systems Neuroscience, Medical Faculty, Heinrich Heine University Düsseldorf, Düsseldorf, Germany. [6]Psychology and Neuroscience of Cognition Research Unit, University of Liège, Liège, Belgium. [7]Federico Raimondo and Athena Demertzi contributed equally to this work. ✉email: a.demertzi@uliege.be

Currently, there is no clear answer as to how MB reports are generated. So far, behavioral studies show that MB can arise after conscious mental effort to empty our mind[7–9], is usually unintentional[5,10,11] and gets reported less frequently during unconstrained thinking compared to MW and sensory/perceptual mental states[5,11–13]. At the brain level, the inability to report mental events after the prompt to "empty the mind" has been associated with activation of the anterior cingulate/medial prefrontal cortex, and deactivation of inferior frontal gyrus/Broca's areas and the hippocampus, which the authors interpreted as the inability to verbalize internal mentation (inner speech)[8]. Recently, we found that the functional connectome of fMRI volumes around MB reports was similar to a unique brain pattern of overall positive inter-areal connectivity[12] which was also characterized by increased amplitude of fMRI global signal (i.e. averaged connectivity across all grey matter voxels), an implicit indicator of low arousal[14–16]. For example, the amplitude of the global signal correlated negatively with EEG vigilance markers (alpha, beta EEG frequency bands), while increases in EEG vigilance due to caffeine ingestion were associated with reduced global signal amplitude[14]. Our findings corroborate recent EEG-related evidence supporting the possibility of "local sleeps" during MB reportability[10,17]. "Local sleeps" refer to the scalp distribution of EEG potentials during wakefulness, in the form of high-intensity, slow oscillatory activity in the theta/delta band, which could differentiate between MB and MW, with more frontocentral potentials tied to MW and parietal to MB[10]. Together, the presence of slow waves preceding MB reports and the high fMRI global signal hint toward the role of arousal in mental content reportability. Starting from this line of evidence, we infer that arousal fluctuations drive MB reportability.

Arousal is a multidimensional construct generally referring to the behavioral state of being awake and alert, supporting wakefulness, responsiveness to environmental stimuli, and attentiveness[18,19]. Anatomically, arousal is supported by the ascending arousal system, the autonomic nervous system, and the endocrine system[18]. Early on, Lacey viewed arousal in terms of behavioral arousal (indicated by a responding organism, like restlessness and crying), cortical arousal (evidenced by desynchronized fast oscillatory activity), and autonomic arousal (indicated by changes in bodily functions)[20]. Cortical arousal is self-generated through the reticulate formation and propagated through dorsal, thalamic, and ventral subthalamic pathways[21], and can be indexed by the alpha, theta, and delta EEG bands during wakefulness[22,23]. Lower levels of cortical arousal in the form of slow waves have been associated with an increased number of missed stimuli in behavioral tasks[11,23] and decreased thought intensity[24]. Also, lower levels of arousal indexed by pupil size have been correlated with a higher probability of MB reports in sustained attention tasks[11,25,26].

Much as it may have been done in terms of cortical arousal, the present study will focus on how autonomic arousal influences MB reportability, which is widely understudied. Our choice is justified by the theoretical assumption that mental function is tightly linked to peripheral body functions, as expressed by the embodied cognition stance[27]. Briefly, embodiment holds that cognition is bound to a living body interacting with a dynamic environment, and conceptualizes cognition as the result of brain-body interactions during dynamic contexts. From that perspective, modifications in autonomic arousal are expected to lead to differential reportability of mental states. Autonomic arousal links the body and the brain through spinal cord projections from peripheral organs to the brainstem and can be indexed by physiological signals reflecting sympathetic/parasympathetic balance, such as heart rate, galvanic skin response, and fluctuations in pupil size[28]. Converging evidence suggests that afferent physiological signals and biological rhythms, such as the cardiac or the respiratory phase, play a modulatory role in conscious perception[29,30], metacognition[31], affective salience of information[32], and perceptual confidence of sensory sampling[33], both during task performance and in-silico simulations[34]. Alterations in autonomic arousal were also found to influence brain activity in that fMRI volumes characterized by lower arousal levels (indexed by decreased pupil size) showed reduced in-between network integration and inter-subject variability in comparison to scans characterized by high arousal levels (indexed by increased pupil size)[35].

Taken together, we here advocated for a link between autonomic arousal and thought reportability. Firstly, we examined how MB report distribution shifted across different autonomic arousal conditions. To this end, we used experience sampling under differently elicited arousal conditions. Experience sampling is a though-sampling methodology, where people are probed to report their mental state at random intervals, probed by an external cue[4]. We employed this task at three distinct arousal conditions: *Baseline*, *High* (post-workout), and *Low* (post-sleep deprivation). Our operational hypothesis was that optimal levels of autonomic arousal (fixed variable) are necessary for optimal mental state reportability (dependent variable). We expected that deviations from optimal levels, such as after sleep deprivation or intense physical exercise, would alter our stream of thought and promote more frequent MB reports (Supplementary Table S1 for the full scope of our hypotheses). Secondly, we opted to identify specific brain-body interaction patterns that would promote MB reportability. To this end, we utilized multimodal neurophysiological recordings and a machine-learning approach to decode MB reports from arousal measurements.

Methods

Design

The study included healthy volunteers recruited after campus poster advertisements, intranet electronic invitations, and through the ULiège "petites annonces" e-campus platform. Inclusion criteria were: (a) right-handedness, (b) age>18 years, (c) minimal exercise background (<2h per week), (d) good subjective sleep quality (Pittsburgh Sleep Quality Index [PSQI] ≤ 5[36]), (e) habitual sleep duration of 8 ± 1 hours. Exclusion criteria were: (a) history of developmental, psychiatric, or neurological illness resulting in documented functional disability, (b) severe anomalies in pupil shape or inability to open both eyes preventing pupil measurement[37], (c) analgesic medication which may affect physiological arousal, (d) history of psychiatric illness pertaining to anxiety disorders or scores < 9 in the General Anxiety Disorder-7 (GAD-7 scale)[38] as anxious participants may experience biased perceptions of their bodily states[39], (e) extreme chronotypes, (f) shift work or traveling over time zones in the past 3 months.

Experience sampling was utilized in a within-participants repeated-measures design. During an experience sampling session, participants laid restfully and were directed to let their minds wander, without any specific instructions towards internal (daydreaming, memories, prospective events) or external thoughts (body sensations, sensory stimuli in their immediate environment). Auditory probes (total n=40, 500 Hz simple tones) invited participants to report what they were thinking at the moment just preceding the probe. The inter-probe interval was sampled from a uniform distribution between 110 and 120 seconds. Report times were monitored online to examine if participants missed the probe or fell asleep due to our experimental manipulation. In case of a report time > 6 s, participants were reminded to report their mental state as soon as they heard the probe and indicate they were awake via button press. In case of unresponsiveness, the experimenters manually awakened the participant. Depending on the probes' trigger times and participants' reaction times, a recording lasted on average 70-90 minutes. We chose to present 40 probes (overall length approximately 1 hour and 15 minutes) to avoid fatigue/drowsiness and the possibility of participants returning to baseline arousal after the experimental manipulations. Also, the relatively large experience sampling interval, compared to previous studies, was used to record enough samples to accurately estimate physiological markers from slow oscillatory signals, such as heart-rate variability. Upon the probe, participants had to choose among four distinct choices describing their mental state: mind blanking (MB), mind wandering (MW), perceptual sensations (SENS), or sleep (SLEEP). These response options were chosen to minimize assumptions about what the actual partition of mental states might be. For example, debates about what can be classified as MW[40] refer to whether MW is a coherent cluster of events[1,41] and how it is separated from awareness and processing of environmental stimuli[40,42]. We believe that our division respects the literature on internal/external thought-orientation brain networks[3,43,44] while introducing minimum assumptions as to the actual content of each state. The introduction of the sleep option facilitated the identification of trials where participants fell asleep due to the reduced vigilance. Participants indicated their responses via button press from a response keyboard placed under their dominant hand. We repeated the experience sampling task on three distinct days, over the span of two weeks under three conditions: (a) experience sampling during spontaneous thinking without arousal modulations (*Baseline*), (b) experience sampling elicited through short, high-intensity interval training (*High Arousal*), (c) experience sampling after total sleep deprivation (*Low Arousal*) (Fig. 1). The goal of both arousal manipulations was to promote distinct changes in physiological and cortical markers associated with arousal mechanisms (Supplementary Table S2). Monitoring of arousal changes was done with physiological and cortical measurements. In case when participants did not show distinct cortical and physiological changes after our arousal manipulations, they were excluded

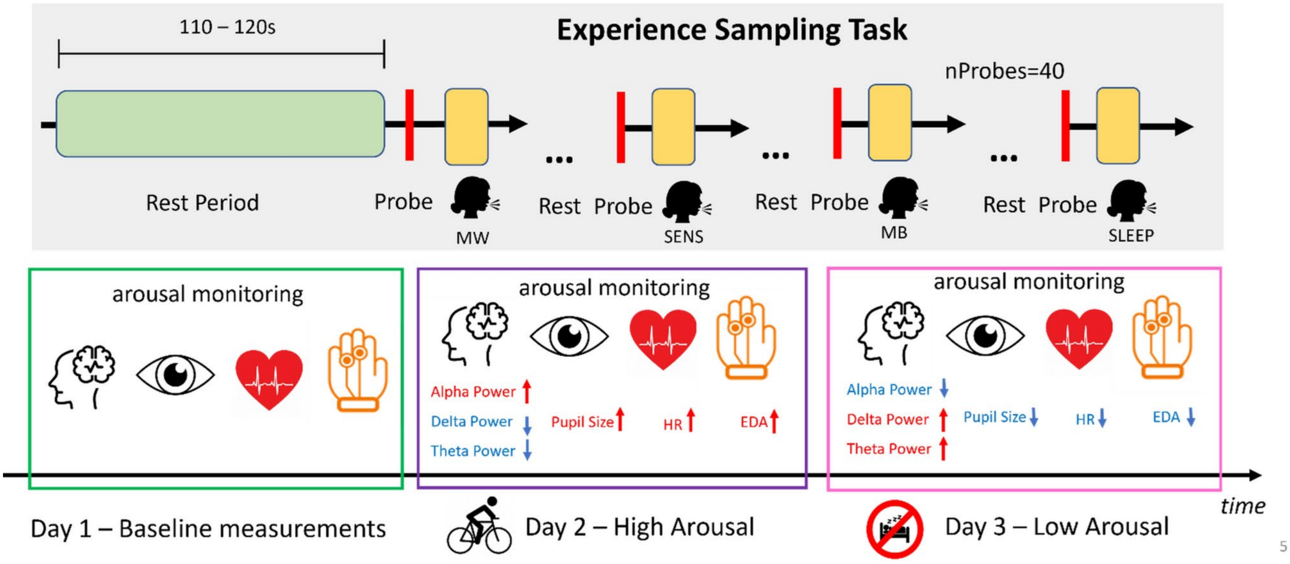

Fig. 1. Experimental protocol. *Top* The experience sampling task invited participants to sit idly and relax, letting their minds wander. Every 110–120 s, a 500 Hz auditory cue probed participants to report what they were thinking at that moment. Participants were able to choose from 4 presented responses: Mind blanking (MB), Mind wandering (MW), Perceptual Sensations (SENS), and Sleep (SLEEP). *Bottom* Repeated-measures autonomic arousal recordings. To test how spontaneous thoughts unfold over time across different arousal conditions, we first invited people for baseline assessments on Day 1 (*Baseline* condition). On Day 2 participants underwent a 15-minute high-intensity exercise (*High Arousal* condition) and on Day 3 they participated in a total sleep deprivation protocol (*Low Arousal* condition). The *High* and *Low Arousal* conditions were counter-balanced across participants. Multimodal physiological recordings were used to monitor arousal manipulations. The dataset was constituted of EEG, pupillometry, ECG, EDA, and respiratory data; the arrows indicate the hypothesized directions of the derived metrics.

from further analysis. Effect monitoring was done by examining the heart rate in *High Arousal* as well as the EEG spectra in both *High* and *Low Arousal*.

In *High Arousal*, participants first performed high-intensity interval activity in the form of static cycling. They started with a warm-up training session of 3 minutes to avoid potential muscle trauma and then cycled for 45 s as fast as possible. A resting period of 15 s followed. A total number of 10 workout cycles was administered. The choice of this timing protocol rested on previous studies indicating that similar exercise routines produce distinct and sustained sympathetic activity[45,46] and cortical excitation[46], which can last between 30 and 90 minutes after exercise cessation[47].

In *Low Arousal*, participants performed the experience sampling task after one night of total sleep deprivation. Sleep deprivation leads to an arousal state that is behaviourally distinct from typical wakefulness[48,49], promotes specific neuronal signatures ("local sleeps" in the delta band)[11], and has a distinct physiological expression. Critically, we do not wish to claim that sleep states are identical to "local sleeps", nor do we suggest an overlap between low arousal due to sleep deprivation and unconsciousness during sleep. To acquire estimates of their mean sleep schedule, participants wore an actimeter for one week before the total sleep deprivation protocol (Supplementary Fig. S1; available for 24/26 subjects due to data corruption). The total sleep deprivation protocol was as follows: A week prior to sleep deprivation, participants were provided with an actimetry device to track wake-sleep schedule, and were instructed to follow a consistent 8 h sleep schedule. On the deprivation day, participants arrived at the lab one hour before their normal sleep time to extract their actimetry baseline data, estimate the optimal sleep deprivation window, and to provide baseline vigilance, drowsiness, and sleepiness measurements. After a total sleep deprivation of 26 h (16 h of typical wakefulness, 8 h of sleep deprivation, and a 2h post-sleep deprivation period) participants began the post-sleep deprivation, experience sampling session. As an example, a participant who typically slept at 12 am would arrive at the lab at 11 pm, start sleep deprivation at 12 am, finish sleep deprivation at 8 am, and perform the experience sampling task at 10 am. Should slow-wave activity during wakefulness follow the same circadian modulation it follows during sleep[50], a potential confound that could have lowered the power of our analysis is the time window of the experience sampling task. However, as suggested in[50], the relative time-window we selected did not fall under a critical point of large reductions in the amplitude of the slow-waves. The 2-hour, post-deprivation waiting window allowed us to match the time of the experience sampling across the 3 conditions, avoiding potential circadian confounds on experience sampling, as we could easier match sleep-wake cycles and the time of the experience sampling within each participant. We chose this sleep manipulation as similar manipulations have been previously used to examine the effects of sleep pressure[51,52], and have been shown to elicit distinct low-arousal cortical profiles[53,54], as well as changes in the sympathetic/parasympathetic balance[55].

Sleep deprivation was controlled with regard to light influence (illuminance = 15 lux), caloric intake (standardized meals every 4 h), and body posture (semi-recumbent position during scheduled wakefulness) to minimize potential masking effects on the sleep-wake regulatory system. Participants were not allowed to stand up except for regularly scheduled bathroom visits and did not have any indications of the time of the day. The experimenters continually monitored participants to keep them awake. In case of a sleep event, the experimenters first tried to awaken the participant through an intercom, and in case of failure, they manually awakened the participant. We also monitored for sleep lapses through the experience sampling tasks. In case participants closed their eyes for a time period of > 30 seconds, they were probed by a tone to wake up. If they did not, the experimenter in the room would awaken the participant.

An one-week interval took place between sleep deprivation and further recordings in order to minimize potential carry-over effects of sleep deprivation on our follow-up conditions. In that way, the participants' sleep schedules would also reset to their respective normal cycles. The order of the three arousal conditions was randomized. As a post-registration note, we randomized only the order between sleep deprivation and post-exercise, to add a training session before the baseline that allowed participants to get acquainted with the protocol, without external task impositions, that might have confounded the protocol understanding.

Sampling plan

We used a Neyman-Pearson frequentist approach to balance false-negative and false-positive rates by setting power to 95% and establishing a Type I error rate (alpha) of 5%. To estimate the desired sample size, a simulation approach was utilized: data were generated consistent with a latent binomial regression model, in which one categorical predictor with 3 levels (Base, High, Low) predicted a binary outcome Y (occurence of MB or not). An original probability $p_{MB} = 0.1$ was specified as the underlying generative probability in the baseline model based on previous research[5,11,12]. We allowed the random intercepts and slopes to vary freely vary around a normal distribution with a standard deviation of s.d. = 0.1. Given that no previous study to our knowledge has provided evidence for the distribution of the effect sizes of arousal on mental reports, and to account for possible reverse effects (such as decreased MB report probability), we reasoned that a meaningful yet conservative effect for the *Low Arousal* condition would be an odds ratio of 1.6 and an odds ratio of 0.55 for the *High Arousal* condition. Since our initial hypothesized distribution is expected to yield ~3–5 MB reports per session[11,12], this effectively translates to a small effect size of interest of at least 3 more reports across conditions.

Considering these parameters, for each population sample, ranging from 5 to 50 participants, we sampled 500 datasets, and fit a binomial model with the participant ID as a random factor, keeping the regression coefficients for the levels of the predictor constant. Based on the simulation analysis, using a false positive threshold of 0.05, we required a sample size of 26 participants to achieve a power of 0.95 (Supplementary Fig. S2).

Data analysis

Behavioral data

Statistical analysis was performed using generalized linear mixed-effects models. To address whether arousal affects MB occurrence, we used a binomial, linear model with arousal as a categorical independent variable, and the proportion of mental reports across a sampling period (40 trials) as our dependent variable. Data were binary coded (occurence or not of MB report) and fit into the model using a "logit" link. Given that the underlying distribution was unknown, a Bernoulli distribution minimized the assumptions about the model. In order to examine whether the multinomial distribution of mental reports itself changes across different arousal conditions, we used the generalized estimating equations (GEE) approach, an extension of generalized mixed-effects models that can account for correlated, repeated-measures count data from multinomial distributions[56,57]. Mental reports were aggregated as counts across participants and conditions, and we examined shifts in reaction time distribution using the three experimental arousal conditions as predictors. We considered as reaction times the intervals between the response probe and the participant's report. To examine reaction times as a function of mental states, we specified a generalized linear mixed-effect model with mental reports and arousal conditions as categorical variables and used a gamma distribution with an "inverse" link function. As reaction times are usually an indicator of arousal effects on the task performance, an effect of arousal condition as a covariate might be informative about a potential shift of the overall slower mental report times distribution and about the arousal condition of the subject itself. This choice of distribution and link minimizes assumptions about the model, respects the positive, skewed distribution of reaction times, and was previously found to provide a better fit compared to other link functions[58]. To examine whether arousal shifts the dynamics of mental reports, i.e. one state might be more likely to be followed by MB in one of the arousal states compared to *Baseline*, we estimated dynamical transition probabilities across different mental states using Markov models. The transition probabilities of MB were then compared using a linear model with an identity link, with the transition probabilities as the dependent variable and the arousal condition as the categorical, independent variable.

All specified models were compared against null models using likelihood ratio tests. We introduced the participant's ID as an a-priori random factor, i.e., we allowed the model's intercept to vary. In case we contrasted multiple models, p-values were corrected using Bonferroni correction. In case of significance of a fixed predictor, we used corrected pairwise comparisons to examine the marginal means of the predictors.

Brain-based measures

Physiological and cortical timeseries were segmented based on the response probe time. We considered the 110-second period before the response probe as a meaningful analysis epoch, representing the neuronal and physiological dynamics that result in a specific mental state. This period was used in subsequent analyses.

We recorded EEG with an EasyCap (64 active electrodes) connected to an actiCHamp system (Brain Products GmbH) using the 10–20 standard configuration. A ground electrode was placed frontally (Fpz in the 10–20 system). Online, we referenced the electrodes to a frontal electrode. Impedance was kept below 20 kΩ. As a post-registration note, we originally registered to keep impedance below 10 kΩ. However, we decided to leverage the strength of active electrodes to follow the research standard of 20 kΩ. To minimize impedance, we used conductive gel. Data were sampled at a sampling frequency of 500 Hz. Preprocessing included band-pass filtering (0.1–45 Hz, FIR filter), notch filtering (50 Hz), and epoch definition (t_start = 110 s preceding the probe, t_max= probe). As a post-registration note, during EEG preprocessing we observed low-frequency (<1 Hz) artifacts, such as sweat during the post-exercise session, that contaminated the quality of the signal. Therefore, we decided to reanalyze our data using a 1 Hz high-pass filter to minimize the presence of those artifacts. By visual inspection, we checked and removed noisy electrodes and epochs. In case of discarding more than 50% of the total epochs for a single participant, that participant was discarded from future analysis. We then used ICA decomposition to remove non-neuronal components such as blinks, heartbeats, muscle artifacts, etc. Finally, channels removed due to rejection were interpolated using neighboring channels, and all channels were re-referenced to the average.

Based on EEG recordings, we estimated three classes of measures: (1) measures estimating spectral power—raw and normalized power spectra, median spectral frequency (MSF), spectral edge 90 (SEF90), and spectral edge 95 (SEF95), (2) measures estimating information content—spectral entropy, Kolmogorov-Chaitin complexity (K) and permutation entropy, and (3) measures estimating functional connectivity—symbolic mutualiInformation (SMI) and weighted symbolic mutual information (wSMI). Power spectrum density (PSD) was computed over the delta (1–4 Hz), theta (4–8 Hz) alpha (8–12 Hz), beta (12–30 Hz), gamma (30–45 Hz) spectral bands, using the Welch spectrum approximation (segments = 512 ms, overlap = 400ms). Segment rejections were windowed using a Hanning window and zero-padded to 4096 samples. Kolmogorov-Chaitin complexity was computed by compressing a discretization of the signal using a histogram approach with 32 bins. Permutation entropy was obtained by computing the entropy of a symbolic transformation of the signals, within the alpha, delta, and theta bands. SMI and wSMI were then computed from the same symbolic transformation, but data was first filtered using current source density estimates to diminish the volume conduction. SMI and wSMI were computed in theta, delta, and alpha bands[59]. From the available connectivity metrics, we chose to use only wSMI as it is the only one that can detect purely nonlinear interaction dynamics and can be computed for each epoch[60].

Physiological measures

Electrocardiogram (ECG) data were acquired using the BIOPAC MP160 system (BIOPAC SYSTEMS Inc.) and the BIOPAC ECG100C amplifier. The data were sampled at a sampling frequency of 2 kHz and recorded using the AcqKnowledge v4.4 software. ECG disposable adhesive skin electrodes were used in a bipolar arrangement of two electrodes and ground. The positive electrode was at the non-dominant wrist of the participant and the negative was on the contralateral ankle. The ground electrode was placed on the ipsilateral ankle.

ECG data were filtered with a notch filter (0.05 Hz) to remove baseline wander artifacts. A Butterworth high-pass filter was applied (0.5 Hz) to attenuate linear drifts and physiological artifacts. Powerline interference was attenuated with a notch filter (50 Hz). Finally, the data were smoothed with a 3rd-order polynomial Savitzky-Golay filter. Peaks were detected using the native Neurokit2 algorithm. Finally, data were epoched based on the partition scheme in the EEG preprocessing section.

ECG metrics were grouped into three domains: time, spectral power, and information content. Time-domain metrics were (a) heart rate (HR), (b) standard deviation of the RR intervals (SDNN), and (c) root mean square of successive differences (RMSSD). Spectral power features were (a) low frequency of the heart rate variability (LF-HRV), (b) high frequency of the heart rate variability (HF-HRV), and (c) LF/HF HRV ratio. Information content metrics were (a) approximate entropy (AE), (b) sample entropy (SE), and (c) multiscale entropy (MSE). Initially, we used the native Neurokit2 algorithm to extract the peaks of the QRS complex. RR intervals were estimated as the sequential difference of the peak times. We estimated the time domain features based on the RR timeseries. For the spectral power metrics, the RR was evenly resampled at 4 Hz. Power spectra were computed over the LF-HRV (0.04–0.15 Hz) and the HF-HRV (0.15–0.4 Hz) frequency bands. The power spectrums were estimated using the Welch procedure.

Respiration. Respiratory data was acquired using a respiratory belt and amplified through the BIOPAC DA100C amplifier. Data were sampled at a sampling frequency of 2 kHz and recorded using the AcqKnowledge v4.4 software.

Respiratory metrics were grouped in the time and information content domain. Time-domain metrics were (a) respiration rate and (b) respiration rate variability. Information content was estimated based on multiscale entropy.

Pupillometry. Eye movements and pupil size in both eyes were recorded using oculometric glasses (Drowsimeter R100; Phasya, S.A) with a sampling frequency of 120 Hz. The eye tracker was calibrated at the start of each recording. Data was epoched based on the epoching scheme in the EEG preprocessing section. We identified 100 ms blink periods around blinks and removed the whole segment, as pre- and post-blink periods can introduce pupil dilation artifacts while the eye is recovering to its standard size. We interpolated segments using 3rd-degree cubic interpolation. Dilation speed outliers were calculated by estimating the median absolute deviation (MAD) of each value. Samples exceeding the deviation threshold were removed. Pupil dilation was smoothed using a moving average filter and baseline-corrected with a 100 ms period 2 s after the probe.

Pupil metrics were grouped in the same three domains: time, spectral power, and information content. Time-domain metrics were: (1) blink rate, (2) pupil size, and (3) pupil size variability. Spectral power metrics were: (1) low frequency pupil component (LFC), (2) high-frequency pupil component (HFC). The information content metric is multiscale entropy. The power spectra were estimated using the Welch procedure. As a post-registration note, we encountered issues extracting pupil metrics at the *Low Arousal* condition, as participants tended to have their eyes closed or partially closed for most of the trials. As our device was not sensitive to capture dilation in this setting, we additionally estimated (a) blink rate, (b) blink duration, (c) blink rate variability, (d) mean eye openness, (e) eye openness variability, (f) percentage of 70% eye closure and (g) percentage of 80% eye closure. As stated below, our registered plan was to reliably estimate all time, frequency, and complexity metrics that can be of use to our classifiers. Therefore, while we do not deviate from our original registered protocol, it is of note that these features could not be estimated reliably.

Electrodermal activity (EDA) data was acquired through skin electrodes on the index and middle finger and amplified through the BIOPAC EDA100C amplifier. Data was sampled at a sampling frequency of 2k Hz and recorded using the AcqKnowledge v4.4 software. All EDA metrics originated from the time domain: (a) galvanic skin response (GSR), (b) tonic EDA, and (c) phasic EDA. Extraction of the phasic and tonic components of the EDA was conducted with deconvolution of the EDA signal with a biologically plausible impulse response function with initially fixed parameters that are iteratively optimized per participant[61].

Pattern recognition

To examine the physiological counterpart of the behavioral shifts in MB reports, we employed a supervised decoding approach. Using the multimodal neurophysiological measurements during the three experience sampling sessions, we trained multiple classifiers to discriminate across MB, MW, and SENS reports and identify whether MB is supported by a unique brain-body interaction pattern. This approach allowed us to extract meaningful brain-body interactions from the proposed arousal metrics without being conservative about the nature of the multiple comparisons between the various brain and body metrics.

As features, we opted to collect meaningful data in the time, frequency, information, and connectivity domain, unless such measurements could not be reliably estimated within our selected time window. The goal of the multiple selected metrics was to capture potential diverse spatiotemporal relationships (low-high frequency interactions, phase-amplitude interactions) that might extend across different recording modalities. Overall, we computed 57 features.

As targets, we used the participants' mental states (MB, MW, and SENS). Since this creates a multiclass classification problem, we focused on the binary classification of MB vs other reports. We expected to acquire 40 samples per participant and condition (i.e. baseline and arousal states), giving a total of 1040 (26*40) samples per condition. We expected that 5% of the samples to correspond to the target report (MB), yielding an imbalanced problem with only 52 target samples per condition.

As learning algorithms, we tested parametric and non-parametric models, such as Support Vector Machines (SVM), Random Forests (RF), and Extremely Randomized Trees (ET). SVM is a classification technique that aims to separate labeled inputs by creating a hyperplane that maximizes the distance of their features. Given a set of n-labeled inputs, SVM provides a hyperplane in an n-dimensional space that maximally separates the differently labeled groups. An RF classifier is a meta-estimator. Various classifiers ("decision trees") are trained in different parts of the input dataset, and each classifier uses only that part of the dataset to predict the label of the input. Then, the predictions of each classifier are pooled ("bagged") together, and an optimal decision is chosen based on the label with the most predictions ("votes"). Finally, an ET classifier is a meta-estimator that employs a similar voting scheme. However, in the case of the ET classifier, trees are trained on all the features and the cutoff point of the trees (how the various metric nodes are arranged to reach a decision) is randomized. Since our problem is highly imbalanced, we also tested outlier detection algorithms (i.e. one-class classifiers), aiming to isolate MB from the other reports by considering MB as either an inlier or outlier. Therefore, we tested the one-class counterparts of the SVM (One-class SVM) and RF (Isolation Forests) algorithms.

For model selection and performance estimation, we employed two different cross-validation approaches. First, we used a 5-fold stratified cross-validation scheme trained with all the samples. This provided us with performance estimates of classifiers aimed at obtaining patterns of brain and body function that can predict MB reports in known participants. As a second approach, we used a 5-fold group stratified cross-validation scheme, using participants as groups. In this scenario, each participant was either on the train or on the test set. Thus, it aimed at learning general patterns of brain and body function that could predict the report of MB in unseen participants. In other terms, the first approach aimed at learning patterns that could discriminate MB from other reports while accounting for each participant's variance, while the second strengthened the claim, aiming to learn general patterns that could be found in unseen participants.

As performance metrics, we report a) recall, b) precision, c) F1-score, d) area under the ROC curve (AUC), and e) balanced accuracy. Recall is the ratio of how often an item was classified correctly as a positive outcome (True Positive / True Positive + False Negative). Similarly, precision is the ability of the model to return only the data points in the relevant class (True Positive / True Positive + False Positive). F1-score is the harmonic mean of precision and recall. The AUC curve is another evaluation metric that summarizes how well the classifier predicts a class based on different thresholds of true positive and false positive ratios. Finally, balanced accuracy is an evaluation metric suitable for imbalanced datasets, where one class appears at significantly different frequencies than the others. Balanced accuracy is useful because it is estimated as the average of specificity and sensitivity, simultaneously controlling for very high precision due to classifying nothing as the infrequent class and very high recall due to classifying everything as the infrequent class.

We selected each model's hyperparameters using nested cross-validation (same scheme as the outer cross-validation), using the F1-score as our optimization metric.

To evaluate the variance in the classifier performance and compare it to chance level, we performed repeated cross-validation (10 times), while training also a "dummy" classifier to obtain the empirical chance level of the training samples distribution. This type of classifier generates predictions based on the distribution of training samples for each class without accounting for the features.

The decoding analysis was implemented in Python using Julearn[62] and Scikit-Learn[63]. Metrics were estimated from existing Python libraries: MNE[64], NICE[65] , Neurokit[66], and custom in-lab Python functions.

Results

Participants

To achieve a power of 0.95 at an alpha threshold of 0.05, we acquired 3 sessions of 40 trials per session from 26 participants (mean age= 26.38, sd= 4.53, min= 20, max= 40; female= 11). As a post-registration note, in case participants could not adhere to the strict 3-week protocol (30% total sessions), they were rescheduled to a later date that respected their sleep schedules to avoid time windows with potential extreme slow-wave activity[50]. Due to data corruption, one participant had 30 trials in one of the three sessions, and one participant had 33 trials in one of the three sessions. The remaining two sessions were completed for both participants.

Behavioral data

Occurrences of mental state reports alter across arousal conditions

We found a main effect for mental states, with MB being reported at significantly lower rates (Mean proportions±SD: MW=0.56±0.21, SENS=0.2±.14, MB= 0.12±0.13; Kruskal H= 124.07, *p*= 1.2e-27, eta^2= 0.53) compared to MW (Dunn's test= -10.75, p_{FDR} = 1.8e-26) and to SENS (Dunn's test= -2.85, p_{FDR}= 4.3e-03). Additionally, MW was reported significantly more frequently compared to SENS (Dunn's test= 7.9, p_{FDR}= 4.3e-15; Fig. 2). As the study was focused on wakeful mental states, "SLEEP" reports were not included in the analysis (Mean proportions ±SD: *Baseline*= 0.03±.05, *High Arousal*= 0.05±.07, *Low Arousal*= 0.26±.21, Total= 0.1±.17).

We found that a model including all conditions outperformed a null model with only an intercept ($Full_{LogLik}$= −1021, $Null_{LogLik}$= −1046.83, χ^2= 51.57, df= 2, p_{Bonf}= 6.1e-12): MB was reported significantly more frequently in *Low Arousal* compared to *Baseline* (Marginal Mean= −0.79, SE= 0.14, CL= [−1.16, −0.43], p_{FDR}= 1.8e-08) and to *High Arousal* (Marginal Mean= −0.97, SE= 0.15, CL= [−1.35, −0.59], p_{FDR}= 7.9e-11) (Fig. 3a). However, MB reports during *Baseline* and *High Arousal* were comparable (Marginal Mean= 0.17, SE= 0.15, CL= [−0.21, 0.56], p_{FDR}= 2.4e-01). A visual inspection of the individual marginal means showed that this effect was mostly consistent across participants and was not driven by extreme cases (Fig. 3b–d).

Additionally, generalized estimating equations (GEE) showed a significant interaction for MW between *Low Arousal—Baseline* (beta= 6, SE= 1.5, CL= [3.06, 8.94], p_{FDR}= 6.4e-05) and *Low—High Arousal* (beta= 8.23, SE=1.6, CL= [5.1, 11.36], p_{FDR}= 2.6e-07). We also found significant interactions in SENS reports, such that SENS tended to be higher in *Baseline* compared to *High* (*SENS Baseline—SENS High*: beta= 2.54, SE= 0.81, CL= [0.96, 4.12], p_{FDR}= 1.7e-3) and *Low Arousal* (*SENS Baseline—SENS Low*: beta= 2.46, SE= 0.77, CL= [0.96, 3.97], p_{FDR}= 1.3e-3). It is of note that this analysis yielded no significant results for MB, but the overall trend of the beta estimates was consistent with our positive results of the logit model above (Supplementary Fig. S3).

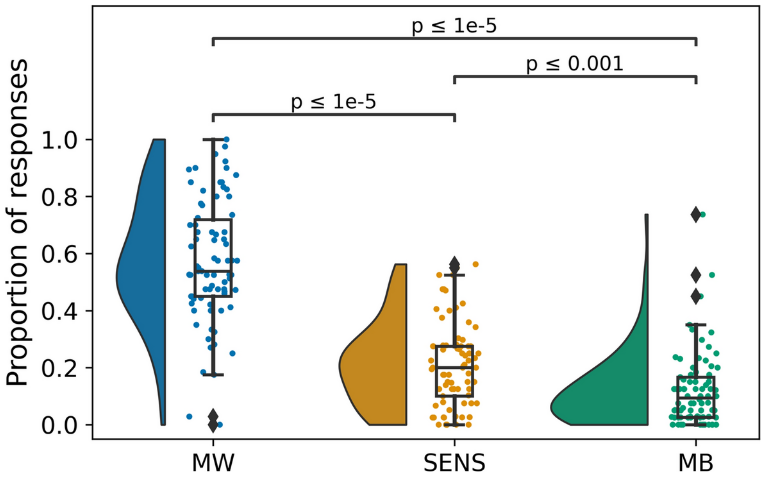

Fig. 2. Mind blanking (MB) was reported significantly less frequently compared to mind wandering (MW) and perceptual sensations (SENS) across all arousal conditions, validating what is generally reported in the literature. Density kernels show overall data dispersion and clustering trends. Point plots are individual subject estimates. Box plots show medians and interquartile ranges, while whiskers indicate extreme values and diamonds indicate outliers.

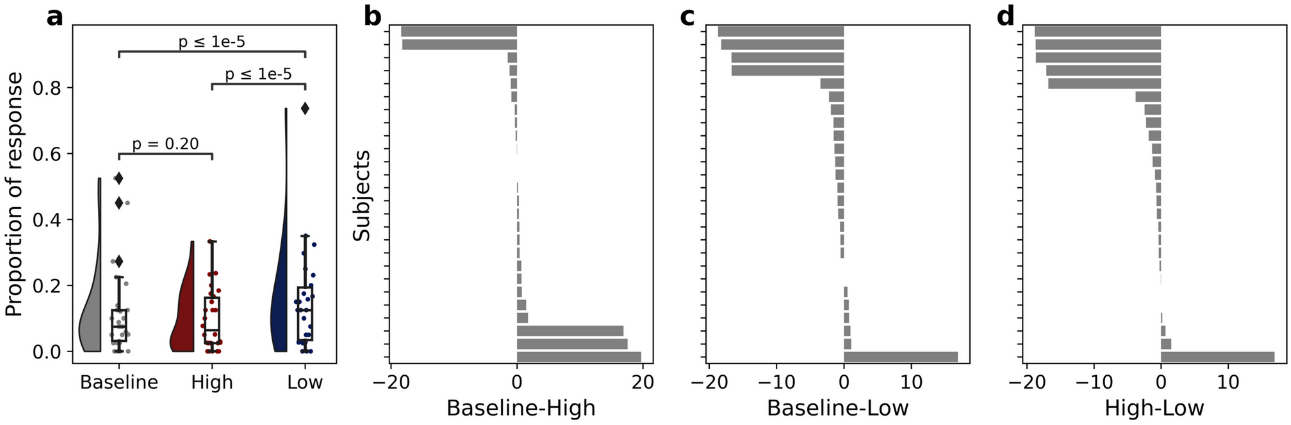

Fig. 3. The frequency of mind blanking (MB) reports altered across the three arousal conditions. (**a**) MB report probability increased in *Low Arousal* (after sleep deprivation) compared to *High Arousal* (after intense exercise) and *Baseline*. Density kernels indicate overall data dispersion and clustering trends. Point plots represent participants' MB report probabilities. Box plots indicate medians and interquartile ranges, whiskers indicate extreme values, and diamonds indicate data outliers. (**b**–**d**) Bar plots denote single-subject marginal means, comparing MB reports across arousal conditions. Compared to *Baseline*, there was no significant change during *High Arousal* (**b**). However, there was a visible trend favoring an increased probability of MB reports in the *Low Arousal* condition compared to baseline and *High Arousal*, signifying that the effect was present in most participants (**c**–**d**).

MB was characterized by higher reaction times

There was a main effect of arousal conditions, with reports during *Baseline* being reported the fastest and during *Low Arousal* the slowest (Fig. 4a). Also, there was a main effect of mental states, with MW reports being reported the fastest and MB reports the slowest (Fig. 4b). A significant interaction between MW and arousal showed that MW was reported the slowest in *Low Arousal* (Fig. 4c). A significant interaction between MB and arousal condition showed that MB was reported the slowest in *High Arousal* and *Low Arousal* (Fig. 4e). A model including both arousal and reaction times outperformed simplified models including only null or main effect terms ($\text{Full}_{\text{LogLik}}$= 2889.76, χ^2= 47.1, df= 4, p_{Bonf}= 1.5e-09; Fig. 4c). For a detailed overview of main effects and interactions, see Supplementary Table S3.

Transition probabilities showed reduced probability to transition to MW in Low arousal

Markov transition probabilities indicated significant differences only between *High* and *Low Arousal* conditions (Fig. 5), such that MW was more likely to be followed by MB (t= 3.26, CI= [0.03,.15], p_{FDR}= 9.7e-03, Cohen's D= 0.74). Also in *Low Arousal*, both MW (t= −3.79, CI= [−0.31, −0.9], p_{FDR}= 7.6e-03, Cohen's D= −0.86) and SENS

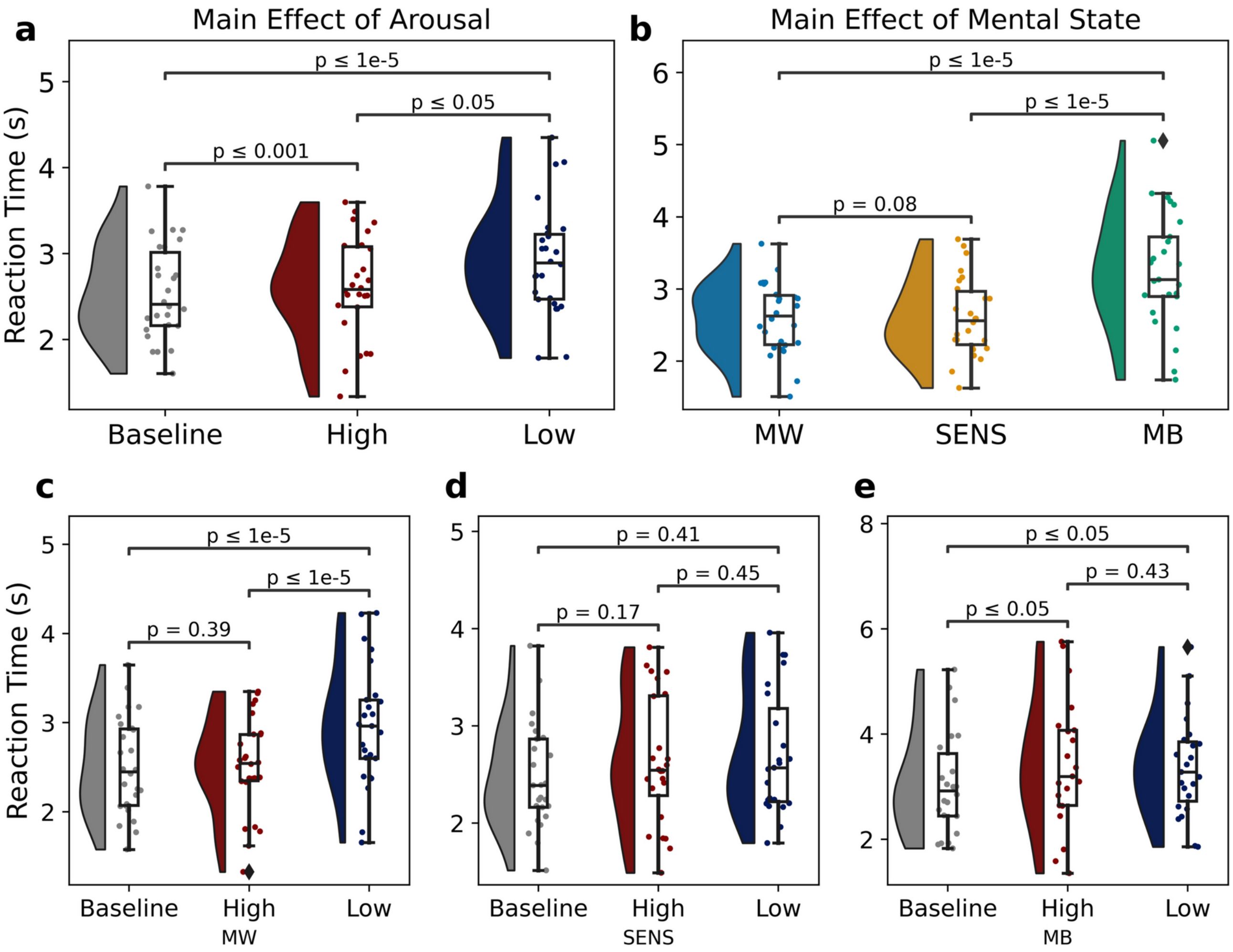

Fig. 4. Mental states had different reaction times depending on arousal conditions. (**a**) Reaction times at *Baseline* arousal were reported the fastestlowest, followed by *High* (after exercise) and *Low Arousal* (after sleep deprivation), collapsed across all arousal levels. Point plots show individual subject estimates. Box plots show medians and interquartile ranges, while whiskers show extreme values. (**b**) Mind wandering (MW) was reported the fastest, followed by Sensations (SENS) and mind blanking (MB), collapsed across all mental states. Point plots show individual subject estimates. Boxplots show medians and interquartile ranges, while whiskers show extreme values. (**c**–**e**) Interaction between arousal condition and mental state reaction times: MW was reported the slowest in *Low Arousal* compared to *Baseline* and *High Arousal*, while MB was reported the slowest in the *Low Arousal* and *High Arousal* conditions compared to *Baseline*.

(t= −3.43, CI= [0.37, −.0 09], p_{FDR}= 9.5e-03, Cohen's D= −0.77) were less likely to be followed by MW (Fig. 5; Supplementary Fig. S4).

Exploratory analysis 1: MB frequency did not correlate with SLEEP frequency

As we wanted to avoid participants confounding MB and SLEEP reports, we opted for a paradigm that allowed participants to report both. Spearman correlations on each condition examined whether these two states were correlated. We did not find any significant correlation between MB and SLEEP report probabilities across any arousal condition. (*Baseline*: r= 0.13, *p*= 5.3e-01, *High Arousal*: r= 0.31, *p*= 1.3e-01, *Low Arousal*: r= −0.05, *p*= 8.2e-01) (Supplementary Fig. S5). To strengthen the claim that MB and SLEEP reports do not covary, we additionally ran separate equivalence tests on each correlation. No test was able to reject an equivalence claim (*Baseline*: z= −0.34, *p*= 3.7e-01, *High Arousal*: z= 0.54, *p*= 7e-01, *Low Arousal*: z= 0.72, *p* = 2.3e-01). Therefore, these results remain indeterminate.

Exploratory analysis 2: High arousal: MB reports increased at the start, but not the end, of the experience sampling session

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While we found that MB reports were more frequently in *Low Arousal*, we did not find any significant effect of *High Arousal*. In our original hypothesis (Supplementary Table S1), we registered a potential alternative explanation for the absence of an effect of high arousal in mental state report frequency. High arousal, as elicited

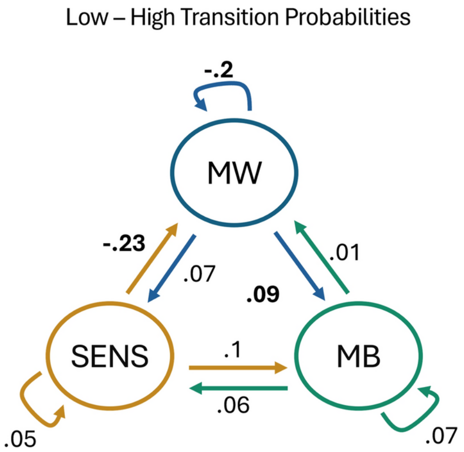

Fig. 5. After sleep deprivation (*Low Arousal)*, participants were more likely to transition from mind wandering (MW) to mind blanking (MB) compared to the condition of physical exercise (*High Arousal)*. Additionally, participants were less likely to transition to MW, either when departing from reports about sensory perception (SENS) or from MW itself. Arrows indicate the direction of the mental state transition. Bold font indicates statistical significance (FDR corrected).

by high-intensity exercise, might not last for the full session, and our session would represent a gradual return to *Baseline Arousal*. To test for potential effects of more frequent MB reports only at the start of the experience sampling we split the *High Arousal* session in two parts and compared the count of MB reports across the start and the end of the experiment. Using a chi-squared test we found a significant effect, with MB reports being more frequent (divergence= 4.08, *p*= 3.2e-02) during the first half of the *High Arousal* condition compared to the second half (MB_{start}= 93, MB_{end}= 66). We additionally attempted to validate this hypothesis by splitting the session into 4 and 6 discrete segments of 10 and 7 trials each and replicated the same analysis. However, this analysis did not reach significance. Finally, to provide further evidence for reduced occurrences of MB across time, we considered only the first and last 10 trials. We found a significant effect of more frequent MB occurrences (divergence= 7.39, *p*= 6.6e-03), with the first 10 trials of the *High Arousal* condition inducing more MB compared to the second half (MB_{start}= 51, MB_{end}= 27).

Classification of MB reports was outperformed by classification containing both BRAIN-BODY markers

We trained a cohort of different classification algorithms and evaluated their capacity to classify MB reports from mental states with content (MW, SENS) based on 26 BRAIN (EEG) and 31 BODY features (12 ECG, 4 EDA, 8 RSP, 7 EYE), spanning time, frequency, information, and connectivity domains for each mental state report. In our original report, we registered that these features would be estimated across the 110 s pre-probe window, with bad epochs being dropped. However, across an 110 s epoch, even a nonlinearity of 1 s would result in epoch removal, leaving a total clean sample of 25 / 78 sessions (29.4%), and a total of 1060/3120 (33.3%) clean epochs. Therefore, to preserve datapoints and data quality and minimize data discarding due to brief non-linearities, we opted for an extra step in bad epoch removal. After the initial epoch definition of 110 s, we followed it up by partitioning that epoch into 5 s sub-epochs, resulting in 22 sub-epochs per epoch. We then proceeded to do bad epoch removal and EEG marker estimation on those sub-epochs. If an epoch consisted of more than 50% bad sub-epochs, it was discarded. Then, we averaged across within each epoch, resulting in no lost sessions, and a total of 2734 / 3120 (87.6%) total sample size.

Having a final 2734 reports x 57 features matrix per report, we trained multiple classifiers on the total dataset, to examine whether a specific brain-body profile would outperform chance level classification of MB reports (Table 1).

Due to the unbalanced nature of our dataset, we evaluated classifier performance based on balanced accuracy, as it avoids inflated performance estimates on unbalanced datasets. Overall, we found that a balanced random forest (a random forest that undersamples the majority class in each bootstrap to equate class count) had above-chance performance and outperformed all other examined classifiers (Fig. 6a). We additionally examined whether we could predict unknown subjects, by leaving a subset of subjects out on each iteration. Due to the high degree of per-fold variance, we do not consider any classifier as meaningfully performing above chance level (Fig. 6b). Importantly, these results were replicated when we trained the classifiers in the 1 Hz filtered data (Supplementary Fig. S6a,b; Supplementary Table S4).

Having established that MB reports can be predicted from known subjects, we then examined whether a brain-body data pattern would outperform classifiers trained solely on either BRAIN or BODY features. To this end, we fit and optimized a separate balanced random forest classifier on discrete feature combinations of our dataset. For a full report of the performance on different features, see Table 2 and Supplementary Table S5.

Overall, we found that a classifier trained on both BRAIN and BODY markers numerically outperformed classifiers trained solely on BRAIN or BODY features across all our performance metrics (Fig. 7a,c; Supplementary Fig. S7a,c; Table 2; Supplementary Table S5). To evaluate the impact of the number of features on the capacity of

Examined	Classifier	Recall	Precision	F1	ROC AUC	Balanced accuracy
Known subjects	Balanced RF	0.62, [0.6, 0.64]	0.26, [0.26, 0.27]	0.37, [0.36, 0.37]	0.71, [0.7, 0.72]	0.66, [0.65, 0.67]
	SVM	0.29, [0.28, 0.31]	0.28, [0.27, 0.29]	0.29, [0.27, 0.3]	0.62, [0.61, 0.63]	0.58, [0.58, 0.59]
	ET	0.16, [0.15, 0.17]	0.61, [0.58, 0.64]	0.25, [0.23, 0.26]	0.73, [0.72, 0.74]	0.57, [0.56, 0.58]
	RF	0.14, [0.13, 0.15]	0.57, [0.53, 0.6]	0.22, [0.21, 0.23]	0.71, [0.7, 0.72]	0.56, [0.56, 0.56]
	IF	0.14, [0.13, 0.16]	0.2, [0.19, 0.22]	0.17, [0.15, 0.18]	0.52, [0.52, 0.53]	0.52, [0.52, 0.53]
	OC SVM	0.89, [0.86, 0.92]	0.15, [0.14, 0.15]	0.25, [0.25, 0.25]	0.51, [0.5, 0.51]	0.51, [0.5, 0.51]
	DUMMY	0.14, [0.13, 0.15]	0.14, [0.13, 0.15]	0.14, [0.13, 0.15]	0.5, [0.49, 0.5]	0.5, [0.49, 0.5]
Unknown Subjects	Balanced RF	0.46, [0.41, 0.51]	0.18, [0.16, 0.2]	0.25, [0.23, 0.27]	0.55, [0.53, 0.57]	0.54, [0.53, 0.56]
	IF	0.23, [0.19, 0.27]	0.18, [0.16, 0.2]	0.19, [0.17, 0.22]	0.53, [0.51, 0.54]	0.53, [0.51, 0.54]
	RF	0.05, [0.04, 0.06]	0.36, [0.29, 0.44]	0.08, [0.06, 0.09]	0.54, [0.52, 0.55]	0.51, [0.51, 0.52]
	OC SVM	0.87, [0.82, 0.92]	0.14, [0.13, 0.15]	0.24, [0.22, 0.26]	0.51, [0.5, 0.52]	0.51, [0.5, 0.52]
	ET	0.03, [0.02, 0.03]	0.36, [0.26, 0.45]	0.05, [0.04, 0.06]	0.53, [0.52, 0.55]	0.51, [0.5, 0.51]
	DUMMY	0.15, [0.14, 0.16]	0.15, [0.13, 0.17]	0.14, [0.13, 0.16]	0.5, [0.49, 0.51]	0.5, [0.5, 0.51]
	SVM	0.2, [0.17, 0.22]	0.16, [0.14, 0.17]	0.16, [0.15, 0.17]	0.49, [0.47, 0.5]	0.5, [0.49, 0.51]

Table 1. A balanced random forest classifier outperformed all classifiers when compared across balanced accuracy. Cells indicate mean and 95% CI. RF = Random Forest; SVM = Support Vector Machine; ET = Extreme Trees; IF = Isolation Forest; OC SVM = One-Class Support Vector Machine

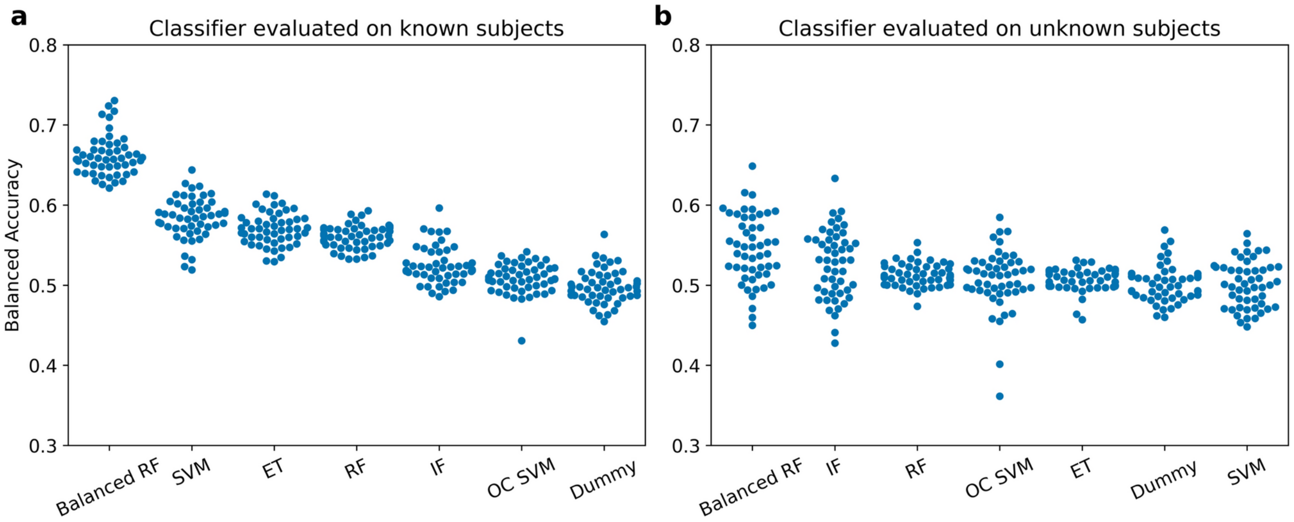

Fig. 6. Classification performance was above chance level when mind blanking (MB) reports were pooled across subjects, but not after training on a subset of participants and classifying the remaining subset. (**a**) A balanced random forest classifier provided the highest classification performance across all examined classifiers including known subjects. (**b**) A balanced random forest classifier provided the highest classification performance across all examined classifiers on unknown samples. However, due to the high variance, we could not consider it meaningful. Individual points indicate performance on the folds of the repeated cross-validation. Results are ordered based on descending order of performance. Chance-level performance is indicated by the Dummy classifier. RF = random forest; SVM = support vector machine; ET = extreme trees; IF = isolation forest; OC SVM = one-class support vector machine.

the learning algorithm to extract relevant information, we also trained the balanced random forest model using randomly shuffled bodily features. EEG features were not altered. The model with the shuffled values showed a decline in classification performance, providing evidence that, when classifying mental states, a model trained on both brain and body data learns unique information from both domains (Fig. 7d; Supplementary Fig. 7d). For feature importance, we calculated Shapley Additive Explanations (SHAP) values for each feature in our dataset. SHAP values estimate the marginal contribution of each feature, averaged across every potential feature combination. In this manner, each value represents how much this feature contributes to the classification, after controlling for the impact of other features on this feature's importance. We found that the model relied mostly on EEG and EYE openness features to discriminate MB reports when pooling MB occurrences across all three conditions. (Fig. 7b; For an extensive list of all SHAP values, see Supplementary Fig. S8). Importantly, feature importance did not substantially change when filtering the data with a 1 Hz filter (Supplementary Fig. S7b; For an extensive list of all SHAP values, see Supplementary Fig. S9). Overall, the comparable performance of the

Classifier	Recall	Precision	F1	ROC AUC	Balanced Accuracy
BRAIN + BODY	0.62, [0.6, 0.64]	0.26, [0.26, 0.27]	0.37, [0.36, 0.37]	0.71, [0.7, 0.72]	0.66, [0.65, 0.67]
BRAIN	0.61, [0.59, 0.62]	0.24, [0.24, 0.25]	0.35, [0.34, 0.36]	0.7, [0.69, 0.71]	0.65, [0.64, 0.65]
BODY	0.59, [0.58, 0.6]	0.22, [0.21, 0.22]	0.32, [0.31, 0.32]	0.66, [0.66, 0.67]	0.61, [0.61, 0.62]
EYE	0.57, [0.55, 0.59]	0.21, [0.21, 0.22]	0.31, [0.3, 0.32]	0.64, [0.63, 0.65]	0.61, [0.6, 0.62]
ECG	0.55, [0.54, 0.57]	0.18, [0.17, 0.18]	0.27, [0.26, 0.27]	0.58, [0.57, 0.59]	0.56, [0.55, 0.57]
EDA	0.6, [0.57, 0.63]	0.17, [0.17, 0.17]	0.26, [0.26, 0.27]	0.57, [0.56, 0.58]	0.55, [0.54, 0.56]
RSP	0.52, [0.5, 0.54]	0.15, [0.15, 0.16]	0.24, [0.23, 0.24]	0.53, [0.52, 0.54]	0.52, [0.51, 0.53]

Table 2. A classifier trained on a combination of BRAIN and BODY features outperformed classifiers trained solely on BRAIN or BODY features, when evaluated with balanced accuracy. Cells indicate mean and 95% CI.

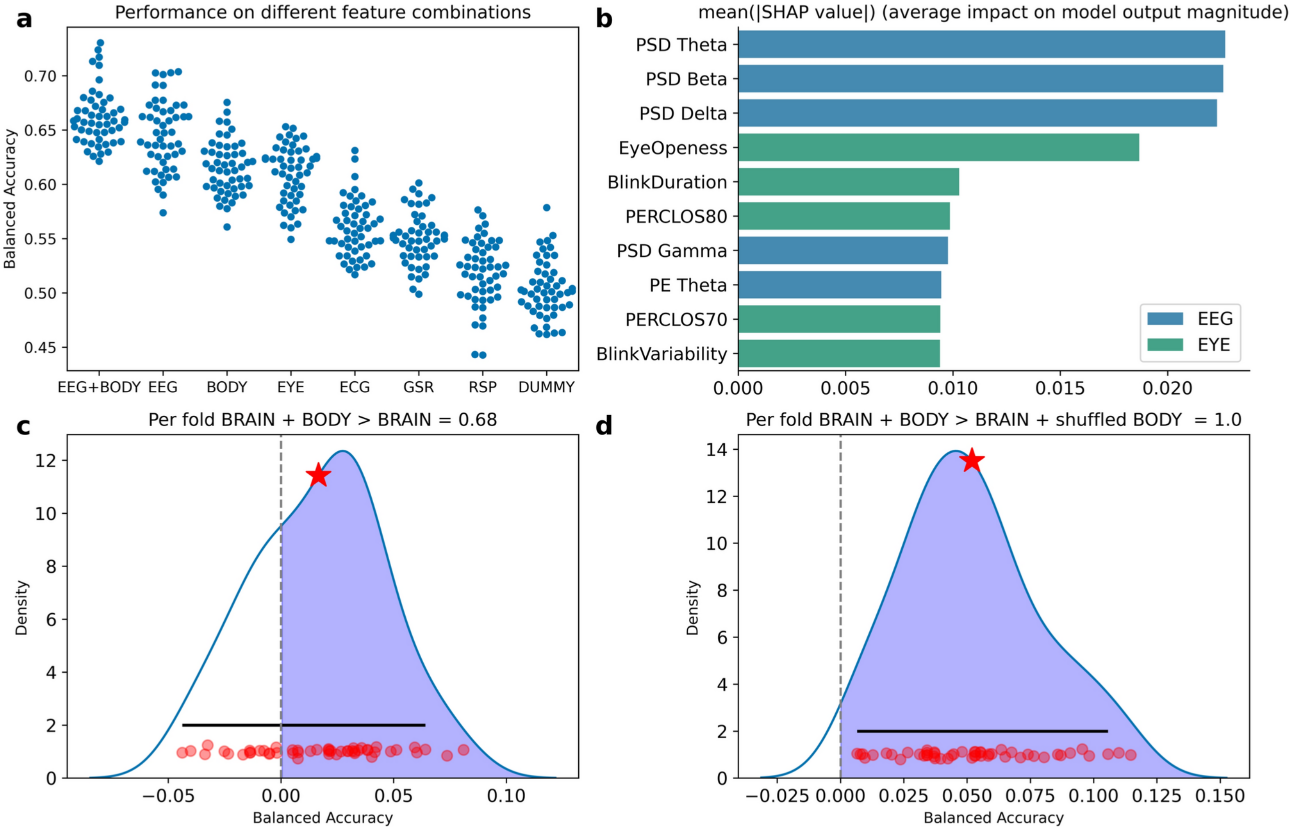

Fig. 7. Classification of MB improves when considering both BRAIN and BODY. (**a**) Balanced random forest classifier trained on a combination of BRAIN and BODY features outperformed classifiers trained solely on BRAIN or BODY features when evaluated with balanced accuracy. Individual points indicate performance on the folds of the repeated cross-validation. (**b**) Subset of the 10 features with the highest mean of the absolute SHAP values obtained from the balanced random forest classifier. (**c**) The per-fold differences between the classifier trained on both BRAIN and BODY features and the one trained only on BRAIN data suggest that incorporating both feature domains provides a slight performance improvement over using BRAIN data alone. The shaded region indicates better performance for the classifier trained on both feature domains. The star indicates the mean difference. The solid, horizontal line represents the 95% highest-density intervals of the distribution. Red dots indicate per-fold differences. (**d**) The per-fold differences between the classifier trained on both BRAIN and BODY features and the one trained on BRAIN and shuffled BODY data suggest that the model with both BRAIN and BODY data does not consider the body markers as noise.

models, and the high degree of overlap in the ranking of the feature importance point to the robustness of the models.

Exploratory analysis 3: Feature importance altered across arousal conditions.

The decoding analysis in known samples showed that we can predict MB instances from the combination of brain-body markers with adequate accuracy when MB instances were aggregated across different arousal conditions.

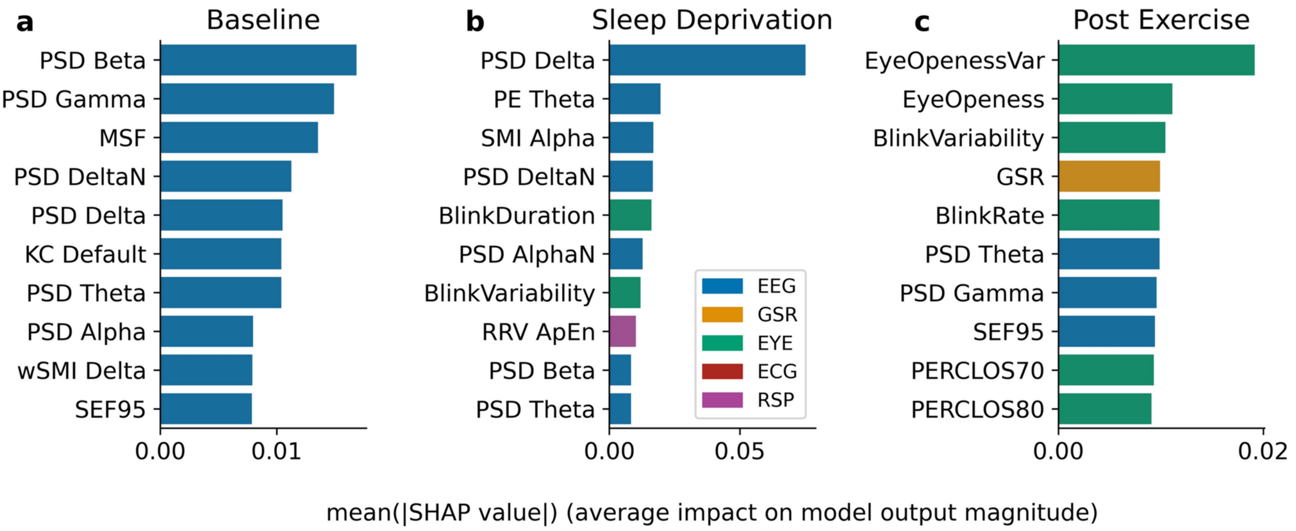

Fig. 8. Ranking of features by mean absolute SHAP value extracted from the balanced random forest classifier varied across different arousal conditions. (**a**) Magnitude of SHAP values for a balanced random forest classifier trained on MB reports collected during the *Baseline Arousal condition*. The model relied mostly on features from the EEG frequency domain. (**b**) Magnitude for SHAP values for a classifier trained on MB reports collected during the *Low Arousal* condition (after sleep deprivation). The model mostly used spectral power in the EEG delta band. (**c**) Magnitude for SHAP values for a classifier trained on MB reports collected during the *High Arousal condition* (after intense exercise). The model relied mostly on features from eye openness, EDA, and the EEG frequency domain

We were further interested in whether this classification was achieved based on a universal mechanism, or whether we could detect arousal-dependent brain-body configurations that predict MB. To this end, we trained a balanced random forest classifier solely on data acquired from *Baseline*, from *High,* and from *Low Arousal*. We found that *Baseline* had the best performance (0.67, [0.65, 0.68]), followed by *Low Arousal* (0.64, [0.63, 0.65]), and finally *High Arousal* (0.61, [0.6, 0.63]). We retained comparable performance when examining the arousal partitions of the 1 Hz filtered dataset (Supplementary Table S6-7). Examining the SHAP values for each arousal state, we saw that the models relied on distinct feature domains. During *Baseline*, the model relied on markers from the frequency domain of EEG (Fig. 8a). During *Low Arousal*, MB classification was obtained using the delta band power, by far the most dominant marker (Fig. 8b). Finally, in *High Arousal*, the model did not rely on a single feature, rather in a combination of eye openness, GSR, and the frequency domain of EEG (Fig. 8c). Similar feature importances were observed in the 1 Hz filtered dataset (Supplementary Fig. S10). However, in the 1 Hz filtered dataset, we observed that ECG features tended to rank higher (Supplementary Fig. S11–16).

Exploratory analysis 4: Feature importance altered based on the pre-probe analysis window

A potential caveat of utilizing the full pre-probe period of 110 s before a report is that we might capture multiple mental states, and the actual statistical regularities might be weakened when averaged across. With this consideration, we examined whether we could improve classification performance when classifying MB from the last 10 s before a report. We defined a secondary brain-body data matrix, with BODY features that could be estimated from 10 s of body activity. Across both 0.1 and 1 Hz filters we retained comparable performance in the classifiers trained on both EEG and bodily markers, as well as solely EEG or BODY markers (Supplementary Fig. S17–20; Supplementary Table S8 and 9). However, we observed decreased performance in the classifier trained solely in the eye openness data (Supplementary Table S8 and 9). An examination of feature importance showed that the beta, delta, and theta bands of the EEG frequency domains remained the most important EEG features, but there was a reduction in the importance of the EYE features and an increase in the importance of EDA (Supplementary Fig. S17b, 18, 19b, 20). Importantly, our results were not affected by the choice of filtering parameters, indicating robustness of our results to preprocessing parameters.

Discussion

We used experience sampling combined with EEG and peripheral physiological recordings under different autonomic arousal conditions to determine whether MB reports in neurotypical individuals were supported by distinct brain-body configurations compared to mental states with reportable content. Overall, our results show that MB is a mental state that becomes more prevalent in low and partially in high arousal states, and that MB is driven by both brain and body processes, providing evidence for an embodied account of MB.

Behaviorally, we found that MB was reported at significantly lower rates compared to sensory experiences or MW, irrespective of the arousal condition. This finding is in line with past research showing that MB rates vary between 5 and 10% of total probe instances, across both uninterrupted thinking[12] and task engagement[11]. We also show that sleep deprivation significantly increased the frequency of MB occurrences. Sleep deprivation has been shown to induce a low arousal state during which cognitive performance declines[67], metabolic and physiological processes change[68], and unique neuronal markers, such as slow-wave activity, emerge[69]. After sleep deprivation, participants also tend to perform worse in sustained attention tasks[70], with results suggesting a true effect of sleep deprivation on more “misses” (no response when necessary) compared to “false alarms” (response when unnecessary)[71], a finding that was recently shown as a behavioral correlate of MB[11]. Additionally, sleep deprivation and mounting sleep pressure have been positively correlated with more MW instances[72,73], suggesting an overall mode shift from task engagement to MW[74]. Our results challenge these past findings by showing that participants were more likely to experience an MB event rather than MW after sleep deprivation. We also found that MW was in fact more likely to decrease after sleep deprivation. This is further supported by the results of the transition analysis, where MW reports were less likely to be followed by another MW report, and more likely to be followed by MB. Such discrepancies in the reportability of MW after sleep deprivation could be possibly explained by the explicit inclusion of MB as a reportable mental state in the experience sampling that our design opted for. In other words, it might be that the observed MW occurrence increases after sleep deprivation can be accounted for by MB reports, once participants have the chance to opt between these two mental states in a more fine-grained way.

In terms of high arousal induced by high-intensity exercise, our analysis did not reveal any significant effects on MB occurrences. As per the provided registered protocol alternative explanation (Supplementary Table 1), we hypothesized that this arousal manipulation might not have been overall effective as it could not have produced effects that would last across the whole experience sampling session. To test whether MB frequency reports would differ between the beginning and at the end of the session, we split the dataset into two parts. When split, we indeed found a significant difference between the frequency of MB reports. This result was replicated when considering only the first and last 10 trials per subject, which maximized the distance between initial and final physiological arousal within the session. However, we were not able to find any differences when the data were split into smaller bins. Together, we consider that these results provide partial evidence for our registered hypothesis, showing that residual high arousal effects after intense exercise can increase the frequency of MB reports.

In addition to the frequency of mental states across arousal conditions, we also examined whether rreaction times differ across arousal conditions and mental states. In general, reports in low arousal tended to be the slowest, consistent with a wide range of attention tasks that show slower reaction times in sleep deprivation compared to baseline arousal[75]. We consider these findings as additional evidence that the arousal manipulation was effective in that it lowered overall vigilance levels of the . We also observed a main effect of mental states, such that MB tended to be reported significantly slower compared to MW and sensations. Contrary to our current results, we recently found that MB was reported faster when compared to other mental states when content had to be evaluated[12]. This apparent mismatch in results can be explained when considering that MB can be a state devoid of content, and therefore, there is the binary consideration of “yes/no” when evaluating thought content, which might be a relatively fast decision. This can be different, for example, from the evaluation of content-full mental states, which demand a sequential evaluation of both content presence (“yes/no”) and content evaluation (“what is the content about?”). This way, the difference in results can be explained by the imposition of an additional cognitive evaluation. Overall, we suggest that these results might reflect a gradient of vigilance, with participants being the most alert at baseline arousal, and progressively declining during high and low arousal conditions, as well as more vigilant when reporting mental states with content compared to MB. Of note, we observed two interesting interactions between mental states and arousal conditions. MW tended to be reported slower in low arousal compared to baseline and high, which is consistent with our interpretation of reaction times as marking vigilant states. However, as we also observed that MB reports tended to be reported slower in both high and low arousal conditions, we speculate that this might be preliminary evidence that arousal modulates how engaged participants are with their current mental states. In this sense, exercise fatigue can lead to an MB state that takes longer to recover from when probed for a report.

A final explanatory analysis revolved around the relationship between sleep and MB. We recently posited that MB is a distinct mental state characterized by a unique phenomenological profile of no content[76], and unique neuronal markers, characterized by high cortical integration and low cortical segregation[12]. This neuronal configuration is atypical of wakefulness[77], and is more closely reminiscent of brain configurations during deep sleep[78]. In conjunction with the presence of slow wave intrusions during wakefulness as a marker of MB reports[11], a classic marker of NREM sleep, an emerging issue is whether MB is a misrepresented instance of sleep. This issue is further complicated by the postulation that in MB there is no content[76], and thus does not functionally represent a wakeful state where people can report content. To avoid this pitfall, we introduced sleep as a potential report during experience sampling. We found that people discretely reported MB and sleep, providing evidence that when provided with such options, people can differentiate between these two experiences. Additionally, we did not find that MB and sleep tended to covary. To strengthen this claim, we ran equivalence tests for each correlation across arousal conditions. However, no test showed a positive result for equivalence. Therefore, these results remain indeterminate, with a trend for no relationship between MB and sleep.

Having established that MB occurrence varied across different physiological arousal conditions, we then examined whether MB could be decoded by brain and body markers. With the aim of showing single trial prediction, we trained different models on EEG and physiological markers, spanning time, spectral, complexity, and connectivity domains. Overall, we were able to achieve above-chance-level classification, showing that there exist unique brain-body patterns that can discriminate MB reports from mental states with content. However, we were not able to show above-chance-level classification when training classifiers on unknown subjects. Therefore, our results are not generalizable to novel populations due to the high amount of variance between subjects. Of importance is the result that a combination of EEG and physiological markers marginally, but consistently, outperformed both EEG and physiological markers. Overall, we observed an improvement of 2–5

% in classification performance in balanced accuracy. This improvement can be attributed to unique information inherent in body signals, as evidenced by the comparison of the classifier trained on both brain and body data compared to classifiers trained solely on brain data or brain and shuffled body data. The classifier trained on both brain and body data does not consider body features as noise or redundant. Overall, while our results suggest a high degree of overlap between brain and body information in MB, they indicate that information about MB extracted from the body is partially independent of the EEG features. Feature importance ranking derived from the classification model indicates that the low and mid frequencies of the EEG power spectrum and metrics of eye openness are useful predictors of MB. This finding was consistent across analysis windows and preprocessing parameters. Importantly, all classifiers trained on body markers had above chance performance with variant degrees of variability, with the highest performing being the EYE (eye openness) and the ECG (heart-rate variability), providing evidence that MB can be decoded solely from bodily signals.

To further validate our protocol, we ran two exploratory analyses, with the aim to examine whether classification performance varies based on the analyzed pre-probe window and whether feature importance alters across arousal conditions (For a full Discussion, see the Supplementary Discussion on Methodology). Overall, when examining a classifier trained on a brief 10 s window before MB reports, we found similar performance compared to the full 110 s classifier. What was interesting was that, while EEG performance remained the same, performance on classifiers trained solely on body features decreased. As brain-physiology coupling occurs at varying time delays across cardiac[79] and respiratory domains[80], we interpret these results as evidence that bodily contributions on MB are based on slow, oscillatory processes that might not be captured from examining short pre-probe periods. At the same time, our classification analysis on separate arousal conditions showed distinct brain-body configurations that can predict MB reports. As our decoding approach did not permit any inference of the directionality effect, or decomposing interactions within and across physiology modalities, at this stage we claim that our results point to discrete physiological pathways that elicit MB reports. Overall, we show that our enhanced classification is retained across different analysis windows and different arousal conditions.

Similarly, enhanced classification when considering a brain-heart matrix compared to solely brain markers was also shown for patients with disorders of consciousness, where the inclusion of cardiac features outperformed classification based solely on EEG markers[81]. To our knowledge, our results are the first to extend multivariate decoding past the brain-heart axis and consider the inclusion of multiple unique bodily afferent sources in classifying mental states. The overall success of the brain-body decoding paradigm in classifying consciousness levels and mental states provides evidence that bodily information is not redundant and is not necessarily fully represented within brain dynamics. Instead, an embodied approach, stressing bidirectional information routes between brain and body can provide better predictive power and assist in more comprehensive, generative models of experience[34,82].

A neurobiological explanation of our results comes from an integrative model of content, task engagement, and arousal which suggests that the relationship between thought and arousal can be conceptualized as an inverted u-curve. This means that an optimal arousal level modeled by the locus coerulius-norepinephrine (LC-NE) release is necessary to actively engage and control our thoughts, either during task engagement or MW[83]. This stance treats thought as an active task, where engagement is necessary for clear content and control of thought dynamics. As arousal tapers off to non-optimal levels of the inverted U-curve, we experience concurrent, opposing thoughts that serve exploratory purposes for optimal performance, such as exploring different strategies. This necessitates flexibility and malleability of content. We here suggest that our results supplement this model by providing an account of the extremities of the optimal U-curve. As the model suggests degradation of thought clarity when we move closer to arousal extremities, we consider MB reports as instances where no content can be clear or present, extending this unifying framework to the entire arousal U-curve. Neurophysiologically, this model has translated to investigations of pupil dilation as a function of mental state and task engagement with pupil size yielding both positive[26,84] and null results[11] in discriminating on-task vs off-task mental states, as well as contrasting MB and MW. Part of the ascending arousal network, the LC modulates cardiac, galvanic, respiratory, and pupillary activity[28,85]. In addition, the LC innervates projections responsible for eyelid openness[86]. The combinatorial high performance of different body markers in classifying MB reports, and the evidence that altered levels of arousal increase MB occurrences provide further support for the modulatory role of the ascending arousal system in mental states and thought reportability.

From a theoretic perspective, our study challenges the conception that brain information is uniquely suitable to understand thought reportability and provides support for an embodied account of the mind. Embodiment moves the seat of mental events away from the brain and reformulates cognition as resulting from brain-body interactions. An extensive literature has shown how cataloged cardiac, respiratory, gut, and pupillary effects on perception[30], action[87], metacognition[31] and consciousness[81], while the collective interplay of peripheral systems has discriminatory power for clinical[88] and consciousness classification[89]. We show here that within embodiment, the body is not only facilitatory, but also might impede access to our mental lives. Under specific brain-body configurations, we are not able to clearly formulate mental content.

Some limitations pertain to our study. First, the nature of experience sampling discretizes the continuous nature of ongoing thinking. As there is no consensus on how long a mental state might last, or whether all mental states last the same length, results might average across different mental states. While we attempted to circumvent this problem by analyzing different pre-probe windows, it remains unclear whether all mental states last the same, and what is their actual duration. Secondly, the post-exercise setup might be suboptimal in examining the effects of high arousal on ongoing cognition. Neuronal and electrophysiological recordings have shown that the duration of the effects of exercise on ongoing brain and physiological activity[45–47] is highly variant. In addition, it is unclear whether brain and body recover to baseline states at the same rates, potentially confounding the post-exercise importance of cortical and physiological markers in cognition. Experience sampling with online probes during exercise could overcome this challenge.

In conclusion, our study suggests that MB is an arousal-modulated mental state, with a unique cortical and physiological profile. We think that our results pave a new paradigm for an embodied account of mental states, where the phenomenology of our mental lives is expressed based on both our body and our brain state. At the same time, our results challenge the neurocentric approach to mental state research, putting emphasis on the constant brain-body interactions that shape our cognition. As MB research continues to evolve, we consider our findings elaborative for clinical and experimental accounts of spontaneous thinking, where we move towards a complex and dynamic conception of our mind.

Data availability

The aggregated raw data in a BIDS format, the trained machine-learning models, experimental and analysis logs, and result dataframes can be found at https://doi.org/https://doi.org/10.58119/ULG/174Q6G.

Code availability

All codes to replicate the power analysis, the experience sampling paradigm, and the present analysis can be found at https://gitlab.uliege.be/Paradeisios.Boulakis/mind_blanking_arousal. An archived version of the code at the time of submission can be found at https://doi.org/https://doi.org/10.58119/ULG/174Q6G.

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Author contributions

Paradeisios Alexandros Boulakis: conceptualization; data curation; formal analysis; investigation; methodology; project administration; software; visualization; writing—original draft preparation. Nicholas John Simos: investigation; software; validation; writing—review and editing. Zoi Stefania: investigation; project administration; writing—review and editing. Sepehr Mortaheb: formal analysis; software; writing—review and editing. Christina Schmidt: methodology; writing—review and editing. Federico Raimondo: formal analysis; methodology; software; validation; supervision; writing—review and editing. Athena Demertzi: conceptualization; methodology; supervision; writing—original draft preparation.

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Declarations

Competing interests

The authors declare no competing interests.

Ethical approval

The experimental procedure has been approved by the CHU Liège local ethics committee and conforms with the Declaration of Helsinki and the European General Data Protection Regulation (GDPR). Before the onset of the protocol, participants provided informed consent for their participation in the study. Participants also received monetary compensation for their participation in the study.

Protocol registration

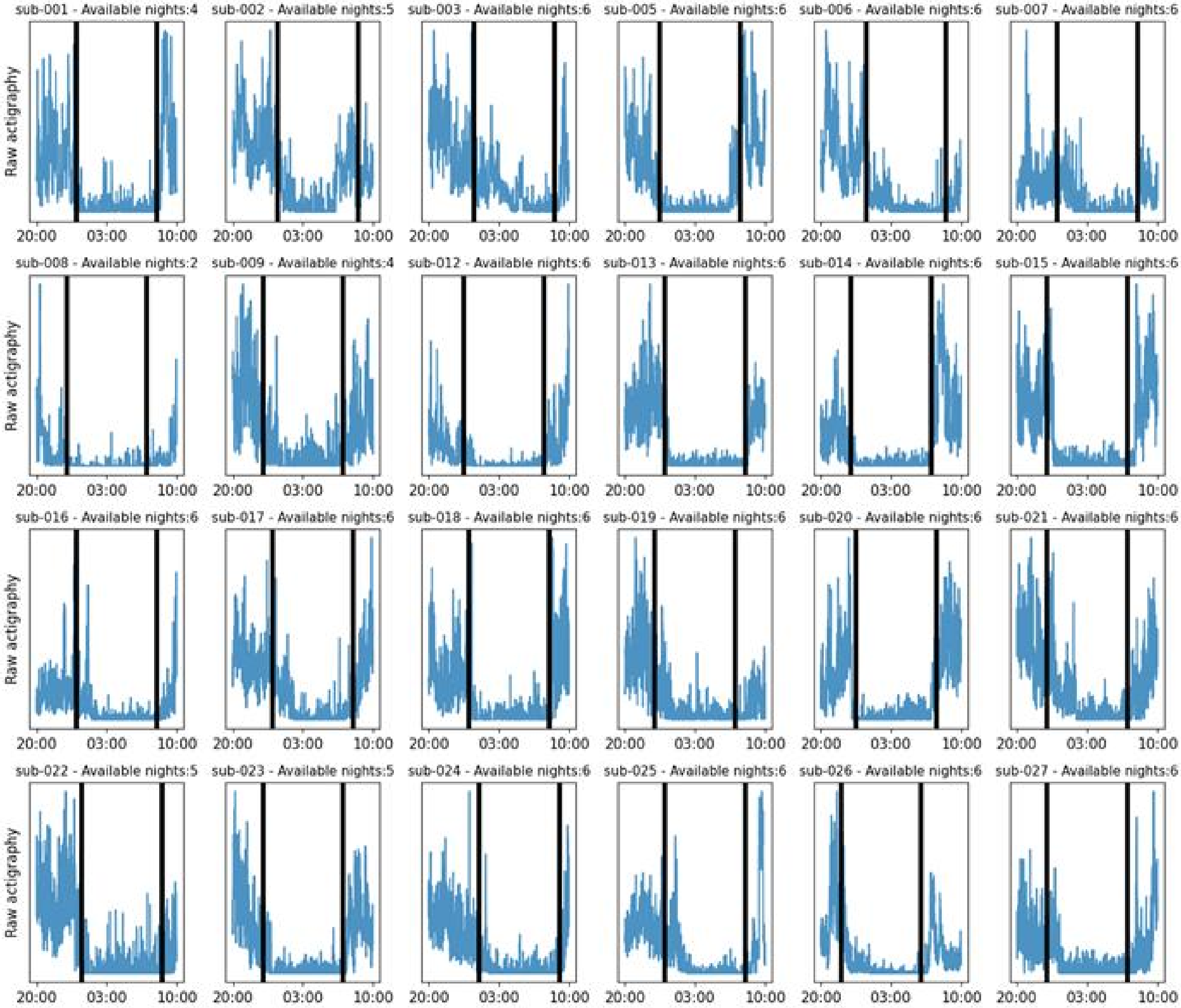
The stage 1 accepted-in-principle protocol can be found at https://osf.io/sh2ye. The authors confirm that no data for the pre-registered study was collected prior to the date of AIP.

Additional information

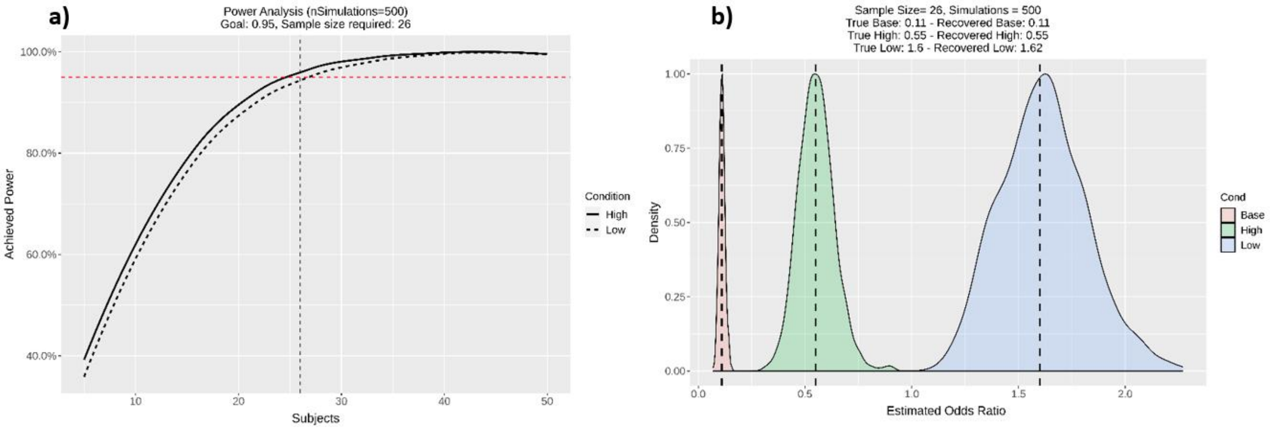
Supplementary Information The online version contains supplementary material available at https://doi.org/10.1038/s41598-024-81618-1.

Correspondence and requests for materials should be addressed to A.D.

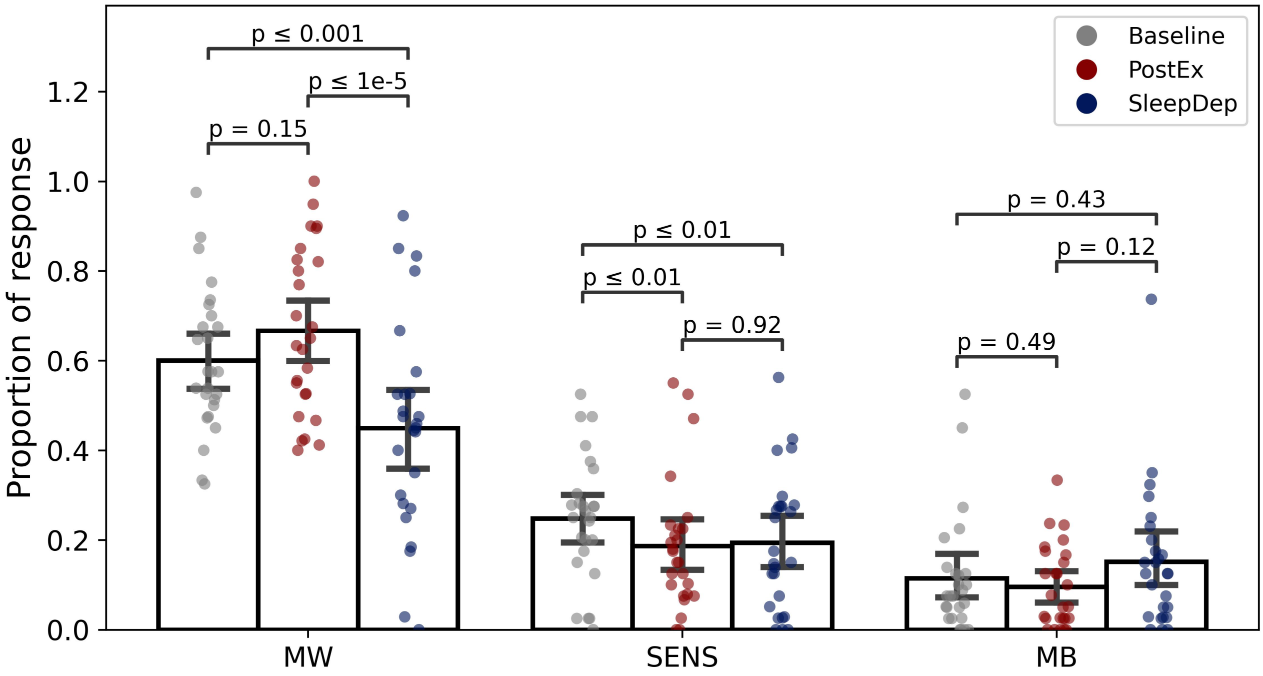
6.2 Supplementary Information - Chapter 3



Supplementary Fig. 6.2-1: Raw actigraphy plots (available for 24/26 subjects). We observed reduced actigraphy activity in the allocated sleep windows, indicating that participants maintained a steady sleep schedule in the week preceding sleep deprivation. Vertical black lines indicate sleep onset and sleep end.

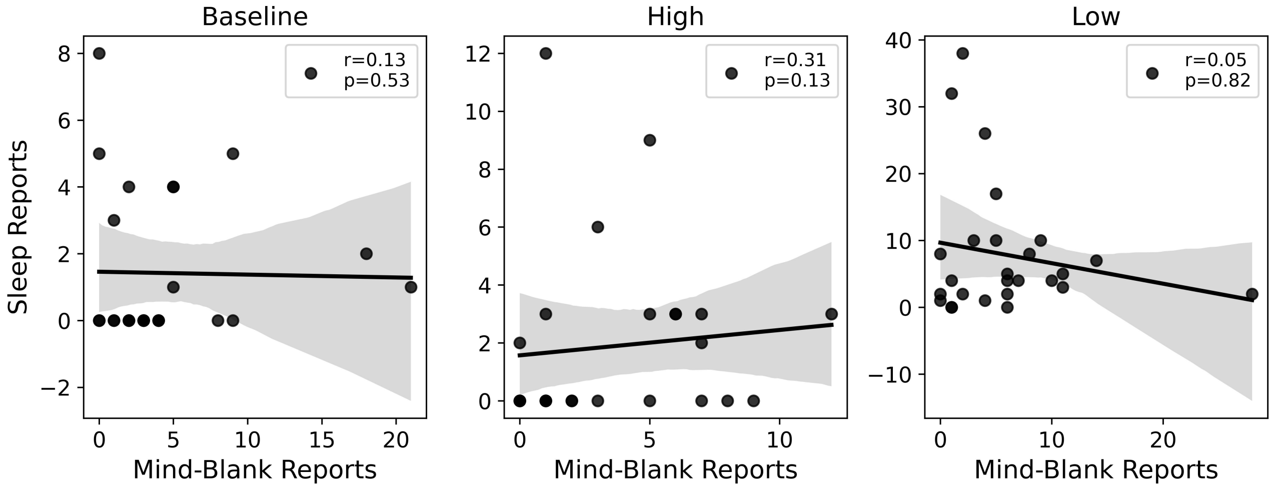


Supplementary Fig. 6.2-2: Simulation analysis for sample size calculation. a) We ran 500 simulations for sample sizes ranging from 5 to 50 participants to estimate the optimal sample size to achieve 95% power. Using a base odds ratio of 0.11 to report mind-blanking (MB) during free thinking, an odds ratio of 1.6 when arousal decreases (Low Arousal, dotted line), and 0.55 when arousal increases (High Arousal, solid line), we estimated that a sample of 26 participants is sufficient to achieve significant power in both arousal conditions. b) To validate whether our model can recover the true parameters, we ran an additional 500 simulations using a sample size of 26 participants. Our results show that our model can indeed estimate the true parameters. Notes: dashed line = true parameters.

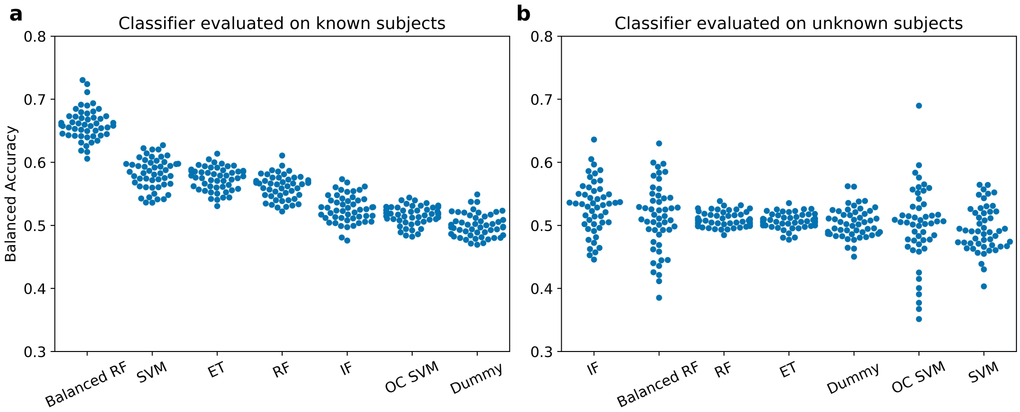


Supplementary Fig. 6.2-3: GEE showed significant differences in mental state occurrences across arousal conditions. We found that while mind-wandering (MW) and sensations (SENS) reports decreased in Low Arousal compared to Baseline and High Arousal, there was no significant effect of Low Arousal on mind-blanking (MB) reports. Coloured points indicate aggregate mean responses per subject. Error bars indicate 95% confidence intervals.

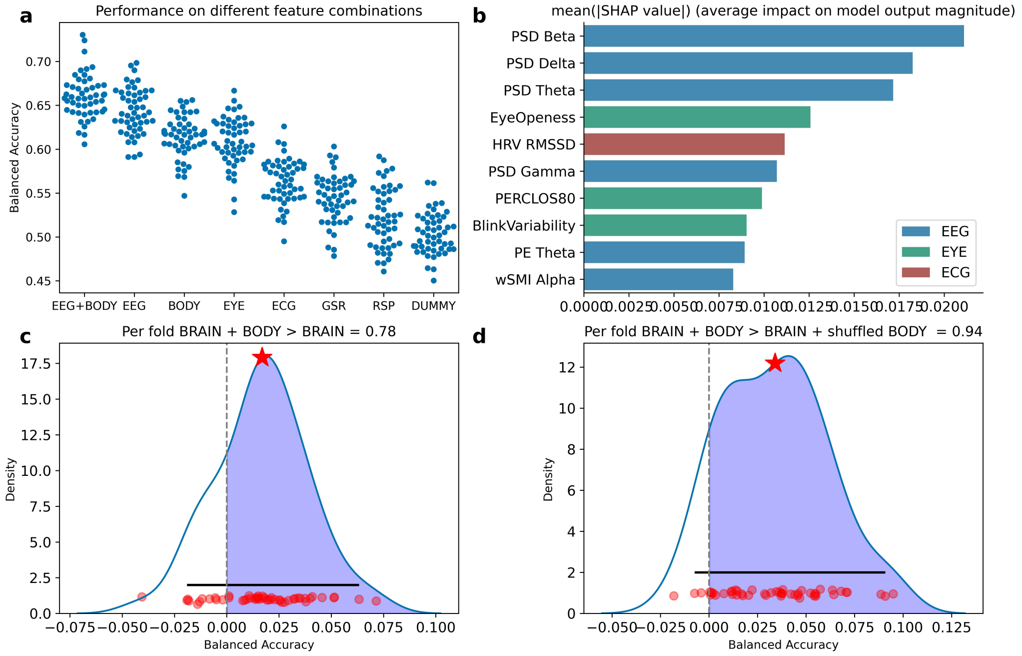
Supplementary Fig. 6.2-4: Arousal conditions modulate mental state transition probabilities. Upper row: Mental state transitions varied across different arousal conditions. Average (green) transition probabilities across Baseline, High (after intense exercise) and Low Arousal (after sleep deprivation). Colour bars and hue intensity indicate probability between 0-1. Lower row: Compared to High Arousal, participants were more likely to transition to MB and less likely to transition to MW in Low Arousal. Transition matrix difference across mental state reports. Numbers in bold indicate statistical significance (FDR corrected). The y-axis represents the origin (from), and the x-axis represents the direction (to).



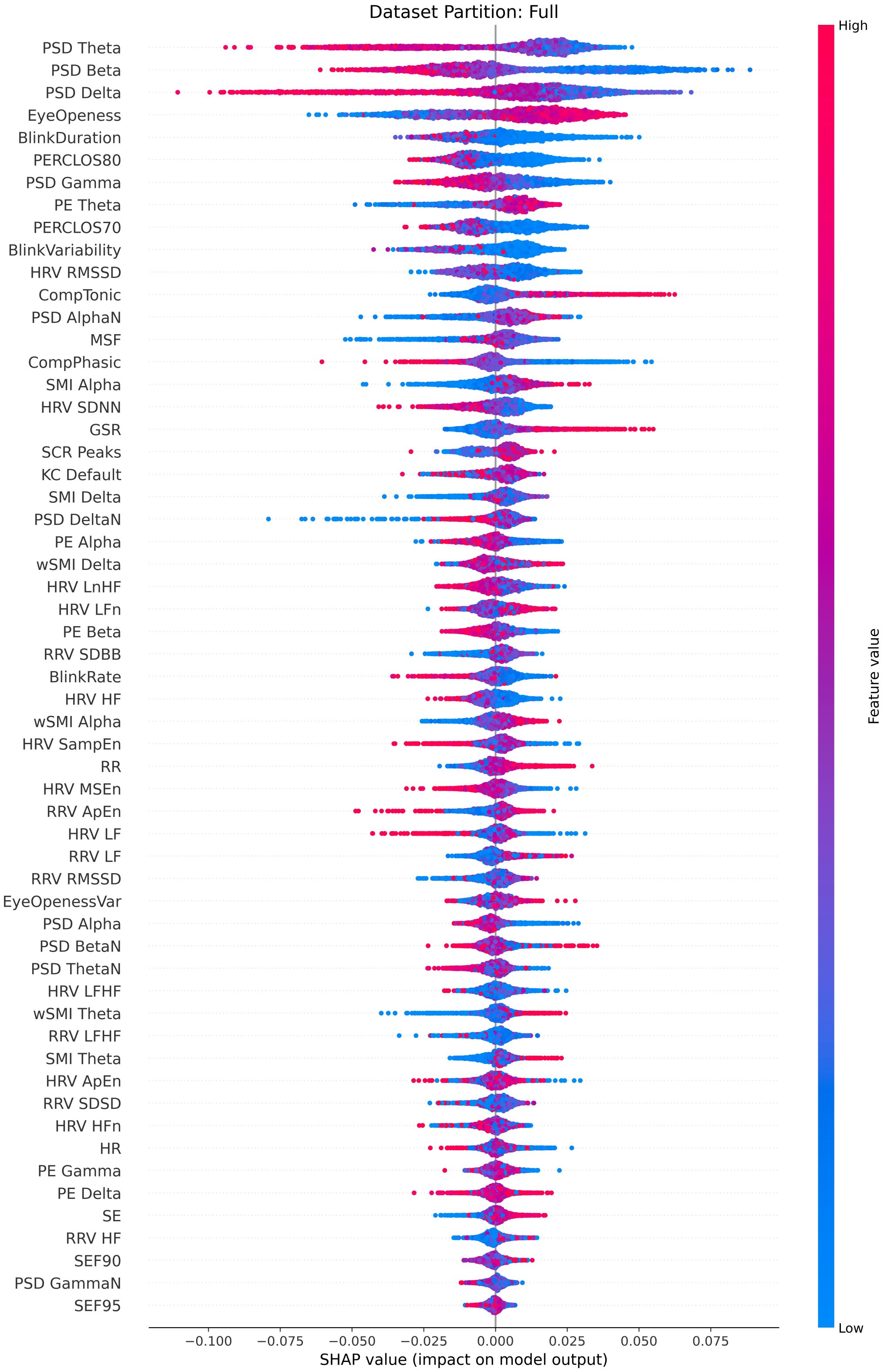
Supplementary Fig. 6.2-5: MB reports did not correlate with Sleep reports across any arousal state. Lines indicate the best fit. Shaded areas represent 95% confidence intervals.



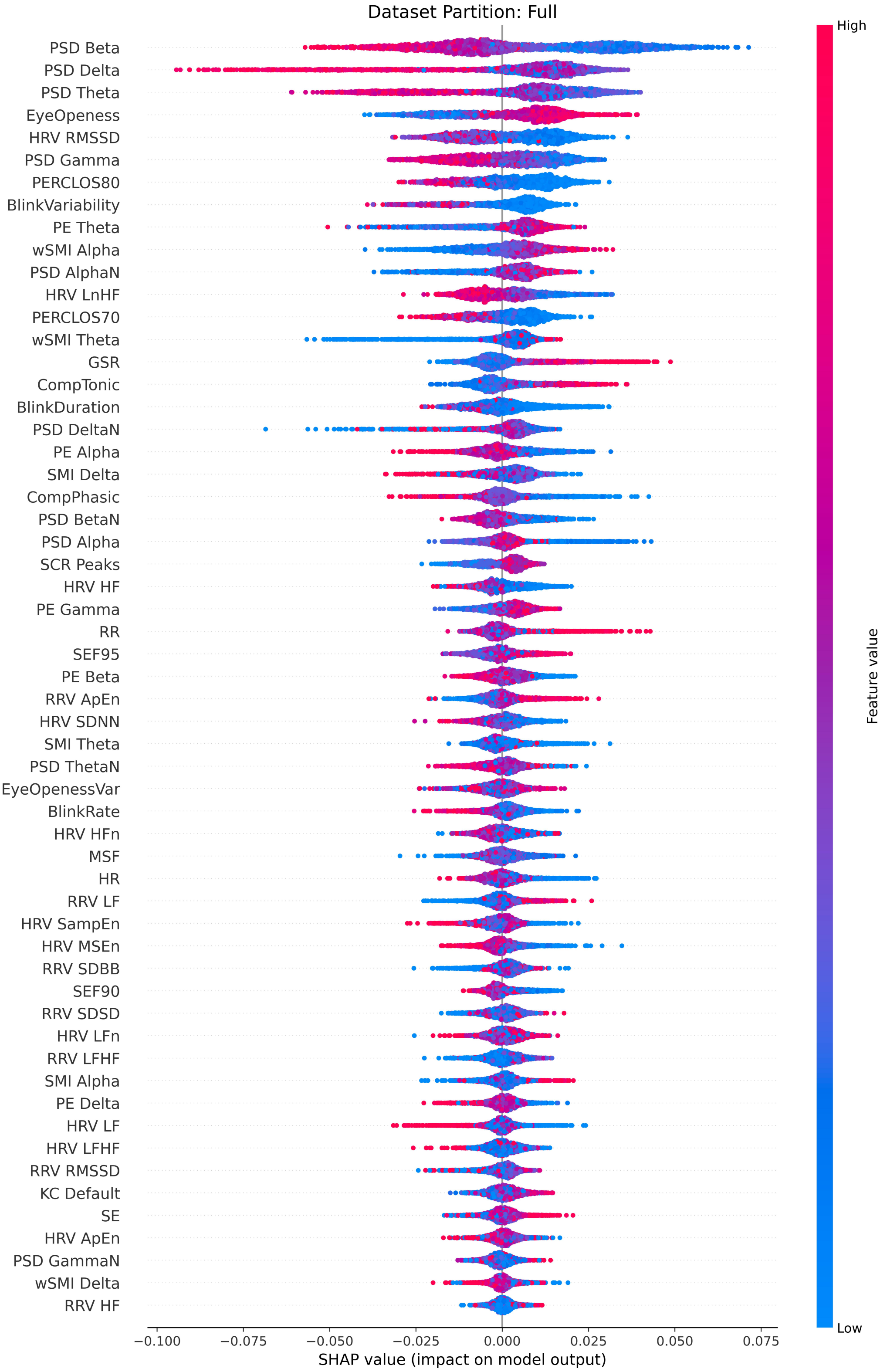
Supplementary Fig. 6.2-6: Classification performance was above chance level when mind-blanking (MB) reports were pooled across subjects, but not after training on a subset of participants and classifying the remaining subset, when training the classifiers on the 1Hz filtered dataset. a) A balanced random forest classifier provided the highest classification performance across all examined classifiers including known subjects. b) An isolation forest classifier provided the highest classification performance across all examined classifiers on unknown samples. However, due to the high variance, we could not consider it meaningful. Individual points indicate performance on the folds of the repeated cross-validation. Results are ordered based on descending order of performance. Chance level performance is indicated by the Dummy classifier. RF = random forest; SVM = support vector machine; ET = extreme trees; IF = isolation forest; OC SVM = one-class support vector machine.



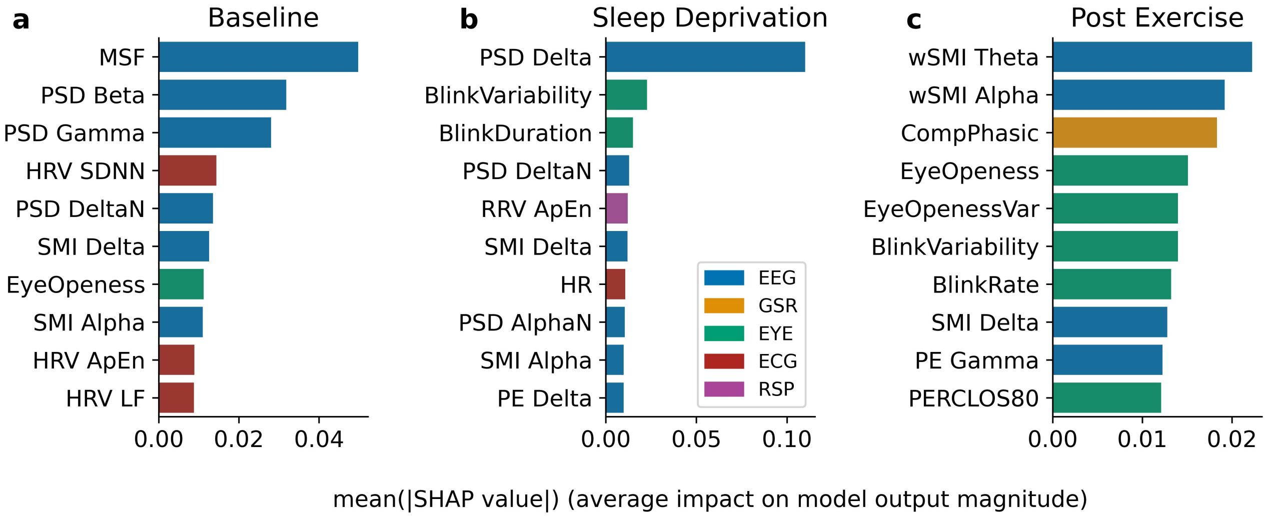
Supplementary Fig. 6.2-7: Combining information from both BRAIN and BODY markers leads to optimal classification performance. a) A balanced random forest classifier trained on the 1Hz filtered dataset on a combination of BRAIN and BODY features outperformed classifiers trained solely on BRAIN or BODY features when evaluated with balanced accuracy. Individual points indicate performance on the folds of the repeated cross-validation. b) Subset of the 10 features with the highest mean of the absolute SHAP values obtained from the balanced random forest classifier. c) The per-fold differences between the classifier trained on both BRAIN and BODY features and the one trained only on BRAIN data suggest that incorporating both feature domains provides a slight performance improvement over using BRAIN data alone. The shaded region indicates better performance for the classifier trained on both feature domains. The star indicates the mean difference. The solid, horizontal line represents the 95% highest-density intervals of the distribution. Red dots indicate per-fold differences. d) The per-fold differences between the classifier trained on both BRAIN and BODY features and the one trained on BRAIN and shuffled BODY data suggest that the model with both BRAIN and BODY data does not consider the body markers as noise.



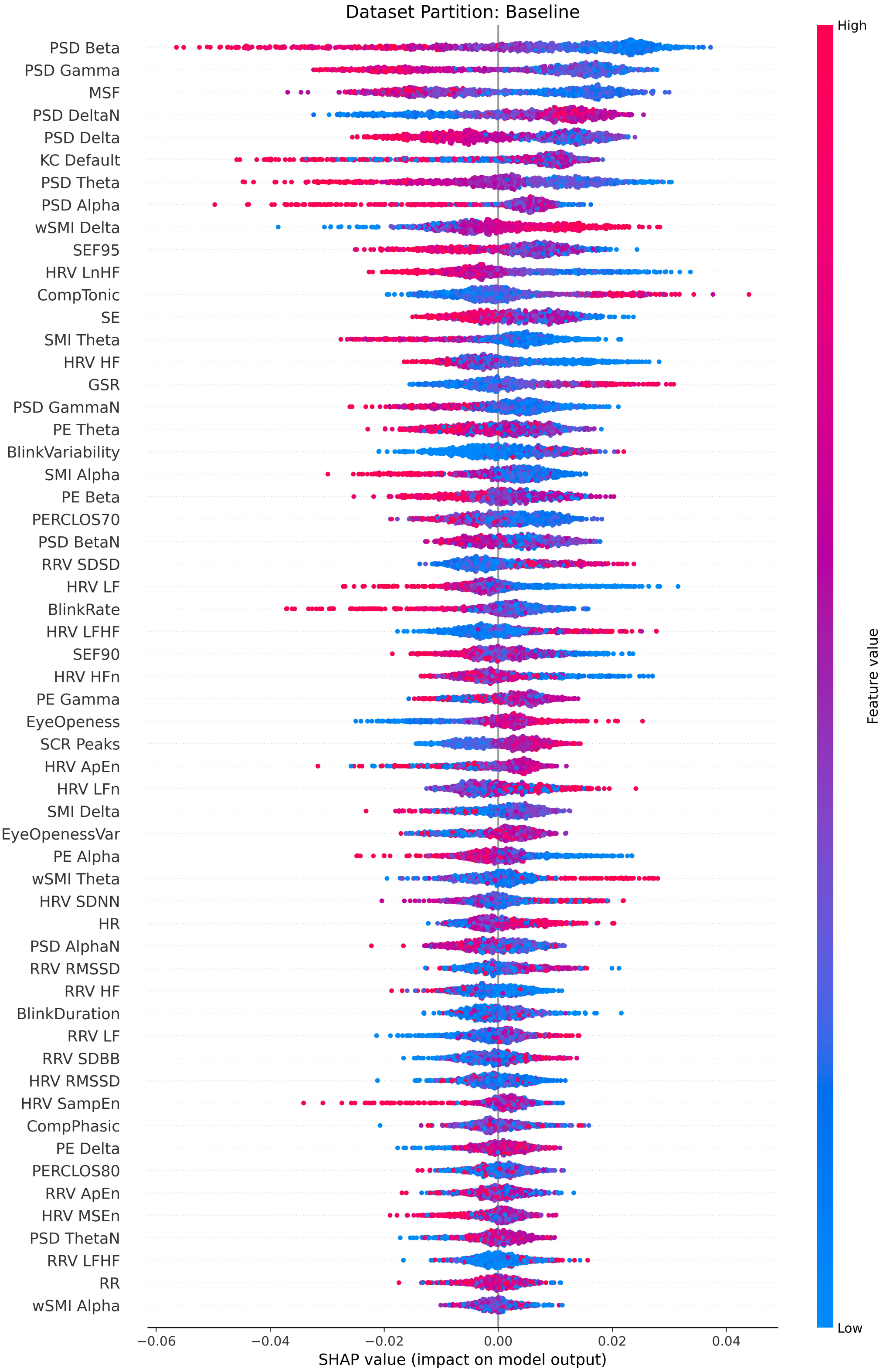
Supplementary Fig. 6.2-8: SHAP values ranking of the .1 Hz filtered dataset. The SHAP value represents the impact of each feature on the model's prediction. Positive SHAP values push the prediction towards MB, while negative SHAP values push away from MB. Effectively, a high feature value with a high SHAP value indicates that when the feature increases, so does the probability of the model classifying a mental report as MB. Inversely, a high feature value with a low SHAP value indicates that when the feature increases, the probability of the model classifying a mental report as MB decreases.



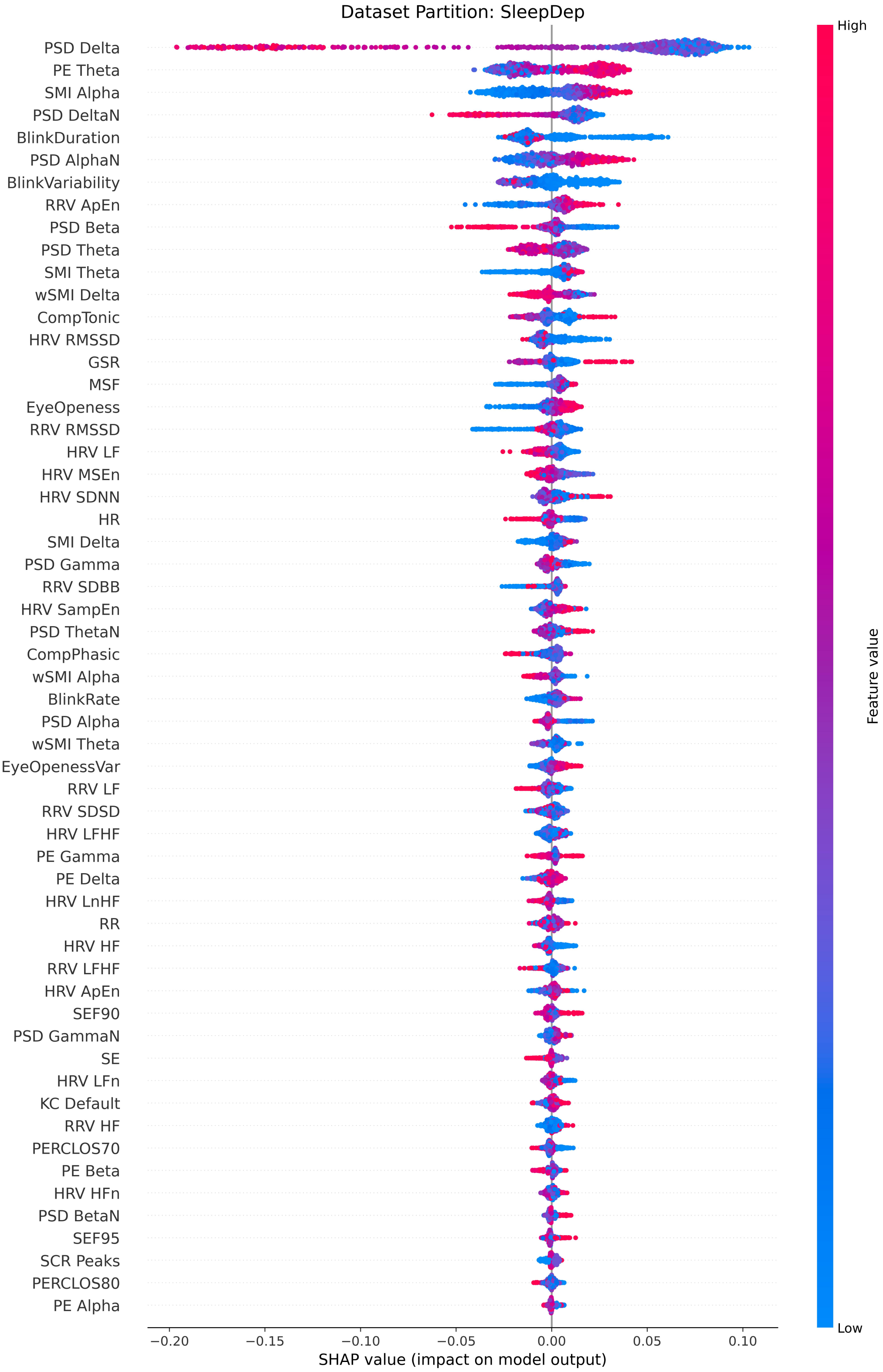
Supplementary Fig. 6.2-9: SHAP values ranking of the 1 Hz filtered dataset. The SHAP value represents the impact of each feature on the model's prediction. Positive SHAP values push the prediction towards MB, while negative SHAP values push away from MB. Effectively, a high feature value with a high SHAP value indicates that when the feature increases, so does the probability of the model classifying a mental report as MB. Inversely, a high feature value with a low SHAP value indicates that when the feature increases, the probability of the model classifying a mental report as MB decreases.



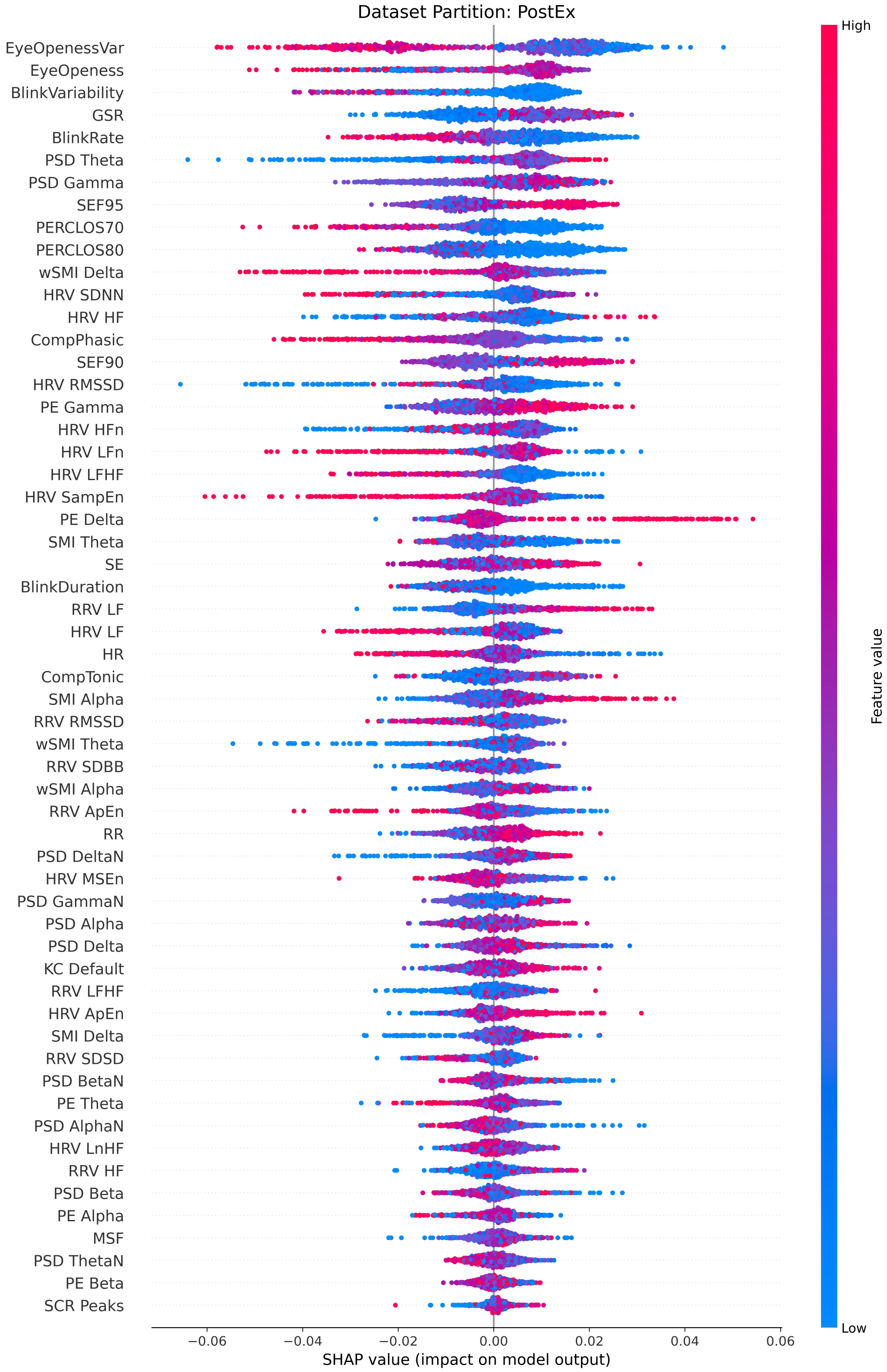
Supplementary Fig. 6.2-10: Ranking of features by mean absolute SHAP value extracted from the balanced random forest classifier varied across different arousal conditions. a) Magnitude of SHAP values for a balanced random forest classifier trained on Baseline Arousal MB reports. The model relies mostly on features from the spectral domain of the EEG, the frequency domain of ECG, and eye openness. b) Magnitude for SHAP values for a classifier trained on Low Arousal MB reports. The model mostly uses spectral power in the delta band. c) Magnitude for SHAP values for a classifier trained on High Arousal MB reports. The model relies mostly on features from the connectivity in EEG, as well as EDA and eye openness.



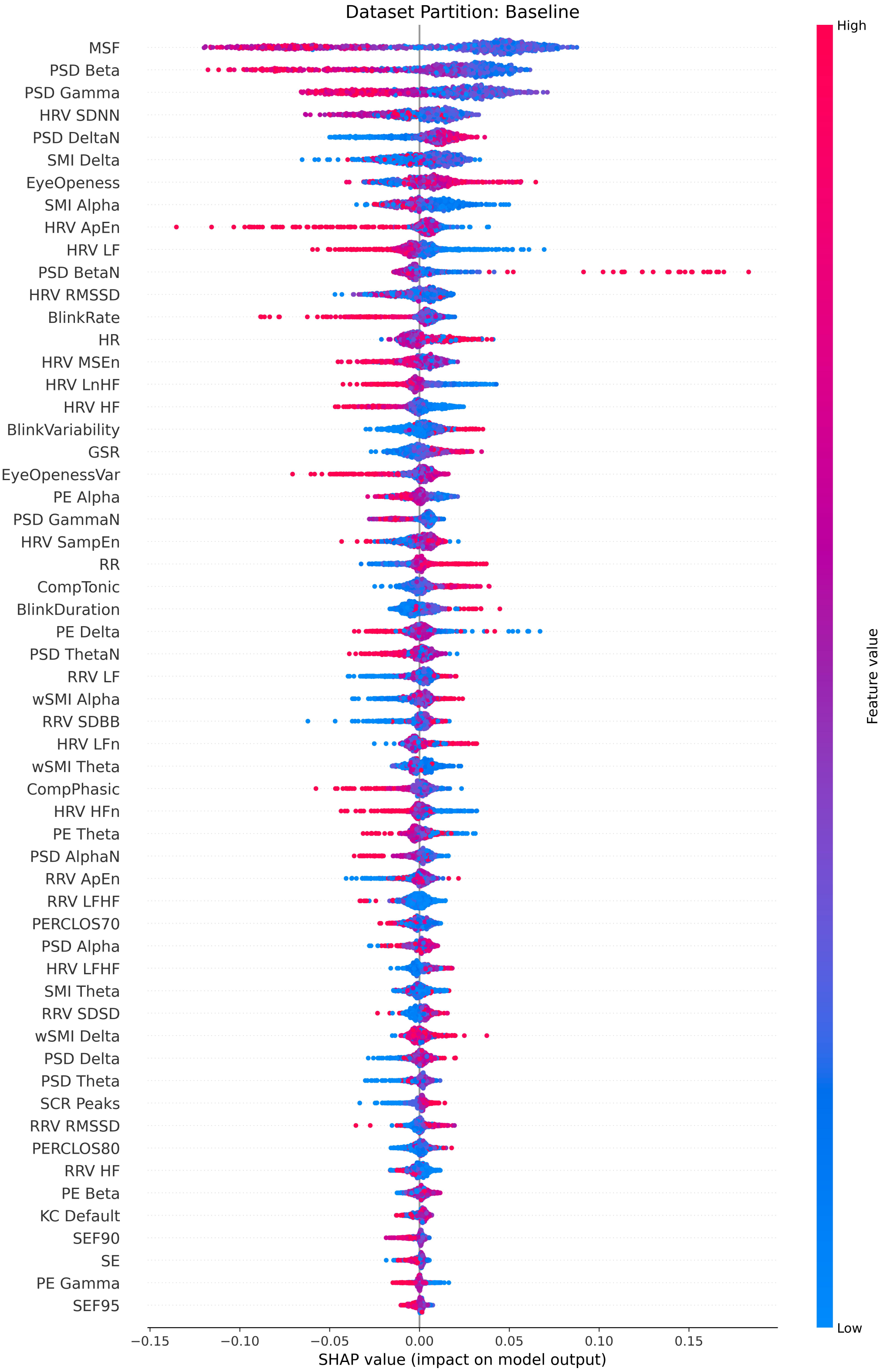
Supplementary Fig. 6.2-11: SHAP values ranking for the Baseline mental state reports of the .1 Hz filtered dataset. The SHAP value represents the impact of each feature on the model's prediction. Positive SHAP values push the prediction towards MB, while negative SHAP values push away from MB. Effectively, a high feature value with a high SHAP value indicates that when the feature increases, so does the probability of the model classifying a mental report as MB. Inversely, a high feature value with a low SHAP value indicates that when the feature increases, the probability of the model classifying a mental report as MB decreases.



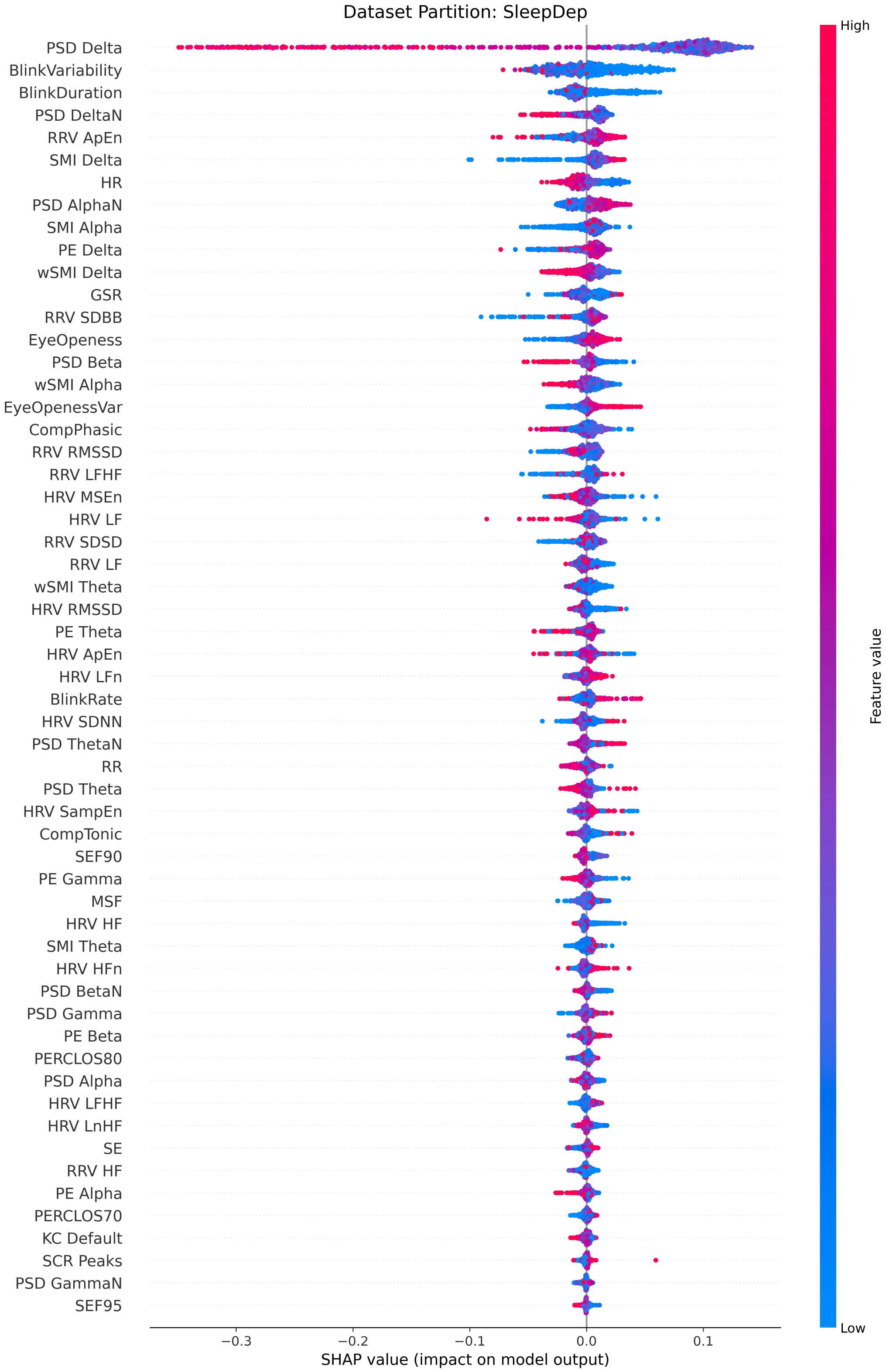
Supplementary Fig. 6.2-12: SHAP values ranking for the Low Arousal mental state reports of the .1 Hz filtered dataset. The SHAP value represents the impact of each feature on the model's prediction. Positive SHAP values push the prediction towards MB, while negative SHAP values push away from MB. Effectively, a high feature value with a high SHAP value indicates that when the feature increases, so does the probability of the model classifying a mental report as MB. Inversely, a high feature value with a low SHAP value indicates that when the feature increases, the probability of the model classifying a mental report as MB decreases.



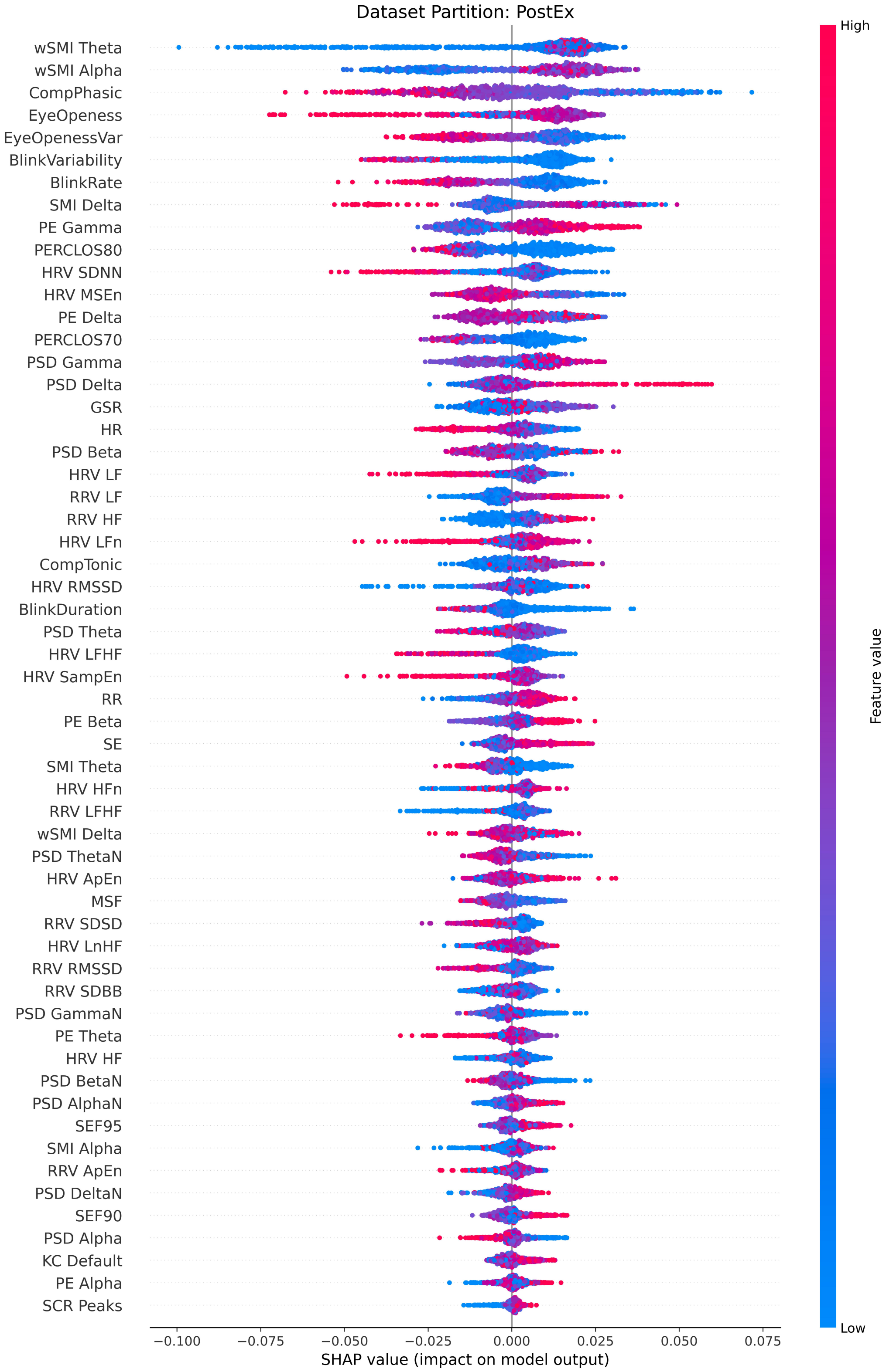
Supplementary Fig. 6.2-13: SHAP values ranking for the High Arousal mental state reports of the .1 Hz filtered dataset. The SHAP value represents the impact of each feature on the model's prediction. Positive SHAP values push the prediction towards MB, while negative SHAP values push away from MB. Effectively, a high feature value with a high SHAP value indicates that when the feature increases, so does the probability of the model classifying a mental report as MB. Inversely, a high feature value with a low SHAP value indicates that when the feature increases, the probability of the model classifying a mental report as MB decreases.



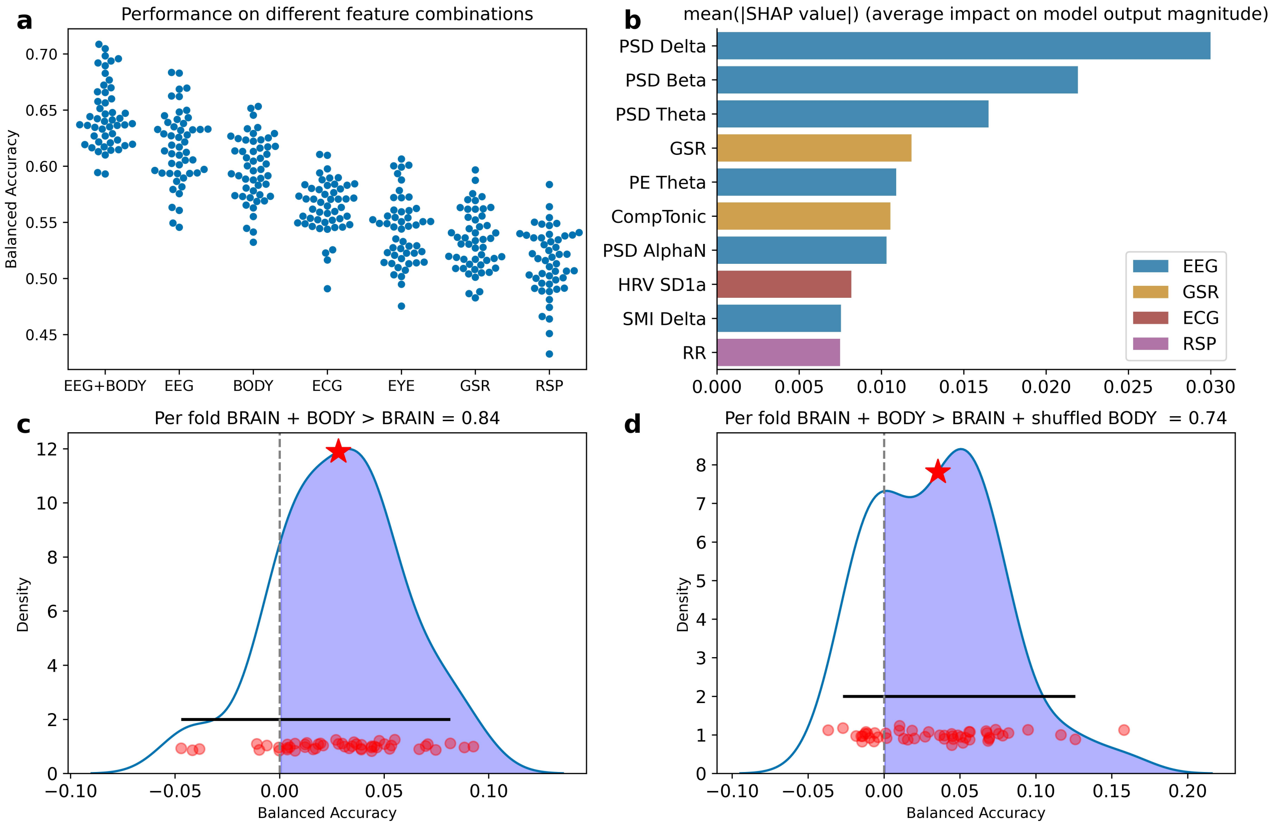
Supplementary Fig. 6.2-14: SHAP values ranking for the Baseline mental state reports of the 1 Hz filtered dataset. The SHAP value represents the impact of each feature on the model's prediction. Positive SHAP values push the prediction towards MB, while negative SHAP values push away from MB. Effectively, a high feature value with a high SHAP value indicates that when the feature increases, so does the probability of the model classifying a mental report as MB. Inversely, a high feature value with a low SHAP value indicates that when the feature increases, the probability of the model classifying a mental report as MB decreases.



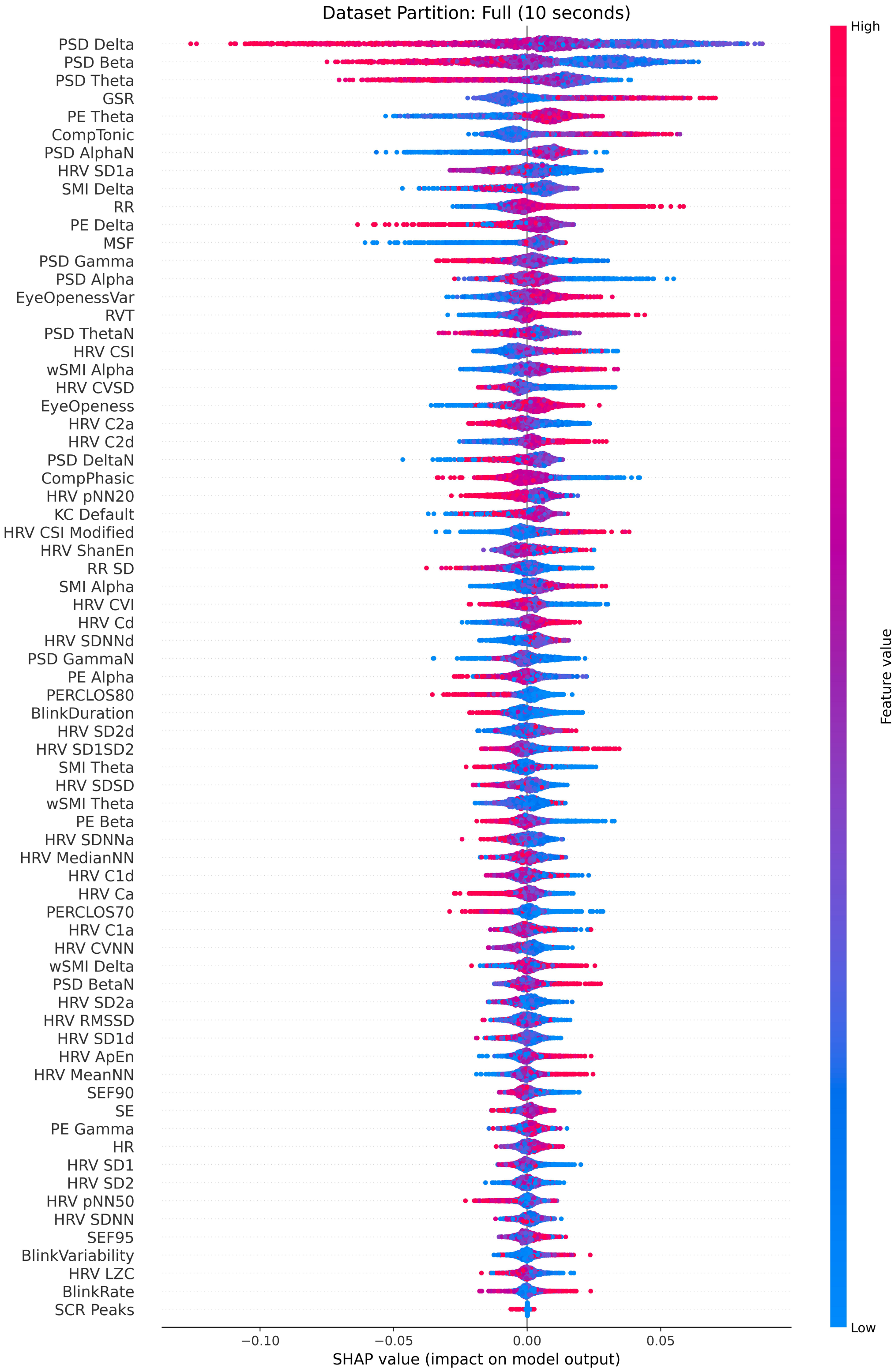
Supplementary Fig. 6.2-15: SHAP values ranking for the Low Arousal mental state reports of the 1 Hz filtered dataset. The SHAP value represents the impact of each feature on the model's prediction. Positive SHAP values push the prediction towards MB, while negative SHAP values push away from MB. Effectively, a high feature value with a high SHAP value indicates that when the feature increases, so does the probability of the model classifying a mental report as MB. Inversely, a high feature value with a low SHAP value indicates that when the feature increases, the probability of the model classifying a mental report as MB decreases.



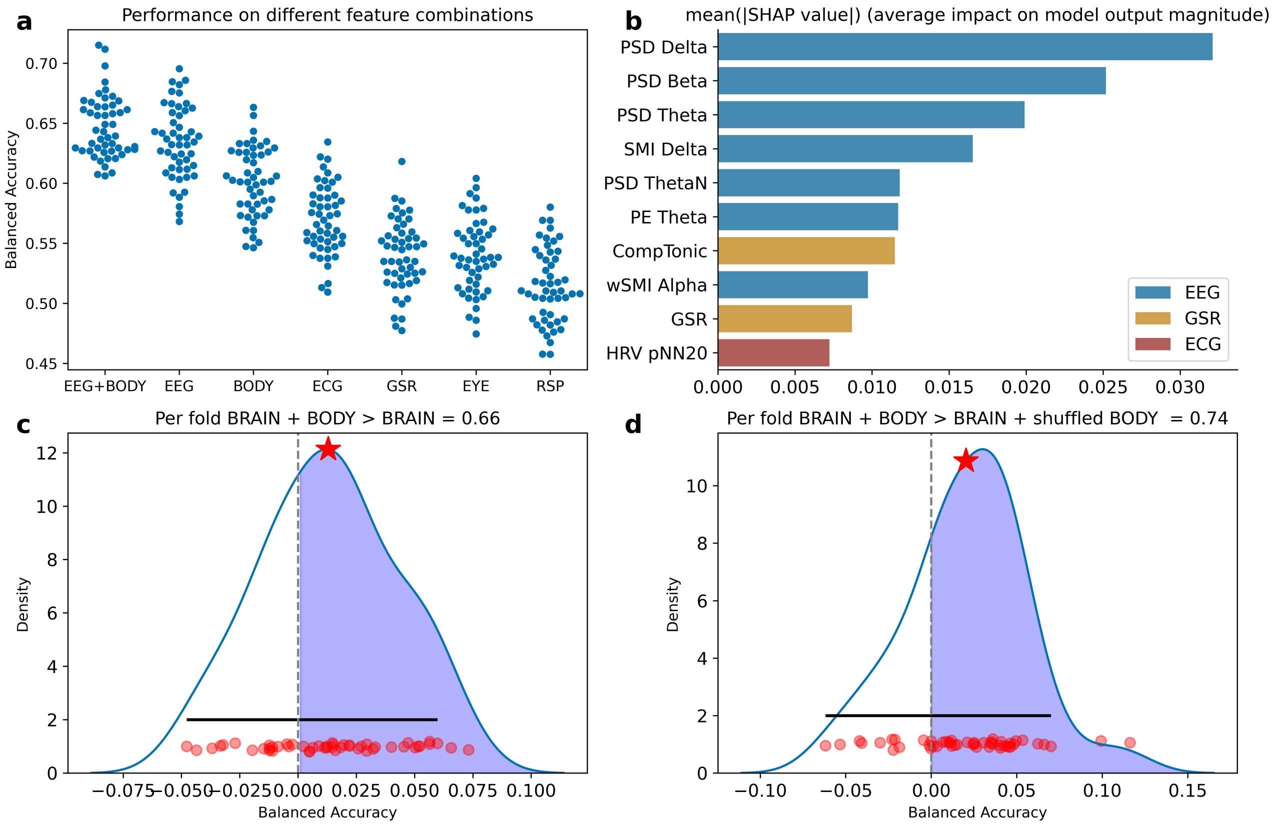
Supplementary Fig. 6.2-16: SHAP values ranking for the High Arousal mental state reports of the 1 Hz filtered dataset. The SHAP value represents the impact of each feature on the model's prediction. Positive SHAP values push the prediction towards MB, while negative SHAP values push away from MB. Effectively, a high feature value with a high SHAP value indicates that when the feature increases, so does the probability of the model classifying a mental report as MB. Inversely, a high feature value with a low SHAP value indicates that when the feature increases, the probability of the model classifying a mental report as MB decreases.



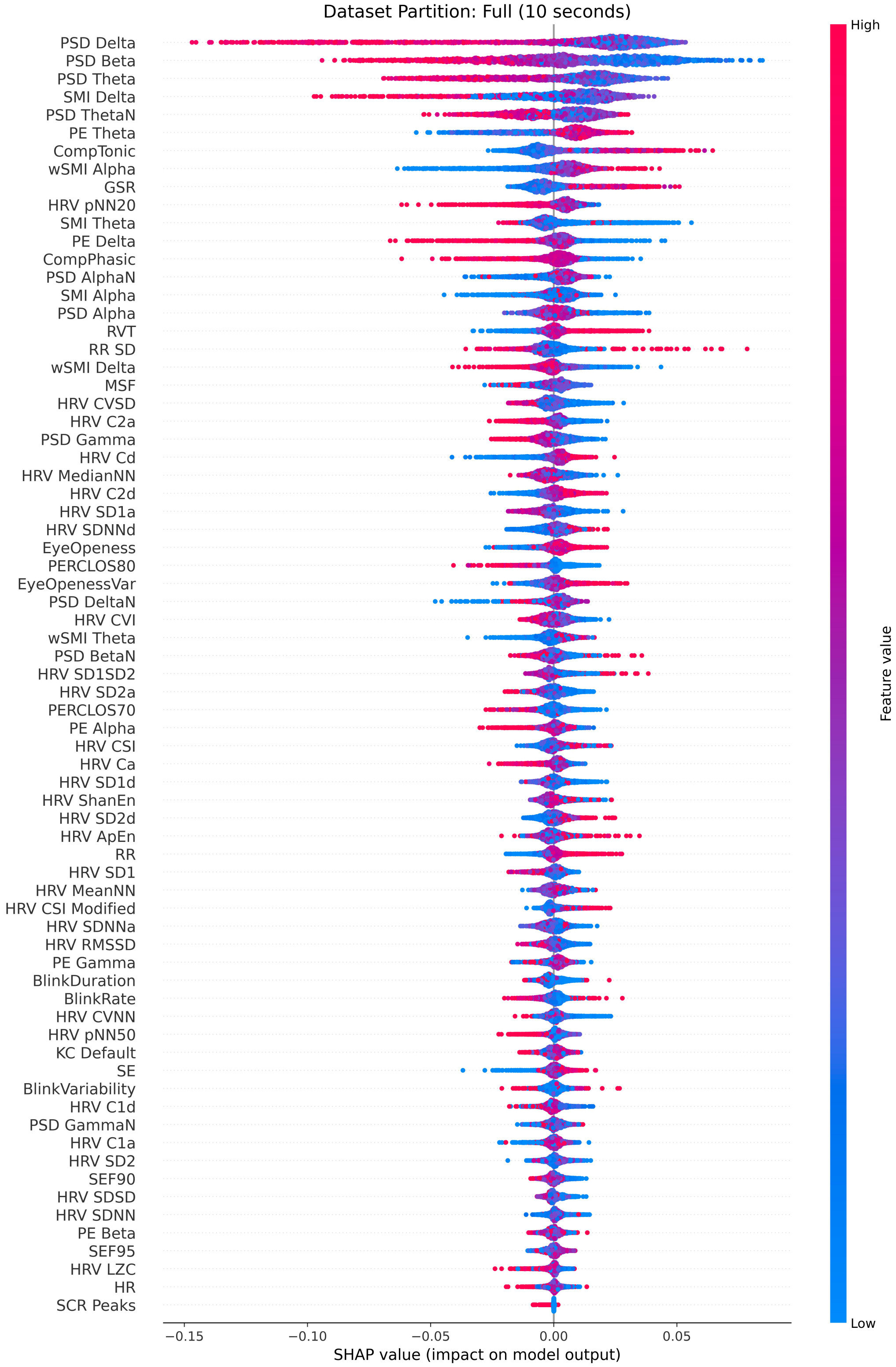
Supplementary Fig. 6.2-17: Combining information from both BRAIN and BODY markers leads to optimal classification performance when considering only a 10 s pre-probe period. a) A balanced random forest classifier trained on the last 10 seconds of the .1Hz filtered dataset on a combination of BRAIN and BODY features outperformed classifiers trained solely on BRAIN or BODY features when evaluated with balanced accuracy. Individual points indicate performance on the folds of the repeated cross-validation. b) Subset of the 10 features with the highest mean of the absolute SHAP values obtained from the balanced random forest classifier. c) The per-fold differences between the classifier trained on both BRAIN and BODY features and the one trained only on BRAIN data suggest that incorporating both feature domains provides a slight performance improvement over using BRAIN data alone. The shaded region indicates better performance for the classifier trained on both feature domains. The star indicates the mean difference. The solid, horizontal line represents the 95% highest-density intervals of the distribution. Red dots indicate per-fold differences. d) The per-fold differences between the classifier trained on both BRAIN and BODY features and the one trained on BRAIN and shuffled BODY data suggest that the model with both BRAIN and BODY data does not consider the body markers as noise.



Supplementary Fig. 6.2-18: SHAP values ranking of the .1Hz filtered dataset (last 10 seconds partition). The SHAP value represents the impact of each feature on the model's prediction. Positive SHAP values push the prediction towards MB, while negative SHAP values push away from MB. Effectively, a high feature value with a high SHAP value indicates that when the feature increases, so does the probability of the model classifying a mental report as MB. Inversely, a high feature value with a low SHAP value indicates that when the feature increases, the probability of the model classifying a mental report as MB decreases.



Supplementary Fig. 6.2-19: Combining information from both BRAIN and BODY markers leads to optimal classification performance when considering only a 10 s pre-probe period and preprocessing data using a 1 Hz filter. a) A balanced random forest classifier trained on the last 10 seconds of the 1Hz filtered dataset on a combination of BRAIN and BODY features outperformed classifiers trained solely on BRAIN or BODY features when evaluated with balanced accuracy. Individual points indicate performance on the folds of the repeated cross-validation. b) Subset of the 10 features with the highest mean of the absolute SHAP values obtained from the balanced random forest classifier. c) The per-fold differences between the classifier trained on both BRAIN and BODY features and the one trained only on BRAIN data suggest that incorporating both feature domains provides a slight performance improvement over using BRAIN data alone. The shaded region indicates better performance for the classifier trained on both feature domains. The star indicates the mean difference. The solid, horizontal line represents the 95% highest-density intervals of the distribution. Red dots indicate per-fold differences. d) The per-fold differences between the classifier trained on both BRAIN and BODY features and the one trained on BRAIN and shuffled BODY data suggest that the model with both BRAIN and BODY data does not consider the body markers as noise.



Supplementary Fig. 6.2-20: SHAP values ranking of the 1Hz filtered dataset (last 10 seconds partition). The SHAP value represents the impact of each feature on the model's prediction. Positive SHAP values push the prediction towards MB, while negative SHAP values push away from MB. Effectively, a high feature value with a high SHAP value indicates that when the feature increases, so does the probability of the model classifying a mental report as MB. Inversely, a high feature value with a low SHAP value indicates that when the feature increases, the probability of the model classifying a mental report as MB decreases.

Supplementary Table 6.2-1: Mental state report frequencies alter across arousal levels

Question	**Hypothesis**	**Sampling Plan**	**Analysis Plan**	**Alternative Explanation**
Is autonomic arousal implicated in mental state reportability?	Low and high arousal promote more frequent MB reports.	Simulate 500 datasets (5 to 50 participants). pMB=.1. Binomial model Final N=26	MB ~Arousal Report ~Arousal RT~Report Transitions~Mental	Low arousal manipulation was not effective in modifying autonomic signals. High arousal manipulation did not last throughout the experience sampling session. Higher arousal levels might facilitate monitoring reducing MB reports.
Can mental absences be attributed to cerebral mechanisms only, or to brain-body interactions?	MB is decodable based on a brain-body profile of lower overall complexity.	NA	SVM OC SVM Random Forest Extreme Trees Isolation Forest Optimize for F1-score Nested CV tuning	Given the unbalanced nature of our dataset, our classifiers might not converge properly to accurate prediction parameters. Physiological time series might be too slow to contribute to short events, such as a mental state.

Supplementary Table 6.2-2: A brief overview of the effects of sleep deprivation and exercise on arousal metrics.

Modality	Metric	Previous Studies
Electrocardiogram (EEG)	Alpha oscillations	Posada-Quintero et al. (2019)
	Delta oscillations	Borbély et al. (1981)
	Theta oscillations	Gutmann et al. (2015)
Electroencephalogram (ECG)	Heart Rate	Glos et al. (2014)
	Heart Rate Variability	Gourine & Ackland (2019)
Pupillometry	Pupil Size	Franzen et al. (2009)
		Ishigaki et al. (1991)

Supplementary Table 6.2-3: People tended to give reports faster in Baseline Arousal. Additionally, people tend to report mind-wandering (MW) the fastest. Bold font indicates significance.

Contrast	**Marginal Mean**	**SE**	**CL**	**pFDR**
Baseline - High	**.02**	**.01**	**[.00,.03]**	**7.3e-04**
Baseline - Low	**.03**	**.00**	**[.02,.04]**	**5e-09**
High-Low	**.01**	**.00**	**[0,.03]**	**1.1e-02**
MB - MW	**-.09**	**.00**	**[-.09, -.07]**	**1.5e-59**
MB - SENS	**-.09**	**.01**	**[-.1, -.07]**	**2.6e-50**
MW-SENS	-.01	.00	[-.02, .01]	1.2e-01
MW Baseline – MW High	.01	.00	[.00, .02]	3.9e-01
MW Baseline – MW Low	**.06**	**.00**	**[.04, .08]**	**1.1e-21**
MW High – MW Low	**.05**	**.01**	**[.04, .07]**	**2e-19**
SENS Baseline – SENS High	.02	.01	[-.01, .05]	1.7e-01
SENS Baseline – SENS Low	.01	.01	[-.02, .04]	4.1e-01
SENS High – SENS Low	-.01	.01	[-.04, .02]	4.5e-01
MB Baseline – MB High	**.03**	**.01**	**[.00, .06]**	**1.2e-02**
MB Baseline – MB Low	**.02**	**.01**	**[-.01, .05]**	**3.4e-02**
MB High – MB Low	-.01	.01	[-.04, .02]	4.3e-01

Supplementary Table 6.2-4: A balanced random forest classifier trained on the 1Hz filtered dataset outperformed all classifiers when compared across balanced accuracy. Cells indicate mean and 95% CI.

Examined	**Classifier**	**Recall**	**Precision**	**F1**	**ROC AUC**	**Balanced Accuracy**
Known Subjects	Balanced RF	.61, [.6, .63]	.26, [.26, .27]	.37, [.36, .37]	.71, [.7, .72]	.66, [.65, .67]
	SVM	.28, [.26, .3]	.29, [.28, .31]	.28, [.27, .3]	.63, [.62, .64]	.58, [.58, .59]
	ET	.16, [.15, .17]	.64, [.6, .67]	.26, [.24, .27]	.72, [.71, .73]	.57, [.57, .58]
	RF	.14, [.13, .15]	.61, [.57, .64]	.22, [.21, .24]	.7, [.69, .71]	.56, [.56, .57]
	IF	.15, [.14, .16]	.21, [.19, .22]	.17, [.16, .18]	.53, [.52, .53]	.53, [.52, .53]
	OC SVM	.91, [.89, .93]	.15, [.15, .15]	.26, [.25, .26]	.52, [.51, .52]	.52, [.51, .52]
	DUMMY	.14, [.13, .15]	.15, [.14, .15]	.14, [.13, .15]	.5, [.5, .51]	.5, [.49, .51]
Unknown Subjects	IF	.25, [.21, .29]	.18, [.16, .2]	.2, [.18, .22]	.53, [.52, .54]	.53, [.52, .54]
	RF	.04, [.03, .05]	.27, [.21, .34]	.06, [.05, .08]	.53, [.51, .54]	.51, [.51, .51]
	Balanced RF	.37, [.32, .42]	.16, [.14, .18]	.21, [.18, .23]	.51, [.49, .53]	.51, [.5, .53]
	ET	.03, [.02, .03]	.34, [.26, .43]	.05, [.04, .06]	.51, [.5, .53]	.51, [.5, .51]
	DUMMY	.15, [.14, .17]	.15, [.13, .17]	.15, [.14, .16]	.5, [.49, .5]	.5, [.5, .51]
	OC SVM	.69, [.61, .77]	.15, [.13, .16]	.23, [.21, .24]	.5, [.48, .52]	.5, [.48, .52]
	SVM	.2, [.18, .22]	.14, [.13, .16]	.16, [.14, .17]	.48, [.47, .5]	.49, [.48, .5]

RF = Random Forest; SVM = Support Vector Machine; ET = Extreme Trees; IF = Isolation Forest; OC SVM = One-Class Support Vector Machine

Supplementary Table 6.2-5: A classifier trained on a combination of BRAIN and BODY features outperformed classifiers trained solely on BRAIN or BODY features on the 1Hz filtered dataset when evaluated with balanced accuracy. Cells indicate mean and 95% CI.

Classifier	Recall	Precision	F1	ROC AUC	Balanced Accuracy
BRAIN + BODY	.61, [.6, .63]	.26, [.26, .27]	.37, [.36, .37]	.71, [.7, .72]	.66, [.65, .67]
BRAIN	.58, [.56, .6]	.25, [.25, .26]	.35, [.34, .36]	.69, [.68, .7]	.64, [.64, .65]
BODY	.6, [.58, .61]	.22, [.21, .22]	.32, [.31, .32]	.67, [.66, .68]	.61, [.61, .62]
EYE	.57, [.55, .58]	.22, [.21, .22]	.31, [.3, .32]	.64, [.63, .65]	.61, [.6, .62]
ECG	.56, [.54, .57]	.18, [.17, .18]	.27, [.26, .28]	.59, [.58, .6]	.56, [.56, .57]
EDA	.6, [.57, .63]	.17, [.16, .17]	.26, [.25, .26]	.57, [.56, .58]	.54, [.54, .55]
RSP	.54, [.52, .55]	.15, [.15, .16]	.24, [.23, .25]	.53, [.52, .54]	.52, [.51, .53]

Supplementary Table 6.2-6: Classification performance was retained when examining mind-blanking (MB) occurrences for each arousal condition on the .1 Hz filtered dataset. Cells indicate mean and 95% CI.

Arousal	Recall	Precision	F1	ROC AUC	Balanced Accuracy
Baseline	.62, [.59, .65]	.24, [.23, .25]	.34, [.33, .36]	.73, [.71, .74]	.67, [.65, .68]
Low	.57, [.54, .6]	.34, [.33, .35]	.42, [.41, .43]	.7, [.69, .71]	.64, [.63, .65]
High	.61, [.58, .64]	.16, [.16, .17]	.26, [.25, .27]	.66, [.64, .68]	.61, [.6, .63]

Supplementary Table 6.2-7: Classifier performance on different feature combinations using 10s of data, filtered at .1 Hz. Performance did not alter when using the BRAIN markers but was reduced in the BODY markers. Cells indicate mean and 95% CI.

Classifier	Recall	Precision	F1	ROC AUC	Balanced Accuracy
EEG + BODY	.62, [.6, .63]	.24, [.23, .24]	.34, [.34, .35]	.69, [.68, .7]	.65, [.64, .65]
EEG	.58, [.56, .6]	.22, [.21, .22]	.32, [.31, .32]	.66, [.65, .67]	.62, [.61, .63]
BODY	.58, [.57, .6]	.2, [.19, .2]	.3, [.29, .3]	.64, [.63, .64]	.6, [.59, .61]
ECG	.52, [.5, .53]	.18, [.18, .18]	.27, [.26, .27]	.59, [.58, .59]	.56, [.56, .57]
EDA	.51, [.49, .54]	.17, [.16, .17]	.25, [.24, .26]	.56, [.55, .57]	.54, [.53, .55]
EYE	.64, [.61, .67]	.16, [.15, .16]	.25, [.24, .26]	.56, [.55, .57]	.53, [.53, .54]
RSP	.67, [.63, .71]	.15, [.14, .15]	.24, [.23, .25]	.52, [.51, .53]	.51, [.51, .52]

Supplementary Table 6.2-8: Classifier performance on different feature combinations using 10s of data, filtered at 1 Hz. Performance did not alter when using the BRAIN markers but was reduced in the BODY markers. Cells indicate mean and 95% CI.

Classifier	Recall	Precision	F1	ROC AUC	Balanced Accuracy
EEG + BODY	.62, [.6, .63]	.24, [.23, .24]	.34, [.34, .35]	.69, [.68, .7]	.65, [.64, .65]
EEG	.58, [.56, .6]	.22, [.21, .22]	.32, [.31, .32]	.66, [.65, .67]	.62, [.61, .63]
BODY	.58, [.57, .6]	.2, [.19, .2]	.3, [.29, .3]	.64, [.63, .64]	.6, [.59, .61]
ECG	.52, [.5, .53]	.18, [.18, .18]	.27, [.26, .27]	.59, [.58, .59]	.56, [.56, .57]
EDA	.51, [.49, .54]	.17, [.16, .17]	.25, [.24, .26]	.56, [.55, .57]	.54, [.53, .55]
EYE	.64, [.61, .67]	.16, [.15, .16]	.25, [.24, .26]	.56, [.55, .57]	.53, [.53, .54]
RSP	.67, [.63, .71]	.15, [.14, .15]	.24, [.23, .25]	.52, [.51, .53]	.51, [.51, .52]

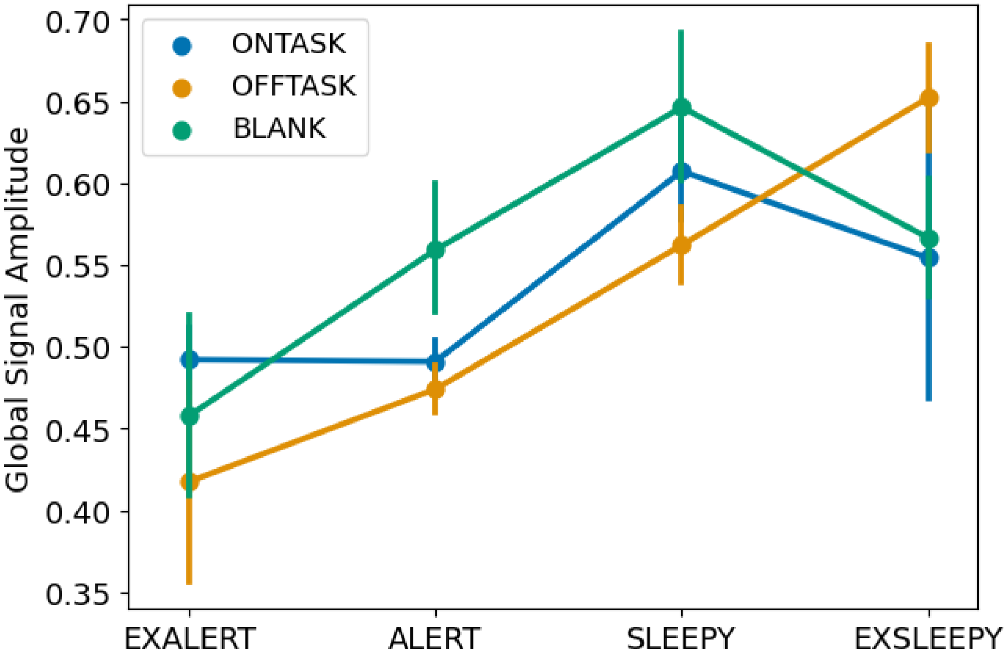
Supplementary Discussion on Methodology

Our analysis examined the whole 110 s period preceding a mental state report. The rationale for this epoch choice was that specific features from slow oscillatory body afferents, such as heart rate variability, cannot be reliably estimated from shorter time windows. Our results advance the discussion of how long mental states last. The study of a mental state is based on a pre-probe window preceding a mental report, akin to our paradigm. The examined pre-probe epoch is varied based on the neuronal or electrophysiological modality used, as BOLD markers are typically slower than EEG. This approach has shown that mental states can be decoded as early as 10s before report (Van Calster et al., 2017; Mortaheb et al., 2022; Boulakis et al., 2023), or as late as 500ms before the report (Andrillon et al., 2021). Here we show that information about a mental state might be available even earlier. However, an important caveat to account for this interpretation is that experience sampling introduces a discrete methodology to sample mental states. Therefore, our analysis of the 110s might encompass multiple mental states, and the patterns of brain-body might represent those as well. To account for this, we performed exploratory analysis by classifying MB considering only a pre-probe period of 10s. The new classifier did not show improved performance. Instead, we observed comparable results across the 10s and the 110s classifier when pooling data across BRAIN and BODY markers. Similarly to the 110s classifier, we examined whether specific BRAIN or BODY markers could decode MB reports separately from other domains of features. While EEG retained high performance, we observed a significant drop in performance across all BODY classifiers, and most prominently, in the eye classifier. Therefore, we speculate that a short pre-probe period might not be adequate to reliably estimate informative BODY features for MB classification.

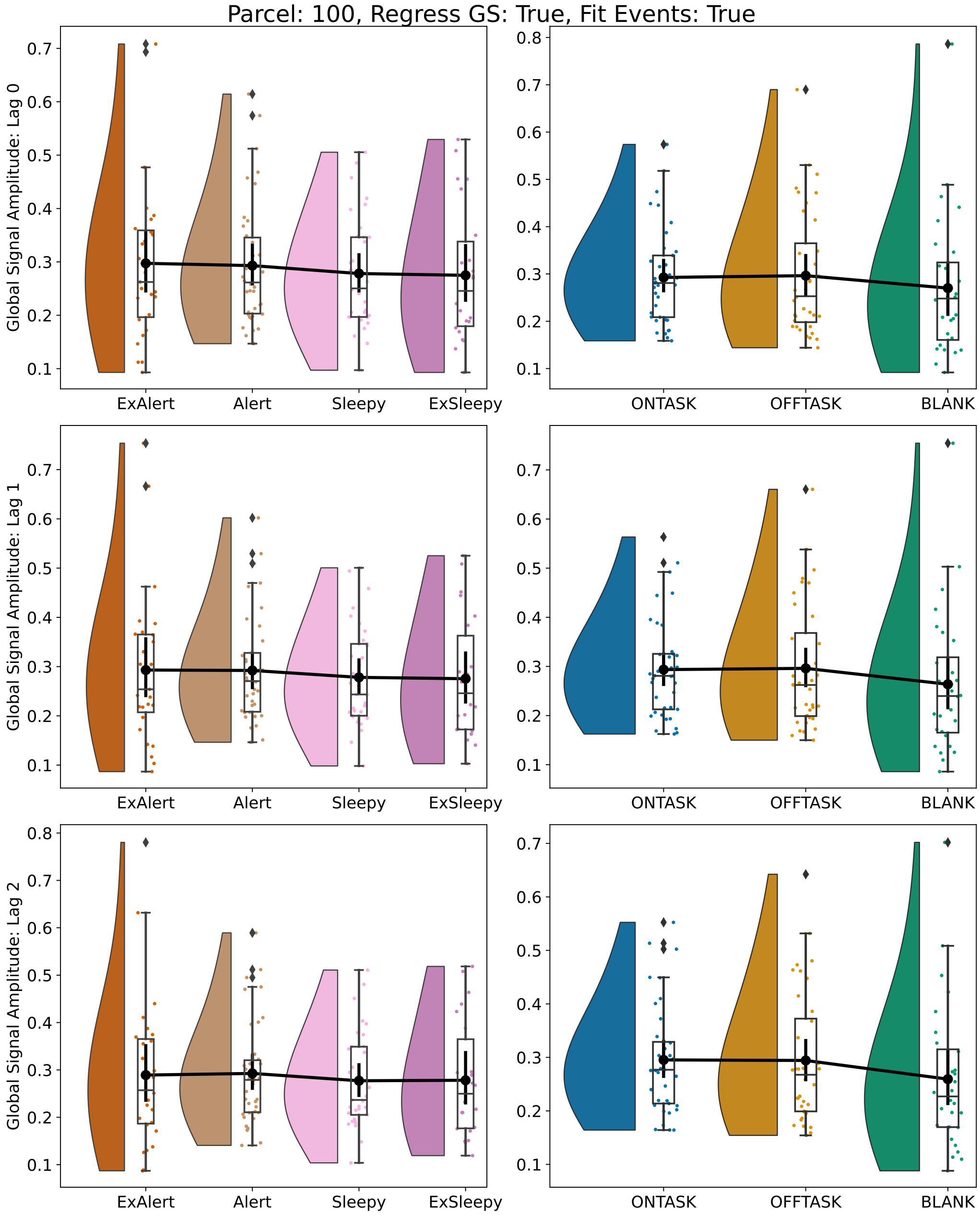
Pooling together MB reports across different arousal conditions might hide arousal-specific effects on MB reports. To examine this hypothesis, we performed exploratory analyses by training our classifier separately on different arousal conditions. While we were able to retain predictive power across these partitions, we observed distinct different brain-body feature importance. During baseline, the feature importance ranking was comprised of a diverse combination spanning EEG, ECG, and EYE markers. There was a clear shift in importance in sleep deprivation, with the power of the delta band being the most important feature. This result is consistent with contemporary accounts of MB (Andrillon et al., 2019, 2021), where

MB is correlated with the presence of the presence of parietal slow-wave intrusions in wakefulness, within the delta band. Mounting sleep pressure has been correlated with an overall increase in localized sleep-like SWs (Hung et al., 2013; Bernardi et al., 2015). As these intrusions in the delta band increase with sleep deprivation, attentional lapses in the form of MB might become themselves more intrusive to cognition, and account for the overall cognitive decline in performance during sleep deprivation (Andrillon & Oudiette, 2023). Contrary to sleep deprivation, post-exercise MB has significantly different feature importance, not driven by delta, but by connectivity in alpha and theta bands, as well as contributions for EDA and EYE markers. Reductions in the alpha and theta bands are consistent with reduced arousal after propofol-induced anaesthesia (Chennu et al., 2016), consistent with the hypothesis of altered arousal during MB. Meanwhile, contributions of the phasic component of the EDA signal provide direct evidence for sympathetic contributions to MB.

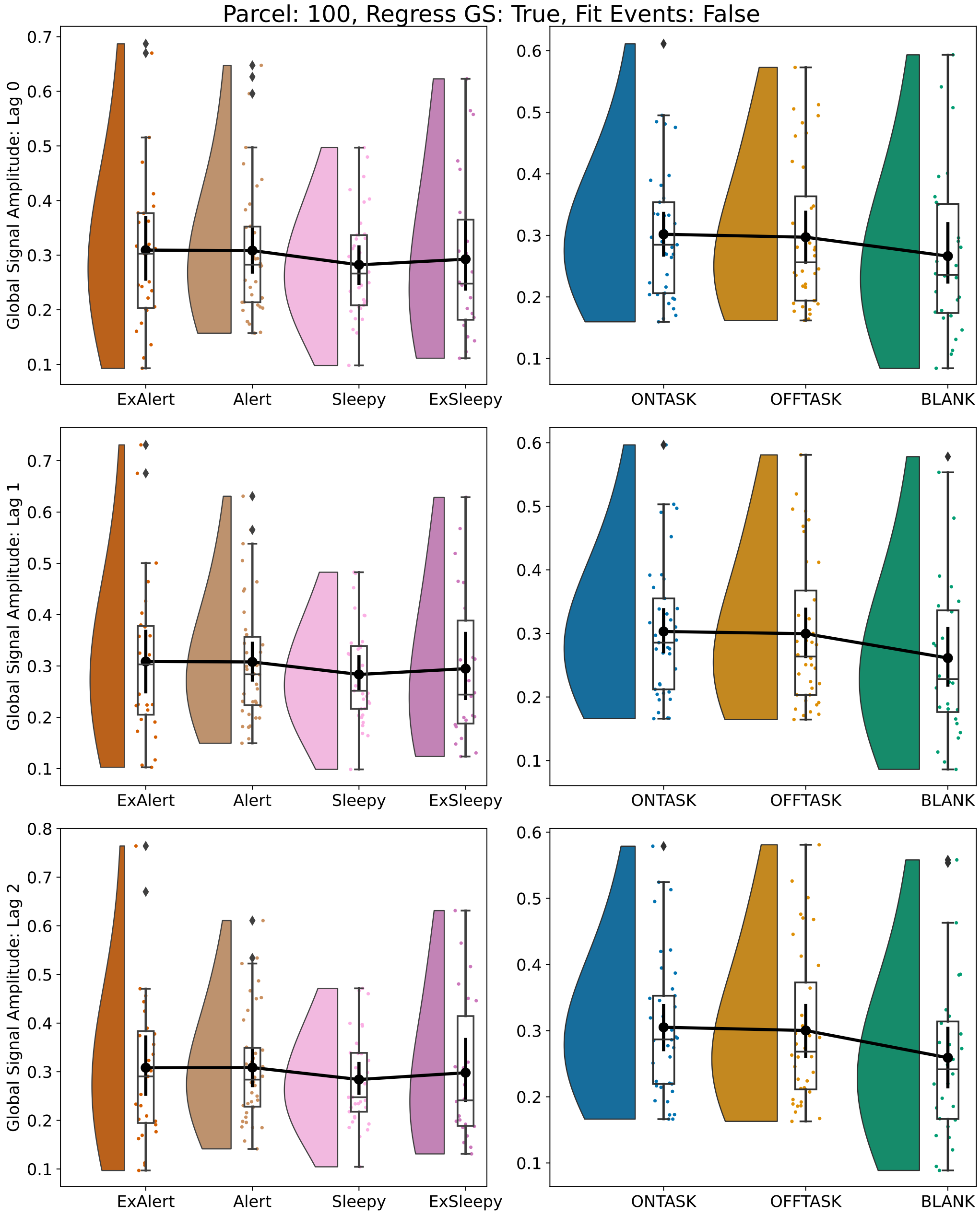
6.3 Supplementary Information - Chapter 4



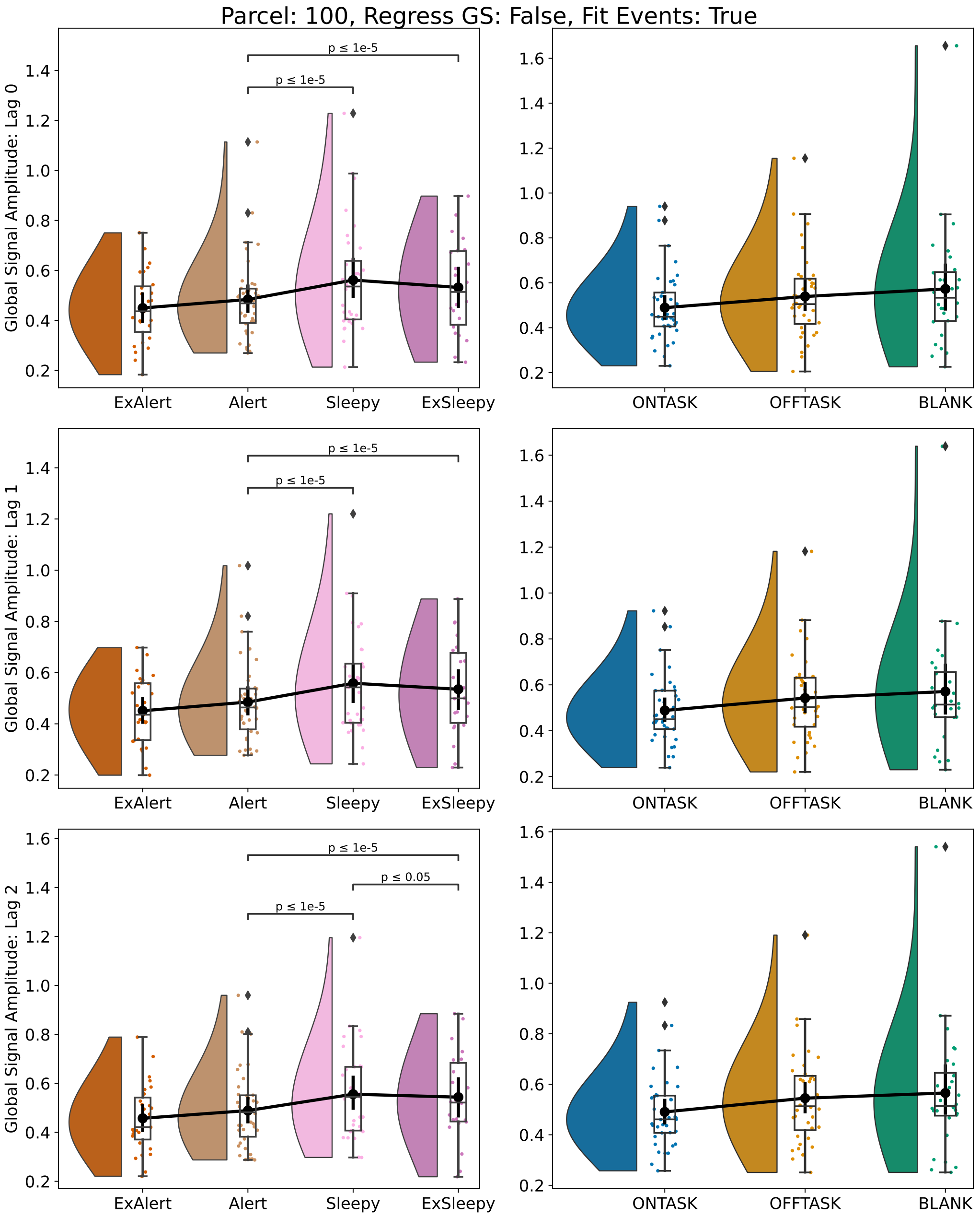
Supplementary Fig. 6.3-1: An analysis of global signal amplitude differences between mental states and alertness indicated showed no significant interaction terms. Line plots indicate means. Error bars indicate 95% confidence intervals.



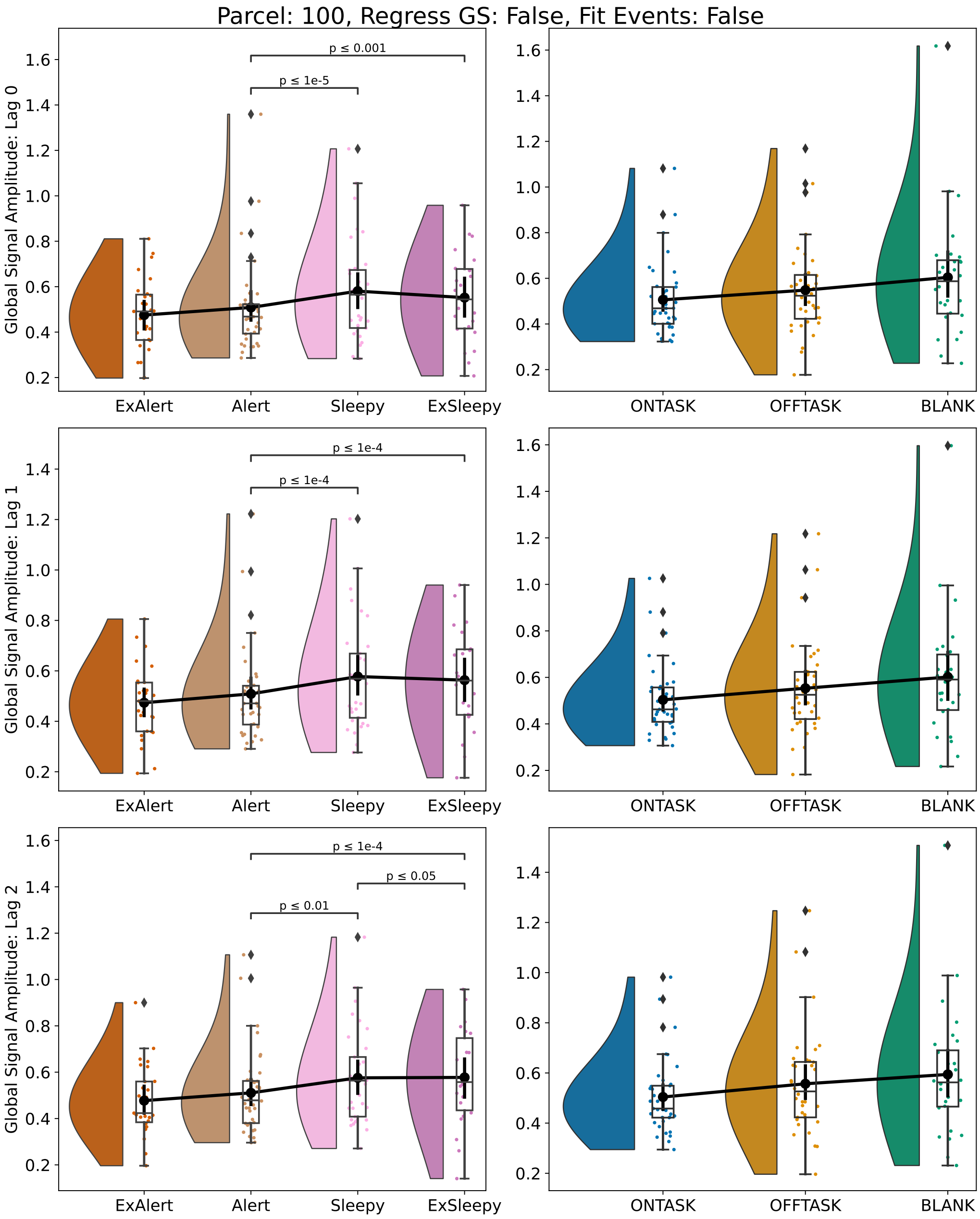
Supplementary Fig. 6.3-2: Global signal amplitude does not differ across alertness levels or mental states when the global signal is regressed out. Analysis parameters: Parcel = 100, Global signal regression = True, Event Regression = True. Raincloud density plots indicate data dispersion. Box plots indicate medians and inter-quantile ranges. Point plots indicate per trial and per run proportion of reports. Line plots indicate means.



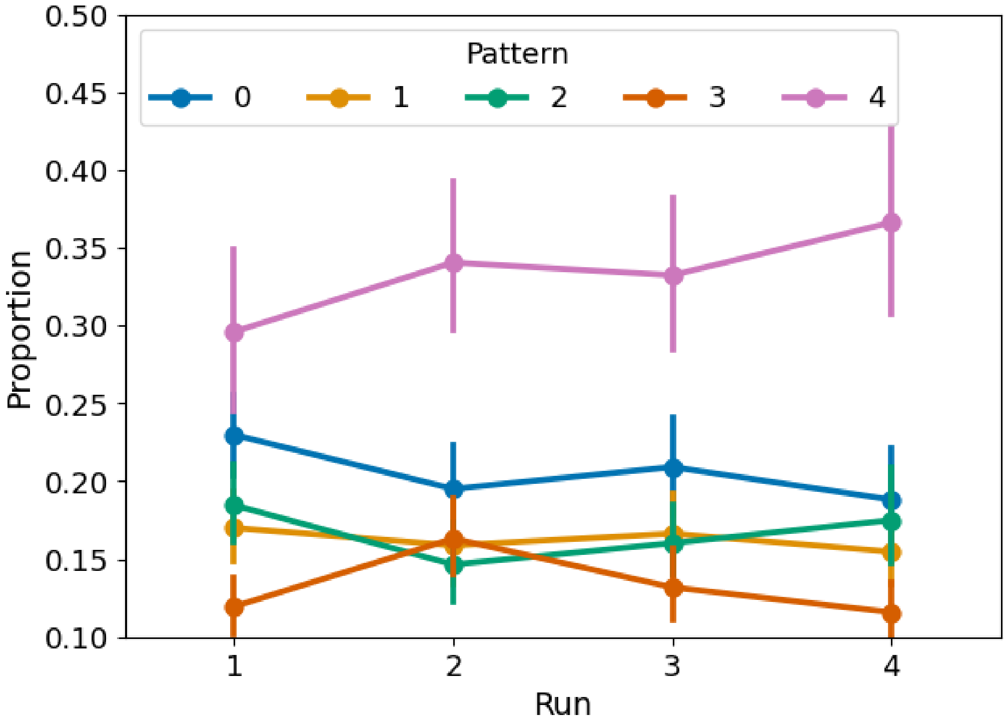
Supplementary Fig. 6.3-3: Global signal amplitude does not differ across alertness levels or mental states when the global signal is regressed out. Analysis parameters: Parcel = 100, Global signal regression = True, Event Regression = False. Raincloud density plots indicate data dispersion. Box plots indicate medians and inter-quantile ranges. Point plots indicate per trial and per run proportion of reports. Line plots indicate means.



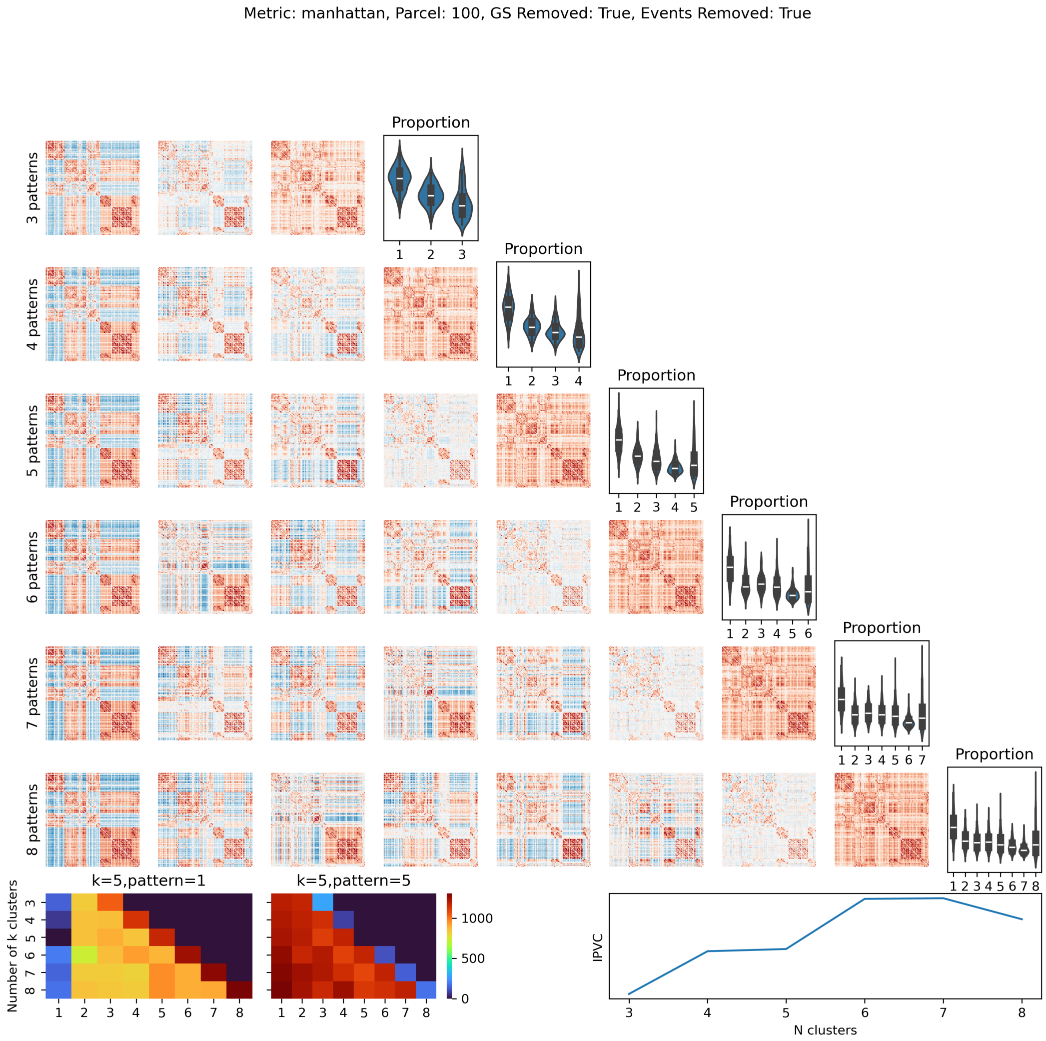
Supplementary Fig. 6.3-4: textbfGlobal signal amplitude is progressively increased as sleepiness increases but does not differ across mental states. Analysis parameters: Parcel = 100, Global signal regression = False, Event Regression = True. Raincloud density plots indicate data dispersion. Box plots indicate medians and inter-quantile ranges. Point plots indicate per trial and per run proportion of reports. Line plots indicate means.



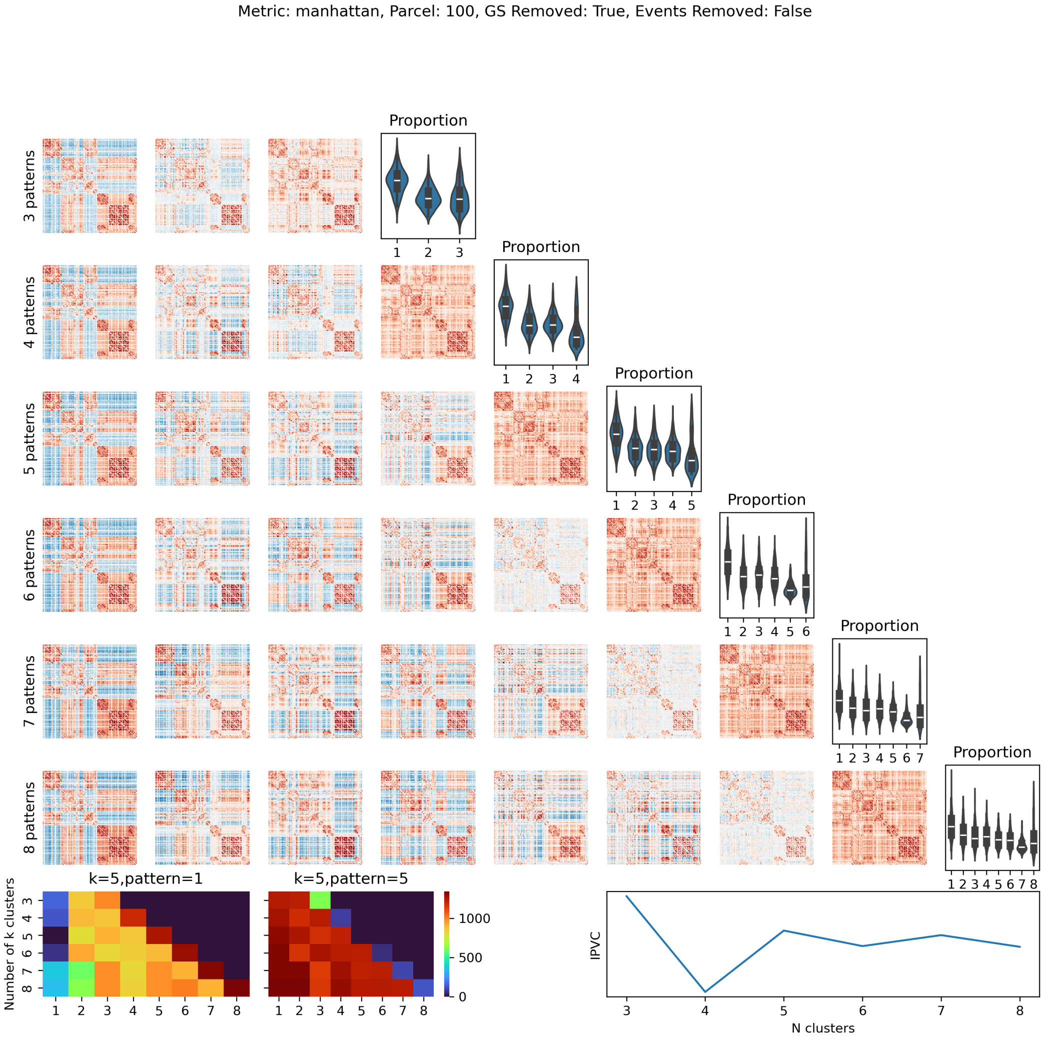
Supplementary Fig. 6.3-5: Global signal amplitude is progressively increased as sleepiness increases but does not differ across mental states. Analysis parameters: Parcel = 100, Global signal regression = False, Event Regression = False. Raincloud density plots indicate data dispersion. Box plots indicate medians and inter-quantile ranges. Point plots indicate per trial and per run proportion of reports. Line plots indicate means.



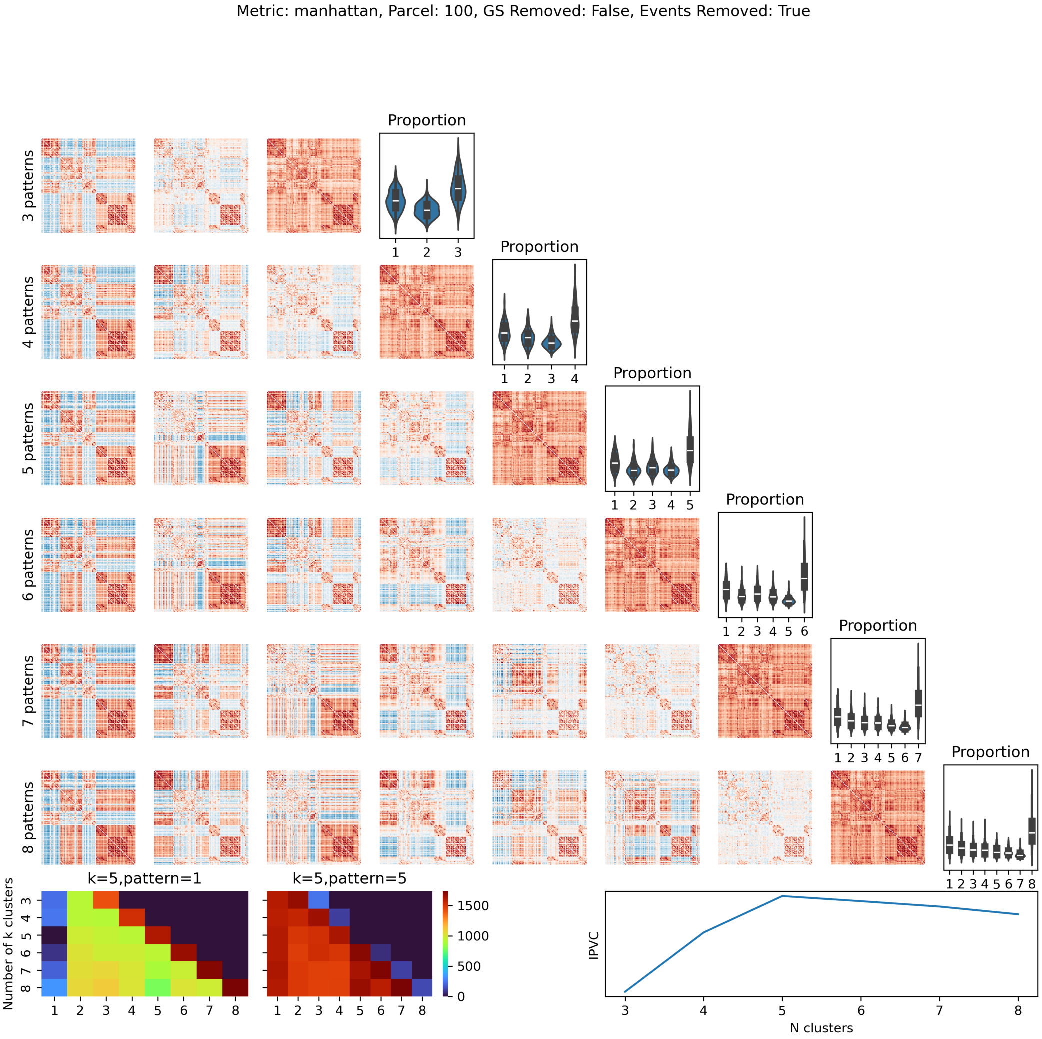
Supplementary Fig. 6.3-6: An analysis exploring whether frequency of brain patterns altered across different run did not yield any significant results. Error bars indicate 95% confidence intervals.



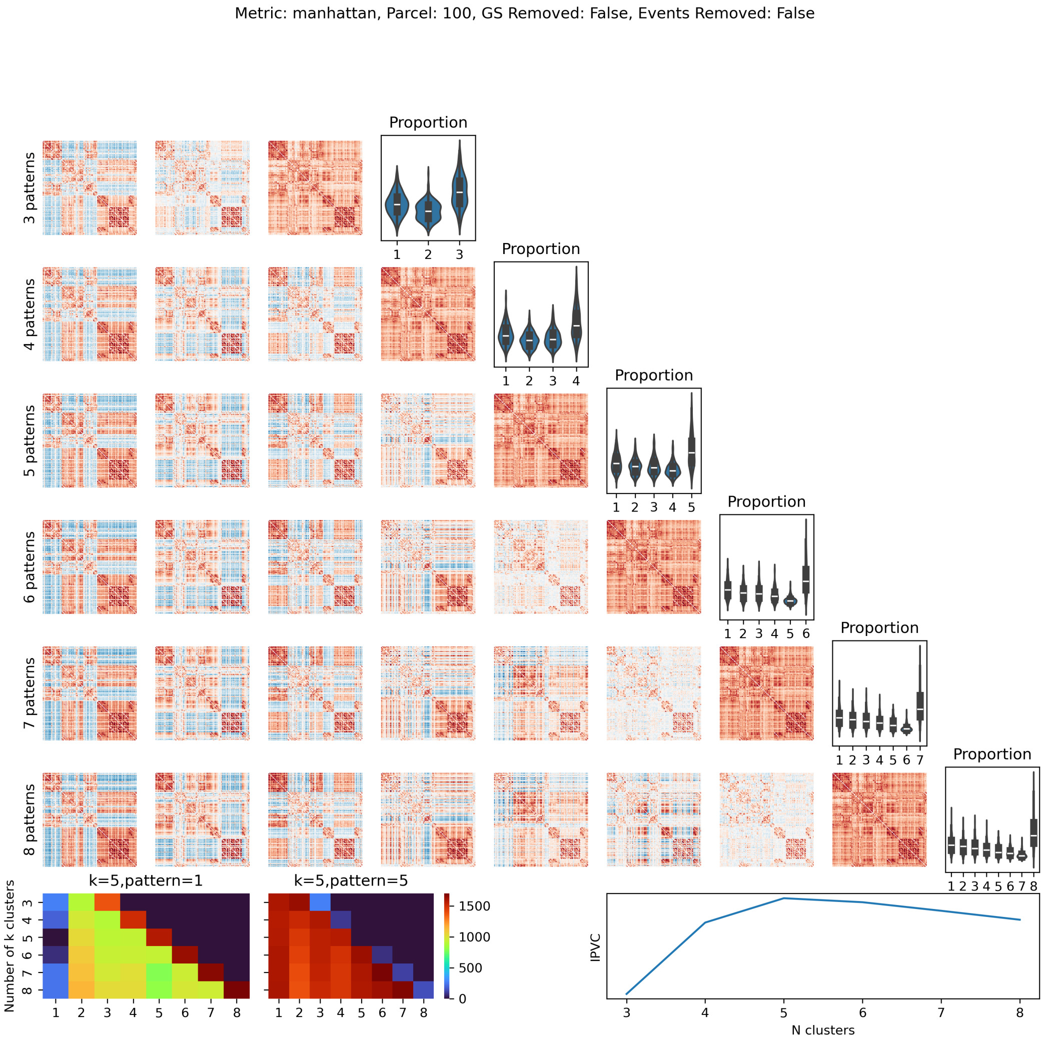
Supplementary Fig. 6.3-7: Recurrent and consistent brain configurations emerge under different clustering dimensionalities. Clustering parameters: Metric = Manhattan distance, Global Signal Regression: True, Event Regression: True. For each value of k, patterns are ordered based on the standard deviation of their connectome, from the most variant (left) to the least (right). The right-most columns indicate per-participant pattern occurrence rate. Violin plots indicate data dispersion. Box plots indicate interquartile ranges and medians. Bottom row - Left. To examine whether patterns produced across different values of k presented correspondence, we estimated the distance of pattern 1 for $k = 5$ with respect to all patterns obtained for $k = 3$ to 8. Similarly,we estimated the distance of pattern 1 for $k = 5$ with respect to all patterns obtained for $k = 3$ to 7. Bottom row - Right. The variability of dynamic coordination patterns found by the clustering procedure is maximal with $k = 7$ clusters. For each selection of number of clusters in the K-means algorithm, we computed the correlation matrices between all the upper triangular parts of the resulting centroids.



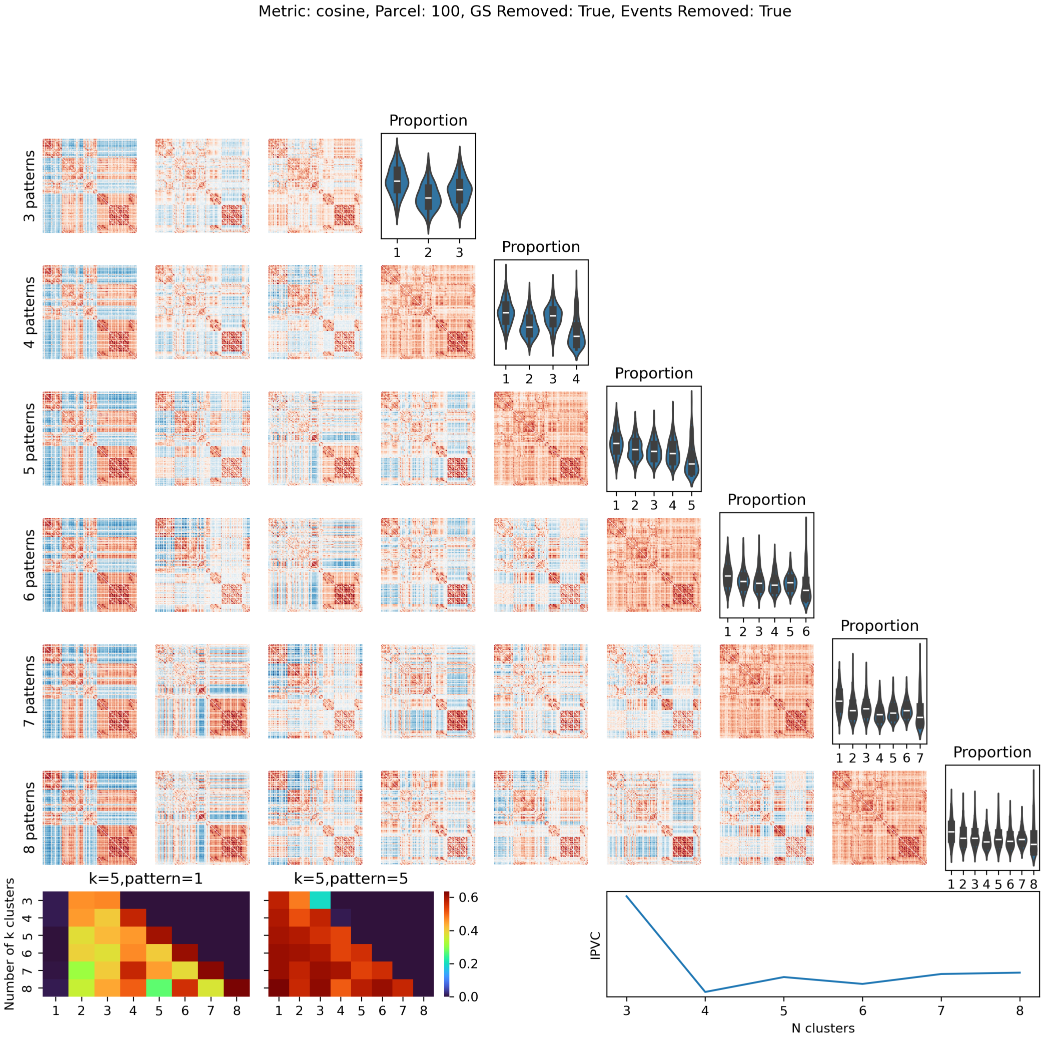
Supplementary Fig. 6.3-8: Recurrent and consistent brain configurations emerge under different clustering dimensionalities. Clustering parameters: Metric = Manhattan distance, Global Signal Regression: True, Event Regression: False. For each value of k, patterns are ordered based on the standard deviation of their connectome, from the most variant (left) to the least (right). The right-most columns indicate per-participant pattern occurrence rate. Violin plots indicate data dispersion. Box plots indicate interquartile ranges and medians. Bottom row - Left. To examine whether patterns produced across different values of k presented correspondence, we estimated the distance of pattern 1 for $k = 5$ with respect to all patterns obtained for $k = 3$ to 8. Similarly,we estimated the distance of pattern 1 for $k = 5$ with respect to all patterns obtained for $k = 3$ to 7. Bottom row - Right. The variability of dynamic coordination patterns found by the clustering procedure is maximal with $k = 7$ clusters. For each selection of the number of clusters in the K-means algorithm, we computed the correlation matrices between all the upper triangular parts of the resulting centroids.



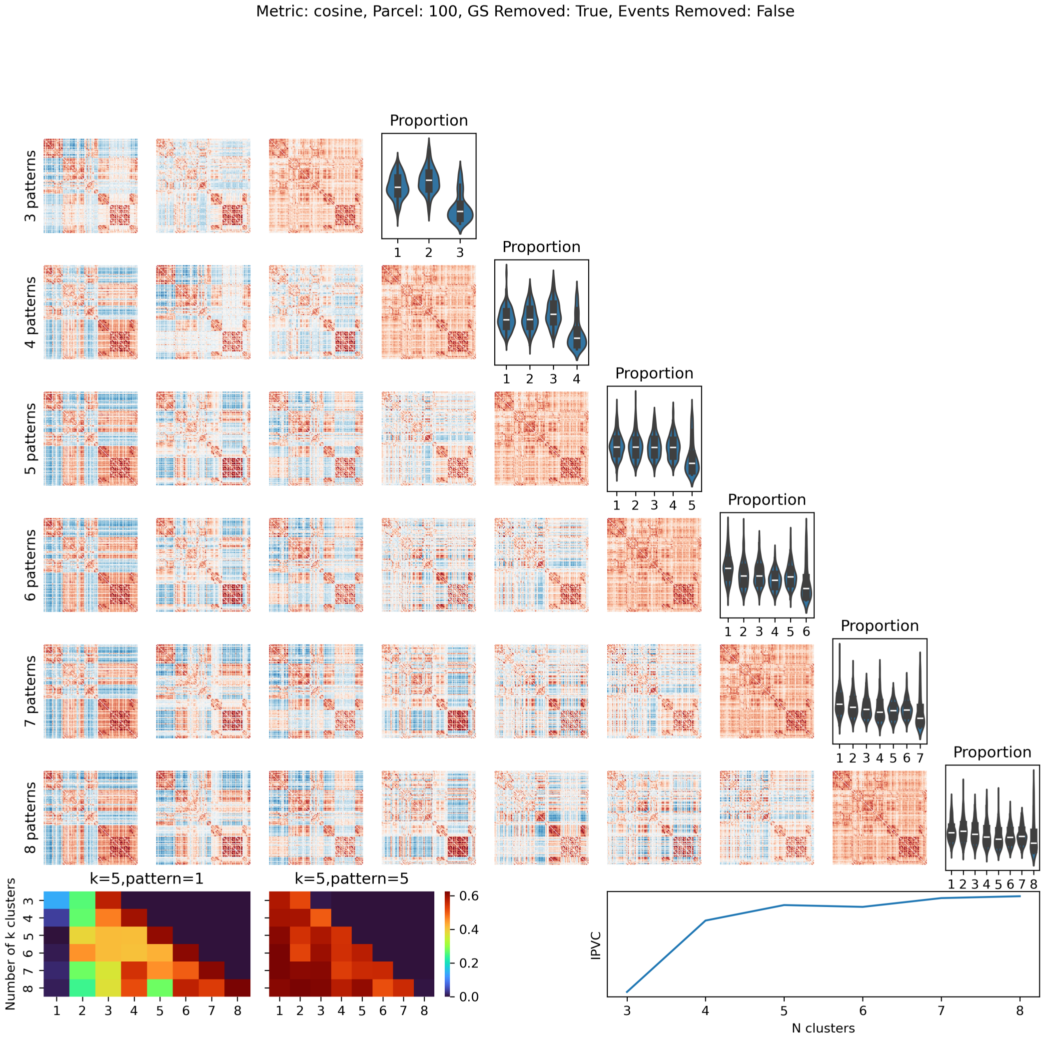
Supplementary Fig. 6.3-9: Recurrent and consistent brain configurations emerge under different clustering dimensionalities. Clustering parameters: Metric = Manhattan distance, Global Signal Regression: False, Event Regression: True. For each value of k, patterns are ordered based on the standard deviation of their connectome, from the most variant (left) to the least (right). The right-most columns indicate per-participant pattern occurrence rate. Violin plots indicate data dispersion. Box plots indicate interquartile ranges and medians. Bottom row - Left. To examine whether patterns produced across different values of k presented correspondence, we estimated the distance of pattern 1 for $k = 5$ with respect to all patterns obtained for $k = 3$ to 8. Similarly, we estimated the distance of pattern 1 for $k = 5$ with respect to all patterns obtained for $k = 3$ to 7. Bottom row - Right. The variability of dynamic coordination patterns found by the clustering procedure is maximal with $k = 7$ clusters. For each selection of the number of clusters in the K-means algorithm, we computed the correlation matrices between all the upper triangular parts of the resulting centroids.



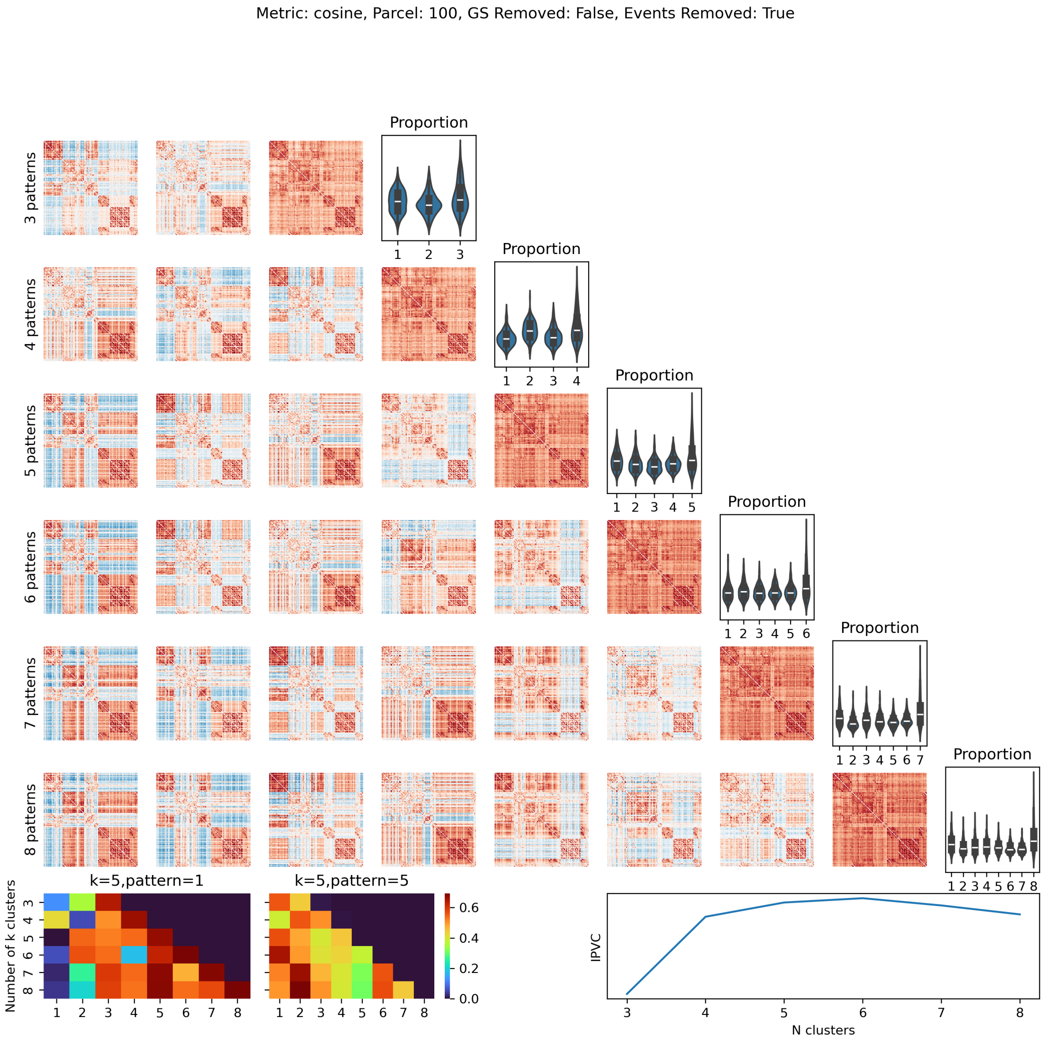
Supplementary Fig. 6.3-10: Recurrent and consistent brain configurations emerge under different clustering dimensionalities. Clustering parameters: Metric = Manhattan distance, Global Signal Regression: False, Event Regression: False. For each value of k, patterns are ordered based on the standard deviation of their connectome, from the most variant (left) to the least (right). The right-most columns indicate per-participant pattern occurrence rate. Violin plots indicate data dispersion. Box plots indicate interquartile ranges and medians. Bottom row - Left. To examine whether patterns produced across different values of k presented correspondence, we estimated the distance of pattern 1 for k = 5 with respect to all patterns obtained for k = 3 to 8. Similarly, we estimated the distance of pattern 1 for k = 5 with respect to all patterns obtained for k = 3 to 7. Bottom row - Right. The variability of dynamic coordination patterns found by the clustering procedure is maximal with k = 7 clusters. For each selection of number of clusters in the K-means algorithm, we computed the correlation matrices between all the upper triangular parts of the resulting centroids.



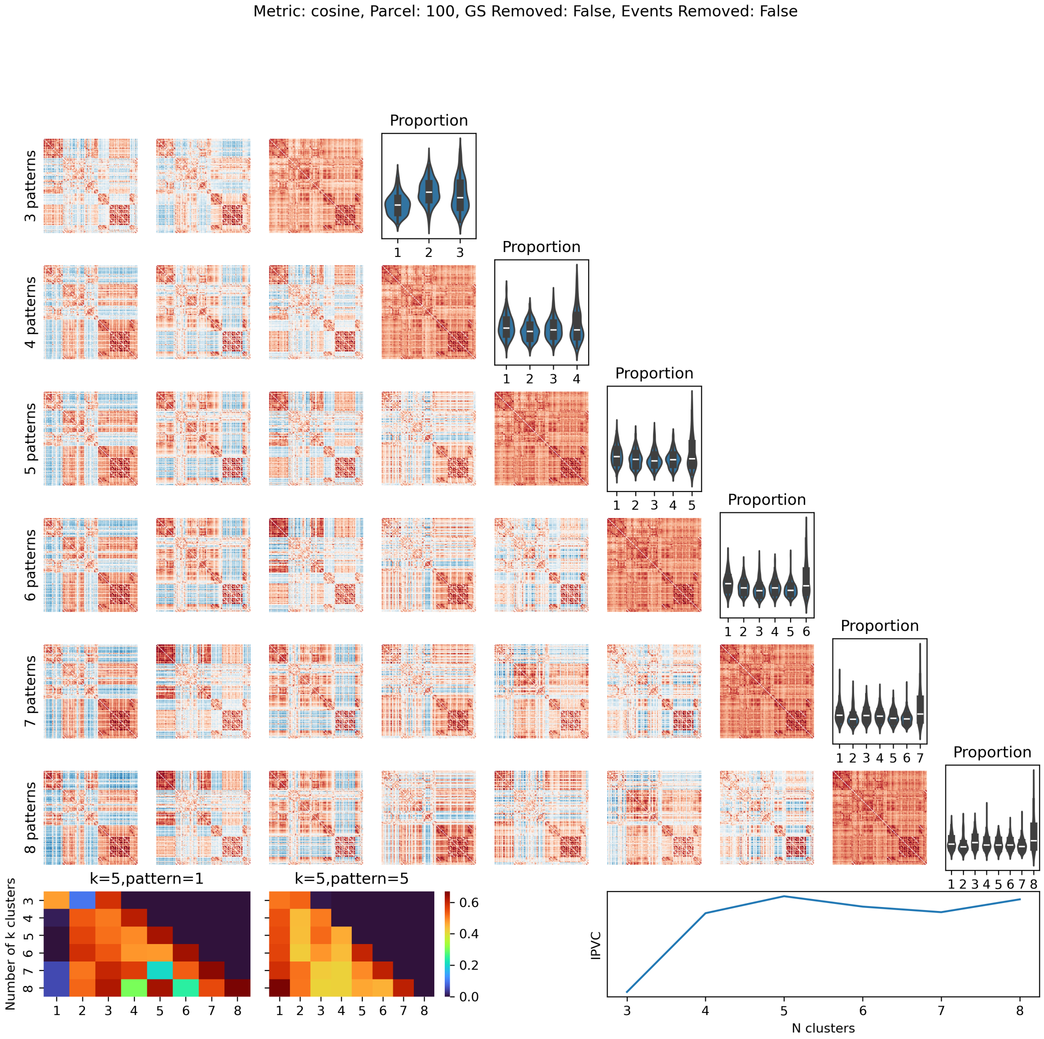
Supplementary Fig. 6.3-11: Recurrent and consistent brain configurations emerge under different clustering dimensionalities. Clustering parameters: Metric = Cosine distance, Global Signal Regression: True, Event Regression: True. For each value of k, patterns are ordered based on the standard deviation of their connectome, from the most variant (left) to the least (right). The right-most columns indicate per-participant pattern occurrence rate. Violin plots indicate data dispersion. Box plots indicate interquartile ranges and medians. Bottom row - Left. To examine whether patterns produced across different values of k presented correspondence, we estimated the distance of pattern 1 for $k = 5$ with respect to all patterns obtained for $k = 3$ to 8. Similarly, we estimated the distance of pattern 1 for $k = 5$ with respect to all patterns obtained for $k = 3$ to 7. Bottom row - Right. The variability of dynamic coordination patterns found by the clustering procedure is maximal with $k = 7$ clusters. For each selection of number of clusters in the K-means algorithm, we computed the correlation matrices between all the upper triangular parts of the resulting centroids.



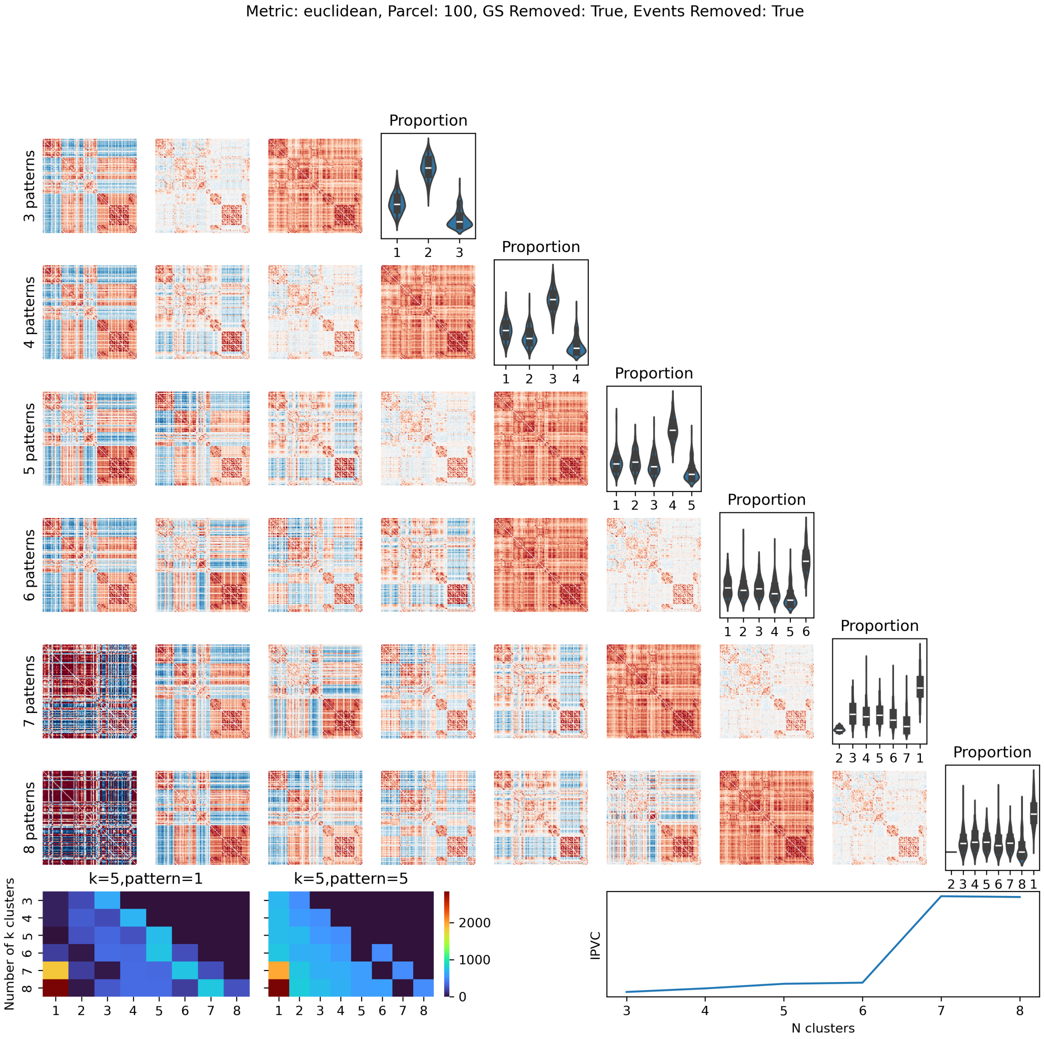
Supplementary Fig. 6.3-12: Recurrent and consistent brain configurations emerge under different clustering dimensionalities. Clustering parameters: Metric = Cosine distance, Global Signal Regression: True, Event Regression: False. For each value of k, patterns are ordered based on the standard deviation of their connectome, from the most variant (left) to the least (right). The right-most columns indicate per-participant pattern occurrence rate. Violin plots indicate data dispersion. Box plots indicate interquartile ranges and medians. Bottom row - Left. To examine whether patterns produced across different values of k presented correspondence, we estimated the distance of pattern 1 for $k = 5$ with respect to all patterns obtained for $k = 3$ to 8. Similarly, we estimated the distance of pattern 1 for $k = 5$ with respect to all patterns obtained for $k = 3$ to 7. Bottom row - Right. The variability of dynamic coordination patterns found by the clustering procedure is maximal with $k = 7$ clusters. For each selection of number of clusters in the K-means algorithm, we computed the correlation matrices between all the upper triangular parts of the resulting centroids.



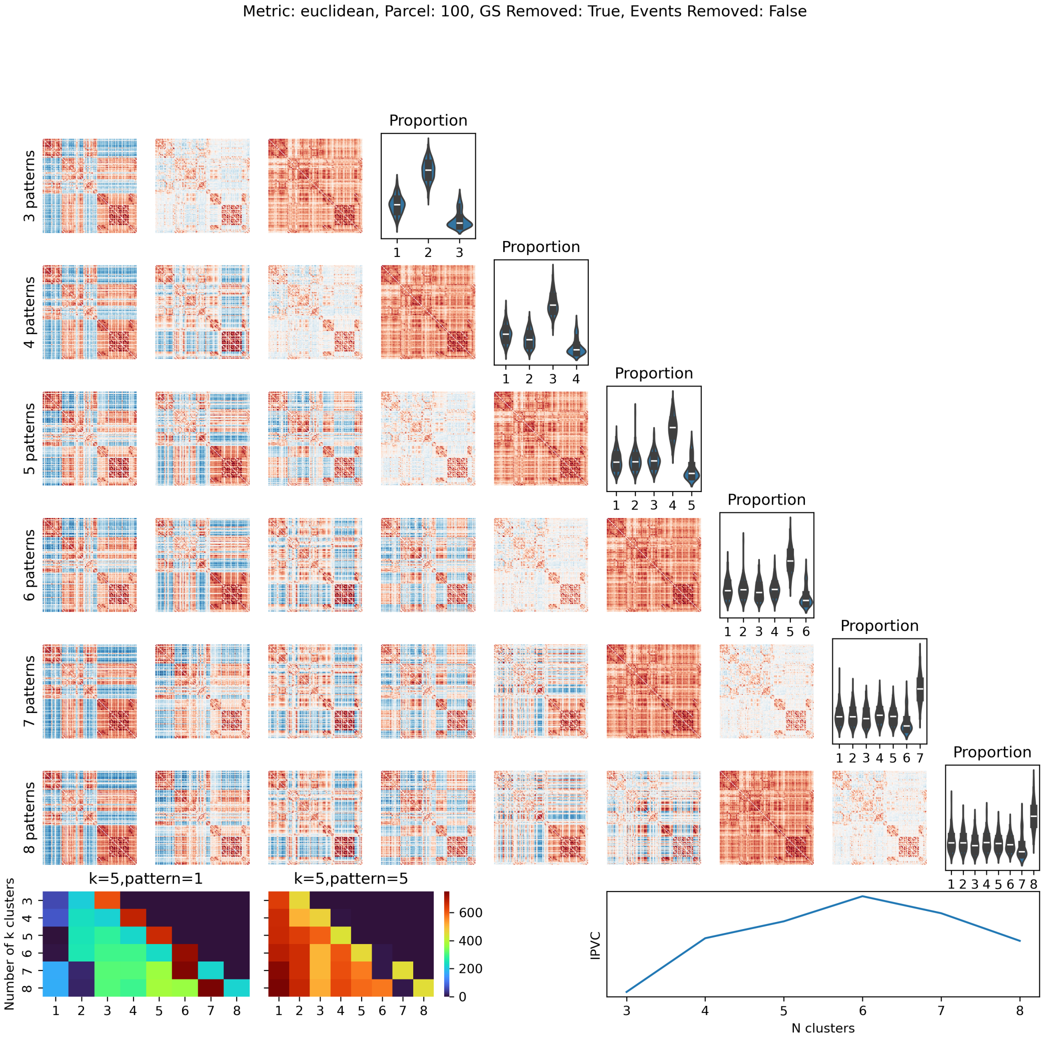
Supplementary Fig. 6.3-13: Recurrent and consistent brain configurations emerge under different clustering dimensionalities. Clustering parameters: Metric = Cosine distance, Global Signal Regression: False, Event Regression: True. For each value of k, patterns are ordered based on the standard deviation of their connectome, from the most variant (left) to the least (right). The right-most columns indicate per-participant pattern occurrence rate. Violin plots indicate data dispersion. Box plots indicate interquartile ranges and medians. Bottom row - Left. To examine whether patterns produced across different values of k presented correspondence, we estimated the distance of pattern 1 for $k = 5$ with respect to all patterns obtained for $k = 3$ to 8. Similarly, we estimated the distance of pattern 1 for $k = 5$ with respect to all patterns obtained for $k = 3$ to 7. Bottom row - Right. The variability of dynamic coordination patterns found by the clustering procedure is maximal with $k = 7$ clusters. For each selection of number of clusters in the K-means algorithm, we computed the correlation matrices between all the upper triangular parts of the resulting centroids.



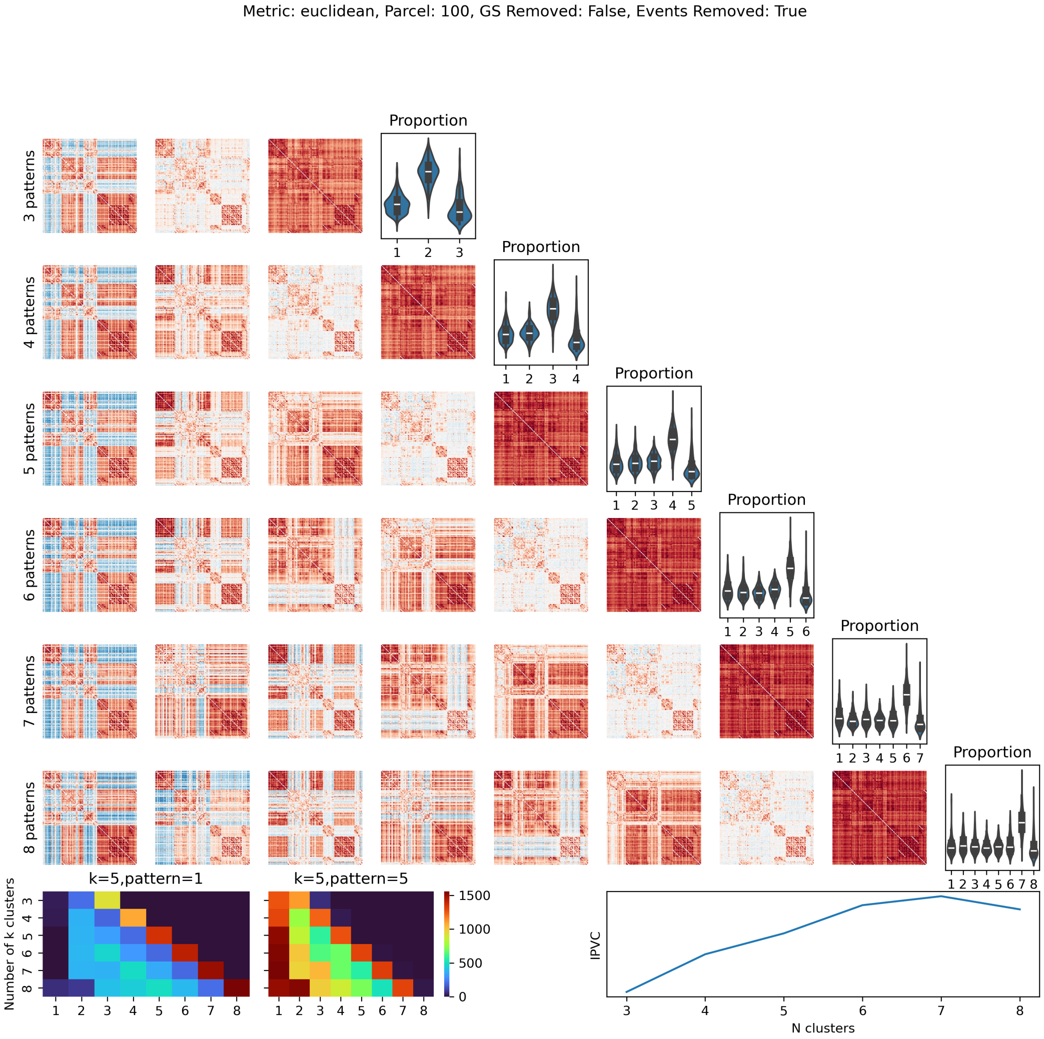
Supplementary Fig. 6.3-14: Recurrent and consistent brain configurations emerge under different clustering dimensionalities. Clustering parameters: Metric = Cosine distance, Global Signal Regression: False, Event Regression: False. For each value of k, patterns are ordered based on the standard deviation of their connectome, from the most variant (left) to the least (right). The right-most columns indicate per-participant pattern occurrence rate. Violin plots indicate data dispersion. Box plots indicate interquartile ranges and medians. Bottom row - Left. To examine whether patterns produced across different values of k presented correspondence, we estimated the distance of pattern 1 for $k = 5$ with respect to all patterns obtained for $k = 3$ to 8. Similarly, we estimated the distance of pattern 1 for $k = 5$ with respect to all patterns obtained for $k = 3$ to 7. Bottom row - Right. The variability of dynamic coordination patterns found by the clustering procedure is maximal with $k = 7$ clusters. For each selection of number of clusters in the K-means algorithm, we computed the correlation matrices between all the upper triangular parts of the resulting centroids.



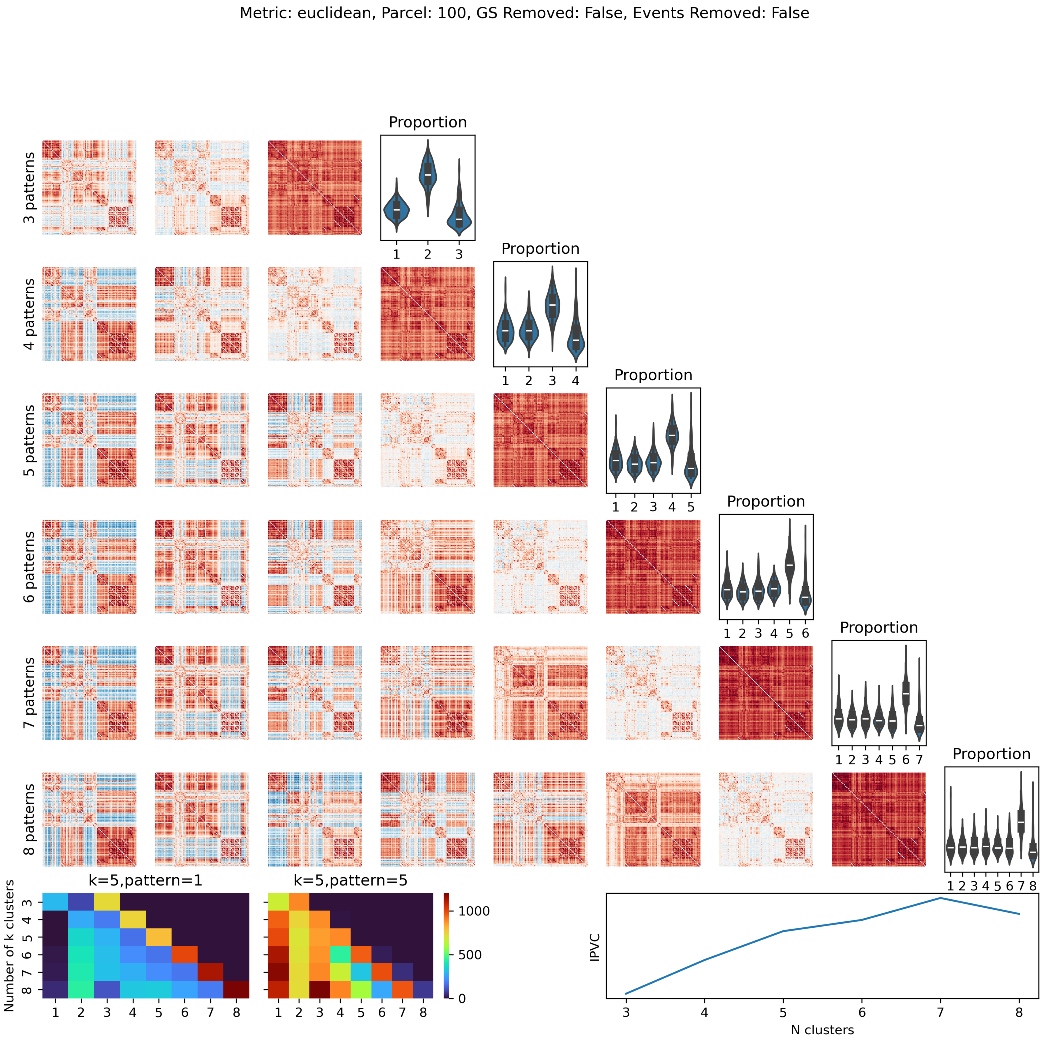
Supplementary Fig. 6.3-15: Recurrent and consistent brain configurations emerge under different clustering dimensionalities. Clustering parameters: Metric = Euclidean distance, Global Signal Regression: True, Event Regression: True. For each value of k, patterns are ordered based on the standard deviation of their connectome, from the most variant (left) to the least (right). The right-most columns indicate per-participant pattern occurrence rate. Violin plots indicate data dispersion. Box plots indicate interquartile ranges and medians. Bottom row - Left. To examine whether patterns produced across different values of k presented correspondence, we estimated the distance of pattern 1 for k = 5 with respect to all patterns obtained for k = 3 to 8. Similarly, we estimated the distance of pattern 1 for k = 5 with respect to all patterns obtained for k = 3 to 7. Bottom row - Right. The variability of dynamic coordination patterns found by the clustering procedure is maximal with k = 7 clusters. For each selection of number of clusters in the K-means algorithm, we computed the correlation matrices between all the upper triangular parts of the resulting centroids.



Supplementary Fig. 6.3-16: Recurrent and consistent brain configurations emerge under different clustering dimensionalities. Clustering parameters: Metric = Euclidean distance, Global Signal Regression: True, Event Regression: False. For each value of k, patterns are ordered based on the standard deviation of their connectome, from the most variant (left) to the least (right). The right-most columns indicate per-participant pattern occurrence rate. Violin plots indicate data dispersion. Box plots indicate interquartile ranges and medians. Bottom row - Left. To examine whether patterns produced across different values of k presented correspondence, we estimated the distance of pattern 1 for k = 5 with respect to all patterns obtained for k = 3 to 8. Similarly, we estimated the distance of pattern 1 for k = 5 with respect to all patterns obtained for k = 3 to 7. Bottom row - Right. The variability of dynamic coordination patterns found by the clustering procedure is maximal with k = 7 clusters. For each selection of number of clusters in the K-means algorithm, we computed the correlation matrices between all the upper triangular parts of the resulting centroids.



Supplementary Fig. 6.3-17: Recurrent and consistent brain configurations emerge under different clustering dimensionalities. Clustering parameters: Metric = Euclidean distance, Global Signal Regression: False, Event Regression: True. For each value of k, patterns are ordered based on the standard deviation of their connectome, from the most variant (left) to the least (right). The right-most columns indicate per-participant pattern occurrence rate. Violin plots indicate data dispersion. Box plots indicate interquartile ranges and medians. Bottom row - Left. To examine whether patterns produced across different values of k presented correspondence, we estimated the distance of pattern 1 for k = 5 with respect to all patterns obtained for k = 3 to 8. Similarly, we estimated the distance of pattern 1 for k = 5 with respect to all patterns obtained for k = 3 to 7. Bottom row - Right. The variability of dynamic coordination patterns found by the clustering procedure is maximal with k = 7 clusters. For each selection of number of clusters in the K-means algorithm, we computed the correlation matrices between all the upper triangular parts of the resulting centroids.



Supplementary Fig. 6.3-18: Recurrent and consistent brain configurations emerge under different clustering dimensionalities. Clustering parameters: Metric = Euclidean distance, Global Signal Regression: False, Event Regression: False. For each value of k, patterns are ordered based on the standard deviation of their connectome, from the most variant (left) to the least (right). The right-most columns indicate per-participant pattern occurrence rate. Violin plots indicate data dispersion. Box plots indicate interquartile ranges and medians. Bottom row - Left. To examine whether patterns produced across different values of k presented correspondence, we estimated the distance of pattern 1 for k = 5 with respect to all patterns obtained for k = 3 to 8. Similarly, we estimated the distance of pattern 1 for k = 5 with respect to all patterns obtained for k = 3 to 7. Bottom row - Right. The variability of dynamic coordination patterns found by the clustering procedure is maximal with k = 7 clusters. For each selection of number of clusters in the K-means algorithm, we computed the correlation matrices between all the upper triangular parts of the resulting centroids.

Supplementary Table 6.3-1: Interaction contrasts between mental states, alertness levels, and distance from brain patterns. Bold font indicates significance.

Alertness	Mental Contrasts	Estimate	SE	L. CL 95%	U. CL 95%	pFDR	Pattern
ExAlert	OFFTASK-ONTASK	-2.7e-07	1.2e-06	-4.1e-06	3.5e-06	8.3e-01	1
ExAlert	BLANK-OFFTASK	4.9e-06	4.0e-06	-7.4e-06	1.7e-05	4.1e-01	1
ExAlert	BLANK-ONTASK	4.6e-06	3.9e-06	-7.2e-06	1.6e-05	4.1e-01	1
Alert	**OFFTASK-ONTASK**	**8.9e-07**	**3.1e-07**	**-5.3e-08**	**1.8e-06**	**1.7e-02**	**1**
Alert	**BLANK-OFFTASK**	**2.2e-06**	**7.2e-07**	**2.3e-09**	**4.4e-06**	**1.2e-02**	**1**
Alert	**BLANK-ONTASK**	**3.1e-06**	**7.0e-07**	**9.6e-07**	**5.2e-06**	**2.2e-04**	**1**
Sleepy	OFFTASK-ONTASK	-5.2e-07	4.3e-07	-1.8e-06	7.8e-07	4.1e-01	1
Sleepy	BLANK-OFFTASK	7.9e-07	5.2e-07	-7.9e-07	2.4e-06	3.0e-01	1
Sleepy	BLANK-ONTASK	2.7e-07	5.6e-07	-1.4e-06	2.0e-06	6.9e-01	1
ExSleepy	OFFTASK-ONTASK	8.2e-07	9.7e-07	-2.1e-06	3.8e-06	6.4e-01	1
ExSleepy	BLANK-OFFTASK	-3.3e-07	6.1e-07	-2.2e-06	1.5e-06	6.9e-01	1
ExSleepy	BLANK-ONTASK	4.9e-07	1.0e-06	-2.6e-06	3.6e-06	6.9e-01	1
ExAlert	**OFFTASK-ONTASK**	**-5.0e-06**	**1.1e-06**	**-8.2e-06**	**-1.7e-06**	**8.9e-05**	**2**
Alert	**BLANK-OFFTASK**	**1.7e-06**	**6.2e-07**	**-1.9e-07**	**3.6e-06**	**3.2e-02**	**2**
Alert	**BLANK-ONTASK**	**2.0e-06**	**6.1e-07**	**1.6e-07**	**3.8e-06**	**9.9e-03**	**2**
Sleepy	OFFTASK-ONTASK	7.1e-07	3.7e-07	-4.3e-07	1.8e-06	1.6e-01	2
Sleepy	BLANK-OFFTASK	-7.6e-07	4.5e-07	-2.1e-06	6.2e-07	2.0e-01	2
Sleepy	BLANK-ONTASK	-5.3e-08	4.9e-07	-1.5e-06	1.4e-06	9.1e-01	2
ExSleepy	**OFFTASK-ONTASK**	**2.6e-06**	**8.5e-07**	**-2.8e-08**	**5.1e-06**	**1.9e-02**	**2**
ExSleepy	BLANK-OFFTASK	-6.6e-07	5.4e-07	-2.3e-06	9.8e-07	3.3e-01	2
ExSleepy	BLANK-ONTASK	1.9e-06	8.8e-07	-7.9e-07	4.6e-06	1.1e-01	2
ExAlert	OFFTASK-ONTASK	-1.7e-06	1.1e-06	-5.1e-06	1.8e-06	2.8e-01	3
ExAlert	BLANK-OFFTASK	-9.7e-07	3.6e-06	-1.2e-05	9.9e-06	7.9e-01	3
ExAlert	BLANK-ONTASK	-2.6e-06	3.4e-06	-1.3e-05	7.8e-06	5.8e-01	3
Alert	**OFFTASK-ONTASK**	**8.5e-07**	**2.8e-07**	**-4.4e-09**	**1.7e-06**	**7.1e-03**	**3**
Alert	**BLANK-OFFTASK**	**2.0e-06**	**6.5e-07**	**-2.4e-08**	**3.9e-06**	**7.1e-03**	**3**
Alert	**BLANK-ONTASK**	**2.8e-06**	**6.3e-07**	**8.9e-07**	**4.7e-06**	**6.3e-05**	**3**
Sleepy	OFFTASK-ONTASK	-2.4e-07	3.9e-07	-1.4e-06	9.4e-07	6.6e-01	3
Sleepy	BLANK-OFFTASK	3.9e-07	4.7e-07	-1.0e-06	1.8e-06	5.8e-01	3
Sleepy	BLANK-ONTASK	1.5e-07	5.1e-07	-1.4e-06	1.7e-06	7.9e-01	3
ExSleepy	**OFFTASK-ONTASK**	**3.3e-06**	**8.7e-07**	**6.9e-07**	**6.0e-06**	**5.5e-04**	**3**
ExSleepy	BLANK-OFFTASK	7.8e-07	5.6e-07	-9.1e-07	2.5e-06	2.8e-01	3
ExSleepy	**BLANK-ONTASK**	**4.1e-06**	**9.1e-07**	**1.4e-06**	**6.9e-06**	**6.1e-05**	**3**
ExAlert	**OFFTASK-ONTASK**	**-4.6e-06**	**1.1e-06**	**-7.9e-06**	**-1.3e-06**	**3.7e-04**	**4**
ExAlert	BLANK-OFFTASK	2.5e-06	3.4e-06	-7.9e-06	1.3e-05	6.0e-01	4
ExAlert	BLANK-ONTASK	-2.1e-06	3.3e-06	-1.2e-05	7.9e-06	6.2e-01	4
Alert	**OFFTASK-ONTASK**	**7.0e-07**	**2.7e-07**	**-1.2e-07**	**1.5e-06**	**4.0e-02**	**4**
Alert	BLANK-OFFTASK	1.2e-06	6.2e-07	-7.2e-07	3.0e-06	1.1e-01	4
Alert	**BLANK-ONTASK**	**1.9e-06**	**6.0e-07**	**3.7e-08**	**3.7e-06**	**1.0e-02**	**4**
Sleepy	OFFTASK-ONTASK	-3.3e-07	3.7e-07	-1.5e-06	8.0e-07	5.6e-01	4
Sleepy	BLANK-OFFTASK	-5.8e-07	4.5e-07	-2.0e-06	7.9e-07	3.2e-01	4
Sleepy	BLANK-ONTASK	-9.1e-07	4.9e-07	-2.4e-06	5.6e-07	1.1e-01	4
ExSleepy	**OFFTASK-ONTASK**	**3.2e-06**	**8.4e-07**	**6.8e-07**	**5.8e-06**	**1.3e-03**	**4**
ExSleepy	BLANK-OFFTASK	-1.5e-07	5.3e-07	-1.8e-06	1.5e-06	7.8e-01	4
ExSleepy	**BLANK-ONTASK**	**3.1e-06**	**8.8e-07**	**4.3e-07**	**5.8e-06**	**3.0e-03**	**4**

Alertness	**Mental Contrasts**	**Estimate**	**SE**	**L. CL 95%**	**U. CL 95%**	**pFDR**	**Pattern**
ExAlert	**OFFTASK-ONTASK**	**-7.6e-06**	**1.6e-06**	**-1.2e-05**	**-2.7e-06**	**2.5e-05**	**5**
ExAlert	BLANK-OFFTASK	4.3e-07	5.1e-06	-1.5e-05	1.6e-05	9.3e-01	5
ExAlert	BLANK-ONTASK	-7.1e-06	4.9e-06	-2.2e-05	7.7e-06	2.1e-01	5
Alert	OFFTASK-ONTASK	-6.1e-07	4.1e-07	-1.8e-06	6.3e-07	2.1e-01	5
Alert	BLANK-OFFTASK	2.0e-06	9.4e-07	-8.8e-07	4.8e-06	1.1e-01	5
Alert	BLANK-ONTASK	1.4e-06	9.1e-07	-1.4e-06	4.1e-06	2.1e-01	5
Sleepy	OFFTASK-ONTASK	-1.0e-06	5.6e-07	-2.7e-06	7.1e-07	1.8e-01	5
Sleepy	BLANK-OFFTASK	-1.2e-07	6.8e-07	-2.2e-06	1.9e-06	9.0e-01	5
Sleepy	BLANK-ONTASK	-1.1e-06	7.3e-07	-3.4e-06	1.1e-06	2.1e-01	5
ExSleepy	OFFTASK-ONTASK	2.6e-06	1.3e-06	-1.3e-06	6.5e-06	1.1e-01	5
ExSleepy	**BLANK-OFFTASK**	**-4.2e-06**	**8.1e-07**	**-6.6e-06**	**-1.7e-06**	**4.5e-06**	**5**
ExSleepy	BLANK-ONTASK	-1.6e-06	1.3e-06	-5.6e-06	2.5e-06	3.3e-01	5

Supplementary Methodology - FMRIPrep Pipeline

Anatomical data preprocessing. A total of 1 T1-weighted (T1w) images were found within the input BIDS dataset. The T1w image was corrected for intensity non-uniformity (INU) with `N4BiasFieldCorrection` (Tustison et al., 2010), distributed with ANTs 2.5.0 (Avants et al., 2008, RRID:SCR_004757), and used as T1w-reference throughout the workflow. The T1w-reference was then skull-stripped with the `antsBrainExtraction.sh` workflow (from ANTs), using OASIS30ANTs as target template. Brain tissue segmentation of cerebrospinal fluid (CSF), white-matter (WM) and gray-matter (GM) was performed on the brain-extracted T1w using `fast` (FSL (6.0.7.14), RRID:SCR_002823, Zhang et al., 2001). Volume-based spatial normalization to one standard space (MNI152NLin2009cAsym) was performed through nonlinear registration with `antsRegistration` (ANTs 2.5.0), using brain-extracted versions of both T1w reference and the T1w template. The following template was were selected for spatial normalization and accessed with *TemplateFlow* (23.1.0, Ciric et al., 2022): *ICBM 152 Nonlinear Asymmetrical template version 2009c* [Fonov et al. (2009), RRID:SCR_008796; TemplateFlow ID: NI152NLin2009cAsym].

Functional data preprocessing. For each of the 4 BOLD runs found per subject (across all tasks and sessions), the following preprocessing was performed. First, a reference volume was generated, using a custom methodology of *fMRIPrep*, for use in head motion correction. Head-motion parameters with respect to the BOLD reference (transformation matrices, and six corresponding rotation and translation parameters) are estimated before any spatiotemporal filtering using `mcflirt` (FSL , Jenkinson et al., 2002). The BOLD reference was then co registered to the T1w reference using `mri_coreg` (FreeSurfer) followed by `flirt` (FSL , Jenkinson & Smith, 2001) with the boundary-based registration (Greve & Fischl, 2009) cost-function. Co-registration was conFig.d with six degrees of freedom. Several confounding time series were calculated based on the *preprocessed BOLD*: framewise displacement (FD), DVARS and three region-wise global signals. FD was computed using two formulations following Power (absolute sum of relative motions, Power et al. (2014)) and Jenkinson (relative root mean square displacement between affines, Jenkinson et al. (2002)). FD and DVARS are calculated for each functional run, both using their implementations in *Nipype* (following the definitions by Power et al., 2014). The three global signals are extracted within the CSF, the WM, and the whole-brain masks. Additionally, a set of physiological regressors were extracted to allow for component-based noise correction (*CompCor*, Behzadi et al., 2007). Principal components are estimated after high-pass filtering the *preprocessed BOLD* time series (using a discrete cosine filter with 128s cut-off) for the two *CompCor* variants: temporal (tCompCor) and anatomical (aCompCor). tCompCor components are then calculated from the top 2% variable voxels within the brain mask. For aCompCor, three probabilistic masks (CSF, WM and combined CSF+WM) are generated in anatomical space. The implementation differs from that of Behzadi et al. in that instead of eroding the masks by 2 pixels on BOLD space, a mask of pixels that likely contain a volume fraction of GM is subtracted from the aCompCor masks. This mask is obtained by thresholding the corresponding partial volume map at 0.05, and it ensures components are not extracted from voxels containing a minimal fraction of GM. Finally, these masks are resampled into BOLD space and binarized by thresholding at 0.99 (as in the original implementation). Components are also calculated separately within the WM and CSF masks. For each CompCor decomposition, the k components with the largest singular values are retained, such that the retained components' time series are sufficient to explain 50 percent of variance across the nuisance mask (CSF, WM, combined, or temporal). The remaining components are dropped from consideration. The head-motion estimates calculated in the correction step were also placed within the corresponding confounds file. The confound time series derived from head motion estimates and global signals were expanded with the inclusion of temporal derivatives and quadratic terms for each (Satterthwaite et al., 2013). Frames that exceeded a threshold of 0.5 mm FD or 1.5 standardized DVARS were annotated as motion outliers. Additional nuisance time series are calculated by means of principal components analysis of the signal found within a thin band (*crown*) of voxels around the edge of the brain, as proposed by (Patriat et al., 2017). All resamplings can be performed with *a single interpolation step* by composing all the pertinent transformations (i.e. head-motion transform matrices, susceptibility distortion correction when available, and coregistrations to anatomical and output spaces). Gridded (volumetric) resamplings were performed using `nitransforms`, conFig.d with cubic B-spline interpolation.

6.4 Reproducibility receipt

Chapter 2

All codes to replicate the statistical analysis in Chapter 2 are available in `https://gitlab.uliege.be/Paradeisios.Boulakis/mb_activation`. The code is based on existing Python libraries and custom functions. The provided repository contains all the necessary information to install an environment and reproduce the analysis on the experience sampling dataset. We used an existing experience sampling dataset, during which participants had the option to report the absence of thoughts (Van Calster et al., 2017). Previous research on this dataset has replicated consistent fMRI findings in other mental states (MW: DMN and executive cortical areas). The raw data are also freely available in BIDS format from: `https://openneuro.org/datasets/ds004134/versions/1.0.0`. The unthresholded maps present in this paper can be found at `https://neurovault.org/collections/14761/`.

Chapter 3

All codes to replicate the power analysis, the experience sampling paradigm, and the statitical analysis in Chapter 3 can be found at `gitlab.uliege.be/Paradeisios.Boulakis/mind_blanking_arousal`. An archived version of the code at the time of study completion can be found at `doi.org/10.58119/ULG/174Q6G`. The aggregated raw data in a BIDS format, the trained machine-learning models, experimental and analysis logs, and result dataframes can be found at `doi.org/10.58119/ULG/174Q6G`. The stage 1 accepted-in-principle protocol can be found at `osf.io/sh2ye`.

Chapter 4

All codes to replicate the statistical analysis in Chapter 4 can be found at `gitlab.uliege.be/Paradeisios.Boulakis/mb_monash`.

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