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# *The Nested States Model*

## *An Empirical Framework for Integrating Brain and Mind*

**Abstract:** *Philosophy of mind has made substantial progress on biologically-rooted approaches to understanding the mind and subjectivity through the enactivist perspective, but research on subjectivity within neuroscience has not kept pace. Indeed, we possess no principled means of relating experiential phenomena to neurophysiological processes. Here, we present the Nested States Model as a framework to guide empirical investigation into the relationship between subjectivity and neurobiology. Building on recent work in phenomenology and philosophy of mind, we develop an account of experiential states as layered, or nested. We argue that this nested structure is also apparent in brain activity. The recognition of this structural homology — that both experiential and brain states can be characterized as systems of nested states — brings our views of subjective mental states into broad alignment with our understanding of general principles and properties of brain activity. This alignment enables a more systematic approach to formulating specific hypotheses and predictions about how the two domains relate to one another.*

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## 1. Introduction

The cognitivist and connectionist paradigms that dominated cognitive science throughout the latter half of the twentieth century defined much of the scope of contemporary neuroscientific investigation, with a consequent lack of emphasis on the direct investigation of subjectivity (Thompson, 2007; Gallagher, 2010; 2017; Kyzar and Denfield, 2023). This lack of emphasis is all the more surprising given that this problem has significant practical import. Subjective experience is what we aim to temporarily prevent during anaesthesia, what we need to identify after brain injury, and what features predominantly in psychopathology.

In recent decades, a new and more firmly biologically-rooted theoretical perspective, known as the enactive approach, has arisen within philosophy of mind. Enactivism emphasizes the continuity between mind and life and returns the investigation of subjective experience to a place of central importance, drawing on the field of phenomenology to do so (Varela, Thompson and Rosch, 1991; Thompson, 2007). Enactivist accounts of mind highlight the reciprocal interaction between body and environment and the role of the organism as a self-organizing, autopoietic system engaged in participatory sense-making with the environment (De Jaegher and Di Paolo, 2007; Thompson, 2007; Di Paolo, 2018). This approach has influenced a number of domains including intersubjectivity (Di Paolo and De Jaegher, 2012), affectivity (Colombetti, 2017), and psychopathology (Fuchs, 2018).

Despite these successes and its natural links to biology, this promising theoretical perspective has not yet translated into an ongoing, empirically-productive dialogue with contemporary neuroscience. This dearth of persistent cross-talk is not for lack of early efforts (Varela, 1996; Varela *et al.*, 2001), but significant hurdles remain. Tackling the complexity of the brain–body–environment system requires different analytic approaches than those emphasized by cognitivism. Additionally, the methods for investigating brain activity on the finest spatial and temporal scales are also the most invasive, limiting much work to animal models and hindering simultaneous studies of subjective experience. Moreover, the scope of enactivism as a full-fledged scientific paradigm is still under debate (Gallagher, 2017; Meyer and Brancazio, 2022). Meyer and Brancazio (2022) note, ‘enactivism does not have a comprehensive story for how the various capacities of the mind can be explained, and how these can

be examined empirically... nor do we see the kind of scientific “divide and conquer” schemes for operationalisation taken up in cognitivist cognitive science.’

Here, our overarching goal is to develop just such an operationalized scheme for the empirical examination of subjective experience in relation to neurophysiological processes. As enactivism takes an holistic view of the relationship between the entire organism and its environment, we are alert to avoid the mereological fallacy highlighted by Fuchs (2018) in which brain activity is mistakenly seen as sufficient to account for the mind. Nevertheless, the nervous system still plays a necessary and vital role, and delineating the full extent of this role is critical in understanding the link between biology and subjectivity. Here, we present an empirical framework to address this question.

We begin by summarizing work in the phenomenological and enactive literature in the preceding decades describing a layered, or nested, quality of subjective experience. While numerous authors have more or less directly engaged with this notion, we are not aware of a dedicated, in-depth exposition of this viewpoint. We, therefore, provide such an account, developing what we call the Nested States Model (NSM). We show that experience can be characterized as a system of nested states, and we show how this nested structure constrains how one mental state flows into another. We then expound on what is, in our estimation, the principal advantage of the NSM — its ability to generate empirical predictions which can be tested using the methods of modern neuroscience. We show that activity in the nervous system can also be described as a system of nested states, and we explore how to build out the bridge between the phenomenological and neurophysiological domains created by this recognition of structural homology. Given that both domains are seen to be systems of nested states, our view of subjective mental states is brought into broad alignment with our understanding of brain activity, allowing us to formulate specific hypotheses and predictions about how the experiential and neurophysiological domains relate to one another. In this manner, the NSM provides a targeted ‘scheme of operationalization’ (Meyer and Brancazio, 2022) from a phenomenological and enactivist vantage point that offers a systematic way to investigate subjective experience from the lens of both neuroscience and philosophy of mind.

## 2. A Phenomenological Analysis of the Nested Structure of Experience

### 2.1. *Emerging views on the layered quality of experience*

Here, we argue that recent work in the enactive and phenomenological literature has begun to converge on a view of mental states and the structure of subjective experience which recognizes the layered quality of experience. We will develop this view of mental states, showing that, while it has primarily been applied to the study of affective and emotional states, the approach applies to the structure of experiential states in general. Importantly, we aim to render this layered, or nested, quality in terms that are empirically tractable.

An exposition of any experiential framework from an enactivist perspective would be incomplete without acknowledging the role of the lived body. While our later discussion will focus on empirically testing the relationship between subjective states and brain dynamics, we do not mean to remove the brain from its proper place — situated within a body. Indeed, embodiment provides the ultimate foundation for experiential states. This point has been discussed at length in the enactivist literature, and the notion that a disembodied ‘brain-in-a-vat’ could somehow replicate lived experience is perhaps best refuted by Thompson and Cosmelli (2011). They argue that body and brain are dynamically entangled to the extent that any ‘vat’ would essentially become a surrogate body. This line of reasoning demonstrates the indispensable nature of the lived body when discussing brain activity, and Thompson and Cosmelli state that it is precisely this embodiment that provides the background for *creature consciousness*, or the feeling of what-it-is-like-to-be a phenomenally conscious organism (*ibid.*). Particularly notable for our purposes, they claim that creature consciousness is intimately tied to background states of consciousness, such as arousal and the sleep–wake cycle, stating: ‘background states of consciousness, such as wakefulness and dreaming, are domain general, not modality specific. They characterize one’s overall phenomenal perspective as a conscious subject’ and constitute ‘global modulations of creature consciousness’ (*ibid.*). Thus, Thompson and Cosmelli discuss the foundational role of the body in enabling subjective experience and allude to a layered structure of experience (through use of words like ‘background’).

The view that experience has a layered structure is most clearly articulated in recent work by Ratcliffe (2008) and Colombetti (2017),

though there are precursors to this idea in earlier phenomenological work. Ratcliffe argues that we catch glimpses of this notion in Heidegger's discussions of affect and mood, which form the basis for Ratcliffe's own work on existential feelings. Ratcliffe interprets Heidegger to claim that 'affective states... amount to a background sense of being situated in a world' that 'shapes all our experiences, thoughts and activities' (Ratcliffe, 2008, p. 42) and which 'is changeable in structure' (*ibid.*, p. 52). Here, we already touch upon the two key themes that we will develop in more detail in this section and which will constitute the core claims of the NSM. First is the notion of a 'background' aspect of experience which can change over time and which implies also the notion of an experiential foreground. Hence, we see an initial sketch of the layered quality of experiential states. Second is the notion that the experiential background 'shapes' other aspects of our experience in some way.

This second concept is hinted at by Heidegger and further elaborated by Ratcliffe. Heidegger characterizes moods as what 'make it possible first of all to direct oneself towards something' (Heidegger, 1962/1988). Ratcliffe makes this notion more concrete through an example of an instance of fear. He notes that 'before one feels afraid, one already has a sense of belonging to the world, of being in a situation *in* which one is afraid', which is thanks to the mood one finds oneself to be in (Ratcliffe, 2008, p. 49). It is through this particular mood that 'one is attuned to the world in such a way that experiences of object-directed fear are possible' (*ibid.*, p. 49). The implication here, which forms the basis for the second key claim of the NSM, is that different background senses of being in a world — different Heideggerian moods in this case — constrain, shape, or make possible certain other aspects of our experiential states.

Ratcliffe delineates the phenomenological category of *existential feelings* as follows: 'an existential feeling is a background sense of belonging to the world, which structures all experiences' (*ibid.*, p. 77). He clarifies that the moods which Heidegger discusses are existential feelings, but more colloquial uses of the term 'mood' do not necessarily reference the 'all-encompassing existential orientations' he means this category to signify; he notes that the term 'affect' would also be appropriate for this category. Continuing on this theme, Ratcliffe states that 'when one experiences an emotion, one already finds oneself in the world. And the way in which one finds oneself in the world disposes one to certain kinds of emotional experience' (*ibid.*, p. 40). Thus, different existential feelings not only operate in

the experiential background, they also dispose us to different emotional experiences, constraining more foreground aspects of our experiential states. Colombetti (2017) describes this structure of affective states and its consequences most clearly when she states that ‘moods appear to facilitate some emotional episodes more than others’ and affect ‘the kinds of emotional episodes [an organism] is likely to enact’ (pp. 77–8). She also touches on the notion of a layered quality of experience more explicitly when discussing Ratcliffe’s existential feelings, noting that existential feelings are ‘deeper’ than specific emotions (*ibid.*, p. 81).

On the topic of depth, both Colombetti and Ratcliffe use the terms foreground and background to differentiate aspects of subjective experience, and it is worth taking a moment to discuss these terms more explicitly. Colombetti (2011) uses these terms when discussing how bodily feelings relate to emotional experiences. She speaks of bodily feelings coming to the ‘foreground of awareness’, noting that a foreground feeling ‘comes into relief, it makes itself apparent, it asserts its presence’ (*ibid.*). In contrast, a background bodily feeling ‘does not “stand out” and is not apparent, but it is still nevertheless *felt*’; elsewhere she states that background feelings ‘are not attended’ (*ibid.*). From these definitions, it is unclear if Colombetti intends to fully equate notions of foreground versus background feelings with attended versus non-attended feelings. Ratcliffe, too, discusses the experiential foreground and background, and it is not always clear whether these terms should be taken as synonymous with attended (foreground) versus present-but-not-attended (background) feelings, or whether a more specific structural claim is intended.

Drawing from their work on the topic discussed above, it seems clear that both authors view affective experience as being layered. What remains unclear is if they mean to use the terms foreground and background to refer to these different layers or if they have a different sense in mind — one that distinguishes different degrees of attention or awareness. As we will see, the NSM provides a more explicit and concrete structural definition for the use of these terms, where foreground and background states explicitly reference different layers of our experiential states.

We have seen how recent work in the phenomenological and enactive literature has honed in on two key features of affective states and emotional experience. First, that they are layered; and second, that deeper, or more background, states constrain what types of more foreground emotional states are likely to occur. The core of our

phenomenological claim is that we agree, and we think that these ideas apply even more broadly, characterizing not only affective states but the structure and dynamics of experiential states in general.

## 2.2. *Experience as a system of nested states*

From a phenomenological standpoint, the NSM makes two core claims:

*Claim 1:* The basic structure of our experience is a system of nested states.

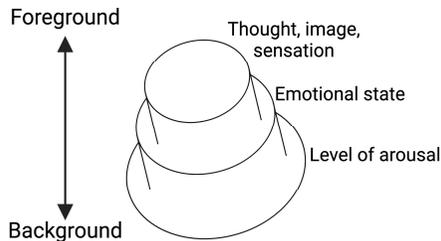
*Claim 2:* This nested structure constrains, and therefore guides, how one mental state flows into another, thereby governing how our experience changes over time.

These claims can be illustrated by examining a hypothetical moment of lived experience. In this example, at moment  $x$ , John is walking outside on the sidewalk when he stubs his toe, feeling a sudden, strong pain. Imagine also that, earlier that day, John and his girlfriend of several years had a big fight and are in the midst of a potential break-up — a situation which has been consuming much of John's attention, up to and including the moment when he stubs his toe. In examining John's mental state at this moment in time, though he may be most acutely aware of the pain in his toe at moment  $x$ , there is, thankfully, more to his experiential state than just pain.

Indeed, his pain occurs in the context of, or, more specifically, is *nested* in, a background of emotions — sadness, anxiety, and perhaps some fear (or, alternatively, happiness or relief if he is not particularly pleased to be in this relationship at this point in his life). All of these features are part of his current experiential state, but the important aspect to note is that these are not all simply co-occurring — there is a particular structure to these features.

This structure is what we refer to as *nested*. By *nested* we mean that some features of the mental state, labelled as the more 'foreground' features, occur in the context of certain other features, labelled as more 'background' features, which in turn occur in the context of yet other, even more 'background' features, and so on. To make this description more concrete, in our example, the feeling of pain would be said to exist in the foreground relative to his emotional state of sadness and anxiety, which are more background features, all of which occur in the yet-more background context of a particular state of arousal, that of wakefulness (as opposed to sleep, for instance).

We can visualize this structure schematically in Figure 1. Here, we get a sense of the relationships between the various features of John’s mental state and their positioning in the foreground to background continuum. It may be helpful to imagine the various levels of foreground to background features of a mental state as sections of a collapsible telescope, with the narrowest piece corresponding to the most foreground features of a mental state — thoughts, images, sensations — and the widest piece to the most background features, our state of arousal (as in the sleep–wake cycle). While our present example articulates only three layers for ease of conceptual illustration, we argue below that our subjective experience is comprised of more than just these layers — though exactly how many is ultimately an empirical question.



*Figure 1.* Example nested state configuration depicting aspects of John’s experiential state at moment  $x$ . Each layer represents a different component feature of a mental state.

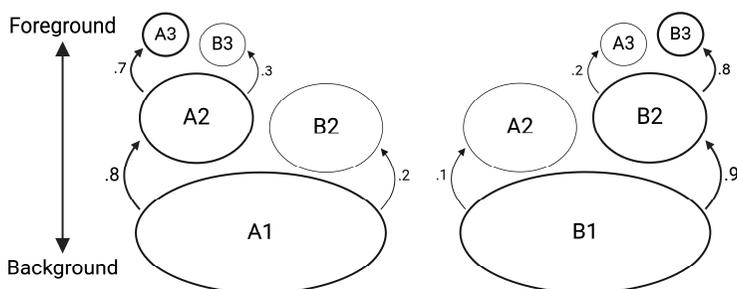
Further variations on this example can help clarify this sense of the nested structure of experiential states. Imagine John and his girlfriend have not spoken in several days, but he has heard from a friend that she is angry towards him. John wants to get a coffee from his favourite café, but this also happens to be his girlfriend’s favourite café too. On the way there, John feels increasingly anxious and nervous about a potential encounter with her. The thought occurs to him, ‘I wonder if she’ll be there’, then, ‘I hope she’s not there’. As he gets closer, he can’t help but focus on their possible encounter and imagine various ways it may play out.

Considering the moment when John has the thought ‘I wonder if she’ll be there’, we would say that this thought is in the foreground, nested in a more background context of anxiety and nervousness, which itself occurs in the context of wakefulness. We could imagine, though, that instead of actually being on the way to the café, John is

simply dreaming about this scenario. In this case, the foreground features (the thoughts) and intermediate background features (the emotions) of his mental state would be the same, whereas they would be occurring in a deeper background context of a level of arousal associated with sleep, likely REM sleep.

As is also apparent in the example above, our subjective experience is inherently temporal; hence the metaphor, as employed by William James, of a stream of consciousness (James, 1890). The way in which subjective experience changes over time relates to Claim 2 of the NSM, and here we emphasize two key points. First, John's thoughts (foreground mental state features) change in the context of an emotional state (intermediate background features) which does not change appreciably over this momentary time span. More accurately, the emotional state changes at a slower timescale than do his thoughts. Additionally, his state of arousal of wakefulness (a deeper background state) changes at an even slower timescale than his emotional state. Thus, we notice that different layers of features of the nested state change over different timescales. Second, in the context of his anxiety, he felt that *he could not help but* focus on certain more foreground thoughts. That is, the more background features of a mental state exert a powerful influence on more foreground features (though as we discuss below, foreground features can modulate more background features as well).

Thus, our notion of nesting entails more than just a relation between layers, it entails constraint. A foreground feature not only occurs in the context of a set of more background features, but those background features constrain which foreground features are likely to occur (as noted for emotion and mood by Ratcliffe, 2008, and Colombetti, 2017). This is the second claim of the NSM. The foreground states that can be or are likely to be expressed at any given moment depend strongly on the more immediate background states operating at that time, such that if background state A1 is active, then it is quite easy for foreground state A2 to occur but difficult for foreground state B2 to occur (which has a much higher probability of occurring if background state B1 is active). Figure 2 depicts this process of constraint across three nested layers, with hypothetical probabilities added to illustrate the point.



*Figure 2.* Background states constrain which more foreground states are likely to occur. On the left, when background state A1 is active, the intermediate state A2 is more likely to occur (with hypothetical probability 0.8) than is intermediate state B2 (probability 0.2). This process of constraint is recapitulated in the next layer, where foreground state A3 is much more likely to occur (with probability 0.7) than is foreground state B3, given that state A2 is active. On the right, background state B1 is active, making intermediate state B2 more likely to occur, which in turns makes foreground state B3 more likely than A3 to occur. Numbers in the figure depict hypothetical probabilities of a state occurring.

Given that he was anxious while on his way to the café, John was much more likely to have the specific, worried thoughts we saw in the above example. Nested in a context of anxiety, it was unlikely John would have been fantasizing about meeting someone new at the café, for instance, rather than anticipating an unwanted encounter with his girlfriend. Alternatively, had John actually been unhappy in this relationship and relieved by the prospect of its ending, we would expect his thoughts would have been biased in a different direction, and perhaps, in that case, he would have been fantasizing about meeting someone new rather than focusing on an unwanted encounter. In this manner, background states constrain or sculpt the space of possibilities for which more foreground states may occur, shaping the riverbed for our stream of consciousness.

Regardless of the specific thoughts John may have had on his way to the café, our example serves to illustrate the general point that background features constrain the foreground features of our mental states. This point can be made even more forcefully if we examine the most background features of our mental states. Take, for instance, the background state of arousal of slow wave sleep (contrasted with wakefulness). While this stage of sleep is critical for our mental functioning, it is generally not one in which we have any clear conscious experiences. That is, it is a background state which essentially

precludes the occurrence of any sort of foreground features like thoughts, images, or feelings whatsoever.

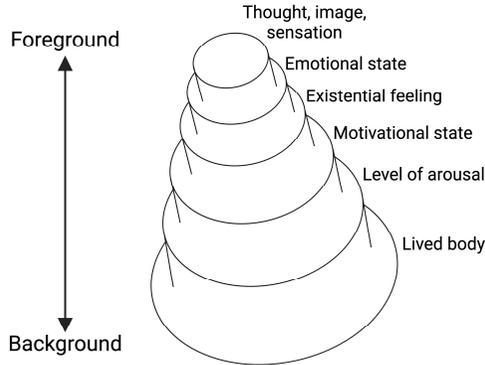
To summarize thus far, we have developed the view of subjective experience as having a layered structure, elaborating this notion through the specific claims of the NSM and clarifying what is meant by an experiential foreground and background. Additionally, specifically through Claim 2, we see how the nested structure of a mental state guides how our subjective experience changes over time, partially accounting for the flow of the stream of consciousness. While we made use of a simple example to illustrate these claims, we end our treatment of the NSM from a phenomenological perspective by outlining an initial proposal for a taxonomy of nested states from an enactive standpoint.

### *2.3. An initial taxonomy for the NSM*

We feel that the principal benefit of the NSM is that it renders subjective phenomena into a structure which is empirically tractable. Neuroscientific experiments can be designed to directly interrogate the various layers of experience, providing critical data which can then inform updated theorizing about the structure of mind and brain from both neuroscientific and phenomenological perspectives. With this sustained dialogue in place, the need for a definitive theory of the *exact* layers of experience is obviated, as repeated cycles of experimentation and updating of hypotheses will bring us closer to a unified understanding of the relationship between subjectivity and brain activity. With these points in mind, we now sketch a proposal for an initial hierarchical taxonomy of the NSM.

We share the view put forward by Thompson and Cosmelli (2011), and others in the enactivist tradition, that the lived body is the vessel through which subjectivity flows, providing the foundation for all other layers of the NSM. Indeed, we suggest that an enactivist hierarchy of nested states begins here, with the body as the deepest background state constraining all more foreground states. As discussed above, states change over time, and more background states tend to change more slowly than more foreground states do. The body, barring the traumatic circumstances of sudden and severe injury, adheres to these requirements of a background state and provides the ultimate constraint on the more foreground layers that can comprise our experiential state as a whole. Nested within the background state of the lived body are several further layers, illustrated in Figure 3.

Arousal states, or background states of consciousness comprising the sleep–wake cycle, appear next in our hierarchy, followed by what we label motivational states.



*Figure 3.* An initial hierarchical taxonomy depicting the various layers of an experiential state.

Motivational states include (at least) biological drives or needs and their occurrent feelings such as hunger, thirst, or lust, and possibly loneliness (in social species). There is a need for further phenomenological investigation of this aspect of our experiential states, and it is beyond the scope of the present article to provide such treatment, but motivational states undoubtedly factor into our experiential states. They act in accordance with Claim 2, influencing the types of more foreground states which are likely to occur given a particular motivational state. We propose that motivational states are deeper in the hierarchy than existential feelings, as it is easier to imagine how states of hunger or thirst, for instance, may influence existential feelings than the reverse, but we emphasize this is ultimately an empirical question. Existential feelings, then, are nested in the foreground of motivational states, followed next by emotional states, and in the foreground of all of this would be sensations, images, and thoughts.

Again, this taxonomy serves as a starting point for an empirical approach to studying its relationship to brain dynamics. We expect that this taxonomy will be clarified and revised through sustained dialogue between experimental and phenomenological investigation. Indeed, work in the psychological literature lends empirical support to features of this proposed hierarchy (e.g. motivational states, like hunger, influence affective states — Ackermans *et al.*, 2022; affective

and emotional states influence thoughts, memory, and imagery — Hollon, Kendall and Lumry, 1986; Beck *et al.*, 1987; Faul and LaBar, 2022).

We next turn to the issue of causal directionality. In which direction do the levels of the NSM hierarchy exert influence? Our examples above principally describe a global-to-local, or background-to-foreground, directionality. Nonetheless, we can imagine that instead of walking along the sidewalk and stubbing his toe in the midst of an angst-ridden break-up, John was having a rather fine day prior to moment  $x$ . Then, immediately following his toe stub, the experience of pain, and of anxiety over any resulting injuries, leads to a more gradual change in his existential feelings and motivational state. In this manner, we see that the causal chain operates bidirectionally, in both a background-to-foreground and foreground-to-background fashion. Colombetti (2017) argues similarly when she notes that ‘the reiteration of certain emotion forms can carve a topology that leads to the relative stabilization of certain mood forms’ over time (p. 78; Ratcliffe, 2008, and Fuchs, 2018, offer similar arguments).

These bidirectional causal chains through layers of subjective experience are reminiscent of the ecological hierarchy identified by Fuchs (2018). He identifies levels of this hierarchy and their interaction with the environment: molecules interacting via metabolism, cells and tissues via homeostatic processes, and the organism via perception and movement. Fuchs describes this hierarchical organization as a structuring influence, which constrains and integrates functions at other levels into emergent patterns. Plainly stated, both local-to-global and global-to-local influences constrain the possibility space in other parts of the hierarchy. This ecological model is extended to the subjective and, crucially, neuronal domains: ‘My thoughts — as agile as they may be — are never absolutely free. Rather they follow various paths which my experiences pre-draft as potential routes... the neuronal processes must also orient themselves along such pathways’ (*ibid.*, p. 234).

This line of reasoning raises the question, is the structure of subjective experience mirrored in the activity of the nervous system? We believe that it is. In the next section, we argue that activity in the nervous system shares an important structural similarity with subjective experience: that it, too, can be described as a system of nested states. Indeed, we see this recognition of structural homology as the key insight of the NSM, leading to its most promising application —

its potential to act as a bridging framework between phenomenological enquiry and neural data.

### **3. The Nested States Model, from a Neurobiological Point of View**

#### *3.1. Brain states exhibit a nested structure*

On a neurobiological level, we assert the same claims with regard to the dynamics of neuronal activity as were made for subjective experience.

*Claim 1b:* The basic structure of activity in the brain is a system of nested states.

*Claim 2b:* This nested structure constrains how one brain state can flow into another.

There is a wide range of evidence from systems neuroscience that supports these claims. We will draw on this work to support the view that brain states share an homologous structure with experiential states, highlighting clear initial points of overlap with certain background states of the hierarchy we proposed in the previous section (Figure 3).

We can conceptualize a brain state in a similar manner as a mental state — as a snapshot of the activity occurring across the brain at a given moment in time. In neuroscience, such brain states are typically identified according to a set of measurable and quantifiable variables related to neuronal activity, such as the firing rate of each neuron being recorded, or the power in different frequency bands of the recorded local field potentials (LFPs) generated by the activity of groups of neurons. The state of the brain is then defined as the point in a multidimensional state space that these identified variables comprise (a mathematical form of the snapshot).

The study of brain states is an active field of research in systems neuroscience (for a review, see McGinley *et al.*, 2015). The earliest studies of brain states focused on characterizing the various states of arousal related to the sleep–wake cycle of mammals. Recall from the previous section that we identified arousal states, or states of consciousness comprising the sleep–wake cycle, as a deeper background layer of our experiential states (Figure 3). Analogously, we argue the neurophysiologically-defined sleep–wake states comprise deeper, background brain states in the hierarchy of nested brain states. These

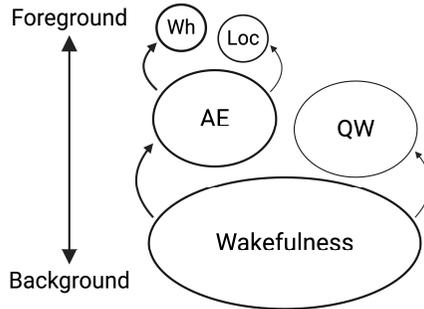
background sleep–wake states are regulated by activity spanning various brain regions, including the brainstem, reticular activating system, basal forebrain, and thalamus (Brown *et al.*, 2012). They can be differentiated through characteristic patterns of neuronal activity associated with each state, such as measurements of the electric field potentials created by that collective activity. Indeed, these patterns are taken to define the various sleep–wake states. Three initial states were identified with these methods: the waking state, slow-wave sleep (SWS), and rapid eye movement (REM) sleep (Steriade, Nuñez and Amzica, 1993; Destexhe, Contreras and Steriade, 1999; Steriade, Timofeev and Grenier, 2001; Brown *et al.*, 2012).

Gervasoni *et al.* (2004) distinguished these three sleep–wake states by constructing a two-dimensional state space with axes defined based on LFP signals recorded from multiple forebrain areas in rats. The waking, SWS, and REM states occupied distinct regions in the state space constructed based on these LFP signals. Further, these states could all be reliably distinguished based on electrophysiological measures alone, without reference to behavioural variables such as movement. Importantly, these background brain states are mutually exclusive — only one state is active at a time.

Nested within these background brain states are specific, more foreground brain states. McGinley *et al.* (2015) discuss ‘sub-states’ of the waking state, and the concept is similar to our notion of a foreground state. This recognition of a variety of sub-states of the waking state is a nascent area of research with no fully characterized taxonomy of layers or more foreground states. One of the key applications of the NSM is that it provides the means to organize an approach within neuroscience studying such states to build out this taxonomy.

Two sub-states that have been relatively well-characterized in animal models are those of the active exploration (AE) state and the state of quiet wakefulness (QW). From the standpoint of the NSM, these states constitute more foreground brain states that occur nested in the context of the background waking state. Though they exhibit a variety of characteristic differences in brain activity patterns, these states can similarly be distinguished based on typical LFP patterns across the brain (*ibid.*). The AE and QW states can be said to exist on the same level of the nested hierarchy because only one or the other appears to exist at a given time. Further, the AE state is associated with specific behaviours such as whisking (the rhythmic, stereotyped movement of whiskers used to explore the environment) or locomotion, which do not occur in the QW state (*ibid.*). Given that

whisking and walking would require different patterns of activity in motor cortical neurons, these behaviours can be said to index different yet more foreground brain states occurring within the AE state, which itself is nested in the waking state. Figure 4 provides a graphical depiction of this nested relationship.



*Figure 4.* Example depiction of nested structure of brain states. The active exploration (AE) and quiet wakefulness (QW) states are seen to exist on the same level in the hierarchy and occur in the context of a background state of wakefulness. Whisking (Wh) or walking (Loc = locomotion) are two foreground states that may occur in the context of the AE state.

We can see how such findings support Claim 2b as well. The AE state is only known to occur in the waking state, suggesting there is something about the SWS state that precludes the occurrence of the AE state (or at least makes it exceptionally unlikely to occur), while the waking state facilitates it. We can see a similar process of constraint in the next layer of this hierarchy when noting that whisking or locomotion do not occur in the QW state.

Recent work in zebrafish also describes two more-foreground brain states nested within the waking state. Marques *et al.* (2020) label these states as the exploitation and exploration states. Behaviourally, the exploitation state in zebrafish is one in which long-range movements associated with exploring an environment are suppressed, but specialized, short-range movements related to hunting for prey are facilitated; while the converse is true for the exploration state (*ibid.*). It is an intriguing and open empirical question whether the exploration state described in zebrafish could be said to be similar to the AE state we encountered above in mice, and, as we argue, this is exactly the type of question that the NSM both helps to highlight as meaningful and offers an approach towards answering.

By imaging activity across the whole brain of zebrafish in these two states, Marques *et al.* identify two opposing brain networks that are respectively more active in the exploration or exploitation state (*ibid.*), thereby demonstrating two opposing brain states nested within the waking state in zebrafish. These brain states facilitate specific more foreground brain states, which have functional advantages depending on the organism's current environmental context. For instance, Marques *et al.* demonstrated that neuronal activity in the exploitation-state network correlated with activity in the cerebellum, which mediates specific hunting-related movements, and was anticorrelated with other brain regions involved in facilitating exploratory movements and behaviours (*ibid.*).

They also raise the question of how hunger and satiety might interact with exploitation and exploration brain states and, specifically, how it might influence transitions between the two states (*ibid.*). This question is well-suited to the NSM framework, as it is asking how a more background state, in this case a motivational state related to hunger, constrains which more foreground state is likely to occur at a given moment. That is, one might predict that a low satiety background state would make the more intermediate exploitation state more likely to occur, given that this is the state supporting hunting behaviours.

While Marques *et al.*'s data do not adequately address this question, a separate study by Allen *et al.* (2019) demonstrates the profound role that deeper background motivational states have on constraining brain activity. This study recorded the activity of over 20,000 neurons across 34 brain regions in the mouse while the mice performed a task for which they received a water reward. The authors compared both spontaneous and stimulus-related brain activity when mice were in a state of thirst or satiation. They found a widespread network of neurons whose activity corresponded to the motivational state of thirst or satiety, as well as significant changes in brain-wide activity patterns that depended on the motivational state of the organism (*ibid.*). That is, they found that the way in which neurons across the brain responded to the presence of specific sensory stimuli was motivational-state-dependent, precisely in a manner that would be expected of a more background level brain state in the NSM framework.

### 3.2. Further evidence for nested brain states in humans

Evidence for a nested structure to brain activity is not limited to animal studies. Human neuroimaging work has identified two seemingly distinct brain states occurring in the context of the background state of wakefulness, which are conceptually similar to the states of active exploration and quiet wakefulness studied in rodents. These brain states involve distinct networks of brain regions exhibiting different activity patterns depending on whether subjects are engaged in tasks requiring goal-directed, focused cognitive function (Fox *et al.*, 2005; Fox and Raichle, 2007). The so-called ‘task-positive network’ (TPN), which includes areas such as the intraparietal sulcus, middle temporal area, and frontal eye fields, is active during goal-directed task engagement, and the ‘task-negative network’ (TNN; also called the default mode network, or DMN; Fox and Raichle, 2007), which includes the lateral parietal cortex and posterior cingulate cortex, amongst other areas, is activated when not engaged in a task, or when in a state of quiet wakefulness. These networks are anticorrelated with one another, thus representing two distinct, more foreground brain states nested in the background state of wakefulness.

Horowitz *et al.* (2009) examined the impact of a different background state of arousal — deep sleep — on functional connectivity within the DMN. They found that connectivity between the frontal brain regions with other DMN regions was disrupted during deep sleep. This work supports our Claim 2b, as we see that a background state of wakefulness can facilitate activity in the DMN, whereas a different background state, deep sleep, inhibits it.

Subsequent research on functional brain networks indicates that there are likely more than just two states at this level of the hierarchy, and the dorsal attention network may constitute a more foreground state nested within the TPN (Yeo *et al.*, 2011). Exactly how many states, in which hierarchical layer each falls, and what are their neuro-anatomical bases are important empirical questions that the NSM highlights.

Additional support for the NSM’s claims is found in studies of affect and emotion in humans. Recall that background states tend to change over longer timescales than do more foreground states. Sani *et al.* (2018) recorded electrical activity from several brain areas associated with the limbic system in humans. They found that specific patterns of brain activity, which were predictive of subjects’ reported moods (assessed using a specific rating scale), varied on a timescale of

3.4 hours or slower. Kragel *et al.* (2016) studied the spontaneous emergence of emotional episodes in human subjects, using a model-based decoding approach of whole-brain functional neuroimaging data, and found that decoded emotional episodes varied over a timescale of minutes or less — shorter than the timescale of affective state variation from Sani *et al.* Notably, EEG studies also support a short timescale — on the order of seconds — for emotional fluctuations (Hajcak, MacNamara and Olvet, 2010). Kragel *et al.* (2016) further obtained subjective reports of mood states, using similar rating scales to Sani *et al.* (2018), and found that the frequency with which certain emotional states occurred was influenced by the subjects' mood states. For example, subjects who reported a more depressed mood exhibited a higher frequency of episodes of sadness, while subjects reporting a more anxious mood exhibited more episodes of fear, exactly as would be predicted through Claim 2 of the NSM. Thus, we find empirical support for the notion that emotional states are nested within the layer of affective, or mood, states.

To summarize the work reviewed thus far, we see that brain states exhibit a nested hierarchical structure, homologous to that of experiential states. Arousal, or sleep–wake, states feature as deeper background states in both brain state and experiential state hierarchies, motivational states appear nested therein in both hierarchies, and research in humans supports the proposed relationship between affective and emotional states as well. How far do these correspondences go? We argue that the ultimate extent and degree of overlap between nested state hierarchies in both domains are empirical questions which the NSM helps to frame and to address. In the remainder of this article, we turn to a discussion of what this empirical approach looks like through the lens of the NSM.

#### 4. Bridging the Gap

Here, we begin to sketch out what an empirical approach to bridging the subjective and neurophysiological domains looks like utilizing the NSM framework. To start, we address two questions, which we label domain-general questions, as they focus on general properties of nested state hierarchies. First, how can we characterize such systems and their dynamics? Second, how do we determine at what level in the hierarchy a particular phenomenon should be placed?

Regarding the first question, we have seen how both our experiential states and patterns of brain activity can be characterized as

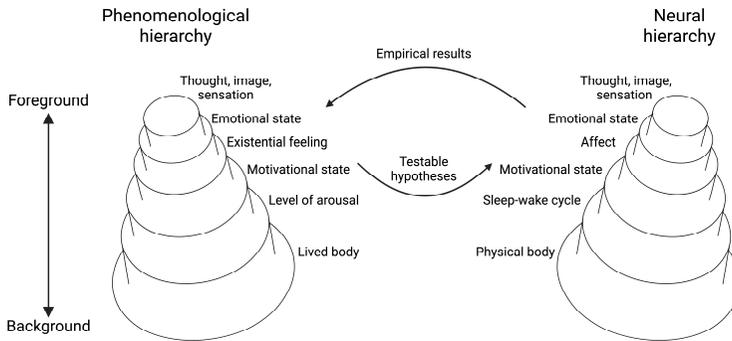
systems of nested states. The methods of dynamical systems theory are well-suited to characterizing and analysing such systems and how they change over time (Colombetti, 2017; Favela, 2021; Freeman, 2000). In the language of dynamical systems, background states partition the overall state space — the space of possible states the system could inhabit — into sub-spaces, restricting the range of foreground states a system may occupy. A background state can be understood as shaping the attractor landscape, creating a tendency for the system to inhabit specific more foreground states. Colombetti (2017) explicitly describes affective, or mood, states and their relation to emotional states in these terms, and many of the studies on brain states cited in the previous section make use of dynamical systems methods as well (Allen *et al.*, 2019; Gervasoni *et al.*, 2004).

Regarding the second question, how do we determine the relative positioning of phenomena in a nested state hierarchy? We have encountered two suggestions in our preceding discussion that help address this question, which we could label an expressive exclusivity principle and a time-constant principle. Regarding expressive exclusivity, it appears that possibly-occurring states within a layer do not occur simultaneously with one another. For instance, we saw that either the AE or QW state is active at a given time point, and that they do not co-occur. If they were on different levels of the hierarchy, however, they could co-occur. Regarding the time-constant principle, we suggested that states in different layers of a nested state hierarchy change over different timescales — that more background states tend to persist over longer timescales than do more foreground states. We applied this principle in Section 3 to argue that emotional states were nested in the foreground of affective states.

This discussion of domain-general questions lays some of the conceptual groundwork needed in order to tackle the central, empirical projects highlighted by the NSM. One project is that of building out the nested state hierarchies in each domain (domain-specific investigation). The other is investigating how nested state configurations in each domain relate to one another (cross-domain investigation). We summarize our initial proposed hierarchies for the phenomenological and neural domains in Figure 5.

In principle, domain-specific investigation to develop and test these hierarchies could proceed in isolation from one another. Phenomenological work, in concert with psychological and clinical studies, can explore the layered qualities of our subjective experience, while neuroscience proceeds to better characterize brain states and how

different levels of such states interact with one another. Indeed, Adolphs and Andler (2018) advocate just such an approach for the study of emotional states in neuroscience through ‘bracketing’ subjective experience. A central project from this standpoint would be to further clarify the neural circuits and dynamics that support the layers of the neural hierarchy outlined in Figure 5. While such domain-specific work is needed and productive from the standpoint of the NSM, relying only on this approach would not help us to make meaningful progress in understanding the relationship between subjective experience and patterns of brain activity. Indeed, it is precisely this cross-domain problem on which the NSM helps us to get a meaningful hold.



*Figure 5.* Proposed nested state hierarchies for experiential states (left) and brain states (right). We hypothesize that a layer in one hierarchy will correspond to a specific layer in the other. The specific levels shown here comprise our initial hypothesized organization, which would be modified with ongoing phenomenological analyses and neural experimentation (as noted by the arrows in the centre). Experiments of the variety proposed in this section would help to clarify further these hierarchies and their relation to one another.

Let us, once again, frame this central problem. It is not that we lack methods to associate aspects of our subjective experience with certain neurophysiological processes. Neurophenomenology provides such means (Varela, 1996; Thompson, Lutz and Cosmelli, 2005; Thompson, 2007) and will factor prominently in the empirical approach we advocate. *What we lack is a framework that brings our views of experiential states into broad alignment with our understanding of general principles and properties of brain activity, through which we can begin to clearly hypothesize about and make*

*specific predictions regarding how alterations in certain brain states might impact our subjective experience in a systematic way.* The NSM provides this framework, which we view as its central contribution.

For instance, how do our motivational states interact with different existential feelings, or moods, to bring about specific foreground aspects of our subjective experiences, such as particular thoughts? Absent the NSM, it is difficult to formulate this question so precisely. The NSM helps us to organize our thinking about this problem while simultaneously offering an empirical approach towards potential solutions. The questions of why we have the experiences we do at the particular moments we have them, and how brain activity might relate to and support these experiences, become questions of how nested state configurations relate to one another in each domain. In this light, we can see why the tasks of building out these hierarchies and examining their overlap are central projects within the context of the NSM.

To illustrate what an empirical approach to studying the relationship between experiential and brain states looks like through the NSM, we will address the question posed in the last paragraph. The work of Sani *et al.* (2018) provides a concrete entry point for this illustration. The authors were interested to decode individuals' mood states from brain activity measured by intracranial electrodes placed over a collection of brain areas known to be involved in both emotional and motivational states — the orbitofrontal cortex, anterior cingulate cortex, amygdala, insular cortex, and hippocampus (Malezieux, Klein and Gogolla, 2023). The electrodes were left in place for multiple days in a row, measuring intracranial electrocorticogram (ECoG) signals continuously over this time, providing an ideal experimental paradigm for pairing phenomenologically-inspired investigations of subjective experience with large-scale recordings of brain activity.

One could then investigate the relationship between motivational states, existential feelings or moods, and their neurobiological correlates using the methods of neurophenomenology (Varela, 1996; Thompson, Lutz and Cosmelli, 2005). Colombetti (2017) gives an excellent outline of how such methods could be incorporated into studies of affect, providing a general blueprint which we argue can be expanded to explore all layers of the two proposed nested state hierarchies. Rather than using pre-specified rating scales, as past studies have, one could use phenomenologically richer methods, with more open-ended prompts, eliciting descriptions of subjects' mood and emotional states in their own words at various time points.

Follow-up prompts could then be targeted to get at different aspects of emotional experience in the moment, possibly using short, semi-structured interviews to do so. All of this would be done while continuously recording activity from distributed regions of the brain associated with the corresponding, relevant layers of the neural hierarchy outlined in Figure 5 (in this case, those of ‘motivational states’ and ‘affect’).

To more fully understand how nested state configurations in the subjective and neurophysiological domains relate to one another, such studies would need to probe more than one layer of experience (and/or brain state) at a time. Continuing with our example, follow-up studies could incorporate manipulations of motivational states, while eliciting descriptions of the experience of those motivational states, of concurrent affective and emotional states, and of how they modify or change the experience of each other in combination. Such studies would provide rich insights into the relationships between our subjective experiences and the neurophysiological processes that support them. Through such studies, we may discover that the positioning in the hierarchy of motivational states, say, relative to affective states needs to be adjusted, or that different brain areas than expected were implicated in motivational or affective experiences. Additionally, we refer the reader to Box 1, illustrating how several clinical examples are conceptualized from this perspective. We envision that the NSM will support an iterative process of investigation, whereby phenomenological analyses inform and integrate with neuroscientific experimentation, with the ultimate goal of providing a ‘scheme of operationalization’ that will help forge a path to a unified understanding of mind and brain.

To further highlight the advantages of our framework, we consider how the NSM compares to some other recent proposals concerned with bridging the gap between mental phenomena and brain activity. Northoff, Wainio-Theberge and Evers (2020) describe an approach emphasizing the analysis of spatio-temporal dynamics of spontaneous brain activity as offering a common reference frame for understanding neural and mental phenomena. While we agree that analysing the dynamics of experiential and neural phenomena will play a central role in bridging this gap, their proposal does not describe a framework to guide a more specific empirical approach to integrating the two domains. Additionally, Badcock, Friston and Ramstead (2019) offer an appealing theoretical approach to bridging the gap between brain–body–environment that combines Karl Friston’s free energy principle

with evolutionary systems theory. It appeals to a nested hierarchical organization of the brain in a similar spirit to the NSM, and it will be important for future work to investigate how this computational approach might relate to the notion of brain states within the NSM. However, neither proposal engages with a principled study of subjective experience, nor do they offer a means to hypothesize and test how *specific* subjective states relate to *specific* brain states, or how changes in brain states might lead to changes in specific experiential states. The NSM offers the means to do so and thus situates the study of the relationship between experiential and neurophysiological phenomena in a more specific empirical context. A complete account of the mind must make room for our conscious, lived experience, and the NSM does this through an approach that is rooted in enactivist thought.

#### Box 1

REM sleep behaviour disorder is a clinical syndrome where dreams are physically acted out, implicating the background states of arousal. Investigation of this disorder from the lens of the NSM could proceed by combining phenomenological reports of dreams and hypnagogic/hypnopompic states with concurrent EEG measurement, targeting more detailed information on the organization and mutual relationship of the more-background layers of the phenomenological and neural NSM hierarchies.

Hyperthyroid states have been clinically associated with anxiety and other psychiatric symptoms. Hormones influence brain activity over longer timescales, so we might expect the primary influence of thyroid hormones to be on more background states, which also tend to persist over relatively longer timescales. The case of hyperthyroid-anxiety implicates the relation of existential feelings and emotions in the phenomenological hierarchy to affective and emotional states in the neural hierarchy. A plausible research avenue would involve detailed phenomenological interviews paired with neurophysiological recordings (either fMRI or EEG) in both hyperthyroid and euthyroid (i.e., pre- and post-treatment) states.

Major depressive disorder (MDD) with delusions is a relatively common comorbid symptom constellation well-exemplified in conditions like the Cotard delusion, where subjects express that they are dead, non-existent, or decomposing. Through the lens of the NSM, this syndrome implicates phenomenological layers including the lived body and existential feelings in relation to the physical body and affective states on the physiological side. One might hypothesize that certain background states that are overrepresented in MDD constrain the state-space of more-foreground layers, such that interactions with the environment are biased towards specific experiences that are expressed in the form of such delusional statements. This hypothesis could be investigated by combining phenomenological reports with neurophysiological recordings in subjects with MDD with and without comorbid delusions, and pre- and post-treatment.

## 5. Conclusion

In our view, the primary contribution of the NSM framework is to make the study of how subjective states relate to neurophysiological processes empirically tractable through the recognition of a structural homology between the two domains. This recognition brings our views of subjective mental states into broad alignment with our understanding of general principles and properties of brain activity,

allowing us to formulate specific hypotheses and predictions about how the two domains relate to one another, as we have just seen. Specifically, we have advanced the notion that both our experiential states and brain states can be described as systems of nested states. In this nested structure, more background states facilitate the occurrence of certain more foreground states, sculpting the riverbed for our stream of consciousness.

It is also worth remarking that, though we have put forward an approach for beginning to unify the subjective and objective domains, this approach remains agnostic about the ultimate reducibility (or irreducibility) of subjective, mental phenomena. That we can develop a principled means of relating the two domains does not indicate how the reducibility question will be resolved one way or another, nor need this question be answered *a priori* for the approach here advocated to be feasible. Additionally, we view this framework as firmly rooted in the enactivist approach. Though this proposal focuses on brain activity, we do not mean to suggest that brain activity alone gives rise to mind and subjectivity. Ultimately, we hope that the NSM framework will provide a productive path forward through sustained, collaborative dialogue geared towards addressing the explanatory gap between biology and subjectivity.

## References

- Ackermans, M.A., Jonker, N.C., Bennik, E.C. & de Jong, P.J. (2022) Hunger increases negative and decreases positive emotions in women with a healthy weight, *Appetite*, **168**, 105746. doi: 10.1016/j.appet.2021.105746
- Adolphs, R. & Andler, D. (2018) Investigating Emotions as functional states distinct from feelings, *Emotion Review*, **10** (3), pp. 191–201. doi: 10.1177/1754073918765662
- Allen, W.E., Chen, M.Z., Pichamoorthy, N., Tien, R.H., Pachitariu, M., Luo, L. & Deisseroth, K. (2019) Thirst regulates motivated behavior through modulation of brainwide neural population dynamics, *Science*, **364** (6437), eaav3932. doi: 10.1126/science.aav3932
- Badcock, P.B., Friston, K.J. & Ramstead, M.J.D. (2019) The hierarchically mechanistic mind: A free-energy formulation of the human psyche, *Physics of Life Reviews*, **31**, pp. 104–121. doi: 10.1016/j.plrev.2018.10.002
- Beck, A.T., Brown, G., Steer, R.A., Eidelson, J.I. & Riskind, J.H. (1987) Differentiating anxiety and depression: A test of the cognitive content-specificity hypothesis, *Journal of Abnormal Psychology*, **96** (3), pp. 179–183. doi: 10.1037//0021-843x.96.3.179
- Brown, R.E., Basheer, R., McKenna, J.T., Strecker, R.E. & McCarley, R.W. (2012) Control of sleep and wakefulness, *Physiological Reviews*, **92** (3), pp. 1087–1187. doi: 10.1152/physrev.00032.2011

- Colombetti, G. (2011) Varieties of pre-reflective self-awareness: Foreground and background bodily feelings in emotion experience, *Inquiry*, **54** (3), pp. 293–313. doi: 10.1080/0020174X.2011.575003
- Colombetti, G. (2017) *The Feeling Body: Affective Science Meets the Enactive Mind*, Cambridge, MA: MIT Press.
- De Jaegher, H. & Di Paolo, E.A. (2007) Participatory sense-making: An enactive approach to social cognition, *Phenomenology and the Cognitive Sciences*, **6** (4), pp. 485–507. doi: 10.1007/s11097-007-9076-9
- Destexhe, A., Contreras, D. & Steriade, M. (1999) Spatiotemporal analysis of local field potentials and unit discharges in cat cerebral cortex during natural wake and sleep states, *The Journal of Neuroscience*, **19** (11), pp. 4595–4608. doi: 10.1523/JNEUROSCI.19-11-04595.1999
- Di Paolo, E.A. (2018) The enactive conception of life, in Newen, A. & Gallagher, S. (eds.) *The Oxford Handbook of Cognition: Embodied, Embedded, Enactive and Extended*, pp. 71–94, Oxford: Oxford University Press.
- Di Paolo, E.A. & De Jaegher, H. (2012) The interactive brain hypothesis, *Frontiers in Human Neuroscience*, **6**, art 163. doi: 10.3389/fnhum.2012.00163
- Faul, L. & LaBar, K.S. (2022) Mood-congruent memory revisited, *Psychological Review*, **130** (6), pp. 1421–1456. doi: 10.1037/rev0000394
- Favela, L.H. (2021) The dynamical renaissance in neuroscience, *Synthese*, **199** (1–2), pp. 2103–2127. doi: 10.1007/s11229-020-02874-y
- Fox, M.D., Snyder, A.Z., Vincent, J.L., Corbetta, M., Van Essen, D.C. & Raichle, M.E. (2005) The human brain is intrinsically organized into dynamic, anticorrelated functional networks, *Proceedings of the National Academy of Sciences USA*, **102** (27), pp. 9673–9678. doi: 10.1073/pnas.0504136102
- Fox, M.D. & Raichle, M.E. (2007) Spontaneous fluctuations in brain activity observed with functional magnetic resonance imaging, *Nature Reviews Neuroscience*, **8** (9), pp. 700–711. doi: 10.1038/nrn2201
- Freeman, W.J. (2000) Emotion is essential to all intentional behaviors, in Lewis, M.D. & Granic, I. (eds.) *Emotion, Development, and Self-Organization*, 1st ed., pp. 209–235, Cambridge: Cambridge University Press. doi: 10.1017/CBO9780511527883.010
- Fuchs, T. (2018) *Ecology of the Brain: The Phenomenology and Biology of the Embodied Mind*, Oxford: Oxford University Press.
- Gallagher, S. (2010) Defining consciousness: The importance of non-reflective self-awareness, *Pragmatics & Cognition*, **18** (3), pp. 561–569. doi: 10.1075/pc.18.3.04gal
- Gallagher, S. (2017) *Enactivist Interventions: Rethinking the Mind*, Oxford: Oxford University Press.
- Gervasoni, D., Lin, S.C., Ribeiro, S., Soares, E.S., Pantoja, J. & Nicolelis, M.A.L. (2004) Global forebrain dynamics predict rat behavioral states and their transitions, *Journal of Neuroscience*, **24** (49), pp. 11137–11147. doi: 10.1523/JNEUROSCI.3524-04.2004
- Hajcak, G., MacNamara, A. & Olvet, D.M. (2010) Event-related potentials, emotion, and emotion regulation: An integrative review, *Developmental Neuropsychology*, **35** (2), pp. 129–155. doi: 10.1080/87565640903526504
- Heidegger, M. (1962/1988) *Being and Time*, New York: Harper and Row.
- Hollon, S.D., Kendall, P.C. & Lumry, A. (1986) Specificity of depressotypic cognitions in clinical depression, *Journal of Abnormal Psychology*, **95** (1), pp. 52–59. doi: 10.1037//0021-843x.95.1.52

- Horovitz, S.G., Braun, A.R., Carr, W.S., Picchioni, D., Balkin, T.J., Fukunaga, M. & Duyn, J.H. (2009) Decoupling of the brain's default mode network during deep sleep, *Proceedings of the National Academy of Sciences USA*, **106** (27), pp. 11376–11381. doi: 10.1073/pnas.0901435106
- James, W. (1890) *The Principles of Psychology*, Vol. I, New York: Henry Holt and Co. doi: 10.1037/10538-000
- Kragel, P.A., Knodt, A.R., Hariri, A.R. & LaBar, K.S. (2016) Decoding spontaneous emotional states in the human brain, *PLoS Biology*, **14** (9), e2000106. doi: 10.1371/journal.pbio.2000106
- Kyzar, E.J. & Denfield, G.H. (2023) Taking subjectivity seriously: Towards a unification of phenomenology, psychiatry, and neuroscience, *Molecular Psychiatry*, **28** (1), pp. 10–16. doi: 10.1038/s41380-022-01891-2
- Malezieux, M., Klein, A.S. & Gogolla, N. (2023) Neural circuits for emotion, *Annual Review of Neuroscience*, **46** (1), pp. 211–231. doi: 10.1146/annurev-neuro-111020-103314
- Marques, J.C., Li, M., Schaak, D., Robson, D.N. & Li, J.M. (2020) Internal state dynamics shape brainwide activity and foraging behaviour, *Nature*, **577** (7789), pp. 239–243. doi: 10.1038/s41586-019-1858-z
- McGinley, M., Vinck, M., Reimer, J., Batista-Brito, R., Zagha, E., Cadwell, C., Tolias, A., Cardin, J. & McCormick, D. (2015) Waking state: Rapid variations modulate neural and behavioral responses, *Neuron*, **87** (6), pp. 1143–1161. doi: 10.1016/j.neuron.2015.09.012
- Meyer, R. & Brancazio, N. (2022) Putting down the revolt: Enactivism as a philosophy of nature, *Frontiers in Psychology*, **13**, art. 948733. doi: 10.3389/fpsyg.2022.948733
- Northoff, G., Wainio-Theberge, S. & Evers, K. (2020) Is temporo-spatial dynamics the common currency of brain and mind? In quest of spatiotemporal neuroscience, *Physics of Life Reviews*, **33**, pp. 34–54. doi: 10.1016/j.plrev.2019.05.002
- Ratcliffe, M. (2008) *Feelings of Being: Phenomenology, Psychiatry and the Sense of Reality*, Oxford: Oxford University Press.
- Sani, O.G., Yang, Y., Lee, M.B., Dawes, H.E., Chang, E.F. & Shanechi, M.M. (2018) Mood variations decoded from multi-site intracranial human brain activity, *Nature Biotechnology*, **36** (10), pp. 954–961. doi: 10.1038/nbt.4200
- Steriade, M., Nuñez, A. & Amzica, F. (1993) A novel slow (< 1 Hz) oscillation of neocortical neurons in vivo: Depolarizing and hyperpolarizing components, *The Journal of Neuroscience*, **13** (8), pp. 3252–3265. doi: 10.1523/JNEUROSCI.13-08-03252.1993
- Steriade, M., Timofeev, I. & Grenier, F. (2001) Natural waking and sleep states: A view from inside neocortical neurons, *Journal of Neurophysiology*, **85** (5), pp. 1969–1985. doi: 10.1152/jn.2001.85.5.1969
- Thompson, E. (2007) *Mind in Life*, Cambridge, MA: The Belknap Press of Harvard University Press.
- Thompson, E., Lutz, A. & Cosmelli, D. (2005) Neurophenomenology: An introduction for neurophilosophers, in Brook, A. & Akins, K. (eds.) *Cognition and the Brain*, 1st ed., pp. 40–97, Cambridge: Cambridge University Press. doi: 10.1017/CBO9780511610608.003
- Thompson, E. & Cosmelli, D. (2011) Brain in a vat or body in a world? Brain-bound versus enactive views of experience, *Philosophical Topics*, **39** (1), pp. 163–180. doi: 10.5840/philtopics201139119

- Varela, F.J. (1996) Neurophenomenology: A methodological remedy for the hard problem, *Journal of Consciousness Studies*, **3** (4), pp. 330–349.
- Varela, F.J., Thompson, E. & Rosch, E. (1991) *The Embodied Mind: Cognitive Science and Human Experience*, Cambridge, MA: MIT Press.
- Varela, F.J., Lachaux, J.P., Rodriguez, E. & Martinerie, J. (2001) The brainweb: Phase synchronization and large-scale integration, *Nature Reviews Neuroscience*, **2** (4), pp. 229–239. doi: 10.1038/35067550
- Yeo, B.T.T., Krienen, F.M., Sepulcre, J., Sabuncu, M.R., Lashkari, D., Hollinshead, M., Roffman, J.L., Smoller, J.W., Zöllei, L., Polimeni, J.R., Fischl, B., Liu, H. & Buckner, R.L. (2011) The organization of the human cerebral cortex estimated by intrinsic functional connectivity, *Journal of Neurophysiology*, **106** (3), pp. 1125–1165. doi: 10.1152/jn.00338.2011

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