First few seconds for flow: A comprehensive proposal of the neurobiology and neurodynamics of state onset

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ABSTRACT

Flow is a cognitive state that manifests when there is complete attentional absorption while performing a task. Flow occurs when certain internal as well as external conditions are present, including intense concentration, a sense of control, feedback, and a balance between the challenge of the task and the relevant skillset. Phenomenologically, flow is accompanied by a loss of self-consciousness, seamless integration of action and awareness, and acute changes in time perception. Research has begun to uncover some of the neurophysiological correlates of flow, as well as some of the state's neuromodulatory processes. We comprehensively review this work and consider the neurodynamics of the onset of the state, considering large-scale brain networks, as well as dopaminergic, noradrenergic, and endocannabinoid systems. To accomplish this, we outline an evidence-based hypothetical situation, and consider the flow state in a broader context including other profound alterations in consciousness, such as the psychedelic state and the state of traumatic stress that can induce PTSD. We present a broad theoretical framework which may motivate future testable hypotheses.

1. Introduction

Flow is an altered state of consciousness that is thought to occur when we are fully engaged in a relatively challenging task or activity that is matched to our skills. The phenomenon has been scientifically investigated for nearly fifty years, after first being elucidated by Mihaly Csikszentmihalyi in the 1970 s (Csikszentmihalyi, 1975), who studied the state from a psychological framework (Csikszentmihalyi, 1990). While researchers built upon this framework for nearly five decades, investigations into the state's underlying neurophysiology are relatively recent. Yet, it is known that flow is associated with specific alterations in brain activity, including changes in neural oscillation, neuro-modulatory processes, dynamic activations of specific brain regions, as well as alterations in large-scale brain connectivity.

Additionally, both cognitively and neurobiologically, the state of flow shares overlap with other altered states of consciousness, including meditative and psychedelic states, states of traumatic stress, and so-called peak or optimal experiences (Carhart-Harris et al., 2012, 2014;

Brandmeyer et al., 2019; Wheeler and Dyer, 2020). While scientists have explored some of the neurobiological changes beneath the aforementioned altered states (Brewer et al., 2011; Nash et al., 2018; Yanes and Loprinzi, 2018), the precise neural mechanisms underpinning the onset of flow and the state itself remain unclear, both empirically and theoretically. In addition, a comprehensive theoretical account of flow's neural dynamics is missing from the literature, yet exists for other altered states (Preller et al., 2019; Girn et al., 2017; Travis, 2020). Thus, the current research leaves open many questions: How does the brain transition into a flow state? What is the temporal nature of this transition, including how long do the changes that facilitate state onset last, and what neural dynamical processes mark the transition into the state itself? From a neuroscientific perspective, how is flow distinct from, or similar to, other altered states of consciousness?

In order to answer the aforementioned questions, we compare and contrast the neurobiological mechanisms for flow with other profound alterations in consciousness, including both psychedelic states and the traumatic stress that can produce Post-Traumatic Stress Disorder

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(PTSD). We argue that this comparative approach is helpful when considering factors such as mood states, fear inhibition, emotional arousal, hyper-vigilance, and contextual cue processing. We propose a comprehensive empirical and theoretical account of the onset of flow. This account includes a number of clear and measurable brain signals that precede the onset of the state, and suggests that there is a large-scale brain network associated with flow.

The goals of this paper are five-fold: First, we review current research on flow, laying the groundwork for a rigorous exploration of the flow's neurobiology, including establishing the criteria that any viable explanation of flow's neural dynamics should meet. The purpose of this paper is to comprehensively draw upon the relevant literature in order to rigorously propose and justify a novel framework for the onset of flow, as well as establish an agenda for future flow research. Second, we outline a conceptual scenario where two fundamental outcomes can occur: the onset of flow, or the onset of traumatic stress that may lead to PTSD. Third, we propose a neural mechanism for the onset of flow that involves selected activation of a large-scale network and a set of brain regions with specific patterns of networked communication. Fourth, by drawing upon recent studies of the neural dynamics of the psychedelic state, we construct a proposal for the brain dynamics of flow, and further suggest that this proposal may yield a computational modeling approach. Fifth, given our comprehensive account of a possible flow network and its dynamics, we link flow's neurobiology with its phenomenology, then compare those dynamics with both trauma, and the psychedelic state. In doing so, we lay a foundation for generating new, testable hypotheses that can add to the empirical literature on the neurobiology of flow.

Finally, given the complexity of the brain and the contextual interaction between the body and environment during flow, a comprehensive explanation of the neurobiology of flow onset must incorporate concepts from a number of neuroscientific domains, explained at multiple levels (Huskey et al., 2020). These include behavioral, theoretical, molecular and systems neuroscience. Thus, our proposal offers a first accounting of relevant mechanisms involved in flow: neurotransmitter systems, neural oscillation, and large-scale functional connectivity, and links each with the phenological characteristics of flow.

2. An overview of flow research

The formal study of flow began in the 1970 s, with Mihaly Csikszentmihalyi's systematic investigations. Csikszentmihalyi defined flow as "an optimal state of consciousness where we feel our best and perform our best" and discovered that flow is a universal phenomenon in humans, arising globally, independent of task, and regardless of class, culture, or creed (Csikszentmihalyi, 1990).

Additionally, Csikszentmihalyi identified six phenomenological characteristics that are commonly present during flow: Hyper-focused, task-specific attention; the merger of action-and-awareness leading to total absorption in task-engagement; the diminishment of self-reflective cognition and awareness of bodily processes; an altered perception of time; a heightened level of task-performance accompanied by a feeling of complete control; and significant positive affect, including high levels of intrinsic reward, enjoyment, pleasure, euphoria and, often, increased feelings of meaning and purpose. Psychometrically, these six characteristics have become the way researchers both define and measure flow. Whether these characteristics are necessary as well as sufficient conditions for the experience of flow remains an open question. In fact, to our knowledge, no research into the neurobiological mechanisms involved in flow have confirmed the presence of all six characteristics. What has been shown is that the intensity of each characteristic helps researchers determine where an experience sits on the spectrum between micro-flow, a low intensity flow experience, or macro-flow, a high intensity flow experience (Csikszentmihalyi, 1975; Csikszentmihalyi and Nakamura, 2002; Engeser, 2012). While this research is based on self-reported subjective assessments, it appears to be largely consistent

as a categorization of the "spectrum" of flow experiences.

More broadly, flow is an altered state of consciousness (Dietrich, 2004; Csikszentmihalyi and Nakamura, 2014; Lee et al., 2016). Altered states of consciousness (Wittmann, 2018) are characterized as significant deviations from normal waking states of consciousness. For instance, flow has been shown to be associated with phenomena found in other altered states, including disassociation, the feeling of oneness with everything, and out-of-body experiences (for disassociation, Wanner et al., 2006; for oneness, see: Newberg et al., 2001; Tsaur et al., 2013; Yaden et al., 2017; Kotler, 2006, 2013; for out of body experiences, see: Kotler, 2006).

Several excellent recent systematic and scoping reviews have been published on flow, which address psychology, physiology, and neurobiology, for both individual as well as group flow, including van der Linden et al. (2021), Knierim et al. (2018), Khoshnoud et al. (2020), Kryston et al. (2018), Fisher et al. (2021), Weber et al., (2016, 2020), Gold and Ciorciari, 2020; Pels et al., 2018, and Peifer et al. (2022). *Our review and proposal draws on this existing work and extends it in two novel ways.* First, we elucidate the underlying neural dynamics of flow, in terms of network and coordination dynamics, something which has not been previously discussed. And second, also for the first time, we discuss the neural dynamics of flow in the context of the dynamics of trauma, and the psychedelic state.

Any viable explanation of flow's underlying neurobiology needs to satisfy several criteria. First, it must account for the altered state of consciousness that characterizes flow. Second, it must link flow's phenomenological characteristics with neurobiological processes. Finally, any viable explanation of flow's underlying neurobiology and neural dynamics must consider both prior research and satisfy an additional number of explanatory requirements, including flow's widely documented impact on performance and the currently theorized "flow triggers," the pre-conditions that have been proposed to produce, or at very least, be correlated with, flow. Although the literature on flow is becoming extensive, the neurobiology underlying the concept and its *antecedent causes*, much like hypnosis (Landry et al., 2017), are not yet fully explained. Flow neuroscience faces many of the same challenges that face the general scientific study of consciousness, creating a unified objective theory of subjective experience (Seth and Bayne, 2022). Nevertheless, the fact that flow and its well-documented effects can be successfully investigated from a psychological and phenomenological perspective (Melnikoff et al., 2022) suggests an optimistic outlook for the neurobiological elucidation of flow. In what follows, we briefly outline currently theorized flow triggers, their possible causal role, and the resulting performance enhancements associated with flow.

2.1. The Functionality of Flow's Triggers

Previous theorizing argues that several "triggers" are causally linked with individual and group flow (Sawyer, 2017; Csikszentmihalyi and Nakamura, 2002; and for a full overview, see Kotler, 2021). As this paper concerns individual flow, it is only the individual flow triggers that are discussed herein. These triggers include: (a) clear goals, immediate feedback and the challenge/skills balance where both the task's challenge and an individual's skills are high (Csikszentmihalyi, 1990; Csikszentmihalyi and LeFevre, 1989, 2012; Nakamura and Csikszentmihalyi, 2005), (b) novelty, complexity, unpredictability, and insight (Kotler, 2006, 2021; Teng, 2011), (c) risk (Martin and Priest, 1986; Celsi, 1993; Kotler, 2013; Schüler and Nakamura, 2013), (d) deep embodiment or the hyper-awareness of cross sensory modalities (Csikszentmihalyi, 1990; Chavez, 2008; Jaque et al., 2020), major intrinsic motivators such as curiosity, autonomy, passion, purpose and mastery (Bakker and Geurts, 2004; Quinn, 2005; Salanova et al., 2006; Kotler, 2021). Additionally, while this idea remains speculative, some researchers have argued that flow triggers operate via independent yet often overlapping mechanisms that govern the allocation of attention to the task-at-hand: the activation of dopaminergic and/or noradrenergic

pathways and/or the perceived low-levels of cognitive load, even when objective measures show otherwise (Harris et al., 2017a, 2017b; Kotler, 2021).

2.2. A hypothetical situation: flow versus PTSD

In order to examine the neurobiological processes that may occur during the onset of flow, consider the following hypothetical situation: A highly skilled motorcycle rider is speeding down the freeway and suddenly gets cut off by a car (the "event"). While other mental states are possible (mind-wandering, for example), assume that pre-event, the motorcyclist is actively engaged in the task of driving down the freeway, with concurrent increases in focus and alertness. Next, to avoid collision, the motorcyclist has an immediate response, swerving around the offending car. Now consider two possible and frequently reported outcomes of high-risk situations, each with their own distinct yet overlapping psychological characteristics.

In one possible outcome, the motorcycle rider starts to swerve, rapidly transitions into flow and skillfully avoids the car. The motorcyclist draws upon prior experience and skills and performs a series of perfectly timed motor actions with a high level of task proficiency. More specifically, the situation elicits the flow's theorized triggers and should be associated with psychological characteristics that are present during the experience, including complete concentration on the task-at-hand, the merger of action and awareness, an altered sense of time (dilation or acceleration), a diminishment in sense of self, a heightened sense of control over the situation, and a post-event increase in positive affect and mood.

Alternatively, the motorcycle rider starts to swerve, feels a sense of overwhelm and panic, yet manages to maneuver around the car and avoid an accident. In this case, the motorcyclist is likely to experience traumatic stress, including heightened anxiety, feelings of terror and powerlessness, and a post-event increase in negative affect, hypervigilance and the distinct possibility of Post-Traumatic Stress Disorder (PTSD). In order to motivate a discussion concerning the transition into a flow state, we emphasize that, in this situation and before the event takes place, the driver is not yet in flow; rather in a state of appropriate arousal and alertness (and valence). The transition into flow may occur when an event takes place that could potentially lead to flow—that is, an event with a confluence of flow triggers.

While these scenarios are not the event's only possible psychological outcomes, both are frequently reported phenomena in high-risk situations, including those found in adventure activities, sports and combat (for flow, see: Allen-Collinson et al., 2018; Jackson, 1992, for trauma, see: Ozer et al., 2003; Van der Kolk and Van der Hart, 1989). We also note that the comparison between flow and the precursors of PTSD in this hypothetical situation may generalize most readily to high-risk situations. Admittedly, not all flow experiences are high-risk (e.g., academic achievement, work productivity, media use, artistry, mental health). Nevertheless, we emphasize that this particular hypothetical situation is useful in that it allows for a broader theoretical investigation concerning flow experiences and an opportunity to consider their relation to PTSD and the psychedelic state. Moreover, we expect the same sequence of neurobiological events should result in flow for both high- and low-risk circumstances. Therefore, we pose this hypothetical situation to underscore a crucial question: What precise alterations in brain function and neural dynamics distinguish these two outcomes, either the transition into flow or the transition into traumatic stress?

Consider that, neurobiologically, the pre-flow/pre-trauma initial conditions are identical. The motorcyclist is experiencing heightened focus and alertness, reflecting increased activity in large scale brain networks, including executive attention, salience, motor action planning and execution. Next, as the "event" begins, the motorcyclist is cut off by the car. Neurobiologically, this produces an immediate increase in activity in the brain's salience network (SN), which is charged with the detection of novel and relevant stimuli (Menon and Uddin, 2010; Weber

and Fisher, 2020). Whether the motorcyclist's experience becomes ecstatic (flow) or traumatic is likely to depend on what happens next. If the experience is overwhelming, terrifying, or there are physical or mental constraints that inhibit the execution of action plans, then the swerve is likely to result in traumatic stress. However, if flow's triggers are present, then we theorize that this should result in a sequence of neural responses that elicit flow, and the corresponding psychological, phenomenological, and behavioral responses.

This emphasis on "action" is particularly important to our discussion. In the literature surrounding both flow and PTSD, action or the inability to act consistently plays a crucial role. "Flow is triggered during a task, thereby implying motor execution" (Michailidis et al., 2018). Additionally, in flow, this action has two phenomenological qualities: effortlessness and empowerment. Effortlessness implies automatic processing (Dietrich and Stoll, 2010), while empowerment refers to one of the flow's core psychological characteristics: a "sense of control." Moreover, the "inability to act" is one of the causal factors involved in PTSD (Van der Kolk and Van der Hart, 1989) and learned helplessness (Miller and Norman, 1979; Seligman, 1972). This suggests that the heightened sense of control in flow may be the opposite of learned helplessness or what could be termed "learned powerfulness," and considered as a possible pre-condition for resiliency and post-traumatic growth, a term coined by Tedeschi and Calhoun (2004) to describe "positive psychological change experienced as a result of the struggle with highly challenging life circumstances".

Similarly, researchers have found that many of flow's performance benefits, including increases in well-being, meaning, empathy, motivation, grit, and environmental awareness are also characteristic of post-traumatic growth (Jayawickreme et al., 2022; Maitlis, 2020; Tedeschi and Calhoun, 2004; Waters et al., 2022). This overlap in performance benefits suggests that flow and post-traumatic growth may share underlying neurobiological mechanisms, an idea that aligns with Selye's (1956) division between eustress (beneficial stress) and distress (harmful stress) and lends additional support to our comparison of flow and trauma (for linkages between flow and eustress, see Hargrove et al., 2013).

As a way to explore these changes, we examine the event temporally, breaking the incident into nine "sequence-coded" sections—starting with T = 0, the moment before the rider is cut off in traffic, and proceeding to T + 9, the post-event moment when the rider drives down the freeway in either flow or traumatic stress—and detail the precise neurobiological changes that underpin each step in the sequence. This framework both allows us to see when, where and why the experiences of flow and trauma overlap then diverge, while further serving to elucidate flow's phenomenology, its performance benefits and the functionality of known flow triggers.

2.3. T = 0: Pre-Flow Events

The specific neurobiological pre-conditions that elicit flow comprise a vast state space. Nevertheless, people get into flow doing all sorts of tasks, suggesting that the exact details of pre-event neurobiology are less important than the increase in salience that marks the onset of the event. Therefore, we maintain our motorcycle hypothetical situation. At the start of the event, our motorcyclist is speeding down the freeway in a state of alert focus. Neurobiologically, the executive attention network (EAN) is engaged, as this network has been shown to facilitate attention while driving (Ball et al., 1993; Clay et al., 2005), including when drivers experience a sudden road hazard then drive away safely, which accurately describes our hypothetical situation (Åkerstedt et al., 2005).

At T = 0, an "unexpected stimulus" arrives, requiring amplification in SN connectivity (Seeley et al., 2007, Menon and Uddin, 2010; Sridharan et al., 2008). This is significant because the SN has been theorized to be involved in facilitating shifts into flow (Huskey et al., 2018, 2021; Weber and Fisher, 2020). Moreover, the SN is involved in the initiation of cognitive control (Botvinick et al., 2004), the coordination of

behavioral responses (Medford and Critchley, 2010) and the maintenance and implementation of task-sets —(Nelson et al., 2010) a term that describes the configuration of cognitive processes that are actively maintained for subsequent task performance (for a review, see Sakai, 2008). Once that unexpected stimulus is detected, the key SN regions that are active in both our flow and trauma scenarios likely include the dorsal anterior cingulate cortex (dACC), the anterior right insula (aRI), the presupplementary motor area (PSA), amygdala, ventral striatum and ventral tegmental area (VTA).

The dorsal anterior cingulate cortex (dACC) is an important cognitive control structure (Holroyd et al., 2004) and is likely involved in detecting the unexpected stimulus (the car), as the dACC is associated with conflict detection and error identification (Carter and Van Veen, 2007; for review: Falkenstein et al., 2000). In conflict detection, the ACC monitors attentional conflicts to signal whenever additional resources are required. In predictive-coding, a series of reciprocal connections between the ACC and the medial prefrontal cortex (mPFC) are involved in the prediction and processing of error messages (Alexander and Brown, 2019). In addition, the aRI may be involved, as this region is also active during performance monitoring and error processing (Ullsperger et al., 2010). In this scenario, the aRI initiates the process, acting as a "cortical outflow hub" that coordinates activity changes across multiple brain networks in response to error detection (Chang et al., 2013, 2012).

Beyond the dACC and aRI, there are three additional regions of interest. The presupplementary motor area (pre-SMA) facilitates the selection of action plans and the suppression of conflicting action plans (Nachev, 2007), allowing the motorcyclist to decide to, say, swerve left instead of right. The amygdala plays, among other things, a role in threat detection (Öhman, 2005; Phelps and LeDoux, 2005), responding to novel events in the environment, though it is especially sensitive to novel dangers—like the motorcyclist being cut off by that car. Finally, the dopaminergic regions including the ventral striatum and the ventral tegmental area are involved in motivation, reward and the reinforcement of behavior (Beier et al., 2015), including unpredictable, high-risk behaviors such as swerving a motorcycle in traffic.

2.4. T + 1: Error Signaling

Moving forward in our sequence, once the salience network detects a perceptual change, the brain generates an error signal that helps lock attention on target. This requires many of the regions involved in the orienting of attention to a perceptual event, including the posterior parietal cortex, as well as the frontal and subcortical control systems of spatial attention (Husain and Rorden, 2003; Mesulam, 1999). Additionally, the dACC remains active, as this region is partially responsible for reorienting.

It is likely that there is an event-related potential (ERP) associated with this error detection. Based on the relevant literature, candidates include an error-relative negativity signal appearing 80–100 ms after the stimulus (Muzammel et al., 2018) or the N200, a negative deflection appearing 200 ms after the stimulus reflecting either conscious attention or an unexpected stimulus or both (Muzammel et al., 2018; Patel and Azzam, 2005). Relatedly, Grahek et al. (2022) have shown that the P3b (a signature of prediction error updating) tracks perceived efficacy at achieving rewards. In short, there is a stronger P3b response when people update from a low-efficacy of achieving a reward to a high-efficacy prediction. Together, these error signals may help guide the allocation of selective attention and control necessary for experiencing flow.

2.5. T + 2: selective attention

At this stage in our scenario, the motorcyclist recognizes the car and its potential danger. A central, but still somewhat unanswered question is how the brain, in a high-risk situation, is able to appropriately filter out an enormous amount of incoming information in order to perform the correct action and make adaptive decisions. This neurobiological filtering phenomenon is known as sensory gating (Jones et al., 2016; Zabelina et al., 2015), and is a core component of cognitive control wherein prepotent stimuli are downregulated to facilitate flexible and adaptive pursuit of a specific goal (Cole et al., 2013; Miller and Cohen, 2001).

This process functions as an attentional regulation mechanism and appears involved in the transition into both flow and PTSD. Importantly, recent research in mice has shown that executive attention—as related to sensory gating—rather than acting as spotlight, is actually regulated by inhibition, similar to a filtering process (Wimmer et al., 2015). In this process, the thalamus serves as a bottom-up relay hub, communicating selected information to large areas within the cortex, including the attentional system in the prefrontal cortex. This process is heavily influenced by motivation and reward processing, which guide control deployment (Botvinick and Braver, 2014).

Yet this is not solely a bottom-up process, as Wimmer et al. (2015) found a top-down feedback loop wherein changes in PFC activity inhibit sensory components of the thalamic reticular nucleus (TRN). Thus, the PFC regulates thalamic activity by allowing relevant information to be processed, while suppressing irrelevant information via various subnetworks. In follow up research, Nakajima et al. (2019), discovered that the relevant inhibitory pathway extends from the PFC to basal ganglia (BG) to TRN.

In the PFC-BG-TRN pathway, the BG inhibits distracting and irrelevant information, while enhancing appropriate cues. In our motorcyclist example, it is likely that the driver experiences the dampening of auditory information in favor of the highlighting of visual information, a commonly reported phenomenon in high-risk situations (Parr and Friston, 2018; Kotler, 2013). This is a form of goal-directed sensory filtering that impacts attention and, via additional BG connections, motor performance. This also means that cognition is intimately tied to action and further underscores the "ability to act" versus the "inability to act" as a key differentiator between experience outcomes (flow or PTSD). Additionally, during threat recognition, two other processes involving the BG are important to this discussion: the phasic response in dopamine (DA), signaling a reward-prediction error (Schultz, 2016; see T + 3 for further discussion), and the inhibition of impulsive behaviors (see below).

On the flow side of our motorcyclist scenario, the selection of appropriate motor plans must correlate with a specific neurobiological mechanism, with the subthalamic nucleus (STN) the likely candidate. Ballanger et al. (2009) found that stimulation of the subthalamic nucleus (STN), via connections with the motor cortex, increases impulsive behavior during high-conflict decision making, while an opposing "proactive inhibition" response (braking, in the motorcyclist's scenario) hinders performance in high-risk situations that demand an immediate motor response. The authors appropriately refer to this model as "release your horses."

2.6. T + 3: task engagement verses disengagement

Concurrent with events described in T + 2, core neuromodulatory processes are likely engaged as the motorcyclist's reorienting response activates noradrenergic and dopaminergic pathways as well as the endocannabinoid system (ECS) in order to enhance executive attention, motor response and reward. We will address these systems individually.

As a core hub in the salience network, the dACC helps focus attention on a single target by triggering the release of norepinephrine from the locus coeruleus (LC), the brainstem nucleus responsible for most of the brain's norepinephrine (Seeley et al., 2007; Berridge and Waterhouse, 2003; Mather et al., 2016; Ventura et al., 2008; Menon and Uddin, 2010). Connections running between the LC and the amygdala and between the LC and the PFC are centrally involved in fear processing, attention switching, task-engagement, and increased learning (Corbetta and Shulman, 2002). Further connections run between the LC and the motor cortex (M1) that extend to our facial muscles and eyes (Ferrucci

et al., 2013). This could explain why changes in facial expression have been repeatedly correlated with flow and trauma (for flow: de Manzano et al., 2010; for trauma: Garrett et al., 2012).

In the amygdala, the arrival of NE begins the process of threat assessment (Gu et al., 2019;LeDoux, 2015). It appears that NE arrives first in the basolateral amygdala (BLA), which is both critical for forming stimulus outcome value representations (Pizzagalli et al., 2011), and as an adaptive response that primes learning. As both flow and trauma result in rapid learning, the presence of NE in the BLA might help explain this phenomenon.

In the PFC, NE increases signal-to-noise ratios in cortical networks (Xing et al., 2016) and triggers many of the top-down processes associated with executive attention. NE projections in the PFC are well-distributed but are particularly active in the medial prefrontal cortex (mPFC). While the amygdala-LC pathway is critical for creating aversive memories, the LC-mPFC pathway is crucial to extinguishing aversive memories, suggesting that this is an important division between flow and PTSD. Additionally, pharmacological targeting of the LC-NE pathways in both the amygdala and mPFC has provided symptomatic relief for people suffering from PTSD (Taylor et al., 2008).

In high-risk situations such as our motorcyclist's, NE is also involved in decreasing and suppressing working memory in favor of flexible attention (Berridge and Spencer, 2016). In times of stress, Snyder et al. (2012) have shown that corticotropin-releasing factor (CRF) acts as a neurotransmitter in the LC, shifting discharge from phasic to tonic in order to promote behavioral flexibility. As there are bidirectional connections between the LC and mPFC and orbital frontal cortex (OFC), this shift from phasic to tonic carries information up to the PFC (Berridge and Waterhouse, 2003). According to Adaptive-Gain Theory (Aston-Jones and Cohen, 2005), this shift reflects a change from the exploitation of a *known* strategy for producing behavioral outcomes (a phasic process) to an exploration of a *novel* strategy for new and potentially preferential outcomes (a tonic process).

Inversely, Sadacca et al. (2017) has shown that depletion of tonic NE in the OFC and, possibly, the mPFC, can result in a lack of attentional flexibility—which could help explain why experiences become either trauma or flow. Based on this evidence, we suggest that, if the motorcyclist does not have enough tonic NE in their system, they may not have enough attentional flexibility to solve the swerve problem, resulting in traumatic stress. Further evidence for this can be found in the fMRI work of Naegeli et al. (2018) who found PTSD patients have exaggerated behavioral and autonomic responses to loud sounds, suggesting sensitized phasic responses of LC neurons (for a review of NE-LC-PTSD research, see: Borodovitsyna et al., 2018).

Another line of evidence for the causal role of the LC-NE system in attentional control, particularly goal-directed attention and impulse control, comes from Bari et al. (2020). Using optogenetics, the authors demonstrate that the LC targets two different areas of the PFC, the dorsal-medial PFC (dmPFC), known to be involved in enhancing focus and performance, and the ventrolateral orbitofrontal cortex (vlOFC), known to be involved in impulse reduction, with each area acting independently, yet synergistically, via ascending efferent connections from the LC (Corbetta and Shulman, 2002). In mice, separately stimulating the LC-NE pathways to the dmPFC and the vlOFC produces two distinct behavioral outcomes, either improved correct performance or impulse control, respectively. Moreover, the LC-NE system also acts as global modulator for arousal in response to a threat or stressor (Morris et al., 2020), which further emphasizes this systems role in the motorcyclist scenario. The LC-NE system has been theorized to play an important role in flow, particularly task engagement verses disengagement (van der Linden et al., 2021). Taken together, the LC-NE system responds to threats during high-stakes situations, regulates the decision to engage or disengage a task, and modulates two distinct attentional pathways, one involved in reducing distracting information and the other in reducing impulsive behaviors.

Interestingly, researchers have also found that both flow and traumatic stress are associated with out-of-body experiences (Blanke and Thut, 2007; Rabeyron and Caussie, 2016; Kotler, 2006), a phenomenon that might be partially explained by NE activity in the temporal parietal junction. In the TPJ, NE is normally linked to failure tracking, but the region (and especially the right TPJ) is also important in empathy, perspective-taking and out-of-body experiences (Shamay-Tsoory et al., 2005; Saxe and Kanwisher, 2003; Blanke and Arzy, 2005). This suggests that an out of body experience might be a NE-triggered radical form of perspective-taking that arises early in perceived crisis situations, arguably during the pre-action plan selection phase, perhaps to aid in that selection.

When the brain detects a salient signal, there is also activity in the mesocorticolimbic dopamine system anchored by the ventral tegmental area (VTA). The VTA provides signals related to novelty, error and reward, yet there is growing evidence that there are two different kinds of DA neurons and that each responds to a specific kind of "reward" (Bromberg-Martin, 2010). The first are *value-coding neurons* that are activated by unexpected rewarding events and inhibited by unexpected aversive events. These value-coding neurons are found in the substantia nigra (SN) and the VTA, while their projections end in the NAcc shell, dorsal striatum (caudate and putamen) and vmPFC (Schultz, 2007).

The second class of DA neurons are saliency-coding neurons that originate in the substantia nigra and VTA and project to the NAcc core, dorsal striatum, and dorsolateral PFC (dlPFC). In both classes of DA neurons in the VTA, activity is both phasic and tonic and relates to both expectation of reward and errors in reward prediction (Schultz, 2016). Additionally, DeYoung (2013) proposed these saliency-neurons are activated by the incentive value of new information; while Di Domenico and Ryan (2017) argue that these neurons alone could underpin intrinsic motivation—two ideas that are relevant to flow's phenomenological characteristics and impact on performance.

Yet, in our motorcycle example, the value-coding DA neurons are activated first, as the unexpected aversive event—the car's arrival in the motorcyclist's visual field—would produce a reward prediction error and a phasic decline in DA activity (Schultz, 2016). This may be the original error signal that starts the entire flow or trauma process (discussed in T + 1). However, this phasic DA decline must be brief, as flow has been consistently linked to heightened dopaminergic activity (Berns, 2005; Weber et al., 2009). Moreover, DA-producing experiences such as risk, unpredictability, complexity, novelty, and insight, appear to precipitate flow (Kotler, 2006, 2021). Finally, flow-proneness is associated with availability of D2 receptors in the dorsal striatum (de Manzano et al., 2013) and increased dorsal striatum gray matter volume (Kavous et al., 2019).

At this step in the sequence, the phenomenology of time perception comes into play. In crisis situations, both anecdotal and empirical evidence (Kotler, 2013) show that time appears to slow down or speed up very early in high-risk situations. Similarly, Arstila (2012) argues that this effect occurs due to a distortion of the relation between the temporal properties of the external world and the internal state. Dopamine may be responsible for this change in temporal phenomenology, as it is the main neurotransmitter involved in time processing (Lustig and Meck, 2005; Meck, 1996). Dopamine agonists tend to speed up time perception, whereas dopamine antagonists slow it down. In our motorcycle example, the initial reward detection error would likely produce a phasic decline in DA that would slow the rider's perception of time. Additionally, Roseboom (2019) correlated the experience of time dilation to the number of salient events which take place during a particular scanning period. The greater the number of salient events, the longer the current moment seems to last. In other words, the activation of the motorcyclist's salience network could begin the process of time elongation, while the presence of dopamine could extend and/or deepen the phenomenon. Importantly, these processes provide a mechanism for time dilation that arises very early in the motorcyclist's experience without requiring the localized deactivation of the medial PFC (see T + 8 for full discussion).

A significant body of research shows the endocannabinoid system (ECS) is a regulator of anxiety and stress (for a review, see Hillard, 2018), and thus implicated in our motorcyclist's response to the event. In a wide variety of situations, the introduction of an acute stressor—the car, in our example—evokes bidirectional changes in the two main molecules produced by the ECS: anandamide (AEA) and 2-archidonoly glycerol (2-AG). These molecules are synthesized on-demand in post-synaptic membranes that feed back into presynaptic terminals (Kano et al., 2009), where they bind to canabiniond receptors (CB) receptors and serve a significant neuromodulatory function. Within the brain, CB receptors are found on GABAergic, glutamatergic, serotonergic, noradrenergic and dopaminergic terminals—a list that includes many of the neurochemicals directly implicated in both flow and trauma, suggesting that the ECS may be something of a master neuromodulator of these experiences.

In the amygdala (see T + 4 for further review), where the threat response is processed, CB receptors are primarily found in the basolateral amygdala (BLA), but also in the central nucleus. When these receptors are inhibited, there is a decline in anandamide (AEA) in the amygdala that contributes to the stress response by activating the hypothalamic-pituitary-adrenal (HPA) axis and increasing anxiety. Additionally, increases in 2-AG, the other major molecule produced by the ECS, contribute to the termination and adaptation of the HPA axis—that is, the end of the threat response—and potentially contribute to pain perception, memory and synaptic plasticity (Gray, 2015). In total, a decline in ECS activity is associated with anxiety and traumatic stress, while (as we will see below) an increase in ECS activity may prevent traumatic stress and enhance correct task-performance and attention, two key components of the flow experience.

2.7. T + 4: threat assessment

In this sequence, the neurobiological changes described in T = 0 through T + 3 reflect the motorcyclist's detection of an aversive and unexpected stimulus. Here, in T + 4, the motorcyclist's brain performs threat assessments and begins the process of action plan selection. We examine these details by focusing on key neuronal regions that are directly implicated in both neurobiological studies of flow and trauma, and by events necessitated by our motorcyclist's scenario—the activation of the salience network by an unexpected stimulus, for example.

In the brain, sensory information about the external environment—such as the sudden appearance of a car in our motorcyclist's visual field—is processed by a pulvino-cortical loop that regulates selective attention (Saalmann et al., 2012) and then relayed to the amygdala through a network of corticothalamic afferents. The amygdala handles preconscious threat detection, emotional valence and, via near-constant bidirectional signaling with the mPFC and the hippocampus, associations with prior experience (Bishop, 2009; Hermans et al., 2014). Bidirectional links between the central amygdala, brainstem and hypothalamus are responsible for mounting fear responses (Adolphs, 2013). In our scenario, in both the flow and trauma conditions, amygdala activity is likely, as the car represents a dire and immediate threat that produces a fear response.

In this fear response, sensory information is funneled into the basal and basomedial cell groups, and the central nucleus of the amygdala (Janak and Tye, 2015). The basolateral amygdala (BLA) is implicated in survival-oriented behaviors such as freezing, fleeing, foraging, and (possibly) fighting, and forms a circuit with the centrolateral amygdala, (CLA) which is a critical structure for fear memory formation and storage (Penzo et al., 2015). In mice, Hartley et al. (2019) found the central amygdala (CeA) is also involved in fear creation and extinction. CeA neurons express corticotropin-release neuropeptide CRF^+, which reduces conditioned freezing responses, impairs fear memory acquisition, facilitates within-activity fear extinction, and is necessary for extinction memory retrieval. Meanwhile, activity in corticotropin-release CRF^- neurons produces fear-based memories.

These facts are relevant for two reasons. First, in order to facilitate the swerve action plan, the motorcyclist had to inhibit automatic braking responses, a function of CRF+ activity. Second, the autotelic nature of flow suggests within-activity fear extinction and post-event fear extinction, both functions of CRF+. This second argument is crucial as no averse affective memory responses have been associated with flow, yet the state frequently arises in high-risk situations that would normally produce them (Csikszentmihalyi, 1990; Celsi, 1993; Kotler, 2013).

Additionally, the endocannabinoid system (ESC) also plays a role in threat assessment, as it can both inhibit or excite CRH response. More specifically, there are both tonic and phasic ECS reactions to stress. In the brain, higher tonic levels of AEA regulate stress and anxiety and play a role in the prevention of PTSD (Gunduz-Cinar et al., 2013; Mayo et al., 2022). AEA is also the tonic signal of the Hypothalamic-Pituitary Axis (HPA), which is partially responsible for mounting the stress response. Under steady-state conditions, Morena et al. (2015) argued that this AEA tone exists in the BLA, where it inhibits the HPA under non-stressful conditions, and activates it under stress. Interestingly, the ECS system is also active in the hippocampus and the mPFC, both regions critical for fear-based associative processing, and over large portions of the PFC in general, including most of the regions active in threat processing, action-plan selection, and the creation or extinction of fear-based memories. In total, mounting evidence suggests that the ECS plays a significant neuromodulatory role in both the onset of flow and the onset of trauma.

During threat assessment, information is also passed to the prefrontal cortex for top-down evaluation (for a review, see Sussman et al., 2016). A network involving the temporal-parietal junction (TPJ), the orbital frontal cortex (OFC) and ventral lateral prefrontal cortex (vlPFC) helps reorient attention to salient stimuli and is particularly sensitive to unexpected events (Corbetta and Shulman, 2002). Beyond these structures, it appears that the specific prefrontal regions activated during threat evaluation will differ depending on the situation, past knowledge, and prior experience. In the flow literature, critical factors that help establish the challenge-skills balance such as tolerance for anxiety, ability to delay gratification, confidence, and optimism, are influential at this stage, and likely determine the exact pattern of prefrontal activity. Yet there are a few areas in the PFC that deserve particular scrutiny for their relevance to our scenario.

In the motorcyclist example, in both flow and trauma, the appearance of an unexpected stimulus makes OFC activity likely. The OFC is considered part of the vmPFC (discussed in greater detail below) and has been implicated in both emotion and emotion-related learning, and is part of the ventral network that reorients attention to salient stimuli and emotional events (Thorpe, 1992; Hartikainen et al., 2012; O'Doherty et al., 2001; Rule et al., 2002). Yet, there are important OFC divisions. In amygdala-generated fear responses, both the medial OFC and the ventromedial PFC (see below) are implicated in fear extinction and reward-processing, while the anterolateral OFC signals the absence of a reward and presence of certain negative stimuli (Milad and Rauch, 2007). In trauma studies, anterolateral OFC dysfunction has been implicated in PTSD.

Relatedly, the vmPFC has bidirectional connection to the amygdala and is involved in threat assessment and response, reward-processing, and decision-making—all tasks that are required at this stage of the event (Botvinick et al., 2001; Fellows, 2007; Rolls, 2000). Moreover, the vmPFC assists in the selection of action plans (Yim, Cai and Wang, 2019) and with solving problems associated with determining the actions of ambiguous agents—the car in this scenario (Vartanian and Mandel, 2011). Evidence also shows that both the amygdala and the vmPFC are active during the extinction of fear memories (Janak and Tye, 2015). This idea aligns with studies of flow in rappers and musicians (Limb and Braun, 2008; Liu et al., 2012) showing heightened activity in the vmPFC—perhaps as a result of the creative decision-making and action plan selection required by improvisation. Yet, other researchers (e.g.,

Barros et al., 2018; Huskey et al., 2018; Klasen et al., 2012; Ulrich et al., 2014, 2016a,b, 2022) found reduced activity across the whole of the mPFC during flow, including the vmPFC. This discrepancy could possibly be resolved with a better understanding of the interrelationship between the mPFC, amygdala and the endocannabinoid system. CB_1 receptors are plentiful in the mPFC and receptor activation by AEA inhibits NE production across the entire region—suggesting a shift in fear processing (Morena, 2015).

Finally, the right ventral lateral PFC (vlPFC) is involved in flexible action plan selection and emotional forecasting (Bechara, 2011), both processes that are relevant to our scenario. Yoshida et al. (2014) discovered vlPFC activity during a study of gamers in flow, a finding they linked to the vlPFC's role in the cognitive control of memory (Badre and Wagner, 2007). Further explanation for vlPFC activity during flow can be found in a frontal-striatal-thalamic loop that allows for the flexibility in behavior seen in high flow activities like improv jazz, video gaming, or a motorcyclist swerving through traffic. As this flexibility is present throughout the entire flow experience and not just at state onset, this could explain why Yoshida et al. (2014) found the vlPFC activated throughout the flow experience, and particularly during later moments in the flow eliciting task. Additionally, upregulating CB_1 receptor binding in the vlPFC promotes stress-coping strategies following unpredictable stress exposure (McLaughlin et al., 2014; Wirz et al., 2018). If the ECS is modulating the vlPFC during flow, this further explains why flow is likely to lead to post-traumatic growth and not post-traumatic stress disorder.

2.8. T + 5: threat processing

Following the threat assessment seen in T + 4, as the motorcyclist recognizes the imminent danger, threat processing occurs T + 5. This will likely require multiple structures within both the executive attention network and salience network, but a full anatomical breakdown is perhaps unnecessary. We know that a threat is detected in our motorcyclist's experience because both of our conditions—flow and trauma—activate the sympathetic nervous system. In humans, when the amygdala detects danger, it sends a threat signal to the hypothalamus that results in the release of cortisol. This phenomenon is well-documented in the study of trauma (Bremner, 2006; Sherin and Nemeroff, 2011), but it appears in flow as well. A number of studies of flow have found that cortisol levels follow an inverted U-shaped curve (Keller et al., 2011; Peifer et al., 2014; Tozman and Peifer, 2016). Tozman and colleagues (2017) for example, examined cortisol levels in chess players in flow, finding a moderate level of cortisol was associated with a higher level of flow absorption, while a higher level of cortisol was associated with a lower level of flow absorption. This finding suggests that flow may require some kind of stress response at the front end of the experience.

2.9. T + 6: the acute stress response in flow and trauma

Returning to our hypothetical situation: The motorcyclist's visuospatial attention is now directed toward the oncoming car, while the driver's threat recognition system (Stein and Nesse, 2011) has identified a significant and imminent danger. From a cognitive-affective perspective, multiple psychobiological systems are now engaged, perhaps most importantly the acute stress or fight-flight-freeze response of the sympathetic nervous system. In this scenario, given the situational context, movement suppression and behavioral inhibition are not likely to occur, thus freezing is not an option (Roelofs, 2017). Instead, from a neurophenomenological point of view, we argue that the transition into flow is likely associated with the *proactive* willingness to approach, and the transition into trauma is associated with the *reactive* inclination to avoid (Roelofs, 2017). From an objective standpoint, the motorcyclist produces the same "swerve" motor action plan, however, phenomenologically, it may be the case that a decision to "approach" leads to the state

of flow, while the decision to "avoid" leads to trauma, with the former producing concurrent feelings of fortitude, and the latter producing concurrent feelings of fear. It is further likely that, subsequent to the event, these two distinct neurobiological reactions would be associated with different psychological outcomes: the absence of fear-based memories in the flow condition, and the presence of fear-based memories in the trauma condition (Izquierdo et al., 2016). A deeper consideration of the underlying neurobiology is warranted here.

Recent work in mice (Salay et al., 2018) has clarified that freeze responses are controlled by xiphoid nucleus (a substructure in the ventral midline thalamus) projections to the BLA. By comparison, fight responses invoke projections from the nucleus reuniens (a structure that surrounds the xiphoid nucleus) to the mPFC. The argument being explored here is that the transition toward flow begins with a signal sent from the ventral midline thalamus to the mPFC that activates the "fight" motor-action plan.

It is unclear if this "fight" signal is always required to create flow, or if flow results from more general approach and avoidance processes (e. g., Cacioppo et al., 1999). Yet, in high-risk situations, three ideas support the activation of the fight response. First, Benson and Proctor (2004) suggested that the psychological experience of "struggle" always precedes entrance into flow. Second, braking is the standard automatic response to a visual threat, yet this instinct is inhibited in this scenario and replaced by the swerve motor-action plan. Temporal constraints dictate that action plan selection must occur immediately after the SN detects a threat, with the nucleus reuniens -mPFC pathway representing the hypothetical "shortest path" to activation. Finally, path selection—fight or flight—is responsible for the reactivation or further suppression of the ECS, which plays a significant role in determining outcomes associated with either flow or trauma. More specifically, at T + 3, the introduction of an acute stressor downregulated tonic AEA production in the amygdala and hippocampus. In the flow condition, after the ventral midline thalamus activates the fight response, we see an increase in sympathetic signaling that releases cortisol and reactivates tonic AEA production in the amygdala. The evidence for tonic AEA reactivation is twofold. First, researchers consistently find amygdala downregulation during flow (Limb and Braun, 2008; Ulrich et al., 2016a, 2022; Liu et al., 2012) and this necessitates the presence of AEA. Second, our flow-condition motorcyclist does not experience in-situation feelings of fear and does not have post-event fear memories, and both require the presence of AEA (Gunduz-Cinar et al., 2013). Additionally, in the trauma condition, continual inhibition of AEA produces fear conditioning, creates fear-memories and is a contributing factor in the later development of PTSD (Wyrofsky et al., 2019).

2.10. T + 7: action plan selection

After threat detection and the sympathetic response detailed in T + 6, the motorcyclist selects the "swerve" action plan. There are a number of lines of evidence that show the dorsal anterior cingulate cortex (dACC) is involved in action plan selection alongside its aforementioned roles (See T = 0 and T + 1). As Brockett et al. (2020) wrote: "Decades of imaging and modeling research in humans have implicated the anterior cingulate cortex in the evaluation of situational demands and the hypothesized alterations of downstream nodes such as the dorsal medial striatum that facilitate appropriate action plan selection." More specifically, Shenhav et al. (2016) has argued that the dACC is particularly sensitive to environmental changes that require a rapid motor response, which is the case in our motorcycle scenario. Furthermore, cognitively demanding tasks—such as swerving in traffic— activate the dorsal ACC and deactivate the posterior ACC (Binder et al., 1999; Drevets and Raichle, 1998; Raichle et al., 2001).

Action plan selection is modulated by dopamine, as D1 DA receptors in the ACC regulate effort-based decision-making (Schweimer and Hauber, 2006). Furthermore, once a decision is made and the action plan selected, as a way to drive reinforcement learning, there is a further

increase in dopaminergic transmission in the right dACC (Holroyd et al., 2004). In the flow scenario, this increase in DA signaling amplifies the signal-to-noise ratio in PFC (Kroener et al., 2009) and could be responsible for the heightened creativity that has been consistently correlated with the state. Additionally, this dopaminergic activity likely explains why "clear goals" and "immediate feedback" function as flow triggers. If "clear goals" are coded into the reward system and DA activity is linked to effort-based decision-making, then having a clear goal may favor action over inaction, and further explain the division between flow and trauma. Meanwhile, the sensitivity of dACC neurons to error responses and error feedback, coupled with DA neurons' well-established reward sensitivity, may explain why immediate feedback facilitates flow onset.

Furthermore, one of flow's most interesting phenomenological attributes is the sensation of flow itself, often described as effortless effort, where the experience is that every action and every decision being performed leads seamlessly, perfectly, fluidly to the next (Csikszentmihalyi, 1990; Kotler, 2013). This suggests that dACC activity is not limited to state onset. As subjects in flow select numerous, sequential action plans, dACC activity may persist throughout the experience. In fact, research shows that the dACC is functionally connected with the dlPFC during flow (Huskey et al., 2018), which may further facilitate phenomenological experience of "clear goals" and "immediate feedback" specifically, and more generally, may explain why so many research subjects have described their phenomenological experience of the state as "flowy." However, a challenge to this interpretation is that other studies have shown lower activation in the ACC during flow (Huskey et al., 2018; Klasen et al., 2012; Ulrich et al., 2016a, 2022).

2.11. T + 8: The onset of flow

At this moment, our motorcyclist executes the swerve action plan and rapidly transitions into flow. For the purposes of this hypothetical situation, assume the swerve consists of three different miniature action plans: an initial swerve away from the car, a second movement to counter-balance the out-thrust of the first, and a final adjustment to re-center the motorcycle along its new trajectory. When the motorcyclist performs the initial swerve away from the car, there is an increase in dopaminergic reward signaling in the mesocorticolimbic pathway that corresponds with the successful execution of this first action plan. Additionally, "rebound-excitation theory" suggests that DA provides a post-acute stress safety signal that inhibits fear-processing neurons in a spatially and temporally controlled manner (J.C. Lee et al., 2016; E.M. Lee et al., 2016). For example, experiments in acute stress conditions showed phasic rebound-excitation of DA neurons in the VTA at the offset of aversive stimuli, with DA signal strength time-locked to the termination of fearful events. A weak signal promotes fearful memories and anxious behavior, while a strong one extinguishes fearful memories and promotes resilience (J.C. Lee et al., 2016; E.M. Lee et al., 2016). In our flow example, once our motorcyclist recognizes that the first of the three mini-action plans is actually working, a DA safety signal should arise.

The initial dopaminergic reward will likely produce a feeling of surprise, as this is the phenomenological signal that arises during the recognition of better than expected results, and provokes a P300 event-related potential (ERP). However, there are two types of P300 ERPs. The P300a is associated with novelty; the P300b with surprise (Polich, 2007). In our motorcyclist's scenario, the signal is a P300b, as an abundance of oddball paradigm experiments show that a novel and unexpected stimulus produces a P300b wave approximately 300–400 ms following presentation (Picton, 1992).

In this scenario, we speculate there are four reasons to predict a P300 at T + 8. First, unless our motorcyclist is a professional, it is unlikely that swerving around a car is a single well-rehearsed motor plan. Thus, the successful execution of each mini-plan would be surprising to our driver. Second, the P300 has also been related to appraisal updating—the threat of the car is updated into something less dangerous as the swerve starts

to work, with the wave's amplitude heightening based on stimulus probability and task-relevance (Donchin and Coles, 1988). Third, studies have shown that flow proneness is associated with DA receptor activity (de Manzano et al., 2013; Gyurkovics et al., 2016). This matters because traits long associated with DA receptor activity—sensation seeking, introversion-to-extroversion, and impulsivity—have also been correlated with the P300 (Stelmack and Houlihan, 1994). Fourth, our in-flow motorcyclist has no post-incident fear despite having accurate memories of the event. It is known that stimulus encoding that promotes successful memory storage and retrieval will increase P300 amplitude (Azizian and Polich, 2007) and that signal latency is related to how long it takes to update a target stimulus, with verbal tasks taking longer than spatial tasks (Kutas et al., 1977). As our motorcyclist has non-fearful memories and responded to a visual stimulus, we predict a P300 wave that is larger in amplitude and shorter in latency.

Additionally, this signal—phasic DA activity—occurs immediately after the first sign that outcomes are better than anticipated, and produces subsequent pulses after each confirming sign (Holroyd et al., 2004). In our example, there are a series of P300 waves, each probably slightly smaller in amplitude, after the successful execution of each of the three mini-action plans (swerve, counter-swerve, straighten out).

2.12. T + 9: Localized hypofrontality

At T + 8, the motorcyclist has executed the action plan and is either experiencing flow or traumatic stress. Early theorizing argued that flow is associated with a significant downregulation of the PFC (Dietrich, 2004), or what has been called "transient hypofrontality" in the literature. Specifically, Dietrich proposed transient hypofrontality as the neuronal process that underlies flow and all altered states of consciousness (Dietrich, 2004). This idea has since been confirmed experimentally, albeit with mixed results (for a review, see Harris et al., 2017a). Some studies have found large-scale PFC deactivation during flow. Both Limb and Braun (2008) and Liu et al. (2012) observed broad deactivations of the PFC in studies of musicians and rappers in flow. In Liu and colleague's work, almost all of the lateral prefrontal cortices, extending from the lateral orbitofrontal cortex (loPFC) to the superior portions of the dorsolateral prefrontal cortex (dlPFC) as well as the dorsal portions of the mPFC, were deactivated.

By comparison, the vast majority of studies have found evidence for more localized hypofrontality, particularly among the medial PFC (mPFC). As was discussed previously, this region is thoroughly implicated in the division between flow and trauma, yet—regarding hypofrontality—it appears that the mPFC is consistently deactivated during flow (Barros et al., 2018; Klasen et al., 2012; Ulrich et al., 2014, 2016a, 2022). In fact, more recent evidence indicates that downregulation of the mPFC is causally implicated in flow experiences (Ulrich et al., 2016b), particularly among people who have low-baseline levels of flow experiences (Ulrich et al., 2018). Other research has shown low levels of mPFC activity (Huskey, Craighead et al., 2018), and mPFC functional connectivity (Huskey et al., 2018, 2021) during flow. Taken together, the data suggests that these PFC deactivations are localized to mPFC regions, and the extent of these deactivations may be based on task-set and task-requirements, rather than the across-the-board shutdown that earlier researchers had proposed (for an extended treatment, see Harris et al., 2017a).

EEG studies of flow show frontal alpha and theta activity (Eschmann et al., 2021; Katahira et al., 2018). In the work done by Katahira et al. (2018), frontal theta was localized to frontal-midline regions, which is implicated in cognitive control (Cavanagh and Frank, 2014) and concentration (Lagopoulos et al., 2009). This finding is related to the increased effort and increased cognitive control required to produce flow (when both task challenge and individual skills are moderate to high) and to task absorption (a complete concentration and merger of action and awareness condition). Eschmann et al. (2021) have shown that increased fronto-medial theta is associated with increased flow, and

increased motor performance, and that neurofeedback training can enhance both flow and motor performance. Similarly, the alpha oscillations in Katahira's study were found over the frontal central and frontal right cortical areas and tended to increase with task difficulty. As alpha has been repeatedly correlated with heightened creativity (Lustenberger et al., 2015) this increase could further account for the amplified creativity seen in flow. Other EEG work has shown increased fronto-alpha power during flow, particularly in midline regions, which has been interpreted as relating to the reward-modulated deployment of cognitive control (Castellar et al., 2019).

In summary, it appears that hypofrontality is localized to the mPFC, a structure that is a core component of the default mode network (Raichle et al., 2001) and is heavily implicated in self-referential processing (Northoff et al., 2006). That the mPFC is consistently downregulated during flow may explain why a core phenomenological characteristic of flow is diminished self-awareness and self-reflection. By comparison, flow seems to require large-scale activity across the PFC, excluding the mPFC, but including the ACC. Together, this accounts for recent theorizing that flow requires high levels of cognitive control (Fisher et al., 2021; Weber et al., 2009, 2016; Weber and Fisher, 2020), which may explain why flow feels simultaneously high-control, but effortless (see also, Harris et al., 2017b; Huskey, Wilcox et al., 2018).

3. A theoretical perspective on the neural dynamics for the onset of flow

In this paper, in addition to the neurobiological mechanisms discussed in sections T + 0 through T + 9, we also propose a neural dynamical framework for the onset of flow. Here, the term "neural dynamics" refers to how the brain exchanges information via oscillation, that is, how neural oscillatory activity in one brain region affects, or is statistically correlated, with neural activity in another brain region. These dynamical networks are how the brain changes its state over time. From a theoretical perspective, understanding the neural dynamics involved in our motorcycle scenario—that is, understanding how the neuronal regions involved in the onset of flow become functionally coupled or uncoupled—may yield new empirical and testable insights about the mechanisms involved, and lay the groundwork for a computational modeling approach.

Functional connectivity (FC) between brain regions is defined as the statistical dependence between neural time series regardless of their direct anatomical connections (Friston, 1994). These patterns of activity, as captured by EEG, MEG or fMRI, can be effectively measured using a variety of functional connectivity analysis (Wang et al., 2014). The resulting data reveals the flow of information among and within brain networks and is critical for linking these networks and their dynamics to cognitive and phenomenological states (such as flow). For example, using correlation either in the time or frequency domains, will yield undirected and symmetrical, shared information among the network (Barnett et al., 2020). Directed functional connectivity analysis, on the other hand, can yield causal connectivity, i.e., the direction of information flow between nodes in the network (Friston et al., 2003; Mannino and Bressler, 2015; Bressler and Seth, 2011).

Given that one of the known phenomenological correlates of flow is hyper-focused, task-specific attention, the underlying neural dynamics should reflect a task-engaged cognitive state. This task-engagement involves the activation of task-dependent networks, such as the dorsal attention network and fronto-parietal control network, and is often contrasted to resting state or task-negative networks, such as the default mode network (DMN; Fox et al., 2005). Typically, the activity of these networks is anti-correlated, though recent evidence has revealed a more nuanced account wherein different network components may be simultaneously active. In fact, evidence shows that tasks performed automatically (Vatansever et al., 2017), or with low levels of difficulty (Huskey et al., 2018b,a, Ulrich et al., 2014, 2016a, 2018, 2022) tend to engage the DMN. Other research shows that, during goal-directed

cognition, the DMN is functionally coupled with both task-positive attentional networks and task-positive frontoparietal control networks (Andrews-Hanna et al., 2014; Christoff et al., 2016; Spreng, 2012; Xu et al., 2020; Dixon et al., 2016).

During flow, typically anti-correlated networks appear to be co-activated. The hyper-focus associated with flow requires activation of task-positive attentional networks. Yet, flow also shares considerable overlap with a task-negative cognitive state, the psychedelic state (Csikszentmihalyi and Nakamura, 2018). This overlap includes phenomenological elements such as the diminishment of self, an altered sense of time (dilation or acceleration), and the merger of action and awareness, as well as behavioral elements, such as a measurable increase in creativity (divergent thinking) and insight. Therefore, a deeper understanding of the neural dynamics of the psychedelic state is useful for informing our examination of flow's neural dynamics.

Using magnetoencephalography (MEG) to investigate the neural dynamics of the psychedelic state, Barnett et al. (2020) found a simultaneous decrease in directed functional connectivity and an increase in undirected functional connectivity (particularly in the LSD condition). The authors interpret this network co-activation as consistent with the "increasing disorder and functional disorganization underlying the psychedelic experience" (Barnett et al., 2020). Essentially, there is a breakdown of ordered communication between critical brain regions. This breakdown reflects a relaxation of constraints in global brain activity that corresponds with an expansion of the possible repertoire of brain states (thereby increasing dynamic diversity). Carhart-Harris et al. (2018) have argued these specific changes in neural dynamics correlate with the uncontrolled cognition and perception that are signature phenomenological aspects of the psychedelic experience.

From a theoretical perspective, the psychedelic brain is at the "edge of criticality" (Carhart-Harris et al., 2018). In any self-organizing dynamical system (like the brain), criticality is the transition point between two tendencies or phases: an ordered state and a disordered, chaotic one. By allowing the brain to best adapt to a wide variety of rapidly changing external conditions, this proximity to criticality facilitates optimal processing and performance. For example, Atasoy et al. (2017), using power-law distributions and connectome-harmonic decomposition, found that a frequency-specific re-organization of brain dynamics—specifically, an increase in repertoire—brings the brain closer to the edge of criticality. This is consistent with the entropic brain hypothesis, metastability, the free-energy principle, and scale-free cortical dynamics (Carhart-Harris and Friston, 2019, Kelso, 2012; Tognoli and Kelso, 2014; Bressler, 2008; Friston et al., 2020, Freeman and Breakspear, 2007). In altered states of consciousness—including psychedelic states—mounting evidence suggests that the brain functions at the edge of criticality, that is, at, or near, a metastable critical state (Carhart-Harris, 2018; Cavanna et al., 2018; Kelso, 2012, 2021; Cocchi et al., 2017).

Two important points considered here are worth elaborating, a theoretical one and a terminological one. Theoretically, given that we are both describing and explaining a phase transition into flow, we consider flow, as an altered state of consciousness described in our hypothetical situation, from a metastable perspective (Fuchs et al., 2000; Kelso, 1992). Crucially, this would mean that flow is a transient phenomenon—a metastable tendency. Metastability (Kelso, 2012; Tognoli and Kelso, 2014) plays a central role in cortical coordination dynamics, and in general, refers to the simultaneous tendency for individual components of system to couple together and for the individual components to remain autonomous. It is a property of a system of coupled oscillators, whereby the systems dynamics tend toward a stable attractor (coordination pattern) but are never fully trapped by that attractor. Instead, the system remains in an unstable pattern near the stable coordination pattern. In cognitive neurodynamics for example, different regions of the cortex, comprised of neuronal populations, can simultaneously couple and coordinate their behavior to produce certain cognitive functions, but also express their own individual oscillatory

behavior, allowing the brain to rapidly shift its functionality in order to make sense of the external world. Thus, cortical metastability produces the simultaneous tendency for cortical areas to remain segregated, manifesting their own intrinsic activity, and to be integrated, influencing each other by reciprocal coupling (Tognoli and Kelso, 2014). Terminologically, although we have used the word "state" as a description of both the neural and phenomenological aspects of flow throughout this paper, this may not accurately reflect reality. By definition, state implies stability, however, considering the dynamics, i.e., the possible metastable nature of the phenomenon, the term state may not, ultimately, be appropriate (Kelso, 2021).

Recently however, Huskey et al., 2021, have theoretically and empirically compared the metastability proposal with the synchronization theory of flow (STF) first proposed by Weber et al. (2009). We carefully consider here the relevance of STF in the context of network control theory and criticality. The STF proposes a functional synchronization of cognitive control (including attentional structures) and reward networks (RNs) in the brain, and understands flow as a synchronized brain state.

One open question is the nature of this connectivity. STF predicts that the brain transitions through a sequence of network topologies, ending up in a functionally connected, highly synchronized state, which corresponds with the flow state (Huskey, Wilcox et al., 2018). This idea is very similar to and sits within the concept of controllability (and network control theory Gu et al., 2015; Lydon-Staley et al., 2021). The concept of controllability states that, in terms of energy efficiency, the brain optimizes its dynamics among distributed neural systems to, in this case, respond to the demands of the environment. Thus, the brain organizes its dynamics to move through various cognitive states, with structurally dense areas facilitating easily reachable states, and more distributed regions facilitating more difficult to reach states (e.g., the flow state). On this account, network control theory offers an underlying theoretical framework for how the brain organizes its dynamics to meet task demands (for everyday living, but also for flow). STF is the specific case where two systems in the brain, cognitive control systems, and reward – based (i.e., intrinsic motivation) systems functionally synchronize to allow the brain to reach the flow state.

Recent work has started to probe the nature of this fronto-parietal control network (FPCN), and the fronto-parietal reward networks (FPRN) connectivity. Using fMRI, Huskey et al., 2021 found increased flexibility among the FPCN and FPRN during flow, but decreased flexibility among the reward network only. They also found comparatively low levels of synchrony in the FPCN and FPRN during flow. Metastability offers one possible explanation for this finding. From a metastability perspective, it is possible that the brain during flow is appropriately segregated or integrated and oscillates between these tendencies, rather than being attracted to them but not entering either. However, Huskey et al., 2021 did not find strong evidence supporting this metastability hypothesis. With that said, other research has shown that the brain does exhibit non-linear criticality during flow (Weber et al., 2018). It may be that the null metastability results observed in (Huskey et al., 2021) was driven by the limited temporal resolution of fMRI.

So far, empirical work shows that the brain is organized into a modular network topology during flow (Huskey et al., 2021), this topology is energetically efficient (Huskey, Wilcox et al., 2018), and exhibits high levels of flexibility (Huskey et al., 2021), which is associated with the successful deployment of cognitive control during difficult tasks (Cole et al., 2013). However, the exact nature of brain-network connectivity during flow is unresolved, and this connectivity may very well exhibit metastable characteristics.

Therefore, we return to our discussion concerning criticality. Contrasted with the increase in disorder accompanying the onset of a psychedelic state, entry into flow appears to require a decrease in disorder—that is, an integration of information—driven by behaviorally salient and cognitively demanding task-oriented input. Thus flow,

especially in the motorcycle scenario considered in this paper, is non-resting and task-dependent. Additionally, while the edge-of-criticality aspect of the psychedelic state increases the repertoire of possible states, we predict that entry into flow will constrain the repertoire of active brain states. We also suggest that this will correspond, empirically, with an increase in directed, and a decrease in undirected, functional connectivity. The brain, upon entry into flow, allocates its resources vis-à-vis distinct connectivity patterns in a manner required for all the requisite performance-enhancing cognitive processes needed for the task at hand—in this case, a successful swerve.

Moreover, research has shown that the brain can quickly tune itself closer to or farther away from criticality depending on external input to the specific network (Zierenberg et al., 2018). Wilting and Priesemann (2019) have called the underlying mechanism driving this process: "homeostatic plasticity." In homeostatic plasticity, neurons and their networks use negative feedback loops to maintain a target spike rate, thereby stabilizing network dynamics. By adjusting their excitability to compensate for unrestrained neural communication, neurons can self-organize into a variety of dynamical regimes. This reorganization moves the brain to a subcritical point, where neural communication is well-constrained. It may be that this same subcritical point is where the flow network manifests and operates.

Given this scenario, it is also important to note that both "neural context" and "situational context" are likely to play central roles in determining exact changes in brain dynamics during flow. Neural context refers to the specific selective functioning of local neural processes as they are modulated by global neural influences, as distinguished from situational context, which involves both internal information from the periphery and external information from the environment, as well as the behavioral demands this information places upon the brain and body (Bressler and McIntosh, 2007). While the relationship between these two categories of context is not completely understood, the research clearly shows situational context shapes neural context—meaning context dependent, task-relevant cues constrain brain connectivity. This dependent relationship likely increases pattern recognition and cognitive flexibility, while decreasing (or constraining) the possible states the relevant networks can operate within (Weber and Fisher, 2020). In other words, in flow, situational context likely influences the sub-critical set point toward which homeostatic plasticity tunes the brain in order to maximize cognitive flexibility and minimize prediction errors.

In flow, the above mechanism would allow the brain to constrain the possible task-specific parameter space between connections of selected cortical areas, but loosen them in other areas, allowing for the unique creativity that is commonly associated with flow. The specific changes in both directed and undirected functional connectivity hypothesized here make it possible for the brain to increase pattern recognition and cognitive flexibility, but within a specific context. Recent evidence from Konovalov and Krajbich (2018) supports this, as they found the brain engages in a novel form of pattern learning. Using a Bayesian pattern-learning inference model, they found that brain networks both predict patterns, while simultaneously developing rules that increase the finding of future patterns. Thus, we surmise here that contextual processing constrains creativity in a flow state, essentially creating a highly constrained novelty detection system that is specifically tuned to increase task-specific performance and learning.

As applied to our hypothetical situation, during flow, and due to homeostatic plasticity, the motorcyclist's brain is much closer to the edge-of-criticality inside a context-constrained search space. This allows the rider to find all possible *best* action-plans for swerving around that offending car, but saves the brain from cue-dependent yet task-irrelevant association—which is something that happens in other altered states, such as dreaming or psychedelic states.

Finally, from a computational perspective, the above analysis suggests that a modelling approach may be useful for exploring flow, given that it is very difficult to study this cognitive phenomenon in an

ecological context. A sufficient model used to simulate the network conditions, as well as the environmental stimulus, may yield more description, explanation and prediction for the onset of the state (see e. g., Bensaid et al., 2019). Melnikoff and colleagues (2022), using the concept of mutual information, recently proposed and empirically validated a computational theory of the subjective experience of flow. This model is based on the concept of Bayesian surprise, which we believe directly corresponds with our proposed involvement of the P300b surprise signal. Likewise, Itti and Baldi (2009) found that this kind of surprise (like our motorcyclist scenario) attracts visual-spatial attention. We suggest that integrating this phenomenological model with some of the underlying neural mechanism described here, would be a reasonable future step.

One interesting element of Melnikoff et al's (2022) model is that it directly contradicts one of the core causal antecedents of flow; that is, the challenge/skill balance. This model shows empirically that flow can occur, even when the challenge/skill balance is low. Such a finding is novel given that the challenge/skill balance is the most common induction in experimental flow research (see e.g., Huskey et al., 2018b,a, 2021; Keller and Bless, 2008; Keller and Blomann, 2008; Ulrich et al., 2014, 2016a,b, 2018, 2022). However, the challenge/skill balance has come under some recent scrutiny as recent experimental work has failed to detect a difference between self-reported flow when challenge ≈ skill (flow) or when challenge < skill (Huskey et al., 2021). Therefore, it will become increasingly important to further verify the extent to which mutual information, rather than the challenge/skill balance, explains when and why flow occurs. Early tests of this mutual information model have been conducted in behavioral contexts (Melnikoff et al., 2022) but could be extended into neuroscientific contexts using existing datasets (e.g., Huskey et al., 2021). If it turns out that mutual information (and Bayesian surprise more generally) do offer a causal explanation for flow, then it becomes possible to link this mechanism with existing neuroscientific research (e.g., Nour et al., 2018; O'Reilly et al., 2013; Schwartenbeck et al., 2016).

4. Linking neurobiology with phenomenology

At the start of this paper, we described criteria any robust explanation of flow-onset should meet, specifically it needs to explain the six core characteristics of flow, the functionality of the state's triggers, and the state's well-documented impact on performance. Does this explanation satisfy these requirements? To answer this question, we revisit the six core phenomenological characteristics of flow and explore this proposal's ability to account for all six.

4.1. Complete concentration

As discussed, flow is a state of complete concentration, but how this concentration arises has yet to be determined. If we assume an error signal (ERP) at the onset of flow, then the resulting activity in the salience network and the NE-induced amplification of attention could serve as the gateway into complete concentration. Similarly, recent computational modeling work (Frömer et al., 2021; Grahek et al., 2022) shows that early prediction errors inform people about task efficacy and the expected value of reward associated with effort. When efficacy or expected reward value is low, people allocate less effort compared to when efficacy and reward are high. Considering that flow is a highly rewarding psychological state that requires high levels of efficacy, it is likely that these early prediction error signals influence subsequent control deployment. Furthermore, it is likely that phasic DA release helps sustain that focus over time.

4.2. Merger of action and awareness

The merger of action and awareness is less empirically tractable, but likely correlates with the efficiency of motor activity. In our motorcycle

example, if the swerve had been highly efficacious (as would be likely during flow), then we would see increased neuronal activation in the corresponding motor areas than would be present in novice, or otherwise low-efficacy swervers. Some preliminary evidence points in this direction. Flow is associated with increased activity in sensorimotor cortex and the cerebellum (which is often implicated in fine-motor coordination) compared to conditions of low-difficulty (Huskey et al., 2018). Interestingly, however, the brain-network topology associated with this activation is more sparsely connected (a measure of energetic efficiency) during flow relative to a low-difficulty condition (Huskey et al., 2018). Research shows that, for well-rehearsed tasks, more efficient brain-network topologies are associated with increased performance (Bassett et al., 2009). Upregulation in sensorimotor cortex and cerebellum, combined with an efficient brain-network topology, might be a neural signature of the merger of action and awareness associated with flow. Indeed, the functionality of the challenge-skills balance as a flow trigger implies expertise and the presence of pre-existing motor plans and/or knowledge structures that expertise demands.

4.3. Time Perception

As discussed, time dilation can be produced by a number of different mechanisms. Phasic DA signaling speeds up and/or slows down our perception of time, as does an increase in signaling in the salience network. Additionally, Dietrich and others have argued that temporal integration is a prefrontal function and that time dilation would be a byproduct of transient hypofrontality (2004). This presents a conundrum as research syntheses (Coull et al., 2011) and meta-analytic work (Wiener et al., 2010) show that accurate time perception requires a distributed network of activation across prefrontal (inferior frontal gyrus, precentral gyrus, supplemental motor area) and basal ganglia structures (anterior putamen, caudate nucleus), regions which have all been implicated in flow (see e.g., Huskey, Craighead et al., 2018; Klasen et al., 2011; Ulrich et al., 2014, 2016). If these regions are all required for accurate time perception, and these regions also show increased activity during flow, then the largescale hypofrontality hypothesis proposed by Dietrich (2004) is not well supported.

A narrower interpretation of Dietrich's (2004) hypothesis may provide an answer. Many of the structures listed above are implicated in "explicit" (how long a stimulus lasts, or the interstimulus interval) or "implicit" (using temporal information to achieve specific task goals) timing (Coull et al., 2011). Both types of time perception may be crucial for accomplishing challenging tasks that are associated with the flow experience. However, there is evidence of localized hypofrontality, particularly in the mPFC, during flow. The mPFC is a core structure in the DMN, and a consistent body of research shows that the mPFC and DMN are downregulated during flow (see e.g., Huskey, Craighead et al., 2018; Huskey, Wilcox et al., 2018; Ulrich et al., 2014, 2016a,b, 2022). The DMN is also implicated in conscious awareness of time's passing (Lloyd, 2012). Therefore, it could be that just mPFC deactivation (as proposed by Dietrich, 2004), but not a large scale downregulation of the DMN, explains temporal dilation during flow.

So far, we have discussed time's passage during flow in terms of dilation. However, research suggests that, in some cases of flow, the perception of time speeds up. Keller and Bless (2008) found subjects reported time went by faster while experiencing flow playing a video game. Additionally, Rutrecht et al. (2021), obtained a similar result in a virtual reality game scenario. Others have found that a perception of time passing rapidly is associated with increased levels of flow and task performance (Christandl et al., 2018). Indeed, ample evidence suggests that time often passes rapidly during flow (for a review see Barthelmäs and Keller, 2021).

Regrettably, this ambiguity between time dilation and the speeded experience of time is prevalent in the flow literature. For instance, prominent self-report measures of flow, including the DFS-2 and FFS-2 (Jackson and Eklund, 2004) fail to distinguish between the two. Even

Csikszentmihalyi has contributed to this ambiguity by noting that time is "distorted", although he does argue that the speeded experience of time may be more common (Nakamura and Csikszentmihalyi, 2005). At the same time, there is some evidence (Heim, 1892, Eagleman, 2009, Kotler, 2013) that time dilation is more frequently reported in high-risk situations than time acceleration. Therefore, the nature of time perception, and its neural substrates during flow, remains an open question.

4.4. The Vanishing of Self

Dietrich and others have correlated the diminishment of our sense of self to transient and localized mPFC hypofrontality (Dietrich, 2004). This also tracks with research by Kotler & Murphy (forthcoming) showing that subjects report time dilation before they report the vanishing of self. If time is first dilated by activity in the salience network and the increase and/or decline in phasic DA (non-hypofrontal mechanisms) and the vanishing of self is a result of localized mPFC hypofrontality, this mechanism could match the reported evidence.

Research shows a consistent downregulation of the DMN during flow (see e.g., Huskey, Craighead et al., 2018; Huskey, Wilcox et al., 2018; Ulrich et al., 2014, 2016a,b, 2022). In addition to temporal perception, the DMN is heavily implicated in self-referential processing (for a meta-analysis, see Northoff et al., 2006). It could very well be that this DMN downregulation explains the diminished self-awareness that is commonly experienced during flow. Additionally, Klasen et al. (2012) found deactivation in the temporal parietal junction during a study of flow in video gamers. As described above, the TPJ has been implicated in both embodied and disembodied (out of body) experiences (Blanke and Arzy, 2005) and could play an additional role in the diminishment of our sense of self.

4.5. A sense of control

A sense of control could be produced by either phasic DA increases and/or a series of P300 ERPs—as both reflect better than expected results from task execution. As DA also increases pattern recognition and amplifies muscle reaction times, these performance benefits could further contribute to the phenomenological experience of control. Indeed, error signals associated with reward and self-efficacy guide the deployment of control (Frömer et al., 2021; Grahek et al., 2022). Moreover, the FPCN, a core network in control deployment, is both flexible and modular during flow (Huskey et al., 2021). This flexibility is associated with successful control deployment during difficult tasks (Cole et al., 2013), and modularity is associated with energetic efficiency (Bullmore and Sporns, 2012) and increased task performance (Bassett, 2009). Finally, as the dACC aids in action plan selection and remote action plan detection—two neuronal activities that, at least hypothetically, should impact our phenomenological sense of control—it is further likely that the dACC activity proposed in this paper would further correspond to that sense of control.

4.6. Autotelicity

In this scenario, autotelicity can be produced by the significant increase in dopaminergic signaling described in T + 3 and T + 7. In their excellent overview of the neurobiology of intrinsic motivation, Di Domenico and Ryan (2017) argue that heightened activity in salience-coding DA neurons accounts for the amplified intrinsic motivation of the autotelic experience. This idea receives further support from both de Manzano et al. (2013) and Gyurkovics et al. (2016) who both found empirical evidence linking DA activity to the autotelic nature of flow. Furthermore, studies consistently associate heightened intrinsic motivation with increased activity in the salience network and the executive attention network and decreased activity in the default mode network (for complete review, see Di Domenico and Ryan, 2017). This is further bolstered by evidence showing that flow is associated with

increased activity within, and functional connectivity between reward processing regions (Huskey et al., 2018b,a, 2021; Klasen et al., 2012; Ulrich et al., 2014, 2016a).

In animal models, acute stress releases dynorphin into the NAcc which downregulates DA and has been correlated with learned helplessness and depressive symptoms (Kram et al., 2002). This may explain the division between flow and trauma, as this would occur in the trauma scenario, while the flow scenario seems likely to require enkephalin release (which is associatd with feelings of euphoria, see Boecker et al., 2008). As applied to our motorcycle hypothetical situation, once the swerve produces better than expected results, enkephalins would be released. These chemicals both increase DA production (Kalivas and Duffy, 1990), which would further enhance motivation and increase autotelicity. Finally, work by Henry et al. (2017) relates heightened enkephalin signaling to the development of resilience, suggesting an opioid-related mechanism for the post-traumatic growth we see in the flow-condition motorcyclist.

4.7. Flow triggers and performance benefits

The neuronal processes outlined in this paper offer a potential explanation of both flow's triggers and flow's performance benefits. We again emphasize that more research is needed for demonstrating the causal role of the triggers and their relationship with performance. On the trigger side, clear goals, immediate feedback, the challenge-skills balance, novelty, complexity, unpredictability, risk, insight, curiosity, passion, autonomy, mastery and purpose, all engage the seeking system and activate phasic DA release. It is likely that any sudden change in DA signaling and activity in the salience network—triggered either externally or internally—can (but will not always) result in flow. Moreover, and as discussed elsewhere, it seems these reward signals appear to bias the deployment of control, which should further facilitate task performance. Now, from a descriptive perspective, flow's triggers engage multiple systems and processes, and thus the proposal in this paper describes how global neurocognitive changes in the brain are associated with those triggers.

On the performance side, the significant increase in salience network activity, especially the LC-NE system, coupled to an increase in dopaminergic signaling could account for flow's heightening of both intrinsic motivation and learning rates (Pekrun, 1992; Seli et al., 2016; Tyng et al., 2017). This increase in DA signaling could also partially explain flow's impact on creativity and innovation, as DA also amplifies pattern recognition. Additionally, as DA signaling correlates with an increase in positive affect and positive affect has been shown to increase the likelihood that the dACC will discover remote associations and activate weakly recalled action plans, this could be a further mechanism for enhanced creativity (Kounios et al., 2006; Kounios and Jung-Beeman, 2014). Myers et al. (2016) found that grit correlated with ventral striatal networks extending to the mPFC and rostral ACC, while Touroutoglou et al. (2018) discovered that the ACC is the central hub for tenacity-persistence in the face of challenges. Both of these systems would be active in a flow scenario and could account for the downstream development of grit and resilience that has been correlated with post-traumatic growth. Moreover, recent neuroimaging studies on grit in academic performance link the trait to heightened spontaneous resting state activity in the right dlPFC (Wang et al., 2017). This finding corresponds to research by Nakagawa et al. (2016), who state: "The dlPFC seems to be the main neural correlate of post-traumatic growth."

5. The flow versus trauma question

In our hypothetical example, why does one motorcyclist experience flow and another traumatic stress? Before we explore alterations in underlying neurobiological mechanisms that account for this difference in psychological outcome, an examination of the similarities between experiences is worth considering. Both flow and traumatic stress are

altered states that arise during waking conscious experience, both require activation of similar large-scale brain networks and neuro-modulatory systems. Yet, it is within the actions of those neuro-modulatory systems that we can start this discussion.

One of the larger neurobiological differences between flow and trauma involves phasic DA. As reviewed earlier, in flow, there is an increase in phasic DA signaling that results from both the "fight response" and/or the successful execution of the initial "swerve" motor-action plan. This surge does not occur in trauma, because, while the execution of the same "swerve" motor-action occurs, in the trauma-scenarios it is a fear-inducing stimulus. More specifically, rebound-excitation theory (J.C. Lee et al., 2016; E.M. Lee et al., 2016) proposes that DA neurons rebound—that is, reactivate phasic DA signaling—at the termination of fearful experiences, putting a "brake" on fear-excitation by supplying intrinsic safety signals. This increase in phasic DA also explains why our flow-condition motorcyclist does not have fearful memories, as the amygdala-connected, ECS-modulated, DA neurons in the mPFC, via connections to the amygdala, play a crucial role in suppressing hyperarousal and promoting fear extinction (Milad et al., 2009; Fenster et al., 2018).

Concurrent to this flow-condition increase in DA signaling, activity in the endocannabinoid system is likely to further down-regulate the amygdala, thus promoting fear-extinction while reducing responses to conditioned fear cues and the retrieval of fearful memories (Atsak et al., 2012, Bitencourt et al., 2008). This would not happen in our trauma condition, which helps explain why PTSD sufferers show heightened activity in the amygdala and anterior cingulate cortex reflecting over-expression of this network and the experience of "hyper-vigilance" (Szeszko and Yehuda, 2019).

Additionally, work by Jasnow et al. (2013) shows that fear-extinction is a less robust process than fear-creation. In this process, inputs from the vmPFC and hippocampus activate when there is safety learning after fearful exposure (Hartley and Phelps, 2010), something that is likely to occur in our flow condition. The opposite is true for trauma, as reduced activation of the vmPFC heightens fearful responses and the creation of fear-based memories (Jovanovic et al., 2012).

6. Summary

The ideas presented herein suggest that there is a cortico-striatal-thalamic loop that governs the onset of flow. We have also proposed that the basal ganglia, thalamus, amygdala and dorsal anterior cingulate cortex are involved. Activity in this loop is modulated by a combination of endocannabinoid, dopaminergic and noradrenergic signaling. More-over, this hypothesis suggests that loop activation is downstream from the fight response and the arrival of a series of P300 waves or, at the very least, an increase of phasic DA in the VTA. More broadly, a "flow network" is beginning to emerge where signals from the FPCN and reward structures are integrated (see also, Weber et al., 2009). In fact, and as argued earlier, it appears that the salience network facilitates the transition into the flow network (for an extended treatment, see Weber and Fisher, 2020).

Overall, our exploration of a neurobiological account for the onset of flow includes various perspectives, including both neuroscientific and phenomenological ones. We believe that, by incorporating this account into a broader framework with other cognitive states—i.e., PTSD and the psychedelic state—we gain a deeper insight into the neurocognitive processes associated with flow.

6.1. Open questions, future directions and research initiatives

While flow's considerable impact on performance is widely documented, these effects are rarely accounted for in the neurobiological descriptions of the state. Yet any theoretical overview of flow should include the state's impact on cognitive performance, with specific attention paid to its impact on the following categories: (a) creativity,

improvisation and innovation (Amabile et al., 2005; Csikszentmihalyi, 1997; Doyle, 2017), (b) learning and education (Rathunde and Csiks-zentmihalyi, 2005; Berka et al., 2007; Craig et al., 2004), (c) motivation and productivity (Bryce and Haworth, 2002; Csikszentmihalyi, 1990; Rheinberg and Engeser, 2018), (d) cooperation and collaboration (Sawyer, 2015; Shehata et al., 2020; van den Hout et al., 2018), (e) well-being, meaning, purpose and eudaimonic values (Bonaiuto et al., 2016; Seligman et al., 2007; Csikszentmihalyi and Nakamura, 2014), (f) appreciation for nature/environmental awareness (Bonaiuto, 2016; anecdotally, also see Kotler, 2006, 2013), (g) empathy (Bachen et al., 2016; Mesurado et al., 2016; Vaillant, 2008), (h) grit, perseverance, and burnout (Aust et al., 2022; Constantinescu et al., 2017; Salanova, 2006; Von Culin et al., 2014; Amabile and Kramer, 2007), (i) intuition (Bolte et al., 2003; Doyle, 2017; Järvilehto, 2016, see "Intuition and Flow" in Flow Experience), and (j) perception (Sinnett et al., 2020).

The theoretical model for the transition into flow outlined in this paper is unique in the literature as it lays out a neurobiologically plausible explanation for the flow's onset thereby offering predictive insights and testable hypotheses — specifically, a set of neuro-markers that may be associated with flow onset and/or flow itself. First, this model predicts that flow comprises a unique pattern of brain network activation, distinct from other similar states of consciousness, e.g., hyperfocus, psychedelic states, and deep meditative states. If this is correct, then flow can be characterized as a phenomenologically distinct experience. Second, although current neuroimaging methods may not be able to ascertain whether some of these neurobiological mechanisms are at work during the transition into flow (particularly as described in our hypothetical situation), future technological advances (e.g., wearable functional near-infrared spectroscopy [FNIRS] or EEG devices) may facilitate the discovery of these mechanisms. Third, and perhaps most importantly, if contrasting neurobiological outcomes distinguish flow from traumatic stress, this would be particularly important as flow could be used as a possible therapeutic approach to PTSD, and resilience more broadly (see Tabibnia, 2020). As initial evidence pointing in this direction, research shows that increased cognitive control (which flow seems to require) is associated with decreased PTSD symptoms (White et al., 2018).

At the same time, there are several important questions that shape inquiry into the neural basis of flow. For instance, we have outlined numerous flow triggers that are thought to causally elicit the flow experience. Excluding the challenge/skill balance, the evidence for nearly all of these triggers is correlational. Therefore, the causal role of these triggers remains uncertain. Similarly, we cannot identify a single study that systematically manipulates all triggers to identify if all are simultaneously necessary to elicit flow. Said differently, the necessary and sufficient conditions that elicit flow require further investigation.

Similarly, we consider the phenomenological characteristics of what it is like to be in flow (complete concentration, merger of action and awareness, time dilation, the vanishing self, a sense of control, autotelicity). Csikszentmihalyi (1990) has argued that all six characteristics describe the flow experience. Here again, the evidence for these characteristics is largely correlational, and based on retrospective-self report measures. There is a dire need to systematically, and experimentally, confirm the presence of all six characteristics during flow.

One challenge is that this confirmation will largely rely on comparing self-reported measures for these six phenomenological characteristics, in a flow condition relative to non-flow conditions. Such an approach makes it possible to claim that a flow condition elicits more self-reported flow than a non-flow condition (for examples, see e.g., Huskey et al., 2018b,a, 2021; Keller and Bless, 2008; Ulrich et al., 2014, 2016a,b, 2018, 2022). Defining flow in comparison to non-flow is useful, but comes with its own challenges. How much self-reported flow is required to say that someone is truly experiencing flow? Surely the score should be above the scale mid-point. But by how much? And by how much on each of flow's six phenomenological characteristics? Are all six characteristics always present during flow? Right now, we do not have

good answers to these questions.

All of these issues present important challenges for neuroscientific investigations of flow. This is especially true when we consider that most neuroscientific methods for linking neural response with psychology or phenomenology are correlational in nature (Ramsey et al., 2010). When considered in conjunction with concerns about reverse inference (Poldrack, 2006), it seems unlikely that neuroscientific investigation will offer clear solutions to these problems. Instead, if we are to better understand the neural basis of flow, then it is incumbent on flow researchers to resolve these theoretical, conceptual, and mechanistic ambiguities. Ultimately, accomplishing these objectives will require careful experimental interventions (Alameda et al., 2022). Our paper lays a foundation for such inquiry.

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