Pedunculopontine-Induced Cortical Decoupling as the Neurophysiological Locus of Dissociation

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Abstract

Mounting evidence suggests an association between aberrant sleep phenomena and dissociative experiences. However, no wake-sleep boundary theory provides a compelling explanation of dissociation or specifies its physiological substrates. We present a theoretical account of dissociation that integrates theories and empirical results from multiple lines of research concerning the domain of dissociation and the regulation of rapid eye movement (REM) sleep. This theory posits that individual differences in the circuitry governing the REM sleep promoting Pedunculopontine Nucleus and Laterodorsal Tegmental Nucleus determine the degree of similarity in the cortical connectivity profiles of wakefulness and REM sleep. We propose that a latent trait characterized by elevated dissociative experiences emerges from the decoupling of frontal executive regions due to a REM sleep-like aminergic/cholinergic balance. The Pedunculopontine Induced Cortical Decoupling Account of Dissociation (PICDAD) suggests multiple fruitful lines of inquiry and provides novel insights.

Keywords: Dissociation, Suggestibility, REM Sleep, Pedunculopontine Nucleus, Functional Connectivity

Dissociation refers to experiences marked by detachment from reality, alterations in the sense of self, disintegration of awareness, and disruptions of memory (Lynn, et al., 2019; Kihlstrom, Glisky, & Angiulo 1994). Accumulating evidence points to weak-to-moderate inter-correlations between dissociation and an array of psychological characteristics that share a family resemblance including absorption, fantasy-proneness, self-transcendence, boundary thickness, schizotypy, hypnotic suggestibility, and openness to experience (Cardeña, & Terhune, 2014; Koffel & Watson, 2009). Cumulatively, these results hint at a higher-order latent trait characterized by pronounced liminality of awareness but the source of this shared variance, and its neurophysiological basis, remains poorly understood.

Multiple empirical studies and theoretical accounts of dissociation and germane phenomena suggest that a common thread among these different characteristics may be a proneness toward atypical, aberrant, or anomalous sleep experiences (DeYoung & Grazioplene, 2013; Hartmann, 1991; Koffel & Watson, 2009; Watson, 2001). For example, highly dissociative individuals exhibit a greater incidence of sleep paralysis, nightmares, sleep disturbances and narcoleptic-like experiences (Koffel, & Watson, 2009; see also Hartmann, 1991). Koffel and Watson (2009) proposed that dissociation, positive schizotypy, and unusual sleep experiences load onto a common latent factor which they referred to as *oddity*. Despite these compelling links, no rapid eye movement (REM) sleep boundary account of dissociation has been advanced that has both a high degree of physiological specificity and a broad focus attempting to explain the connection between the diverse phenomena comprising the domain of dissociation.

The pedunculopontine induced cortical decoupling account of dissociation: a synthesis

Here we present a neurophysiological theory of dissociation (Pedunculopontine Induced Cortical Decoupling Account of Dissociation [PICDAD]) that advances a set of testable

predictions. This theory starts from the proposal that dissociative and germane phenomena comprise a latent trait (henceforth, dissociation). We propose that this trait is partly derived from activity in the REM-promoting cholinergic nuclei of the Pedunculopontine Nucleus (PPN) and Laterodorsal Tegmental Nucleus (LDT). According to this account, dissociation reflects the extent to which the waking balance of neuromodulation resembles the neuromodulatory conditions of REM sleep. In turn, dissociation emerges from a propensity for cortical decoupling that is a function of this wake-REM sleep neuromodulatory resemblance and is partly shaped by contextual factors, other psychological dispositions, and developmental trajectories.

PICDAD attempts to integrate preexisting ideas regarding unusual sleep experiences and the domain of dissociation. After describing the central features of this theory and the principal characteristics of dissociation and pertinent aspects of PPN/LDT physiology, we outline how cortical decoupling may underlie atypical cognitive control and other features of dissociative experiences. We conclude by presenting potential means of testing the theory and describe how this account is commensurate with dominant theoretical accounts of consciousness and human brain function (Friston, 2010; Spratling, 2017; Tononi, Boly, Massimini, & Koch, 2016; Tononi, & Edelman, 1998).

The Core Tenets of PICDAD: A Neurophysiological Theory of Dissociation

The central premise of PICDAD is that dissociative experiences arise from a cascade of neurophysiological effects originating from aberrant activity in the PPN and LDT. Mahowald and Schenck (1992) similarly proposed that disruptions of transitions between states (wakefulness, NREM sleep, and REM sleep) could lead to state dissociations (ambiguous states with characteristics of multiple states) and concomitant dissociative symptoms. PICDAD expands upon this idea by proposing a specific kind of state boundary abnormality and describes

how this thin boundary between states affects the cortex in a way that yields dissociative phenomenology. In particular, it proposes that high levels of dissociation result from REM sleep regulatory abnormalities similar to those found in narcolepsy.

If the thinness of the boundary between wakefulness and REM sleep is responsible for dissociation, the PPN/LDT are likely to exhibit abnormal waking activity. The phenomenology of REM sleep seems to resemble the phenomenology typically associated with the domain of dissociation (Hobson, 2002). During REM sleep, with the exception of dopamine, aminergic (norepinephrine and serotonin) neuromodulation is reduced and cholinergic neuromodulation is dominant (Hobson, Pace-Schott, & Stickgold, 2000; Solms, 2000). The PPN/LDT play a critical role in the promotion of REM sleep. Electrical stimulation of the LDT increases REM sleep in cats and the destruction of cholinergic neurons in PPN/LDT leads to a reduction in REM sleep (Jones, 1991; Thakkar, Portas, & McCarley, 1996). Additionally, REM sleep is marked by greater cholinergic release (from PPN/LDT projections) in the thalamus relative to NREM sleep (Williams, Comisarow, Day, Fibiger & Reiner, 1994).

PICDAD has five core tenets, the first being that the domain of dissociation is unified by a latent trait (dissociation). The second tenet is that dissociation is at least in part a product of REM sleep associated cholinergic nuclei in the PPN/LDT. The third tenet is that dissociation is marked by a waking state with a neuromodulatory balance resembling that found during REM sleep. The fourth tenet is that this REM-like neuromodulatory balance and/or changes in the PPN/LDT interactions with thalamic nuclei elicit dissociative experiences through cortical decoupling (a breakdown in communication) within higher-order control regions and between high-order and lower-level processing regions. A critical form of decoupling for PICDAD is the weakening of the casual influence of higher order control related regions on lower order areas.

The fifth tenet is that dissociation manifests in many different ways depending on a range of factors including developmental trajectories and other psychological dispositions.

Beyond its core tenets, PICDAD views dissociation as a cognitive style, that in combination with life events and other predispositions, shapes personality. Accordingly, PICDAD is a theory of both pathological and non-pathological dissociative experiences. We do not present a theory of the origin of aberrant PPN/LDT activity, which we consider only briefly, and are not committed to specific pathways underlying it. A peripheral tenet that follows from PICDAD's fourth core tenet and the dorsolateral prefrontal cortex (DLPFC) deactivation observed during REM sleep is that cognitive control disruptions are in some way related to the domain of dissociation. Cognitive control could be hindered in highly dissociative individuals at baseline or only during dissociative states, resulting in greater intra-individual variability in cognitive control. PICDAD is similarly neutral regarding whether highly dissociative individuals are characterized by a tonic waking REM-like neuromodulatory balance or whether this balance is restricted to transient states.

The Domain of Dissociation

The Structure of Dissociation and Measurement Challenges

Dissociative experiences are characterized by a disruption of the integration of psychological processes that typically exemplify normal waking states (Ellickson-Larew, Stasik-O'Brien, Stanton, & Watson, 2020; Kihlstrom et al., 1994). Evidence suggests that dissociation is a risk factor for many forms of psychopathology (Ellickson-Larew et al., 2020). Researchers have proposed that dissociative experiences comprise two distinct but interrelated phenomena: *detachment* and *compartmentalization* (Brown, 2006; Holmes et al., 2005). Detachment is

characterized by the experience of feeling distanced from one's self or the external world (e.g., absorption, depersonalization). By contrast, compartmentalization includes the perceived loss of control over typically volitional processes like memory or movement, and thus includes phenomena such as dissociative amnesia and functional neurological symptoms (e.g., nonepileptic seizures). It has been argued that both forms of dissociation could be explained by sleep-wake cycle regulation abnormalities (Van der Kloet, Giesbrecht, Lynn, Merckelbach, & de Zutter, 2012a).

A special note needs to be made regarding functional neurological symptoms and dissociation. Historically, functional neurological disorder was considered a dissociative disorder (Brown, Cardeña, Nijenhuis, Sar, & Van Der Hart, 2007) and it is still classified as such in the ICD-11 (World Health Organization, 2019) but this is not the case for the DSM-5 (American Psychiatric Association, 2013). Although there is still disagreement in the field (Brown et al., 2007), multiple lines of evidence support the view that FND represents a dissociative condition. A recent meta-analysis of 19 psychiatric disorders (Lyssenko, Schmahl, Bockhacker, Vonderlin, Bohus, & Kleindienst, 2018) demonstrated that FND was among the top five disorders in the reporting of dissociative symptoms (alongside dissociative identity disorder, dissociative disorders, posttraumatic stress disorder, and borderline personality disorder), and was even numerically higher than depersonalization-derealization disorder, which is classified as a dissociative disorder in the DSM-5 (American Psychiatric Association, 2013). Relatedly, dissociative amnesia has been classified as a subtype of functional cognitive disorder (McWhirter, Ritchie, Stone, & Carson, 2020). Given this evidence, we treat functional cognitive/neurological symptoms as a form of dissociation.

The propensity for dissociative experiences is typically measured with psychometric measures or interview schedules (Cardeña, 2008). The gold standard measure of dissociation is the *Dissociative Experiences Scale* (DES; Bernstein, & Putnam, 1986; Carlson et al., 1993), a self-report measure that indexes the frequency of a diverse array of neurotypical and pathological dissociative experiences (Lyssenko et al., 2018). Factor analyses of the DES have yielded inconsistent results (Mazzotti et al., 2016) although most researchers use a three-factor model of the DES with inter-correlated subscales for depersonalization-derealization, amnesia, and absorption (Ross, Joshi, Currie, & 1991). There is disagreement regarding whether the factor structure of dissociation is similar in non-clinical and dissociative disorder samples (Olsen, Clapp, Parra, & Beck, 2013; Ross, et al., 1995; Sijbrandij et al., 2012; Waller, Putnam, & Carlson, 1996; Waller, & Ross, 1997). If the factor structure is not invariant between groups it could stem from different relationships between latent variables (Revelle, & Wilt, 2016) or it could be due to the same latent variable structure manifesting itself differently (Molenaar, & Campbell, 2009; Nesselroade & Ford, 1985; Nesselroade, Gerstorf, Hardy, & Ram, 2007). The latter possibility is interesting from the perspective of PICDAD but modeling it requires overcoming a few challenges including the need for multiple measurements per manifest variable per individual. Consensus has not yet formed regarding whether dissociative experiences are best understood by a hierarchical model comprised of a general factor and ancillary factors or correlated factors (Goldberg, 1999; Stockdale et al., 2002). However, a recent application of the Rasch model, a psychometric approach that circumvents limitations of classic test theory methods, yielded evidence in favor of the unidimensionality of the DES (Saggino et al., 2020). Replication and extension of this research is required but it suggests that dissociation is best explained by a hierarchical model with a single general factor.

Multiple models have suggested that high absorption and/or (hypnotic) suggestibility acts as a diathesis for pathological dissociation in response to stress (Butler, Duran, Jasiukaitis, Koopman, & Spiegel, 1996; Kihlstrom et al., 1994; Wieder, & Terhune, 2019). We expect that dissociation is fostered through dissimilar developmental trajectories. A related issue is that many low frequency dissociative experiences (e.g., dissociative amnesia) are considered pathological but this is not the case in all contexts. For example, the trance dancers of Bali and dang-ki mediums report amnesia for possession rituals (Haley, & Richeport-Haley, 2015; Lee, 2016). This illustrates PICDAD's fifth tenet that the expression of dissociation can be shaped by the developmental context (see also Dalenberg et al., 2012).

Another aspect of PICDAD's fifth tenet is that the factors that set developmental trajectories could moderate dissociation's relationships with other traits. Hartmann (1991) proposed that his mental boundaries construct represented a foundational feature of personality. The profile of a person with thin boundaries matches Herbert Spiegel's clinical observations of extremely hypnotizable individuals (Spiegel, 1974; Spiegel, 2007). What Hartmann and Spiegel observed, not to mention the domain of dissociation more broadly, might be better thought of as a cognitive style or rather a mode of thinking and perceiving (Witkin, Moore, Goodenough, & Cox, 1977). A cognitive style might interact with other biological dispositions and life events to shape the development of personality. Accordingly, when examining trait-level associations, it will be imperative to model constellations of cognitive and personality traits rather than simple bivariate associations. Certain constellations might occur with greater frequency at different levels of dissociation proneness. In addition, the moderating influence of stressful life events on dissociation's relationship with personality variables and other factors will have to be taken into consideration.

PICDAD is neutral as to whether or not a diathesis is best thought of as different manifestations of the same underlying psychological constructs or as different traits that load on a higher order trait. Regardless, the dissociation research domain would benefit from greater use of latent variable modeling methods in order to assess the full domain of dissociation and to mitigate measurement error (Loehlin, 1998) and refined measures using contemporary, rather than classic, test theory approaches (e.g., Saggino et al., 2020). A commonly-cited limitation of dissociation scales, that they do not adequately index non-pathological manifestations of dissociation, hinders our ability to evaluate PICDAD's fifth tenet (Fisher, Johnson, & Elkins, 2013; Saggino et al., 2020). Similarly, these scales measure the frequency of dissociative experiences and less so a respondent's capacity to dissociate in certain contexts. Critically, the field needs to pay greater attention to non-pathological forms of dissociation.

Absorption and Its Correlates

Absorption is the quintessential form of dissociation that is commonly experienced in the general population (Kihlstrom et al., 1994; Tellegen, & Atkinson, 1974). Absorption is defined as an openness to self-altering experiences involving engrossment in imagination and perceptual states often at the cost of environmental awareness with downstream cognitive-perceptual consequences, such as underestimation of the passage of time. Psychometric meaures of absorption (Tellegen, & Atkinson, 1974; Jamieson, 2005) reliably predict the tendency to experience alterations in awareness and perception in a variety of contexts including hypnotic suggestibility (responsiveness to suggestion following a hypnotic induction) (Glisky et al., 1991; Tellegen, & Atkinson, 1974; Zachariae, Jo rgensen , & Christensen, 2000), openness to experience (Glisky, et al., 1991), fantasy proneness (Angiulo & Kihlstrom, 1993; Fassler, Knox, & Lynn, 2006; Lynn & Rhue, 1986; Rhue & Lynn, 1989), and proneness to anomalous

experiences in a variety of contexts (Granqvist et al., 2005; Lifshitz, van Elk, & Luhrmann, 2019; Maij, & Van Elk, 2018; Studerus, Gamma, Kometer, & Vollenweider, 2012) (for a recent critique of the use of absorption scales in this context, see Terhune & Jamieson, 2021). These effects are potentially inflated by context effects (Council, Kirsch, & Hafner, 1986) (but see Barnier & McConkey, 1999) but multiple studies are at odds with this (Cardeña, & Terhune, 2014; Nadon, Hoyt, Register, & Kihlstrom, 1991; Zachariae, et al., 2000). In accordance with PICDAD, the relationship between absorption and hypnotic suggestibility was shown to depend on a higher order factor (Jamieson, 2005). Despite being widely considered as a non-pathological form of dissociation (Kihlstrom, 1994), absorption seems to confer vulnerability to various pathological conditions or accompany other symptoms, including idiopathic environmental intolerance (Witthöft, Rist, & Bailer, 2008), obsessive compulsive symptoms (Soffer-Dudek, Lassri, Soffer-Dudek, & Shahar, 2015), panic attacks (Lilienfeld, 1997), and externalizing symptoms (Ellickson-Larew et al., 2020).

Dissociation and Hypnotic Suggestibility

Dissociation is historically intertwined with hypnosis although the former's relation with hypnotic suggestibility is complex (Butler et al., 1996). Dissociation only weakly correlates with hypnotic suggestibility (Butler, & Bryant, 1997; Covino, Jimerson, Wolfe, Franko, & Frankel, 1994; Frischholz et al., 1992) although highly suggestible individuals seem to be prone to dissociative states following a hypnotic induction (Cleveland, Korman, & Gold, 2015; Maxwell, Lynn, & Condon, 2015; Terhune, Cardeña, & Lindgren, 2011). By contrast, there is consistent evidence that patients with dissociative and germane disorders reliably display elevated hypnotic suggestibility (for reviews, see Bell, Oakley, Halligan, & Deeley, 2011; Dell, 2019; Terhune & Cardena, 2015; Wieder et al., 2021). Additionally, NMDA receptor antagonists are known for

their dissociative effects (Farber, 2003) and they produce increases in suggestibility (Whalley, & Brooks, 2009; for a review, see Acunzo, Oakley, & Terhune, 2021). These seemingly inconsistent findings can potentially be reconciled by a diathesis stress model, according to which (hypnotic) suggestibility confers predisposition to dissociation in the wake of traumatic stress (Butler et al., 1996; Kihlstrom et al., 1994). Evidence in favor of this model has been found in both functional neurological disorder patients (Roelofs, Keijsers, Hoogduin, Näring, & Moene, 2002) and neurotypical adults (Wieder & Terhune, 2019) and is consistent with links between hypnotic suggestibility and posttraumatic stress (Yard, DuHamel, & Galynker, 2008), which is known to facilitate dissociation (Kihlstrom et al., 1994).

This complex association is in keeping with a wealth of research pointing to heterogeneity among highly suggestible individuals. Phenomenological, behavioral, cognitive, and developmental data suggests different modes of responding to verbal suggestions and dissimilar neurocognitive profiles of highly suggestible individuals (Terhune & Cardena, 2015). One model attributes this heterogeneity to the interaction between a core latent trait of hypnotic suggestibility and ancillary componential traits that facilitate response to certain suggestions (Barnier, Terhune, Polito, & Woody, 2020; Woody & McConkey, 2003). As in other research domains (Feczko et al., 2019), an alternative interpretation models heterogeneity by reference to a latent typology in which a dissociative subtype of highly suggestible individuals experiences suggestions through dissimilar mechanisms than a second non-dissociative subtype (Barber, 1999; Carlson & Putnam, 1989). Although the debate between these models is ongoing, evidence is accumulating that dissociation can elucidate heterogeneity among highly suggestible individuals (King & Council, 1998; Terhune, & Cardeña, 2010; Terhune et al., 2011b). PICDAD is agnostic regarding these models and thus this theory is irrelevant to explanations of

suggestibility that reference compliance, positive attitudes, or active cognitive strategies but has direct bearing on hypnotic responses characterized by pronounced distortions in volition (the *classic suggestion effect*; Bowers, 1981). A key feature of PICDAD is that a shared mechanism (cortical decoupling) explains the commonality of dissociation and suggestibility.

Dissociation and Cognition

There is mounting evidence that dissociation is at least weakly negatively associated with cognitive control abilities but there is considerable inconsistency in the literature. Some studies have failed to find a relationship between performance-based measures of cognitive control and dissociation (Schurle Bruce, Ray, Bruce, Arnett, & Carlson, 2007; Dimitrova, Vissia, Nijenhuis, Draijer, & Reinders, 2020; Wright, & Osborne, 2005) and others have even found that divided attention and working memory capacity are superior in high relative to low dissociators (De Ruiter, Phaf, Elzinga, & Van Dyck, 2004; De Ruiter, Phaf, Veltman, Kok, & Van Dyck, 2003; DePrince & Freyd, 1999; Elzinga et al., 2007). Also, superior shifting ability has been observed with higher dissociation when controlling for other executive functions (Chui et al., 2016). Yet, many studies have reported poorer cognitive control in high dissociation (Amrhein, Hengmith, Maragkos, & Hennig-Fast, 2008; Giesbrecht, Geraerts, & Merckelbach, 2007; Giesbrecht, Merckelbach, Geraerts, & Smeets, 2004; Giesbrecht & Merckelbach, 2009). Dissociative absorption has been shown to weakly negatively correlate with intelligence in addition to being associated with lower accuracy on cognitively demanding tasks (Bregman-Hai et al., 2018). Similarly, there is evidence for an association of reduced frontal functioning following a hypnotic induction in highly suggestible individuals (Farvolden, & Woody, 2004; Jamieson, & Sheehan, 2004; McGeown, Mazzoni, Venneri, & Kirsch, 2009; Parris, 2016; Parris, 2017; Sheehan, Donovan, & MacLeod, 1988; Terhune et al., 2011b; Wagstaff, Cole, & Brunas-

Wagstaff, 2007), although such an effect might be specific to, or more pronounced, among those who are highly dissociative (Marcusson-Clavertz, Terhune & Cardeña, 2012; Terhune et al., 2011b). Complementary research suggests that highly dissociative-highly suggestible participants exhibit poorer upregulation of cognitive control, elevated involuntariness and more automated responses following a hypnotic induction (King & Council, 1998; Terhune et al., 2011b). Related research points to elevated automaticity in highly suggestible individuals at baseline (Dixon, Brunet, & Laurence, 1990; Dixon & Laurence, 1992; Srzich, Cirillo, Stinear, Coxon, McMorland, & Anson, 2019). Dissociation is also associated with the tendency to make commission errors (Bregman-Hai, et al., 2018; Candel, Merckelbach, & Kuijpers, 2003; Merckelbach, Zeles, Van Bergen, & Giesbrecht, 2007). Given that REM sleep is associated with decreased activity in the DLPFC (Hobson, et al., 2000), these findings are in general accordance with PICDAD.

Dissociation seems to be characterized by memory errors. When dissociation was induced in subjects with Borderline Personality Disorder working memory performance was impaired (Krause-Utz et al., 2018). Dissociation has been reported to be negatively associated with memory for both negative and neutral items as well (Matsumoto, & Kawaguchi, 2020). Children and adolescents with functional neurological symptoms have been shown to have poorer performance on a battery of memory and cognitive control tasks relative to healthy control subjects but displayed no difference in intelligence (Kozlowska et al., 2015; see also O'Brien et al., 2015; McWhirter et al., 2020).

Some of these inconsistencies are plausibly attributed to many studies not taking adverse life events into consideration (Dimitrova et al., 2020) and/or to the vagaries of the specific tasks used. It is very likely that adverse life events can have deleterious effects on cognition which are

independent of the pathological forms of dissociation that they foster (see also Chiu, 2018). Independently of this potential confound, many measures of inhibiting and shifting rely on difference scores that tend to have poor reliability (Draheim, Mashburn, Martin, & Engle, 2019). Additionally, the tasks typically used in the assessment of cognitive control might not correspond with the level of cognitive control that is impaired in dissociation (Badre & Nee, 2018). Rather, paradigms with high levels of task nesting and/or temporal extension are more likely to assess performance differences that covary with dissociative tendencies. Previous research on working memory in dissociation relied on tasks with minimal interference (e.g., De Ruiter et al., 2004) but the DLPFC seems to play a vital role in tasks that involve distractors and/or the processing of new information during the delay period, i.e., paradigms with interference (Kane & Engle, 2002). Research demonstrating superior working memory updating and greater recognition of ignored items in dissociation (Chiu, 2018) suggests that highly dissociative individuals tend to keep more memory elements in an active state. It has been proposed that working memory is the product of storage capacity and attentional control that mitigates interference and manipulates information (Cowan, 1999; Engle, Tuholski, Laughlin, & Conway, 1999). Thus, it is possible that dissociative tendencies are only negatively correlated with attentional control processes in working memory and either uncorrelated or positively correlated with storage as measured by simple short term memory tasks. Although this explanation cannot account for high dissociators' superior performance in some tasks (e.g., Elzinga et al., 2007), it can explain the positive relationship between dissociation and commission errors (Bregman-Hai, et al., 2018; Candel et al., 2003; Merckelbach et al., 2007). With less attentional control and normal or higher numbers of active memory elements, inaccurate items might intrude into consciousness awareness with greater frequency. This aligns with the proposal that REM sleep cognition is hyperassociative,

leading to the activation of remotely connected memory items (Llewellyn, 2013) and that higher dissociation is associated with a superior ability to generate word association chains (Huntjens, Janssen, Merckelbach, & Lynn, 2021).

Dissociation and germane characteristics also tend to be reliably associated with metacognitive deficits (Dehon et al., 2008; Glicksohn, & Barrett, 2003; Kunzendorf, & Karpen, 1997; Lush, Naish & Dienes, 2016; Terhune, & Hedman, 2017). In particular, dissociative experiences, absorption, and hypnotic suggestibility have been associated with misinformation effects, imagination inflation, and other forms of false memory (Eisen & Carlson, 1998; Eisen, Morgan, & Mickes, 2002; Heaps & Nash, 1999; Hekkanen & McEvoy, 2002; Hyman & Billings, 1998; Nichols, & Loftus, 2019; Platt, Lacey, Iobst, & Finkelman, 1998). Dissociation is associated with reduced sense of agency and poorer memory for self-generated writing (Bregman-Hai et al., 2020) and poorer source monitoring (Chiu et al., 2016). Given that metacognition is likely disrupted during REM sleep (Hobson, 2009) deficient metacognition in highly dissociative subjects is consistent with PICDAD. Along similar lines hallucination proneness is associated with dissociation (Varese, Barkus, & Bentall, 2011). Overall, dissociation seems to be associated with subtle deficits in cognitive control, perception, and metacognition, as predicted by PICDAD, although further high-powered studies incorporating latent variable modeling are required.

Dissociation and Social Resonance

Dreaming that occurs during REM sleep might be implicated in social cognition (McNamara, 1996; Revonsuo, Tuominen, & Valli, 2015) and reflect an association between wake-sleep and self-other boundaries (Hartmann, 1991). REM sleep has been hypothesized to play a role in the promotion of social bonding (McNamara, 1996). Individuals with anxious

attachment styles, who are typically highly dissociative (Wieder, & Terhune, 2019), exhibit higher dream recall and enter REM sleep earlier than those with a secure attachment style (McNamara, Andresen, Clark, Zborowski, & Duffy, 2001; McNamara, Pace-Schott, Johnson, Harris, & Auerbach, 2011). Peptides implicated in attachment, oxytocin and prolactin, have been shown to promote REM sleep (Braga, Panaitescu, Bădescu, Zăgrean, & Zăgrean, 2014; Machado, Rocha, & Suchecki, 2017; Obál et al., 2005; Roky et al., 1995) and there is evidence that both are positively associated with dissociation (Bob et al., 2007; Bob et al., 2008; Jalal & Salim Jehangir, 2015; Li, Hassett, & Seng, 2019; Seng et al., 2013). Additionally, oxytocin receptors are found in the PPN of the rhesus macaque (Freeman, Inoue, Smith, Goodman & Young, 2014). If REM sleep is involved in offline simulation of social situations, it might be associated with waking experiences of social resonance (Revonsuo et al., 2015). The frequency of dream enactment behaviors (behavioral expressions of dreaming that usually occur during sleep to wake transitions) and nightmares are positively related to mirroring behaviors in everyday life, especially those involving emotional contagion (Nielsen, & Kuiken, 2013; Nielsen, Powell, & Kuiken, 2013).

Interpreting these effects in the context of PICDAD leads to the prediction that dissociation should be associated with greater social resonance. Indeed, various contagion experiences, such as emotional contagion, the spontaneous triggering of an emotion by the mere observation of another person's affective state, and empathy are positively correlated with dissociation, unusual sleep experiences and germane traits (Cardeña, Terhune, Lööf, & Buratti, 2008; Kotov, Bellman, & Watson, 2004; Neufeld, Brown, Lee-Grimm, Newen, & Brüne, 2016; Sapkota, Brunet, & Kirmayer, 2019; Wickramasekera, & Szlyk, 2003). Also, individuals high in depersonalization are more susceptible to the rubber hand illusion than those exhibiting low

depersonalization scores (Kanayama, Sato & Ohira, 2009). These effects are consistent with work showing that highly suggestible individuals are more prone to vicarious experiences (Fiorio, Modenese, & Cesari, 2020; Lush et al., 2020; Walsh et al., 2015) and bodily illusions (Keizer, Chang, O'Mahony, Schaap, & Stone, 2020; Stone, Bryant, & Gonzalez, 2013). The precise cognitive locus of these associations is unclear as it is likely that bodily illusions in these paradigms are at least partly influenced by implicit and/or explicit suggestions in these procedures (Lush et al., 2020), however, weak-to-moderate correlations between these illusions and suggestibility do not necessarily indicate that these illusions are suggestion effects per se. In addition, mu suppression, a phenomenon that occurs when engaging in a motor action and when observing actions, has been shown to be greater for highly suggestible individuals relative to lows while watching video clips of intentional actions during hypnosis (Neufeld et al., 2016).

Vicarious experiences can have dissociative pathological manifestations as well, such as in mass psychogenic illness (Jones et al., 2000; Van Ommeren et al., 2001) and recent work highlights the importance of dissociation and hypnotic suggestibility in predicting proneness to mass psychogenic illness (Sapkota, Brunet, & Kirmayer 2020). However, the relationship between dissociation and social resonance is likely complex as certain features of dissociation, such as absorption, may facilitate such effects, other features, such as depersonalization, may hinder vicarious emotional experience (Barrett, 2016).

If a hereditary predisposition towards dissociation is shaped through development to manifest itself as depersonalization resulting in alexithymia, awareness of resonance phenomena could be disrupted. Elementary forms of empathy (fantasy and personal distress) might remain somewhat intact whereas advanced forms of empathy (empathetic concern and/or perspective taking) might fail to develop (Guttman, & Laporte, 2000). Lower cognitive empathy in high

dissociators has been shown to be partially attributed to impaired emotional awareness (Chiu, Paesen, Dziobek, & Tollenaar, 2016) and might be related to broader alterations in attachment (Joireman, Needham & Cummings, 2002; Troyer, & Greitemeyer, 2018). In a healthy environment the hereditary predisposition towards dissociation might manifest itself primarily as non-pathological forms of dissociation (e.g., absorption) that could enhance empathy. This example is one illustration of PICDAD's fifth tenet, dissociation's potential to manifest itself differently depending on context.

The fourth tenet of PICDAD proposes that dissociative phenomena emerge from cortical decoupling. Individual differences in social resonance might be partially explained by the degree of frontal coupling. Individuals scoring high in absorption and with a propensity to ruminate displayed a decrease in beta band coherence between anterior and posterior electrode sites during emotional stimulation (watching or listening to people expressing sadness or anxiety) while individuals low in the two traits exhibited an increase in coherence (Reiser et al., 2012). From a psychological standpoint, PICDAD proposes that social resonance phenomena are facilitated and shaped by suggestion. In physiological terms, PICDAD explains the relationship between vicarious experiences and the domain of dissociation through the up-regulation of regions, at intermediate levels of a perception or action hierarchy, and the disruption of frontal regions, responsible for the regulation of social resonance, brought about by a REM sleep-like neuromodulatory balance.

Dissociation and Stress

A longstanding controversy concerns the role of trauma, especially early life trauma, in the genesis of dissociative experiences and symptoms (Dalenberg et al., 2012). The trauma model (TM), which is widely endorsed among clinicians and researchers, posits that traumatic

life events play a causal role in the development of dissociative experiences (Dalenberg et al., 2012) whereas the sociocognitive model (SM) proposes that dissociation is multi-causal and that the association between dissociation and self-reported trauma is likely inflated by fantasy proneness and a propensity to form false memories (Lynn et al., 2014; Lynn et al., 2019). PICDAD acknowledges the relationship between traumatic stress and dissociation but shares the SM's emphasis on dissociation being explained by factors beyond a history of stressful life events and the SM's proposed link between dissociation and aberrant metacognition. On the other hand, PICDAD provides the TM with a biological pathway through which stressful life events could promote and/or shape dissociative experiences.

When incorporating studies with different sample types, on average ~10% of the variance in dissociation is explained by trauma (Buchnik-Daniely, Vannikov-Lugassi, Shalev, & Soffer-Dudek, 2021; Dalenberg et al., 2012; Rafiq, Campodonico, & Varese, 2018). Meta-analytic research has similarly found evidence for dissociation as an important mediating variable between trauma and hallucinations (Bloomfield et al., 2021) and self-reported distress predicts dissociative experiences over and above potential confounds, such as sleep quality (Buchnik-Daniely et al., 2021). The relationship between dissociation and trauma is stronger when looking at sexual abuse samples in isolation but still this only amounts to ~29% of the variance (Dalenberg et al., 2012; Vonderlin, Kleindienst, Alpers, Bohus, Lyssenko, & Schmahl, 2018). Moreover, although present at a higher rate than in the general population, trauma does not represent a core etiological feature of some dissociative conditions (e.g., FND) (Keynejad, Frod, Kanaan, Pariante, Reuber, Nicholson, 2018). Thus, a model of dissociation has to be able to explain individuals with strong dissociative tendencies that lack a significant trauma history and the factors that determine why dissociation is present in some people with a history of severe

trauma but not others. Future research should focus more on how stress in general, rather than extreme stress, relates to dissociation and what factors moderate this relationship.

The connection between dissociation and stress is related to PICDAD's fifth tenet, that dissociation can manifest itself in different ways depending on developmental factors. At a fundamental level, this implies that dissociation can be understood through a diathesis stress or differential susceptibility framework (Morgan, Shaw, & Olino, 2012). A connection between dissociation and stress complements the assumptions of PICDAD. REM sleep is associated with affective disorders (e.g., PTSD) and has been postulated to weaken next day amygdala and behavioral responses to previously experienced emotional stimuli (van der Helm, & Walker 2010; van der Helm, Yao, Dutt, Rao, Saletin, & Walker, 2011). Given these findings, excessive REM sleep drive could explain the experiences of detachment associated with some cases of posttraumatic stress (Steuwe, Lanius, & Frewen, 2012). Also, some adherents of the TM maintain that dissociation is a manifestation of something akin to tonic immobility (Lloyd, Lanius, Brown, Neufeld, Frewen, & McKinnon, 2019). Although this is link is speculative, a large set of behavioral and physiological commonalities has inspired the hypothesis that there is an evolutionary kinship between tonic immobility and REM sleep (Tsoukalas, 2012). An even more speculative connection is the triad between REM sleep, insecure attachment, and dissociation (McNamara et al., 2001; McNamara et al., 2011; Wieder, & Terhune, 2019). If REM sleep has a special role to play in modulating social bonding, traumatic stressors that affect attachment might be more likely to lead to pathological dissociative experiences than other kinds of traumatic stressors.

A point of contention related to the TM vs. SM debate concerns whether dissociation is better thought of as a continuum or as a typology. The SM views dissociation as a continuum

whereas some adherents of the TM endorse the view that certain dissociative experiences comprise a pathological taxon (Waller & Ross, 1997). Generally, the continuum model is more compatible with PICDAD. The appearance of a taxon might be an artefact arising from heterogeneity in the manifestation of the same underlying latent trait with some patterns of manifestation being less common than others. That is, the behavioral expression of dissociative experiences might differ across individuals, such as immersion in music in one person or extreme engagement in reading in another. In the West, dissociative amnesia may only have pathological manifestations but in Bali this factor might manifest itself in a non-pathological manner during trance rituals (Haley, & Richeport-Haley, 2015). Additionally, dissociation has a similar factor structure in clinical and non-clinical populations, thereby casting doubt on the view that non-pathological and pathological manifestations of dissociation are qualitatively different (Olsen, et al., 2013; Ross, et al., 1995; Sijbrandij et al., 2012). PICDAD could be thought of as a third way (other than the TM and SM models) that appreciates links between dissociation, metacognitive deficits, and suggestibility while acknowledging the role that stressful life events likely play in the manifestation and expression of certain dissociative experiences.

Sleep Experiences

Over the past few decades, evidence has converged to suggest that atypical sleep experiences are more prevalent among highly dissociative individuals (Fassler, Knox, & Lynn, 2006; Giesbrecht, & Merckelbach, 2006; Giesbrecht, Smeets, Leppink, Jelicic, & Merckelbach, 2013; Hartmann, Elkin, & Garg, 1991; Koffel, & Watson, 2009; Van Der Kloet et al., 2013; Van der Kloet et al., 2012a; Watson, 2001; Watson, 2003). Dissociation and germane phenomena reliably correlate with dream recall (Schredl, Wittmann, Ciric, & Götz, 2003; Spanos, Stam, Radtke, & Nightingale, 1980; Tonay, 1993; Watson, 2003) and unusual sleep experiences such

as sleep paralysis and hypnagogic hallucinations (Belicki & Belicki, 1986; Fassler, et al., 2006; Giesbrecht & Merckelbach 2006; Levin, & Fireman, 2001; Spanos, McNulty, DuBreuil, Pires, & Burgess, 1995; Watson 2001; Watson 2003). Dissociation is also associated with insomnia and parasomnia symptoms and nightmares have been shown to mediate the relationship between trauma and dissociation (Nobakht, & Dale, 2019). Among patients with insomnia, dissociation positively predicted REM sleep percentage and fewer awakenings after sleep onset (Van der Kloet et al., 2013). Dissociative absorption is similarly associated with greater sleepiness following sleep deprivation (Soffer-Dudek et al., 2017). Many of the sleep experiences indexed in these studies (Watson, 2001) are common among narcoleptic subjects (e.g., hypnagogic hallucinations), and narcolepsy type 1 is characterized by pronounced dissociative symptomatology (Hanin, Arnulf, Maranci, Lecendreux, Levinson, Cohen, & Laurent-Levinson, 2021; Quaedackers, Droogleever Fortuyn, Van Gilst, Lappenschaar, & Overeem, 2021; see also Van der Kloet et al., 2012; Vannikov-Lugassi, & Soffer-Dudek, 2018). Complementary evidence is provided by preliminary research linking insomnia and unusual sleep experiences to hypnotic suggestibility (Perlstrom, & Wickramasekera, 1998), habitual daytime sleepiness (Móró, Noreika, Revonsuo, & Kallio, 2011) and self-report measures of dream mentation (Evans, 1977; Nadon, Laurence, & Perry, 1987).

Different theoretical strands have advanced accounts of how dissociation relates to unusual sleep experiences. One proposal suggests that dissociative experiences stem from a labile sleep-wake cycle that allows dream-like mentation to break into the waking state (Van der Kloet et al., 2012b). Kahn and Hobson (2003) also proposed that both hypnosis and REM sleep involve a neuromodulator balance shift from aminergic dominance towards cholinergic dominance. Sleep fragmentation plausibly has a causal role in dissociation: a longitudinal study

of sleep normalization showed that a decrease in dissociative experiences with sleep normalization was accompanied by a reduction in narcoleptic symptoms, but not insomnia symptoms (Van der Kloet et al., 2012a). The dual reduction of dissociative experiences and narcoleptic symptoms in response to sleep normalization hints at a role for PPN/LDT over-activation given that narcolepsy involves dysregulation of REM sleep. PICDAD provides a parsimonious explanation for an association between dissociative experiences and REM sleep percentage in addition to the relationship between sleep fragmentation and dissociation (Van der Kloet et al., 2012a; Van der Kloet et al., 2013).

The Neuroanatomy of the PPN/LDT

In this section, we provide a description of the anatomy of the PPN/LDT and their roles in psychosis, sensory gating, and sleep. We demonstrate how the PPN/LDT are well positioned to foster the phenomenology of dissociation. In addition, we describe potential sleep circuit abnormalities that might act as the source of PPN/LDT REM-ON cell activity intruding into wakefulness.

Anatomy of the PPN and LDT

The PPN and the LDT are located in the dorsolateral portion of the midbrain-pontine junction (Rye, 1997). Traditionally the PPN has been viewed as having two components based on cellular structure: diffuse pars dissipata (PPN-d) and dense pars compacta (PPN-pc); the latter comprises the caudal half of the nucleus and contains most of the cholinergic neurons in the PPN (Rye 1997). The LDT is located caudal to the PPN and similarly contains cholinergic, GABAergic and glutamatergic cells (Mena-Segovia, & Bolam, 2017). The rostral and caudal

PPN receive inputs from the substantia nigra, the globus pallidus, the dorsal raphe (DR), the cortex, and other regions, respectively (Martinez-Gonzalez et al., 2011). Projections from the rostral PPN innervate the substantia nigra, the hypothalamus, the basal forebrain, and globus pallidus (Rye, 1997). The caudal PPN projects to the thalamus (as does the LDT), the tectum, the ventral tegmental area (VTA), and brainstem regions. PPN cholinergic neurons that project to the thalamus also send collaterals to the basal ganglia, basal forebrain, the pontine reticular formation, and superior and inferior colliculi (Losier & Semba, 1993; Mena-Segovia et al., 2008; Semba et al., 1990), suggesting a coordinated modulation of these regions. The PPN's intimate relationship with the basal ganglia is one potential pathway through which it could have a role in the genesis of dissociative phenomena. In addition to its roles in associative learning and motor control, the basal ganglia functions as a working memory gate (Badre, 2012). Disruptions of working memory updating could potentially explain some dissociative symptoms.

The PPN seems to have a rostral-caudal connectivity gradient. The rostral PPN has greater connectivity with motor regions whereas the caudal PPN are linked with associative and limbic-related structures (Dautan et al., 2014; Huerta-Ocampo, Hacioglu-Bay, Dautan, & Mena-Segovia, 2020; Mena-Segovia, & Bolam, 2017). The LDT sits at the caudal extreme of this axis innervating the VTA, thalamic midline, and the dorsomedial striatum. The anterior, laterodorsal, and mediodorsal thalamic nuclei, not to mention the rostral thalamic reticular nucleus, receive LDT inputs and are implicated in limbic functioning (Hallanger, Levey, Lee, Rye, & Wainer, 1987; Rye, 1997; Spreafico, Amadeo, Angoscini, Panzica, & Battaglia, 1993). The connectivity profile (rich projections to the thalamus and inputs from the cortex) of the caudal PPN suggests that it may modulate brain states through the manipulation of thalamocortical loops (Martinez-Gonzalez et al., 2011). The manipulation of thalamocortical loops is a key avenue through

which the PPN could foster dissociative phenomena. The PPN/LDT's rich connectivity with a large set of thalamic nuclei, especially those implicated in limbic and associative circuits (Huerta-Ocampo et al., 2020), implies multiple routes toward the alterations in awareness that define dissociation. Garcia-Rill and colleagues have highlighted how the main targets of the PPN, the intralaminar thalamic nuclei, contain cells with intrinsic gamma oscillations and that through these projections the PPN likely promotes cortical coherence during the waking state but not during REM sleep (Garcia-Rill, Mahaffey, Hyde, & Urbano, 2019). Additionally, the intralaminar nuclei connect with frontoparietal regions and may regulate information transmission across these areas (Saalmann, 2014). This is one avenue through which the PPN may be implicated in decoupling.

The basal forebrain is another pathway by which the PPN/LDT may be involved in decoupling. A recent theory of brain network communication postulates that the cholinergic basal forebrain and the noradrenergic locus coeruleus regulate the amount of segregation and integration in the cortex (Shine, 2019). The basal forebrain is proposed to promote segregation while the locus coeruleus, which is inactive during REM sleep, promotes integration. Basal forebrain acetylcholine release is greater during REM sleep relative to wakefulness and stimulation of the cholinergic basal forebrain neurons during NREM sleep induces transitions to REM sleep and wakefulness (Han et al., 2014; Vazquez, & Baghdoyan, 2001). As previously stated, the basal forebrain receives PPN projections (Rye, 1997). Aberrant PPN/LDT might shift the balance of power between these nuclei in favor of segregation.

The PPN/LDT and Psychosis

Numerous strands of evidence indicate that insights into the physiological basis of dissociation might come from research concerning the biological origins of psychosis. Meta-

analytic research consistently demonstrates robust associations between dissociative symptoms and positive psychosis symptoms, such as hallucinations (Kotov et al., 2020; Longden et al., 2020; Pilton, Varese, Berry, & Bucci, 2015). Although distinct conditions, dissociation and schizophrenia have overlapping symptomatology including hallucinations, abnormalities in metacognition, disruptions in wake-sleep boundaries, and dissociative disorders are sometimes misdiagnosed as schizophrenia (Longden et al., 2020; Shibayama, 2011). These effects have led multiple researchers to propose that specific psychosis symptoms (e.g., hallucinations) may be better understood as expressions of dissociative psychopathology (Longden et al., 2020).

Multiple lines of evidence implicate the PPN/LDT in psychosis (Yeomans, 1995). Patients with schizophrenia exhibit a greater number of neurons in the PPN (postmortem) and suggestively so in the LDT (Garcia-Rill et al., 1995). Given that PPN cholinergic projections have been shown to provide excitatory input to substantia nigra and the VTA (Beninato, & Spencer, 1987; Oakman et al., 1995), abnormally high PPN output might overdrive these dopaminergic regions leading to less habituation to repetitive stimulation and greater sensory reactivity (Garcia-Rill et al., 1995). A common measure of sensory gating, *prepulse inhibition* (PPI), is operationalized as the attenuation of the startle response induced by a moderately intense preceding stimulus of close temporal proximity (Hoffman, & Searle, 1968). Patients with schizophrenia reliably exhibit reduced PPI relative to controls (Braff, Geyer, & Swerdlow, 2001; Grillon, Ameli, Charney, Krystal, & Braff, 1992; Geyer, Krebs-Thomson, Braff, & Swerdlow, 2001). The PPN is generally believed to represent a critical component of the PPI circuit (Fendt, Li, & Yeomans, 2001; Koch, Kungel, & Herbert, 1993; Reese, Garcia-Rill, & Skinner, 1995), thereby indirectly implicating the PPN in schizophrenia. Additionally, schizophrenia is associated with shorter REM latency and 10-30% of schizophrenics have been

shown to enter their first REM epoch during the first 15 minutes of sleep (a rare occurrence in neurotypical participants), both of these findings would be expected if schizophrenia is characterized by elevated PPN activity (Taylor, Tandon, Shipley, & Eiser, 1991; Yeomans, 1995; Zarcone, Benson, & Berger, 1987). These and other effects led Garcia-Rill et al. (1995) to propose that some schizophrenia symptoms might be manifestations of REM sleep intrusions into the waking state (see also Waters et al., 2016).

Dreaming is plausibly partly the product of REM sleep's neuromodulatory balance and the topography of PPN connectivity (Mena-Segovia, & Bolam, 2017). Greater modulation of limbic and associative regions might allow them to override input from primary sensory regions which are already reduced during sleep. Yeomans (1995) suggested that muscarinic antagonist-induced psychosis may be caused by blocking m2 autoreceptors, which act as a breaking mechanism for the PPN; the resulting over-activity in PPN could lead to greater stimulation of dopamine nuclei, resulting in hallucinations. Alternatively, the muscarinic antagonist could attenuate the PPN's modulatory power by blocking the receptor sites of postsynaptic cells of its efferent connections. The cholinergic system has a complex relationship with hallucinatory experiences. Anticholinergic drugs trigger hallucinations, acetylcholine can enhance the signal-to-noise ratio in sensory regions (Everitt, & Robbins, 1997; Minces, Pinto, Dan, & Chiba, 2017), and many conditions associated with hallucinations (e.g., schizophrenia, Parkinson's disease, and Lewy body dementia) are associated with cholinergic deficiencies (Perry, & Perry, 1995). However, REM sleep is characterized by heightened cholinergic activity (Hobson, Goldberg, Vivaldi, & Riew, 1983; Jasper, & Tessier, 1971; Jones, 1991; McCarley, & Hobson, 1975; Williams et al., 1994). Perry and Perry (1995) proposed that this apparent discrepancy results from cortical acetylcholine exciting GABAergic and glutamatergic neurons and thalamus

cholinergic inputs inhibiting GABAergic neurons leading to thalamic disinhibition which facilitates hallucinations. This potentially explains how increased PPN/LDT activity could result in hallucination proneness and dissociative experiences.

Sensory Gating and Dissociation

Preliminary evidence suggests that dissociation is characterized by sensory gating abnormalities as would be expected by PICDAD. One study observed that patients with dissociative identity disorder displayed weaker PPI than controls at short stimulus onset asynchronies but stronger PPI at a long asynchrony whereas patients with other dissociative disorders followed the same pattern as controls (Dale, Flaten, Elden, & Holte, 2008). Multiple studies have similarly observed reduced PPI in highly suggestible participants (Levin et al., 2011; Lichtenberg et al., 2008; Storozheva, Kirenskaya, Gordeev, Kovaleva, & Novototsky-Vlasov, 2018). Another study observed the converse (De Pascalis & Russo, 2013), which may be attributable to heterogeneity in dissociative tendencies in highly suggestible individuals (Terhune et al., 2011b; see also Acunzo, Cardeña, & Terhune, 2020). The germane construct of self-transcendence (Cloninger, Svrakic, & Przybeck, 1998; Cardeña, & Terhune, 2014; Grabe, Spitzer, & Freyberger, 1999), also negatively correlates with the magnitude of PPI (Takahashi et al., 2012). PPI is also reduced in patients with narcolepsy–cataplexy, a condition associated with REM sleep dysregulation and unusual sleep experiences, relative to neurotypical subjects (Frauscher et al., 2012). Research showing that sleep deprivation reduces PPI provides further indirect evidence for an association with dissociative experiences (Petrovsky et al., 2014). These results are broadly in agreement with Garcia-Rill et al.'s (1995) predictions of the effects of PPN over-activation extended to the domain of dissociation. Also, it should be noted that many culture-bound syndromes involving dissociative episodes and heighted suggestibility are startle

induced (Simons, 1996; Woody, & Szechtman, 2003), suggesting an interaction between a physiological substrate and cultural context (Simons, 1996).

The Genesis of Aberrant PPN/LDT Activity

Multiple models propose that dissociative phenomena arise from a disruption in transitions between waking and sleep (NREM/REM) states (Mahowald & Schenck, 1992) and it has been hypothesized that narcolepsy-like mechanisms might underlie dissociative phenomena (Van der Kloet et al., 2012b). Deficits in the regulation of REM sleep, like narcolepsy, have been linked to the pontine cholinergic nuclei. Narcolepsy with cataplexy is hypothesized to be caused by a depletion of orexin neurons (neuropeptides that regulate arousal and appetite) in the hypothalamus (Chen, Brown, McKenna, & McCarley, 2009; Reid, Siegel, Dement, & Mignot, 1994). The LDT neurons of orexin receptor knockout mice display an elevated capacity to synthesize, package, and release acetylcholine (Kalogiannis et al., 2010). Also, narcoleptic subjects have been reported to have short REM latency and sleep onset REM sleep episodes (Chen et al., 2009; Rye, 1995).

PICDAD assumes a process resembling the REM sleep regulation abnormalities found in narcolepsy is responsible for the cascade of events that allows for the emergence of dissociation. This account is agnostic regarding what drives individual differences in PPN cholinergic neuron activity as well as different REM circuit models (Grace,Vanstone, & Horner, 2014; McCarley, Greene, Rainnie, & Portas, 1995; McCarley, & Hobson, 1975; Lu, Sherman, Devor, & Saper, 2006; Sapin et al., 2009). It has been proposed that the PPN has three cell types: REM-ON, Wake-ON, and Wake-REM-ON, which are associated with different calcium channel subtypes (Garcia-Rill eta al., 2015). Individual differences in calcium channels might be linked to individual differences in dissociation. REM sleep circuit models offer multiple avenues through

which aberrant PPN/LDT activity can be reached. From the standpoint of pacemaker models, PPN/LDT over-activation could stem from deficits in REM sleep inactive cells in the dorsal raphe (DR) and locus coeruleus (LC) or a weakness in the inhibitory connections projecting from these nuclei to the PPN/LDT. Flip-flop switch models of REM sleep regulation are grounded on competition between REM-ON and OFF cells (Lu et al., 2006; Grace et al., 2014) potentially located in the ventrolateral periaqueductal gray (Sapin, et al., 2009; Weber et al., 2018). Notably, this region seems to be implicated in the dissociative subtype of PTSD (Harricharan et al., 2016), which suggests that disruption of ventrolateral periaqueductal gray functioning could be responsible for individual differences in dissociation. Another possibility is that aberrant PPN/LDT activity could stem from individual differences in the integrity of the orexin system.

Decoupling: Disruptions of Networks and Hierarchies of Control

Cognitive control allows for adaptive behavior involving the management of competing goals, extended action sequences, and overcoming habitual responses. Phenomena within the domain of dissociation include multiple disruptions of cognitive control, such as fugue states and functional neurological symptoms. According to PICDAD, the atypical cognition characteristic of high dissociation is attributable to the decoupling of control-related regions and is consistent with both cognitive control theories emphasizing prefrontal hierarchies based on some definition of abstraction (Badre, & Nee, 2018) and those proposing that large scale intrinsic connectivity networks are responsible for different features of cognitive control (Dosenbach et al., 2006; Dosenbach et al., 2007).

Control Hierarchies and Networks

A central feature of both pathological and non-pathological dissociative experiences is that they involve a reduction or disruption in the integration of mentation. Dissociation can manifest itself as a decoupling of intention and action (e.g., functional movement symptoms, fugue states), and/or of perception and reality (e.g., derealization, hallucinations). These phenomena can be grounded within hierarchies of control (e.g., Badre, 2008).

Researchers have attempted to understand the lateral PFC as a caudal to rostral abstraction gradient that is based on the extent of task nesting or a task's degree of temporal extension (Badre, 2008; Badre, & D'Esposito, 2007; Koechlin, & Summerfield, 2007). The PFC has been similarly described as a perceptual decision making axis with caudal regions associated with stimulus selection, the DLPFC with decision processing and the anterior PFC responsible for confidence judgments (Rahnev, 2017; Rahnev, Nee, Riddle, Larson, & D'Esposito, 2016). Evidence similarly suggests that, like the lateral PFC, the medial prefrontal cortex (mPFC) has a functional hierarchy that engages in goal selection by modulating the cascade of control, in the lateral hierarchy, in a direction that corresponds with motivation (Badre, & Nee, 2018; Pezzulo, Rigoli, & Friston, 2018; Venkatraman, Rosati, Taren, & Huettel, 2009). Given that no single dimension of abstraction (e.g., task nesting, temporal extension) holds a monopoly on lateral prefrontal activation, it has been proposed that the lateral frontal cortex comprises three zones, the sensory-motor, contextual, and schematic control zones, each defined by its degree of abstraction (Badre, & Nee, 2018). Schematic control involves the use of models of the external world to support forward thinking decision making, memory-based inferences, and the use of knowledge structures to guide the organization of lower processing levels (Badre, & Nee, 2018). Higher order schemas engender widespread integration of cognitive processing. Since dissociation is characterized by lower cognitive-perceptual integration, the disruption of

schematic control's integration into a control hierarchy plausibly underlies dissociative experiences involving distortions of identity and incongruence between higher order intentions and actions.

Intrinsic connectivity networks are sets of brain regions linked by inter-correlated activity. Dissociation can also be conceptualized as arising from breakdowns of, or reductions in, communications within and between large scale brain networks (Dosenbach et al., 2006; Dosenbach et al., 2007; Raichle, 2015). The frontoparietal network (FPN), widely associated with cognitive control, includes regions spanning from the DLPFC to the inferior parietal lobule and (Dosenbach et al., 2007) and the FPN has been proposed to be responsible for online tactical control processes (Dosenbach et al., 2007). By contrast, the cingulo-opercular network (CON), which includes the anterior cingulate cortex (ACC), anterior insula/frontal operculum, anterior thalamus and the anterior PFC, has been shown to play a fundamental role in error processing and might be involved in maintenance of a task set, the mental representation of the rules, operations, stimuli, and responses of a task, given its sustained activation during task blocks (Dosenbach et al., 2006; Dosenbach et al., 2007) and/or tonic alertness (Sadaghiani & D'Esposito 2014). Finally, disruptions in the default mode network (DMN), which has been reliably implicated in self-referential processing (Raichle, 2015), might serve as one neural substrate of dissociation, including experiences of depersonalization, or atypical self-processing or metacognition, but decoupling of control-related networks may have a role to play in the emergence of other dissociative experiences, particularly those involving suggestion.

Decoupling: The Intersection of Dissociation and Suggestibility

The disengagement of mentation from higher order schemas can manifest itself in a variety of different ways. The mechanisms supporting responsiveness to verbal suggestions have

been proposed to overlap with those underlying *environmental dependency syndrome* (Lhermitte, 1986; Woody & Bowers, 1994; Woody, & Szechtman, 2003). Lhermitte reported on frontal lobe patients that exhibited behaviors similar to typical utilization and imitation behavior but of a more complicated nature (Lhermitte, 1986). For example, when the word museum was mentioned, a patient began touring the apartment he was visiting as if it were a museum. The similarity of these reports to responses to suggestions among highly suggestible individuals helped inspire the dissociated control theory of hypnosis (Bower, 1992; Woody, & Sadler, 2008; Woody & Szechtman, 2003), which posits that Norman and Shallice's (1986) contention schedules are activated by suggestions independent of the supervisory attentional system. One shortcoming of the original dissociated control theory is that it cannot account for hypnotic suggestions that require overcoming a habitual response (Brown & Oakley, 2004) but this can be overcome by adopting a hierarchical view of cognitive control.

The parallels between hypnosis, dissociative fugue states, and the actions of Lhermitte's patients are perhaps better characterized as a disruption of schematic control and/or a disruption of a medial motivational hierarchy as opposed to the direct activation of contention schedules (Badre, & Nee, 2018). PICDAD posits that decoupling can manifest itself as canonical dissociative experiences or as responsiveness to suggestion thus explaining the link between dissociation and suggestibility. Some examples of situations that might arise from a breakdown in an intentional hierarchy or the links between networks of control include certain cases of functional (or suggested) motor paralysis, hypnotic challenge suggestions, and maladaptive daydreams (Somer, 2002). Disruptions in communication between different levels of a rostro-caudal control hierarchy and/or in the integration of motivational and control hierarchies can allow for flexibility present in hypnotic behavior (Barnier et al., 2008; Noble, & McConkey,

1995). Alternatively, a reduction in the integration of strategic task set oriented processing in the CON and tactical control related processing in the FPN might explain why certain types of hypnotic behaviors consume attentional resources but in other ways are experienced as automatic (King, & Council, 1998; Kirsch, Burgess, & Braffman, 1999; Tobis, & Kihlstrom, 2010). In addition, breakdowns in CON-FPN communication might be able to account for high dissociative highly suggestible participants failing to up-regulate cognitive control on post-conflict trials after a hypnotic induction (Terhune et al., 2011b).

Given the prefrontal deactivation observed during REM sleep, a more REM sleep-like waking neuromodulatory balance would likely disrupt prefrontal hierarchies and networks of control (Hobson et al., 2000). REM sleep disrupts the connectivity of the left prefrontal pole, a region that corresponds with the schematic control zone (Badre, & Nee, 2018; Zou et al. 2018). Dopamine, which is believed to exercise an important role in frontal hierarchies (Vogelsang, & D'Esposito, 2018), is lower in mPFC in rats during REM sleep than wakefulness (Lena et al., 2005), thus allowing for the possibility of weaker integrity of frontal hierarchies in individuals exhibiting a waking neuromodulatory balance approximating that during REM sleep. There is evidence of a weakening of prefrontal control in the domain of dissociation. Patients with functional movement disorder exhibit weaker left supplemental motor area (SMA) activity during movement relative to healthy controls and decreased connectivity between left SMA and bilateral DLPFC during internally vs. externally generated movement (Voon, Brezing, Gallea, & Hallett, 2011). Additionally, research has shown that repetitive transcranial magnetic stimulation of the right, and possibility the left, DLPFC augments hypnotic suggestibility (Coltheart et al., 2018; Dienes, & Hutton, 2013).

Automaticity has been conceived as functional decoupling of higher-order processing regions from lower order regions (Bezdek, Godwin, Smith, Hazeltine, & Schumacher, 2019). This should be reflected in a breakdown in cause-effect relations between regions (effective connectivity) that can lead to changes in functional connectivity. In dual-task situations, decoupling between areas involved in the respective tasks may occur strategically. Sticky decoupling (or persistent disintegration between sets of regions) could lead to maladaptive or outright pathological outcomes (Bezdek et al., 2019). Additionally, sticky decoupling provides a means of explaining both abnormalities in action control and perception which define the domain of dissociation. A breakdown of a perceptual/metacognitive hierarchy can account for the metacognitive deficits found in high dissociators (Kunzendorf, & Karpen, 1997), the dissociation-positive schizotypy association, and hypnotic hallucinations which have been difficult for most hypnosis theories to explain (Lynn, Kirsch, & Hallquist, 2008; Woody, & Sadler, 2008). Likewise, disruptions of control hierarchies and/or networks can free action from the grasp of higher order intentions. Alterations in cognitive control and perception brought about by sticky decoupling play a central role in PICDAD.

Decoupling and REM Sleep

PICDAD's fourth tenet, cortical decoupling, stems from the large body of literature reporting decoupling of various forms in REM sleep. In rodents and cats, gamma band coherence has been shown to be reduced in REM sleep relative to wakefulness (Castro et al., 2014; Cavelli et al., 2015; Torterolo, Castro-Zaballa, Cavelli, Chase, & Falconi, 2016; see also Dimitriadis et al., 2009). In humans, the intrahemispheric EEG correlation in the gamma band between frontal and perceptual regions (and within perceptual regions) was weaker during REM than NREM sleep (Perez-Garci, et al., 2001; Corsi-Cabrera et al., 2003). Similarly, one study

observed that cross-frequency band coupling, particularly for higher frequency bands, was reduced in REM sleep relative to wakefulness between frontal, central, and occipital channels (Liu, Bartsch, Lin, Mantegna & Ivanov, 2015). Intracranial recordings in human patients have shown that gamma band coherence is reduced in REM sleep relative to wakefulness in neocortex and between the neocortex and the hippocampus (Cantero et al., 2004). REM sleep percentage has also been shown to inversely relate to FPN connectivity, as measured by fMRI (Zou et al., 2018). By contrast, the evidence for altered effective connectivity during REM sleep is limited (Hein, Lanquart, Loas, Hubain, & Linkowski, 2018; Massimini et al., 2010).

Within a predictive processing framework, PICDAD, postulates that priors in the intermediate regions of perceptual and action hierarchies might be afforded excessive precision whereas precision in certain prefrontal regions might be reduced. High precision causes more weight to be placed on prior predictions relative to sensory information (likelihood) causing both perceptual states (posteriors) and updated predictions to more greatly resemble prior predictions (see below). From the perspective of predictive coding, sleep acts as a pruning period that reduces the complexity of the brain's models of the world (Hobson & Friston, 2012). During REM sleep, aminergic neuromodulation is toned down and cholinergic modulation dominates. In turn, the precision of priors at high (prefrontal) and low (sensory) levels is reduced, in addition to a lack of sensory input, and precision is increased in intermediate sensory regions due to cholinergic modulation, thus allowing for dream content unconstrained by sensory input (Hobson & Friston, 2012; Hobson, Hong & Fristion, 2014). This account aligns with the connectivity profile of the PPN (Mena-Segovia, & Bolam, 2017). Increased precision at intermediate levels reduces the ability of regions higher in the perceptual hierarchy and lower tier sensory regions to

influence the predictions generated by intermediate levels, amounting to reduced effective connectivity in higher-level regions.

Patterns of activation during REM sleep are consistent with an attenuation of prefrontal control. DLPFC deactivation has been observed during REM sleep whereas activation occurs in limbic, paralimbic, unimodal visual and auditory association areas, the anterior cingulate, and the mPFC (Hobson et al., 2000). PICDAD does not posit that highly dissociative individuals are in a constant state of REM sleep but rather that they have a more REM sleep-like waking neuromodulatory balance and/or are prone to transient episodes of such a balance. Therefore, DLPFC deactivation, relative to individuals low in trait dissociation, is unlikely to be a characteristic of such individuals; rather, they might exhibit transient episodes of deactivation or decoupling.

Most of the research on REM sleep connectivity assesses functional connectivity (Cantero et al., 2004 Castro et al., 2014; Cavelli et al., 2015; Dimitriadis et al., 2009; Torterolo et al., 2016). However, changes in the correlations between regions does not necessarily mean that causal relationships have changed. It should be noted that rhythmic changes in postsynaptic excitability are essentially rhythmic changes in synaptic input gain and inputs that arrive at time points of high synaptic input gain on a consistent basis would benefit from superior effective connectivity. The communication through coherence hypothesis posits that effective connectivity depends on oscillatory coherence and is supported by multiple lines of evidence (Fries, 2005; Fries, 2015). The breakdown in coherence observed during REM sleep might be in part a manifestation of weaker prefrontal regulation of more posterior regions (Hobson et al., 2000). Also, holding other factors constant, reductions in functional connectivity between two

regions would be expected if effective connectivity was reduced by an experimental manipulation.

Decoupling and Dissociation

As with REM sleep, decoupling has been associated with the domain of dissociation. Recent research in patient populations showed that functional connectivity between FPN nodes and nodes in the visual, somatomotor, and dorsal attention networks was negatively associated with dissociative symptom severity whereas DMN-FPN connectivity was positively associated with dissociative symptoms (Lebois et al., 2020). These results are consistent with EEG research showing that dissociative symptoms are associated with lower frontal-occipital and central-parietal connectivity in multiple frequency bands (Soffer-Dudek, Todder, Shelef, Deutsch, & Gordon, 2018; see also Reiser et al., 2012). Similarly, when recounting autobiographical experiences related to attachment, neurotypical controls, but not patients with a dissociative disorder, exhibited global increases in lagged coherence across multiple frequency bands, especially in the beta and gamma bands (Farina et al., 2014). Functional connectivity has also been shown to negatively correlate with dissociation in schizophrenia (Bob, Susta, Glaslova, & Boutros, 2010). Although these results suggest that dissociation is characterized by lower anterior-posterior connectivity, PICDAD does not predict a generalized reduction in connectivity. In particular, it expects that areas more/less coupled during REM sleep versus wakefulness will display greater/reduced connectivity in high dissociation. The overall waking connectivity profile would be more similar to REM sleep in individuals with high trait dissociation. Critically, preliminary research indeed shows that patients with the dissociative subtype of PTSD exhibit greater resting state functional connectivity between the PPN and the ACC, ventromedial prefrontal cortex, the amygdala, and the parahippocampal gyrus (Thome et

al., 2019). Although these results align with PICDAD, they should be interpreted with caution given the poor signal quality in the brainstem and because the scanner resolution was not well suited for examining regions as small as the PPN.

NMDA receptor antagonism, such as through administration of ketamine or nitrous oxide, presents somewhat of a challenge for PICDAD as it seems to impair REM sleep (Stone, Walker, & Gold, 1992) and inhibit muscarinic receptor function (Durieux, 1995), yet reliably triggers dissociative states (e.g., Kamboj et al., 2021; Niciu et al., 2018). Nevertheless, there is reason to believe that the dissociative effects of these drugs are congruent with PICDAD. NMDA antagonists promote cholinergic release in the cortex (Kim, Price, Olney, & Farber, 1999). The NMDA receptor hypofunction theory of psychosis posits that reduced NMDA function results in excessive release of glutamate and acetylcholine (Farber, 2003). Critically, similar to REM sleep, ketamine and nitrous oxide produce decreases in functional connectivity and gamma band coherence (Castro-Zaballa et al., 2013; Castro-Zaballa et al., 2018; Kuhlmann, Foster, & Liley, 2013). Such decoupling might be the source of the dissociative phenomenology associated with NMDA receptor antagonists.

A multi-species study has recently demonstrated that a ~3Hz rhythm in the posteromedial cortex plays a causal role in dissociation (Vesuna et al., 2020). The HCN1 pacemaker channel was shown to be responsible for the production of the rhythm. The scope of dissociative phenomenology related to this rhythm is still unknown as the linked symptoms mostly included out-of-body experiences and depersonalization, although such experiences have been associated with REM sleep (Jalal, & Ramachandran, 2017; Levitan, LaBerge, DeGracia, & Zimbardo, 1999). Another key result of this study was that ketamine produced a decoupling of both the laterodorsal nucleus and anterior ventral nucleus, which connect to posterior forebrain circuitry,

with the anterior medial nucleus, which connects to frontal circuitry (Vensuna et al., 2020). These findings are generally in accordance with the predictions of PICDAD.

Some of the reported changes in functional connectivity observed following a hypnotic induction in highly suggestible individuals align with a decoupling account of dissociation (Cojan et al., 2009; Egner, Jamieson, & Gruzelier, 2005; Egner, & Raz, 2007; Terhune et al., 2011a; Terhune et al., 2017). Behavioral findings that imply some sort of functional decoupling have been reported as well but only in the highly dissociative subtype of highly suggestible individuals (King, & Council, 1998; Terhune et al., 2011b; Terhune et al., 2017). On the other hand, Terhune and colleagues observed lower alpha2 phase synchrony between frontal and posterior electrodes following a hypnotic induction in highly suggestible individuals irrespective of dissociation status relative to low suggestible controls (Terhune et al., 2011a; see also Fingelkurts, Fingelkurts, Kallio, & Revonsuo, 2007; Jamieson & Burgess, 2014). Similarly, imaginary coherence in the beta1 frequency band has been shown to drop going from baseline to hypnosis in highly suggestible subjects relative to lows (Jamieson, & Burgess, 2014).

The neurons of the PPN have been shown to fire at beta/gamma frequencies and it has been proposed that the PPN has a role in the regulation of cortical gamma rhythms (Garcia-Rill, D'Onofrio, & Mahaffey, 2016; Garcia-Rill et al., 2013). Also, two nodes of the CON, the ACC and the SMA, are coupled with the PPN in the alpha and beta frequency bands respectively (Jha et al., 2017). A detailed account describing the innerworkings of decoupling is beyond this incarnation of PICDAD. A recently proposed circuit based framework for understanding information processing and control posits that local cortical circuits marked by gamma oscillatory activity interacting with long corticothalamic circuits associated with the alpha and beta frequency bands could allow for the selection and extended maintenance of representations

(Gratton, 2018). If high frequency activity bursts occur during phases of a lower frequency oscillation the observed reductions in beta coherence might have a role to play in gamma band decoupling (Egner et al., 2005; Jamieson, & Burgess, 2014; Reiser et al., 2012). As previously stated, inter-frequency coupling is reduced during REM sleep relative to wakefulness (Liu et al., 2015). Future research should examine cross-frequency coupling during states of dissociation and at baseline across the spectrum of dissociation proneness.

There is complementary evidence of a negative relationship between dissociation and functional connectivity measured with fMRI data at different spatial scales (Scalabrini, Mucci, Esposito, Damiani, & Northoff, 2020). Along similar lines the integrity of the FPN is negatively associated with the commonality of openness and psychoticism (Blain, Grazioplene, Ma, & DeYoung, 2020). Yet, some fMRI findings are not easily explained by PICDAD. Recent reviews have highlighted how increased frontal activation (ACC, DLPFC, and mPFC) was frequently associated with dissociation but there was little regional consistency across studies and the same held true for connectivity findings (Lotfinia, Soorgi, Mertens, & Daniels, 2020; Roydeva & Reinders, 2020), potentially because of differences in experimental paradigms and control groups. Findings of increased functional connectivity between prefrontal regions and the amygdala in the dissociative subtype of PTSD (Nicholson et al., 2015) are not incongruent with PICDAD but evidence of greater top-down effective connectivity between prefrontal cortex and the amygdala is difficult for PICDAD to explain depending on the prefrontal region (Nicholson et al., 2017). During exposure to previously viewed emotional images after sleep, ventromedial PFC-amygdala connectivity was increased and both amygdala and self-reported affect were attenuated (van der Helm, Yao, Dutt, Rao, Saletin, & Walker, 2011). The reduced amygdala activity was dependent on reduced gamma power during REM sleep. Thus, the ventromedial

PFC to amygdala effectivity connectivity findings of Nicholson and colleagues (2015) could be attributed to a REM sleep-related mechanism. It should be noted that unlike the DLPFC, mPFC has been shown to be reactivated during REM sleep (Muzur, Pace-Schott, & Hobson, 2002). Also, among highly suggestible individuals, DLPFC functional connectivity is greater with the salience network at baseline (Hoeft et al., 2012) and with the insula following a hypnotic induction (Jiang, White, Greicius, Waelde, & Spiegel, 2017). However, these studies did not take individual differences in dissociation into account and the segregation of participants into high and low hypnotic suggestibility groups was based on scales that are not well suited for identifying subjects with high suggestibility.

Human neuroimaging studies of dissociation should be considered in the context of the shortcomings of the methodologies used. Most studies have not accounted for potential heterogeneity in the neural substrates of dissociation, patient samples, and germane phenomenological factors or relevant confounding factors (e.g., trauma). In regards to the connectivity findings, a potential problem in this literature is that many studies have not taken sufficient measures (global signal regression, physiological data based nuisance regressors, component based noise correction, etc.) to mitigate artifacts (Power, Plitt, Laumann & Martin, 2017). Critically, groups (healthy controls, non-dissociative PTSD, dissociative subtype PTSD) could exhibit differences in artifacts that could drive connectivity differences. This could be especially problematic for symptom elicitation paradigms during which it is not unlikely that groups would differ in their respiratory responses. In addition, most fMRI studies of dissociation have utilized scan times (Hoeft et al., 2012; Jiang et al., 2017; Nicholson et al., 2015; Nicholson et al., 2016; Nicholson et al., 2017; Thome et al., 2019) that are substantially shorter than those required to achieve high individual level test-retest reliability of functional brain networks

(Laumann et al., 2015). Research in this domain should shift focus from group to individual level analyses (Gratton et al., 2020) and collect a larger amount of within subject data (deep data) in order to ensure reliable estimates of individual connectivity profiles and account for heterogeneity in functional anatomy (Gratton et al., 2020; Smith et al., in press). Recent research utilizing more within-subject data than what is typical, artifact mitigation procedures like global signal regression, and individually-defined functional regions represents a step in this direction (Lebois et al., 2020).

Integration with Contemporary Theories of Consciousness and Brain Function

Predictive Coding

A prominent theoretical framework views the brain as a hierarchical Bayesian inference machine (Friston, 2010; Spratling, 2017). Perceptual and motor processes have been modeled as hierarchies with levels that contain two types of neural populations: prediction units and error units. Predictive coding hierarchies work towards minimizing prediction error (Edwards, Adams, Brown, Pareés, & Friston, 2012; Spratling, 2017). Prediction units predict the "beliefs" of the level below and transmit predictions to the lower level's prediction error units which compute the discrepancy between beliefs and predictions (prediction error). This error is transmitted to the upper level and triggers an adjustment in the upper level's predictions. The competition between sensory evidence (prediction errors) and prior beliefs is biased by the precision (inverse variance) of the prior beliefs and sensory data. Updated predictions will resemble the prior predictions if predictions had high precision relative to the prediction error (Edwards, et al., 2012; Friston, 2010). The physiological basis of the precision of prediction error is believed to be the synaptic gain of the neurons that encode the error. Neuromodulators associated with attention influence synaptic gain (Feldman, & Friston, 2010).

Predictive Coding and Dissociative Psychopathology

Predictive coding mechanisms have been advanced for a variety of pathological conditions (Horga, Schatz, Abi-Dargham, & Peterson, 2014; Van de Cruys, Evers, Van der Hallen, Van Eylen, Boets, de-Wit & Wagemans, 2014) including functional neurological disorder (Edwards et al., 2012). According to the latter model, attentional bias towards the body increases the precision of false symptom expectations stored in an intermediate level of a sensory (e.g., functional pain) or motor (e.g., functional paralysis) hierarchy. The effect of bottom-up prediction errors on the intermediate level is attenuated and a precise prediction error is transmitted to higher levels. The abnormal prediction error received from the intermediate level dominates higher-level prediction error thus the intermediate-level predictions have more weight in determining the new higher-level beliefs and the functional symptoms are maintained. This account represents an example of decoupling with the intermediate level of a cortical hierarchy becoming insensitive to inputs from lower and upper levels. In the case of dissociation, intrusions of PPN-LDT REM ON cell activity into wakefulness would be expected to produce an effective connectivity disturbance similar to the one proposed to explain schizophrenia symptoms (Adams, Stephan, Brown, Frith, & Friston, 2013; Friston, Brown, Siemerkus, & Stephan, 2016). Such an account is largely compatible with PICDAD.

Edward and colleagues propose that scenarios like those they described for functional symptoms are applicable to dissociative symptoms more broadly (Edwards et al., 2012). PICDAD predicts that a REM sleep-like neuromodulatory balance affects the precision landscape in two ways that facilitate dissociative symptoms: increased precision in intermediate levels (e.g., somatomotor) and reduced precision of higher levels (e.g., prefrontal) of a cortical hierarchy. Both of these effects independently can yield the previously described phenomena but

the nature of REM sleep suggests that precision is changing at multiple levels (Hobson, Hong, & Fristion 2014). The predictive coding model of functional symptoms predicts that symptoms should be mitigated by distraction but if the precision imbalance underlying dissociative states are simply driven by atypical attentional fixation on symptoms it would make sense that individual differences in attentional abilities would contribute to dissociation. According to PICDAD, attention to a dissociative symptom might help tip the precision balance but the precision landscape that allows for these experiences is primarily driven by activity in the PPN/LDT.

Predictive Coding, Intentions, and Suggestibility

Viewing PICDAD through the lens of predictive coding makes it clear how intentional processing might be disrupted in those with a tendency to dissociate. Intentions might be best understood as temporally extended higher order plans (Gallagher, 2006). It is plausible that an intentional cascade comprising distal (long time scale abstract goal setting), proximal (organizing and initiation of subgoals while on route to the primary objective), and motor (mostly unconscious short time scale decisions regarding the nuances of movement) is compromised during dissociative experiences (Pacherie, 2008; Pacherie, & Haggard, 2010). Functional connectivity between the SMA and other motor regions is reduced in a hypnotically suggested movement condition relative to a normal voluntary movement condition (Deeley et al., 2013; see also Cojan et al., 2009). In the latter study, preparatory activation in right motor cortex was preserved during suggested paralysis suggesting presence of a movement intention (Cojan et al., 2009). Intentions to meet the challenge may be formed during motor challenge suggestions, which bear resemblance to functional motor symptoms, but their potency, or rather their precision, might be limited. Highly suggestible subjects have been shown to exhibit aberrant

metacognition of agency at baseline (Terhune & Hedman, 2017) and less intentional binding, the subjective reduction of the time interval between a voluntary action and its sensory consequence, for hypnotic suggestions (Lush et al., 2017). In addition, multiple lines of evidence suggest that patients with FND, as well as highly suggestible individuals display delayed awareness of motor intentions (Baek et al., 2017; Edwards et al., 2011; Lush et al., 2016). FND patients also display impaired voluntary movement as measured by the finger tapping task, a measure of voluntary motor control (Criswell, Sterling, Swisher, Evanoff & Racette, 2010). When these results are considered together with findings of reduced functional connectivity, in FND patients, in areas associated with cognitive control and the processing of intention it seems likely that the domain of dissociation is marked by disruptions of both intention awareness and potency (Baek et al., 2017; Maurer et al., 2016; Voon et al., 2011; Voon et al., 2010).

In the context of a motor paralysis suggestion, why is the precision in higher levels responsible for the intention to move not increased? If a participant was trying to move their arm would it not make sense to redirect attentional resources to high-level movement predictions? Other predictive coding based accounts of hypnotic suggestibility do not present a clear explanation for this but PICDAD explains this through constraints imposed on the degree of prefrontal precision due to a REM sleep-like neuromodulatory balance (Martin & Pacherie, 2019). Additionally, lower levels of a sensory hierarchy likely have down-regulated precision during REM sleep so increased lower-level sensory precision is unlikely to hold in the context of dissociation, according to PICDAD (see also Hobson et al., 2014).

Integrated Information Theory

Integrated information theory, a prominent theory of consciousness, postulates that conscious systems are characterized by integrated, yet differentiated states (Tononi, 2004;

Tononi, 2011; Tononi & Edelman, 1998). Functional clusters, complexes, in the brain are the physical substrate of consciousness. This theory allows for the possibility of two or more non-overlapping complexes being present in a brain simultaneously. The complex with the highest degree of integrated information, *phi*, will act as the substrate for the typical phenomenology of consciousness but in special cases, such as split-brain patients, two major complexes could emerge (Tononi et al., 2016). Tononi and colleagues have suggested that dissociative disorders might be manifestations of complex splitting (Tononi, 2004; Tononi et al., 2016). This is compatible with PICDAD's fourth tenet, cortical decoupling.

Dual-task situations might reflect a context that promotes benign complex splitting (Sasai, Boly, Mensen, & Tononi, 2016). For example, in one study (Sasai et al., 2016), participants completed a driving simulation involving listening to GPS directions (integrated task) or to a radio show (split task) while undergoing fMRI scanning. Integrated information was measured by comparing the results of modeling future states with current activity patterns in the listening and driving networks separately with a model of the two networks jointly predicting their future states. Integration, quantified as the ratio of the error for the split mode over the error for the integrated model, was greater in the integrated task than in the split task and covaried with driving performance (Sasai et al., 2016). This approach may hold promise for future testing of the predictions of PICDAD, particularly the decoupling tenet. The neuromodulatory balance associated with increased PPN/LDT activation could facilitate complex splitting. Rogue complexes are essentially rogue representations (Brown, 2004). They are the product of decoupling and integrated information theory supplies a means for determining the extent of decoupling (Sasai et al., 2016).

Predictions and Future Directions

Psychometric Considerations

Among the clearest challenges facing PICDAD is the measurement of the proposed latent dissociation factor. Testing of PICDAD should make use of latent variable modeling approaches involving multiple, complementary measures in order to provide a more robust estimate of this latent factor and minimize scale-specific measurement error (Loehlin, 1998). Model comparisons can determine how well a unifying latent trait of dissociation explains the domain of dissociation relative to alternative factor structures. Implementing latent variable methods will require data sets with large sample sizes and this represents a formidable challenge for imaging studies. This challenge can potentially be circumvented through the use of large sample latent variable analyses followed by imaging of select subgroups along the latent dimension.

Neuroimaging Approaches

One clear neurophysiological test of PICDAD would be an assessment of the prediction that high (trait or state) dissociation is characterized by atypical REM sleep features especially elevated REM sleep percentage and shorter REM latency. Anterior-posterior decoupling, disruptions of the causal relations within prefrontal hierarchies, and most importantly the reduction of influence of lower and higher order sensory regions on intermediate association areas could be tested with methods like dynamic causal modeling (in the context of a task) and the Group Iterative Multiple Model Estimation (GIMME) approach (Friston, Harrison, & Penny, 2003; Gates, & Molenaar, 2012). Yet, with fMRI the measurement of effective connectivity is difficult given the assumptions associated with the aforementioned methods and the fact that the timing of the hemodynamic response is not homogenous across brain regions (David et al., 2008).

Activation and connectivity profiles could also be used to test predictions derived from PICDAD. Highly dissociative individuals should have a waking state (or at least be prone to periods of time during the waking state) that appears more similar to REM sleep than controls. Similarity metrics could be applied to activation and connectivity profiles of wakefulness and REM sleep (Kriegeskorte, Mur, & Bandettini, 2008). In addition, Positron Emission Tomography may hold promise considering recent advancements in acetylcholine related radiotracers (Aghourian et al., 2017; Roy, Niccolini, Pagano, & Politis, 2016). Cholinergic activity should be higher, especially in the thalamus given the trajectories of PPN projections, in those high in dissociation. It could be also be used to determine if the neuromodulatory balance during the waking state among highly dissociative individuals is more similar to REM sleep.

Another approach to assessing the neurophysiology of dissociation is afforded by the use of information integration indices to assess the relative independence of complexes (Sasai et al., 2016). For example, the set of regions involved in the implementation of a suggestion and those involved in a voluntarily performed task could be assessed for integration when the suggestion and the task are being performed together. The integration metric for the suggestion condition could be compared to a condition in which the suggested activity is performed voluntarily along with the same task that was performed voluntarily during the suggestion condition. PICDAD would predict, at least in high dissociative highly suggestible participants, less integration in the suggestion relative to the conventional dual-task condition (see also King & Council, 1996).

Additionally, future fMRI research should make use of individual level functional brain maps (Gratton et al., 2020). Similarly, graph theoretic metrics should be applied to data in order to gain a better understanding of how differences in network properties relate to dissociation (Rubinov, & Sporns, 2010). Connector hubs, regions exhibiting a high about of between-

network connectivity that seem to play a role in inter-network integration, should be of particular interest to dissociation researchers and such regions can be identified with graph theoretic metrics like the participation coefficient (Power, Schlaggar, Lessov-Schlaggar, & Petersen, 2013).

Pharmacological Approaches

Pharmacological manipulations provide another means of testing PICDAD. One potentially promising avenue would be to determine the role that decoupling plays in the link between NMDA receptor antagonists and their dissociative effects. Recent research has shown that the dissociative effects of ketamine can be attenuated using benzodiazepines (Gitlin et al., 2020), which may allow for more precise assessments of the neurophysiological loci of dissociation. In addition, cholinergic agonism would represent a salient vehicle for testing PICDAD but the proposed mechanism depends on the distribution of cholinergic projections from the PPN/LDT and pharmacological agents will lack this degree of specificity. Moreover, given the autoregulatory role of m2 receptors in the PPN cholinergic drugs could inhibit PPN/LDT activity (Yeomans, 1995). Orexin agonists that can cross the blood brain barrier might hinder the expression of dissociation by reducing the activation of REM-ON regions in the PPN/LDT and have been shown to mitigate narcolepsy-cataplexy symptoms in rodents (Irukayama-Tomobe et al., 2017; Suzuki, Yukitake, Ishikawa, & Kimura, 2018). Accordingly, orexin antagonists would be expected to increase dissociation. The orexin receptor antagonist, suvorexant, which is used to treat insomnia reduces REM latency (Snyder et al., 2016). In addition, suvorexant occasionally produces narcolepsy-like symptoms (Kripke, 2015). GlaxoSmithKline's SB-649868 (a dual receptor orexin antagonist) has been shown to increase the amount of time spent in REM sleep, reduce the REM latency, and induce sleep onset REM

episodes (Bettica et al., 2012). These agents represent potentially valuable candidates for pharmacological evaluations of PICDAD's predictions.

Neural Stimulation

A final means of testing PICDAD would be deep brain stimulation. The PPN is a common target region in deep brain stimulation in patients with Parkinson's disease (Stefani et al., 2007). Aside from challenges associated with patients' symptoms, generalization to dissociative populations, PPN pathology in Parkinson's disease (Pahapill, & Lozano, 2000), and different PPN cell types (Garcia-Rill et al., 2015), deep brain stimulation applied to PPN would be expected to increase the frequency of dissociative experiences assuming REM-ON cells can be preferentially stimulated.

Conclusions

PICDAD integrates the domain of dissociation into wider theoretical frameworks and provides a diverse set of testable predictions. In particular, PICDAD provides a model that explains the established association between dissociation and sleep phenomena. Like all models, it rests on certain assumptions, including cortical decoupling and a latent trait of dissociation, but many of these are empirically tractable. In addition, it predicts that dissociation emerges from activation of REM associated cells in the PPN/LDT. The central features of PICDAD are that dissociative experiences emerge from a particular REM-like neuromodulatory balance. Cortically, the change in neuromodulation is proposed to manifest itself as a propensity for decoupling, particularly along anterior-posterior and medial-lateral lines.

PICDAD opens up new avenues of research and a mode of thinking about the domain of dissociation. PICDAD can explain the complex link between dissociation and direct verbal

suggestibility, not to mention many of dissociation's cognitive correlates. The theory accounts for the relationship between PPI and many of the traits that comprise the domain of dissociation and why dissociation relates to hallucinations. It reconceives dissociation as a cognitive style and emphasizes the importance of understanding non-pathological dissociative experiences. A better understanding of non-pathological forms of dissociation will allow clinicians to identify individuals at risk of developing dissociative psychopathology. PICDAD is challenged by some findings hinting at superior top-down control in dissociation (De Ruiter et al., 2003; De Ruiter et al., 2004; Nicholson et al., 2017) and further robust assessments of these effects is necessary to evaluate and/or revise the theory. In addition, PICDAD does not advance a concrete prediction regarding the level of task nesting and/or degree of temporal extension where one would expect to find dissociation-related individual differences in performance.

A key limitation of PICDAD is that it does not contain a comprehensive account of decoupling. Hopefully, new versions of the theory, informed by future findings, will contain detailed mechanistic accounts describing decoupling and how it could yield dissociative phenomenology and suggestibility. Also, it should be noted that there is some inconsistency in the recent literature regarding the role of PPN/LDT cholinergic neurons in REM sleep. On one hand, chemogenetic stimulation of PPN cholinergic neurons promotes light NREM sleep but not REM sleep (Kroeger et al., 2017). On the other hand, Optogenetic activation of cholinergic PPN/LDT neurons during NREM sleep has been shown to increase the number of REM sleep episodes (Van Dort et al., 2015). Similarly a wide body of studies suggest that PPN/LDT cholinergic neurons promote REM sleep (Datta, & Siwek, 1997; Datta et al., 2001; Grace, & Horner, 2015; Shiromani, &McGinty, 1986; Webster, & Jones, 1988). Another shortcoming of PICDAD is the theory's lack of commitment to an explanation of the genesis of aberrant

PPN/LDT activity. Future findings might allow for versions of PICDAD that make such commitments. Currently the orexin system seems to be the most viable source. Individual differences in the integrity of the orexin system could potentially lead to aberrant PPN/LDT activity (Kalogiannis et al., 2010). Orexin has widespread interactions with the arousal system including the regulation of the LC and DR aminergic nuclei (Brown, Sergeeva, Eriksson, & Haas, 2001; Gompf, & Aston-Jones, 2008; Hagan et al., 1999). A reduction in the facilitation of inter-regional communication via down regulation of the aminergic nuclei might along with aberrant PPN/LDT play a critical casual role in decoupling (Shine, 2019). Poorer integrity of the orexin system might lead to a REM sleep-like aminergic/cholinergic balance and individual differences in the orexin system certainly merit attention from dissociation researchers.

Assuming a latent trait that unites the domain of dissociation can be reliably observed and measured, neuroimaging can be used to determine if decoupling is associated with this latent trait and whether it is associated with the extent to which the waking neural profile is similar to the profile of REM sleep. More critical tests of this theory are afforded by deep brain stimulation and pharmacological manipulations. Overall, PICDAD provides a synthesis of numerous findings showing a link between sleep related factors and the domain of dissociation. It is well integrated with theories of brain function (predictive coding) and consciousness (integrated information theory), thereby enabling a healthy dialogue with germane research fields outside the domain of dissociation. In addition, it adds a degree of specificity and provides a synthesis for many ideas regarding the domain of dissociation.

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