Embodiment Across the Schizophrenia Spectrum

By

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I dedicate this dissertation to all the individuals with lived experiences I had the privilege to meet, learn from, collaborate with, treat, and cross paths with in my research and clinical work so far. Your stories and your resilience inspired and motivated this work. I hope this dissertation will fuel more research that will bring meaningful interventions into your lives.

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CHAPTER I

Introduction

SCHIZOPHRENIA AND SCHIZOTYPY

Schizophrenia

Schizophrenia is a chronic psychotic disorder affecting about 1% of the population worldwide (Murray et al., 2002). The prognosis for individuals diagnosed with schizophrenia is poor and the burden of the disorder large for societies. In fact, in a study by the World Health Organization, schizophrenia was ranked the most debilitating condition, above and beyond other mental or physical disorders such as multiple sclerosis or untreated spinal cord lesions (Salomon et al., 2012). Though relatively rare, the burden of schizophrenia therefore warrants research efforts to understand the symptomatology, phenomenology, course of illness, and factors influencing outcome. However, little progress has been made regarding the etiology of the disorder and, consequently, current treatments for schizophrenia continue to have limited efficacy (Jones et al., 2018; Samara et al, 2019). This lack of progress likely reflects changes in schizophrenia conceptualization and the underlying shifts in psychiatry focus throughout history.

Early theories of schizophrenia placed a weakened sense of self and anomalous bodily experiences at the core of the disorder. Kraeplin, who is credited as one of the first to recognize schizophrenia as a unique disorder, believed in its physiological underpinnings. He highlighted the importance of studying "the processes of metabolism and blood chemistry" in understanding the etiology of schizophrenia (Kraeplin, 1896). When coining the word schizophrenia, Bleuler combined two Greek words that, together, mean "splitting of the mind." Bleuler's thorough clinical observations led him to believe that the fragmentation of the self and the disintegration of cognitive, emotional, and social functions are at the core of schizophrenia (Bleuler, 1911). Schneider, who famously defined schizophrenia's first rank symptoms for diagnostic purposes, also recognized the importance of self-disorders in the etiology of schizophrenia (Schneider, 1959). However, this conceptualization of schizophrenia as a disorder of the self began to wane in the 1920s, overshadowed by the growing influence of Freud and Jung's psychoanalytic models, and continued to decline through the ages of Behaviorism and Cognitive Neuroscience until it almost disappeared from the scientific literature on psychosis.

Since the 1980s, the focus in psychology and psychiatry shifted from construct validity to clinical reliability. As a result, self-disturbances, which are inherently difficult to measure due to their subjective nature, have been notably absent from the Diagnostic and Statistical Manual of Mental Disorders since the third version of the manual (DSM-III; APA, 1980). In this search for clinical parsimony, some argue that the clinical core of the disorder was lost (Andreasen, 2006; Parnas, 2011).

The current conceptualization of schizophrenia, as defined by the DSM-5, considers positive (e.g., hallucinations, delusions) and negative (e.g., diminished emotional expression, anhedonia, asociality) symptoms the hallmarks of the disorder (APA, 2013). Disorganization (i.e., thought disorder, bizarre behavior) and cognitive deficits (e.g., attention and memory deficits) are also considered common symptoms of the disorder. In contrast, self-disturbances, which are central to the daily experiences of individuals with schizophrenia and therefore of outmost clinical relevance, are notably absent from this contemporary view designed to "guide clinical practice" (APA, 2013, p. xli). Thus, though disturbances of the self are still recognized as salient to the everyday experience of individuals with schizophrenia, contemporary clinicians seldom target them in treatment (see Nasrallah, 2012).

A slow re-emergence of the conceptualization of schizophrenia as a self disorder begun in the recent decades (see Park & Nasrallah, 2014), partly owing to the vast progress in empirical methods that now allow subjective experiences to be systematically investigated. This steady increase in awareness of the importance of self-disturbances in schizophrenia research triggered a shift back to Bleuler's early conceptualization of the disorder (Parnas & Handest, 2003), leading to the inclusion of distortions of the self-experience as one of eight core symptoms of schizophrenia in the latest revision of the International Classification of Diseases (ICD-11; World Health Organization, 2018). Self-disturbances were also documented in the prodromal stages of the illness (Nelson et al., 2008), and shown to predict transition for those at risk for psychosis (Nelson et al., 2012). Thus, there has been a growing acceptance of the self-disorder as critical to understanding the core and/or phenomenology of schizophrenia, as well as a recognition of its clinical utility. To gain insight into the etiology of the disorder and inform treatment, researchers have therefore begun to investigate self-disturbances along the schizophrenia spectrum. In particular, studying embodiment in individuals at varying levels of risk for psychosis can cast light into the nature of *dis*embodiment in schizophrenia.

Schizotypy

According to the diathesis-stress model of psychopathology, schizophrenia results from the interaction of (1) a genetic predisposition (i.e., latent liability) and (2) exposure to risk factors/ life stressors. Schizotypy was first introduced as a set of inherited personality traits that yields a vulnerability for schizophrenia (Meehl, 1962). In fact, increased levels of schizotypy have been reliably identified in first-degree relatives of patients with schizophrenia (e.g., Kremen et al., 1998). More recently, a review by Walter et al. (2016) confirmed that schizotypal traits (i.e., schizotypy) increase with genetic liability for schizophrenia.

Beyond the realm of the familial risk, schizotypy broadly refers to the set of personality traits and experiences related to subthreshold psychotic experiences in the general population (Debbané et al., 2015). Schizotypy is multidimensional, and its factors are analogous to the three major symptom clusters in schizophrenia: positive, negative, and disorganized (Raine et al., 1994). As such, positive schizotypy refers to unusual perceptual experiences, magical thinking, and referential ideation; negative schizotypy is characterized by decreased interest in social engagement; and disorganized schizotypy refers to odd behavior and language. We note that measures of schizotypy (see next paragraph) are often based on DSM criteria, which might explain the similarity between the factor structures of schizotypy and schizophrenia.

Schizotypy is most commonly measured using self-report instruments (for a comprehensive review of schizotypy instruments, see Kwapil & Chun, 2015; Mason, 2015). The Chapman Scales, which include the Perceptual Aberration (Chapman et al., 1978), Magical Ideation (Eckblad and Chapman, 1983), and Physical and Social Anhedonia (Chapman et al., 1976) scales, were one of the earliest measures of schizotypy. The Schizotypal Personality Questionnaire (SPQ; Raine, 1991) is a 74 true/false items questionnaire designed to assess schizotypal traits based on DSM-III criteria (APA, 1980). It yields nine subscales (Ideas of Reference, Excessive Social Anxiety, Odd Beliefs/Magical Thinking, Unusual Perceptual Experiences, Odd/Eccentric Behavior, No Close Friends, Odd Speech, Constricted Affect, and Suspiciousness) that load on to the three factors of schizotypy: Cognitive/Perceptual deficits, Interpersonal deficits, and Disorganization. The Oxford-Liverpool Inventory of Feelings &

Experiences (O-LIFE; Mason et al., 1995) is a 43-item questionnaire designed to assess schizotypal traits in the general population. The O-LIFE yields four subscales: unusual experiences, cognitive disorganization, introvertive anhedonia, and impulsive nonconformity. More recently, Kwapil et al. (2018) developed the Multidimensional Schizotypy Scale (MSS), a 76-item scale which probes positive, negative, and disorganized schizotypy. At present, the SPQ remains the most widely used tool to assess schizotypy in research settings. We note the heterogeneity in methodology and designs used to assess schizotypy, reflecting the conceptual variability around the construct.

The nature of schizotypy and its relation to schizophrenia remain debated in the field (see Lenzenweger, 2015; Grant et al., 2015). Some argue for a dimensional model in which schizotypy is a continuous personality trait in the general population (Claridge, 1985; Eysenck, 1952). In this dimensional view, high schizotypy can, in some extreme cases and/or under unfavorable conditions, unfold into a schizophrenia-spectrum disorder (Debbané et al., 2015). Others argue for a categorical model in which schizotypy is a discrete latent taxon (i.e., present or absent) representing schizophrenia illness and risk (Lenzenweger, 2010, 2015; Meehl, 1962, 1989). According to this disease-based model of schizotypy, about 10% of individuals in the general population are "schizotypes," which includes schizophrenia-spectrum disorders (i.e., schizophrenia, delusional disorder, schizotypal and paranoid personality disorders) as well as endophenotypes (Lenzenweger, 2015; Meehl, 1990).

Though the nature of the schizotypy construct remains debated, there is a broad consensus that schizotypy correlates with schizophrenia liability (Grant et al., 2015). In this dissertation, we therefore use schizotypy to investigate embodiment in a population that presents qualitatively similar to, and may have latent liability for, schizophrenia. **Fig 1.** Summarizes the diathesis-stress model of schizophrenia-spectrum disorders.

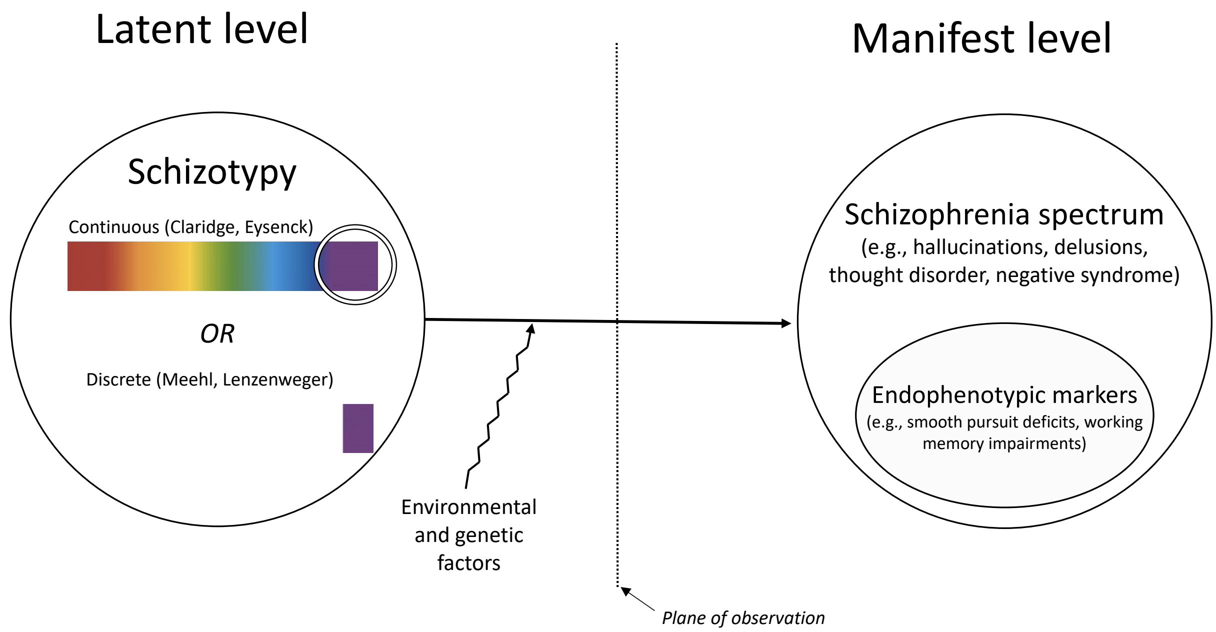

Fig. 1. Adapted from Lenzenweger (2015). Diathesis-stress model of schizophrenia-spectrum disorders. Schizotypy is a latent personality organization conceptualized as continuous (i.e., normally distributed in the general population) or discrete (i.e., schizophrenia liability that affects about 10% of the population). When combined to environmental risk factors and polygenetic influences, (elevated) schizotypy can pass a critical threshold at which various manifest variables occur (i.e., schizophrenia-spectrum disorders). Endophenotypic markers, which are stable across time (unlike clinical symptoms), can be detected using technology.

Neurodevelopmental models of schizophrenia (Rapoport et al., 2005) posit a gradual worsening of symptoms, in which elevated schizotypy, when combined with environmental risk factors, gives rise to cognitive and behavioral abnormalities which precede the onset of full-blow psychosis. Thus, different schizophrenia-spectrum disorders can be considered prodromal stages of schizophrenia. For instance, Schizotypal Personality Disorder (SPD) is characterized by "social and interpersonal deficits […] as well as cognitive and perceptual distortions and eccentricities of behaviors" (APA, 2013, p.655) in conjunction with self-reported occupational and interpersonal impairments. Critically, 40% of individuals with SPD will progress to a psychotic disorder within the next two years (Nordentoft et al., 2006). SPD is therefore considered part of the prodrome of schizophrenia (Salokangas & McGlashan, 2008). This change in conceptualization of SPD is evidenced by its move from the Personality Disorders section of the DSM-IV (APA, 1994) to the Schizophrenia Spectrum and Other Psychotic Disorders section of the DSM-V (APA, 2013).

In sum, schizotypy is a multidimensional personality trait that can help identify individuals who have a vulnerability for schizophrenia spectrum disorders. Importantly, not all individuals with high levels of schizotypal traits will transition to psychosis or experience functional impairments. Thus, the study of schizotypy is not only valuable in understanding the etiology of schizophrenia and informing early intervention programs, it also allows to investigate protective factors for those individuals who do not develop clinical impairments. Barrantes-Vidal and colleagues (2015) in fact argue that schizotypy research facilitates the identification of causal, resilience, and compensating factors at play in the development of schizophrenia and offers a multidimensional structure that captures etiological heterogeneity.

In line with early models of schizophrenia, anomalous bodily experiences and self-disturbances were also regarded as central to schizotypy or psychosis-proneness by early investigators (e.g., Chapman, 1978; Meehl, 1962; Rado, 1953). In fact, Chapmans' Perceptual Aberration Scale (PAS; Chapman et al., 1978), which largely probes bodily self-disturbances, was originally called the Body Aberration Scale. In a seminal longitudinal study of 543 young adults, scores on the PAS predicted elevated rates of schizophrenia spectrum disorders at the ten year follow-up (Chapman et al., 1994). More recently, Raballo and Parnas (2011) measured self-disorders in 218 unaffected family members of a person diagnosed with schizophrenia. They grouped participants into four groups based on their clinical presentation (i.e., no mental illness, no mental illness with schizotypal traits, other personality disorders, and SPD), and found that self-disorders increased as a function of the diagnostic category after accounting for demographic and subclinical factors. Thus, bodily disturbances and self-disorders seem closely linked to schizotypy and schizophrenia risk, though research in this area remains scarce.

In this dissertation, we study embodiment in schizophrenia and schizotypy to gain insight into the etiology and nature of schizophrenia phenomenology, and to inform treatment research. In the following sections, we describe embodiment in the general population before reviewing the empirical evidence documenting *dis*embodiment in the schizophrenia spectrum, and highlighting the gaps in the literature this dissertation aims to address.

EMBODIMENT AND THE SENSE OF SELF

The concept of embodiment allows us to approach to study of mental disorders from a multidisciplinary perspective to investigate the "circular interaction of mind, brain, organism and environment in the etiology of psychiatric disorders" (Martin et al., 2016). Specifically, the embodiment paradigm focuses on the role of the body in everyday experiences and functioning (Fuchs, 2012; Fuchs & Koch, 2014; Fuchs & Schlimme, 2009; Gallagher, 2005; Merleau-Ponty, 1962). Embodied actions are thought to begin shaping the sense of self early in infancy, and embodied sensations are the basis for emotional experiences throughout life (Rochat, 2011; 2019). Embodiment also scaffolds the distinction of the self from the other, thereby laying the groundwork for social functioning. In this section, we review the role of embodiment in human experience and behavior and highlight the role of interoception.

Sense of Self

Over the course of human history, scholars across a variety of areas (i.e., philosophy, theology, sociology, history, psychology) have investigated the construct of the self, leading to a variety of conceptualizations (for a review see: Brown, 2014; Hunt, 2014). Though the ultimate reality of the concept of the self remains controversial, psychologists and phenomenologists have avoided this ontological debate by focusing on the experiential, subjective aspect of the self: the sense of self (Dainton, 2008; Zahavi, 2008). The subjective self is experienced at different levels.

Two main levels of selfhood are routinely described: the *minimal self* and the *narrative self*. The minimal self or "ipseity" is the most basic, foundational level of selfhood (Gallagher, 2000). It is the level at which one acquires the first-person perspective through which they experience (i.e., see, feel, hear, taste, smell) life. For instance, my minimal self gives me the sense that *I* am the one writing this dissertation, *I* need coffee. Importantly, ipseity is pre-reflexive such that the experience of the minimal self is implicit and automatic. The minimal self is the most primal level of selfhood from which higher levels, such as the narrative self, stem. The narrative self binds together various aspects of personality, personal history, and social experiences to build an explicit self-identity. The narrative self gives rise to a self-concept: an individual's beliefs about themselves that influences their interactions with others and determines their self-identity (Baumeister, 1999). It is a coherent self-story incorporating our past and used to build our future. The following section details the role of the body in creating a reflective self-awareness. **Fig. 2** represents these levels of selfhood.

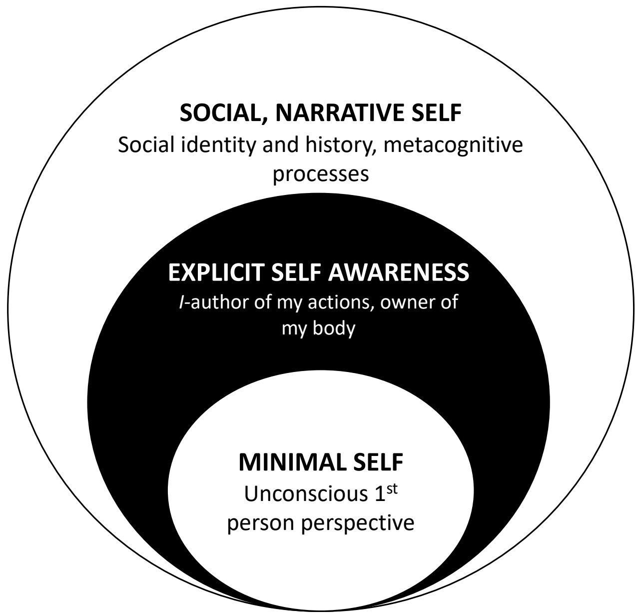

Fig. 2. Adapted from Raballo (2012). Levels of selfhood.

The Embodied Self

The body plays a critical role in the development of the sense of self. Newborns build an explicit sense of self through repeated sensorimotor actions. ***Agency***, the sense of control one feels over their own actions, gives rise to a map of body representations. For instance, when a baby exercises agency (i.e., reaching for their bottle), they receive sensory feedback resulting from their motor action (i.e., feeling the bottle in their hand), which scaffolds the creation of a mental representation of the body. This mental representation of our body in turn yields a sense of ownership over it. In fact, Gallagher (2000) pointed out that agency scaffolds the development of the sense of ***body ownership*** (i.e., "the special perceptual status of one's own body, which makes bodily sensations seem unique to oneself;" Tsakiris et al., 2007). However, once a stable sense of body ownership is established, it becomes independent of our sense of agency (e.g., my arm is mine even when someone else moves it).

Beyond its role in development, the body anchors the sense of self and scaffolds social and emotional functioning throughout life. The body is the physical anchor for ***emotional experiences***, thus serving a key role in social functioning. In fact, the subjective experience of emotions depends on our perception of physiological changes in the body (James, 1884; Damasio & Carvalho, 2013). Producing and recognizing emotional expressions is, in turn, crucial to communicating internal feelings and intentions to others (Ekman & Oster, 1979). The fundamental role of somatosensory signaling in emotional experience is clearly captured by the common metaphors we use to describe and communicate our internal states (e.g., "butterflies in the stomach") (Lakoff & Johnson, 1980). In line with folk knowledge, neuroimaging studies implementing pattern recognition techniques have established that somatosensory cortices hold a unique neural "fingerprint" for different emotions (Saarimäk et al., 2016). Using a computerized mapping tool, Nummenmaa and colleagues (2014) also showed that different emotional experiences are associated with unique patterns of bodily sensations, and statistical analyses confirmed the independence of the topographical representation of different emotions. A recent study using the same tool found evidence for the universality of these bodily signatures of emotions (Volynets et al., 2019). Thus, distinct "bodily signatures" of emotions, analogous the unique neural signatures of basic affective states (Saarimäki et al. 2016), were identified. Lastly, the bodily self allows for the self-other distinction, which forms the foundation of social cognition (Palmer & Tsakiris, 2018).

The sense of bodily self is constructed from the integration of exteroceptive, proprioceptive and interoceptive information, in conjunction with internal models of the body and predictive processing (Giummarra et al., 2008). For instance, Tsakiris (2010; 2011) proposed a neurocognitive model of the sense of body ownership based on multiple comparisons between bottom-up signals and top-down models: 1. the visual characteristics of the object are compared against the stored representation of the body, 2. the postural and anatomical features of the object are compared against the current state of the body, 3. multisensory inputs (e.g., the sight of an exteroceptive signal reaching the object) are compared to the felt sensations (e.g., touch). If these three comparisons yield a match, a sense of body ownership over the object will result. This subjective experience of body ownership will in turn update the stored body model. Beyond body ownership, Seth (2012) proposed an interoceptive predictive coding model of conscious presence. In short, the model proposes that conscious presence and agency result from the successful match between interoceptive predictions and direct (i.e., autonomic control signals) and indirect (i.e., bodily responses to afferent signals) inputs, resulting in the suppression of prediction errors (Seth, 2012).

In sum, embodiment is a key aspect of both self-experience and socio-emotional functioning. Though a stable sense of bodily self relies on the integration of exteroceptive, proprioceptive and interoceptive signals, empirical research has historically ignored interoceptive aspects of the self-experience (Quigley et al., 2021). We turn to a discussion of interoception, one of the key mechanisms underlying the sense of bodily self this dissertation focuses on.

Interoception

Interoception refers to the perception of the internal state of the body (Craig, 2002). Interoception plays a crucial role in cognitive, behavioral, emotional, and social functioning (Quigley et al., 2021). The ability to sense, interpret, and integrate our internal bodily signals guides our behaviors from the most primal (e.g., knowing when to use the restroom, eat, or drink), to the most mundane (e.g., knowing when to stop a workout) and crucial (e.g., knowing when to seek medical help). Thus, the perception of our autonomic signals ensures homeostasis through allostatic responses. Beyond its role in basic aspects of human functioning, interoception is also central to the sense of the self (Damasio, 2012) as well as emotional and social functioning (James, 1922). Given its critical role in various aspects of functioning, interoception has become a key focus of psychology research, exemplified by *Trends in Neuroscience*'s recent special issue on the topic (Furman, 2021).

Interoception and Sense of Self. Theoretical models of interoception and consciousness have highlighted the role of interoception in providing a physical anchor to self-experiences (Metzinger, 2004). In fact, the steadiness of interoceptive signals is thought to be a building block of the unitary sense of self.

Empirical evidence highlights the role of interoception in critical aspects of the embodied self such as self-recognition, self-other distinction, and peripersonal space. For instance, the Enfacement Illusion, a multisensory illusion designed to evoke alterations in self-recognition, was found to be more strongly induced in individuals with low interoceptive accuracy (Tajadura-Jimenez & Tsakiris, 2014). This illusion was also shown to decrease interoceptive accuracy in individuals with high interoceptive ability (Filippetti & Tsakiris, 2017). Conversely, Ainley et al. (2012) showed that looking at a picture of one's self increases interoceptive accuracy. Enhancing or dampening the saliency of interoceptive signals also modulates participants' ability to recognize their own face, especially in those with high interoceptive ability (Sel et al., 2017). Additionally, interoceptive ability predicts the size of one's peripersonal space (i.e., the space of the bodily self, or the reachable space, which extends beyond the physical boundary of one's body). In fact, Ardizzi & Ferri (2018) showed that the higher the interceptive accuracy, the narrower the peripersonal space. Interoception was also found to play a key role in self-other distinction, which forms the foundation of social cognition (Palmer & Tsakiris, 2018).

Empirical evidence also links interoception to the sense of body ownership. Tsakiris et al. (2011) showed that the Rubber Hand Illusion (RHI; Botvinik & Cohen, 1998; discussed further subsequently) can be induced more strongly in individuals with lower interoceptive accuracy. This finding suggests that individuals with higher interoceptive ability might have a stronger, more stable sense of bodily self, such that they are less susceptible to illusions of the bodily self. Suzuki et al. (2013) showed that watching a rubber hand pulsating in synchrony with one's heartbeat yields a sense of ownership over it in the absence of any visuo-tactile stimulation, thereby causally linking interoceptive signals to body ownership.

Interoception and Socio-Emotional Functioning. As previously established, bodily sensations are a central aspect of emotional experiences. More precisely, the perception of physiological changes (i.e., interoception) is essential to emotion recognition and social functioning (James, 1922). In fact, individuals with heightened interoception were shown to experience emotions with greater intensity (Wiens et al., 2000). On the other hand, interoceptive deficits are thought to underlie the difficulty identifying and describing feelings characteristic of alexithymia (Bonaz et al., 2021). At the neural level, the role of interoception in emotional experience is evidenced by the overlap between the neural networks underlying interceptive functioning, body regulation, and emotional experiences (Quigley et al., 2021). Beyond emotions, interoception has also been linked to social functioning. In fact, interoception helps appraise physiological signals during social interactions (Arnold et al., 2019). Based on empirical evidence, Crucianelli et al. (2018) argue that the ability to temporarily down-regulate interoceptive signals to favor exteroceptive information might be adaptive in challenging social situations. Interoception has also been linked to cognitive processes such as memory (Garfinkel et al., 2013; Werner et al., 2010) and decision making (Werner et al., 2013). Overall, a wealth of evidence highlights the key role of interoception across psychological processes, making it a pillar of both physical and mental wellbeing (Khalsa et al., 2018; Quadt et al., 2018). Some even argue that interoceptive dysfunction during adolescence could underlie the onset of psychopathology and risky behavior (Murphy et al., 2017).

Dimensions and Measurement. Interoceptive ability is multidimensional. Garfinkel et al. (2015) make an empirically-driven distinction between (1) interoceptive accuracy, (2) interoceptive sensibility, and (3) interoceptive awareness:

1. *Interoceptive accuracy* refers to the objective performance on behavioral tasks aimed at assessing the ability of a participant to perceive their own internal signals (Garfinkel et al., 2015). For pragmatic reasons, these tasks have largely focused on the ability to detect one's heartbeat. Two main versions of the heartbeat task exist. In the Heartbeat Counting Task (Schandry, 1981), the participant is asked to count the number of times their heart beats in a given period of time. Their response is compared to the actual number of heartbeats recorded by a heart monitor to yield an interoceptive accuracy score. In the Heartbeat Discrimination Task (Brener & Kluviste, 1988; Whitehead et al., 1977) the participant is asked to report the timing of their heartbeats, either by tapping, or by gauging the synchrony of their heartbeat with an external auditory stimulus. We note that though heartbeat counting tasks have been criticized (e.g., Zamariola et al., 2018), they

remain the gold standard for behavioral tasks measuring interoception to date. In fact, though alternative behavioral measures of interoceptive accuracy have been developed (e.g., the Water Load test; van Dyck et al., 2016) they are deemed impractical and therefore sparsely used by researchers.

2. Interoceptive sensibility is the subjective evaluation of one's own interceptive ability (Garfinkel et al., 2015). It is measured using self-report measures such as questionnaires or interviews.
3. Interoceptive awareness is the experimentally measured metacognitive awareness of one's interoceptive ability (Garfinkel et al., 2015). Interoceptive awareness is measured by comparing subjective ratings of confidence with objective performance in behavioral tasks.

***DIS*EMBODIMENT IN THE SCHIZOPHRENIA SPECTRUM**

Consistent with early conceptualizations of the disorder, contemporary evidence points to disturbances of the embodied self as the core of schizophrenia pathology. Broadly, the loss of sense of ownership over one's thoughts, actions, and body, is believed to be central to the schizophrenia experience (de Vries et al., 2013; Park & Narsallah, 2014). We note that the majority of this contemporary evidence comes from phenomenological studies and first-person accounts. In an attempt to bridge the gap between empirical research and the phenomenology of the disorder, *Schizophrenia Bulletin* includes a first-person account in each of the journal's issues. In one of them, Clara Kean explains that she feels detached from herself (Kean, 2009).

Elyn Saks, a professor of Law at the University of Southern California, writes in her autobiography that in the midst of a psychotic episode, she felt like she was "dissolving like a sand castle with all the sand sliding away" (Saks, 2007).

Embodiment disturbances are also evident from clinical observations and reports of autoscopic (i.e., the perception of one's *surroundings* from an outside perspective) and heautoscopic (i.e., the perception of one's *self* from an outside perspective) experiences in schizophrenia (Blanke & Mohr, 2005; Brugger et al., 1997). For instance, individuals with schizophrenia are prone to out-of-body experiences (OBEs), the sensation of being located outside of one's physical body (Blackmore, 1986; Tyrell, 1943). In a rare spontaneous case study, a participant with schizophrenia experienced an OBE during the induction of a multisensory illusion (Thakkar et al., 2011). He reported "*[It] feels like we're a foot off the floor, turning in a circle,*" following which, *"[it] feels like we're coming back down; [it] felt like there wasn't a floor beneath my feet"* (Thakkar et al., 2011, p. 6). Previous research also linked positive schizoptypy to OBEs (e.g., McCreary & Claridge, 1995; 1996; 2002). Another example of heautoscopic experiences is the Feeling of a Presence (FoP), which refers to the illusion of being in the company of another being or entity (Cheyne, 2001). FoPs are thought to result from the external projection of one's internal bodily representation, which results in the subjective sensation of an "other" (Brugger et al., 1996). FoPs can thus be seen as the heautoscopic experience of one's invisible doppelgänger (Brugger et al., 1996). Wibel (2012) argues that many symptoms of schizophrenia can be reframed as the FoP of someone watching, doing, speaking, etc. Schizotypy has also been linked to FoPs (Barnby & Bell, 2017).

Empirical evidence for embodiment disturbances in the schizophrenia spectrum comes from (1) the quantification of phenomenological experiences via self-report measures and (2) the experimental assessment of various aspects of embodiment using behavioral tasks. While both empirical (i.e., quantitative), these two types of assessment answer fundamentally different questions. In fact, while self-report instruments aim at understanding and quantifying disembodiment as a whole, experimental tasks aim at isolating and individually assessing different aspects of disembodiment (i.e., agency deficits, body ownership disturbances, anomalous emotional embodiment, interoceptive deficits).

Self-report and Interview Measures

Given their subjective nature, bodily self-disturbances are often assessed using self-report and interview measures. These instruments generally survey various anomalous bodily/self experiences and aim at quantifying overall embodiment disturbances in an individual. Though an exhaustive review of all these self-report instruments is beyond the scope of this dissertation, we briefly review some self-report instruments commonly used in schizophrenia-spectrum research and highlight key results.

Examination of Anomalous Self-Experiences (EASE; Parnas et al., 2005). The EASE is, to our knowledge, the only semi-structured interview designed to assess self-disturbances across the schizophrenia spectrum. It assesses five domains of self experience, including Bodily Disturbances. Individuals with schizophrenia and SPD were shown to score higher than control individuals across domains of anomalous self-experience (Raballo & Parnas, 2012). EASE scores correlate with overall schizophrenia symptomatology, positive symptoms, negative symptoms, and reduced social functioning (Raballo & Parnas, 2012). Furthermore, total EASE scores predict transition to psychosis in high-risk individuals (Nelson et al., 2012). In a First

Episode Psychosis (FEP) population, individuals who meet criteria for a schizophrenia diagnosis scored significantly higher on the bodily experiences cluster compared to those who met criteria for other psychotic disorders (Nelson et al., 2013), suggesting that self-disorders are specific schizophrenia spectrum disorders.

Inventory of Psychotic-Like Self Experiences (IPASE; Cicero et al., 2017). The IPASE is a 57-item self-report questionnaire that was developed in an effort to create an easy-to-administer, short self-report version of the EASE. It surveys five domains of self experience, including Somatization. Individuals with high positive schizotypy scored higher than individuals with high negative schizotypy on all five scales, including bodily-self-disturbances (Cicero et al., 2017). Furthermore, individuals with schizophrenia or schizoaffective disorder scored significantly higher than control participants on all IPASE scales (Cicero et al., 2017).

Perceptual Aberration Scale (PAS; Chapman, et al., 1978). The PAS is a 35 true/false items scale designed to measure perceptual disturbances (especially related to the body) in both clinical and healthy populations. The scale was initially titled the "Body Image Aberration Scale," which consisted of 28 items measuring bodily disturbances. The PAS measures five types of anomalous bodily experiences: (1) unclear body boundaries, (2) feelings of unreality or estrangement of body, (3) feelings of deterioration of one's body parts, (4) perceptions of the change of size of one's body parts, and (5) changes in the appearance of the body. However, the authors suggest computing a total score representing the overall level of anomalous perceptual aberration experienced by the participant. Chapman et al. (1978) found that individuals with schizophrenia reported significantly higher levels of body aberrations compared to matched controls. The degree of body-image disturbance reported by individuals with schizophrenia negatively correlated with illness duration, such that the more chronic the patient, the less body aberration they reported. Thus, the authors concluded that body image disturbances are more common in the early stages of schizophrenia illness.

Benson et al. Body Disturbances Inventory (B-BODI; Benson et al., 2019). The B-BODI is a 25-item picture-based instrument assessing various anomalous bodily experiences (i.e., dissociations, flexibility of the body boundary, body aberrations, loss of agency, body ownership disturbance, self–other transformations, feeling-of-presence, anomalous sense of time, autoscopic hallucinations). Each item includes a statement and a corresponding drawing depicting a unique unusual bodily experience. If a participant endorses an item, they are instructed to rate the frequency, vividness, and level of emotional disturbance brought on by the experience. The original study showed that individuals with schizophrenia scored higher than control individuals on the B-BODI (Benson et al., 2019). Similar results were found when comparing individuals at high versus low risk for developing schizophrenia. Interestingly, when comparing people diagnosed with schizophrenia and college student at psychometric risk of developing schizophrenia, the authors found that the at-risk groups scored significantly higher than the chronic schizophrenia group, again suggesting that bodily disturbances might be particularly salient in early schizophrenia (Benson et al., 2019).

In sum, studies using self-report instruments have consistently documented a heightened level of bodily disturbances in the schizophrenia spectrum. This seems to be particularly true in the early stages of illness, and the assessment of anomalous bodily disturbances has been proposed as an efficient tool to identify at-risk individuals. Furthermore, bodily disturbances appear to correlate with both positive and negative symptomatology/schizotypy and seem to be specific to schizophrenia versus other psychotic disorders remains unclear.

Experimental investigations of the bodily self

As previously mentioned, experimental tasks are used to measure one specific aspect of embodiment. In this section, we review the empirical evidence for interoceptive deficits and specific types of anomalous bodily experiences (i.e., anomalous emotional embodiment, agency deficits, body ownership disturbances) in the schizophrenia spectrum, which lays the groundwork for the studies presented in Chapters II-IV.

Interoception. Case studies documenting reduced internal pain perception in schizophrenia have long been present in the literature. A review identified nine case studies of individuals with schizophrenia reporting no pain to severe medical conditions such as ruptured appendix, peritonitis, peptic ulcer, perforated bowel, compartment syndrome, or fractures (Olivier et al., 2009). Another, more recent, systematic review concluded that both the prevalence and intensity of pain is reduced in schizophrenia compared to control individuals, specifically for severe pain with an apparent medical cause (Engels et al., 2014). These findings suggest reduced interoceptive ability in schizophrenia. We note, however, the potential confounding effect of antipsychotic medication. In fact, antipsychotics are known for their analgesic effect such that atypical antipsychotic drugs are sometimes prescribed for pain management (e.g., Seidel et al., 2010; Shin et al., 2019).

Surprisingly few studies have empirically investigated interoceptive ability in the schizophrenia spectrum. To our knowledge, the only two studies that used a behavioral task to experimentally measure interoception in individuals with schizophrenia found reduced interoceptive accuracy in this population (Ardizzi et al., 2016; Koreki et al., 2021). Reduced interoceptive ability was not accounted for by other demographic of clinical factors (i.e., age, BMI, anxiety, heart rate), but significantly correlated with positive symptoms (Ardizzi et al., 2016, Koreki et al., 2021). Koreki et al. (2021) also found evidence for difference in the subjective experience of interoception (i.e., interoceptive sensibility) in schizophrenia. To our knowledge, no study to date has experimentally assessed interoceptive ability in relation to schizotypy.

Indirect evidence for interoceptive deficits in the schizophrenia spectrum comes from the neuroimaging literature investigating the insula. In fact, the anterior insular cortex supports interoceptive functioning (Craig, 2009) and insular dysfunction has been documented in a few studies conducted on individuals with schizophrenia. For instance, Linnman et al. (2013) found a lack of insula reactivity to aversive stimuli in schizophrenia, though typical neural responses were observed during shock anticipation. This deficit was linked to the severity of positive symptoms (Linnman et al., 2013). In addition to functional abnormalities, the structure of the posterior insula was also found to be altered in individuals with schizophrenia compared to control individuals (Palaniyappan et al., 2011). The authors discuss their results in relation to interoceptive deficits in this population (Palaniyappan et al., 2011). In their review of the role of the insula in schizophrenia, Wylie and Tregellas (2010) directly link documented insula dysfunction to a variety of interoceptive deficits (e.g., emotional processing, pain perception, self- versus other-generated stimuli) in this population.

Overall, neuroimaging studies reliably document insula dysfunction and structural anomalies in schizophrenia, which suggests interoceptive deficits in this population. The only two studies that directly assessed interoceptive functioning in individuals with schizophrenia noted a marked deficit in interoceptive accuracy. The link between interoceptive functioning and schizotypy remains unexplored. This lays the groundwork for study 1.

Emotional Embodiment. Disruptions in facial emotional expressivity have long been documented in the schizophrenia literature. In fact, Kraepelin and Bleuler believed that “flat” and “inappropriate” affect were core features of the illness (see Trémeau, 2006 for a review). Empirical studies also found that the facial expression of emotions is reduced in individuals with schizophrenia (Berenbaum & Oltmanns, 1992; Kring & Moran, 2008). However, studies using facial electromyography (fEMG) showed that the recruitment of facial muscles underlying the production of facial expressions is intact in this population (Kring et al., 1999). Though spontaneous facial mimicry was originally believed to be impaired (Varcin et al., 2010), two recent studies documented intact automatic facial mimicry in schizophrenia (Chechko et al., 2016; Torregrossa et al., 2019a). Interestingly, intentional facial imitation and action imitation are impaired in schizophrenia (Schwartz et al., 2006; Thakkar et al., 2014). Together, these findings suggest that emotion recognition deficits in schizophrenia arise from a faulty interpretation of one’s own bodily signals rather than anomalous physiological responses to affective stimuli (i.e., false inference model of embodiment; Tschacher et al., 2017). However, studies investigating emotional embodiment at the whole-body level suggest disrupted bodily sensation of emotions in this population.

In a previous study, we used Nummenmaa et al. (2014)'s body mapping tool to assess embodied emotions in schizophrenia (Torregrossa et al., 2019b). We found anomalous emotional embodiment in individuals with schizophrenia (see **Fig. 3**). To our knowledge, bodily maps of emotions have not been examined in schizotypy, which motivated Study 2.

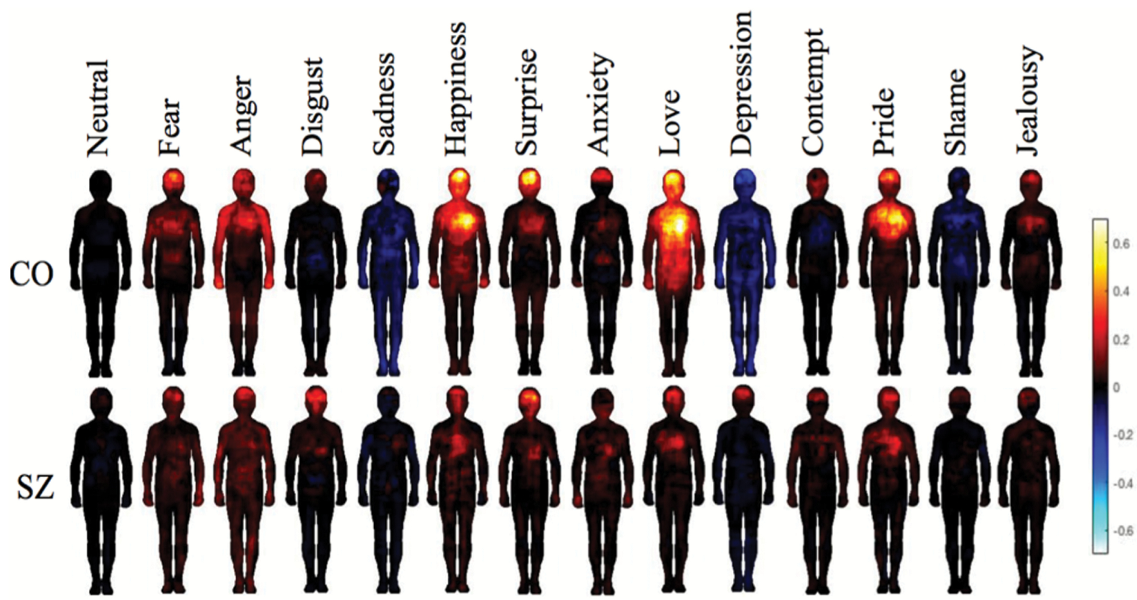

Fig. 3. Reprinted from Torregrossa et al., 2018. Anomalous bodily maps of emotions in individuals with schizophrenia (SZ) compared to matched controls (CO). The color bar indicates the proportion of endorsement at each pixel ranging from -1 (group consensus for deactivation) to 1 (group consensus for deactivation).

Agency. Agency is the higher-order mechanism responsible for the sense of control we experience over our voluntary actions. When we complete an intentional motor command, an efference copy (i.e., corollary discharge) of that movement is generated and compared with the re-afference signal (i.e., the sensory feedback) to yield a sense of intentionality over our actions.

Agency disturbances are well documented across a variety of paradigm in schizophrenia (e.g., Bulot et al., 2007; Frith, 1987; Frith, 2005; Graham et al, 2014; Hauser et al., 2011a; Hauser et al., 2011b; Hur et al., 2014; Jeannerod, 2009; Kircher & Leube, 2003; Lafargue &

Franck, 2009; Lallart et al., 2008; Maeda et al., 2012; Metcalfe et al., 2012; Sato & Yasuda, 2005; Schimansky et al., 2010). In a seminal study, Blakemore et al. (2000) showed that individuals with schizophrenia could tickle themselves, which provide further evidence for deficits in the corollary discharge system in this population. Agency deficits are also well documented in schizotypy. In fact, various studies found an anomalous sense of agency in individuals with high levels of schizotypy (Asai & Tanno, 2007; Asai & Tanno, 2008; Moore et al., 2020).

In a meta-analysis of empirical studies assessing self-disturbances in schizophrenia, 60% of the identified studies assessed agency deficits (Hur et al., 2014). The overall effect size for agency deficits was found in the medium range (g= 0.49). In sum, agency deficits have been extensively studied and documented along the schizophrenia spectrum. Given the wealth of existing research on agency deficits in the schizophrenia spectrum, the present dissertation will not examine this aspect of the bodily self.

Body Ownership. Though agency disturbances in schizophrenia have long been documented, body ownership was thought to be intact until recently (Klaver & Dijkerman, 2016). However, in the meta-analysis previously mentioned, the authors found the largest effect size for body ownership disturbances (g= 0.91) as compared to other types of self-disturbances in schizophrenia (Hur et al., 2014).

The Rubber Hand Illusion (RHI; Botvinik & Cohen, 1998) is the most widely used behavioral task to measure body ownership. The RHI uses conflicting visual and tactile information to create a sense of bodily ownership over a foreign object (i.e., a rubber hand). The discrepancy between the tactile stimulation (i.e., feeling the stoking on one's real hand) and the simultaneous visual feedback (i.e., watching the rubber hand being brushed) results in the illusion of ownership over the rubber hand.

To date, 13 studies have used the RHI to measure body ownership across the schizophrenia spectrum (Asai et al., 2011; Ferri et al., 2014; Germine et al., 2013; Graham et al., 2014; Kaplan et al., 2014; Lev-Ari et al., 2015; Mirucka, 2016; Mirucka, 2019; Peled et al., 2000; Peled et al., 2003; Prikken et al., 2019, Thakkar et al., 2011; Zopf et al., 2021). These studies consistently documented an increased sensitivity to the illusion in individuals with schizophrenia compared to matched controls. Two studies investigated the RHI sensitivity in relation to schizotypy (Asai et al., 2011, Germine et al., 2013). They both found a link between positive schizotypy and susceptibility to the RHI. Asai and colleagues (2011) also found a positive relationship between RHI susceptibility and negative schizotypy. This line of research motivated study 3.

ETIOLOGIES OF BODILY DISTURBANCES

As previously established, the sense of bodily self relies on the processing and multisensory integration of a variety of bottom-up signals (i.e., interoceptive, proprioceptive, and exteroceptive), as well as top-down contributions from internal models and predictive processes. Thus, disturbances in any of these mechanisms can lead to embodiment abnormalities. In this section, we selectively review the literature pointing at neurological and environmental factors contributing to disembodiment both within and outside of the schizophrenia spectrum.

Neural Bases

Neuroimaging studies have been instrumental in exploring the mechanisms underlying bodily disturbances. In fact, pharmacological studies examining ketamine-induced disembodiment and case studies of clinical syndromes and conditions characterized by embodiment deficits (e.g., asomatognosia, Body Integrity Identity Disorder, Cotard delusion) shed light on the neural basis of bodily disturbances. In this section, we briefly review the literature investigating these conditions and their proposed neurological etiology. When relevant, we draw the link between findings from these studies and schizophrenia phenomenology.

Ketamine is an analgesic agent known to induce altered states of consciousness characterized by dissociative experiences (Vlisides et al., 2018), aberrant agency (Moore et al., 2010), and body ownership disturbances (Morgan et al., 2011). An EEG study showed that these bodily disturbances were linked to reduced alpha power in the precuneus and tempo-parietal junction (TPJ) following ketamine administration (Vlisides et al., 2018). Corlett et al. (2006) also showed that ketamine induces aberrant prediction error signaling, which is linked to increased activation of the frontal cortex. Importantly, aberrant prediction errors also predict delusion severity in clinical samples (2007) and correlate with sub-threshold delusions in individuals with high schizotypy (2012).

Consistent with the glutamate hypothesis of schizophrenia, ketamine, a N-methyl-D-aspartate glutamate receptor (NMDAR) antagonist, has been proposed as a pharmacological model of the disorder (for a review, see Frohlich & Van Horn, 2014). Ketamine administration is known to mimic not only acute symptoms of schizophrenia (Krystal et al., 1994) but also the bodily disturbances characteristic of the illness (Pomarol-Clotet et al., 2006). Thus, the brain regions (i.e., precuneus, TPJ, frontal lobes) and top-down mechanisms (i.e., predictive coding) underlying ketamine-induced bodily disturbances might be important targets for research aiming at elucidating the etiology of disembodiment in schizophrenia.

Asomatognosia describes a category of neurological disorders characterized by a lack of ownership over a specific limb (Feinberg et al., 2010). Hemispatial neglect (i.e., deficits in attention to, and awareness of, one side of the visual field following brain damage) is likely necessary, yet insufficient for asomatognosia to occur (Feinberg et al. 2010). Feinberg and colleagues' study (2010) in fact suggests that medial frontal lesions are critical to body ownership disturbances. More precisely, Arzy et al. (2006) pointed at the role of premotor cortex damage in body ownership disturbances. Right orbitofrontal lesions have been shown to be specifically implicated in somatoparaphrenia, a subtype of asomatognosia in which the perceptual abnormality is explained by delusional beliefs. Vallar and Ronchi (2009) showed that 91% of the 56 somatoparaphrenia cases they studied had right-sided brain lesions. These authors, along with others, point at the critical role of the right TPJ (rTPJ) in body ownership disturbances (Feinberg et al., 2010; Vallar & Ronchi, 2009). To our knowledge, asomatognosia have not been systematically studied in schizophrenia.

Body Integrity Identity Disorder (BIID) is a special case of somatoparaphrenia in which the perceptual aberration and delusion result in a strong desire to amputate or disable the affected limb. This desire is believed to result from a mismatch between the actual and perceived body schema, such that the individual does not perceive the affected limb as part of their body (First, 2005). BIID is not included in the DSM-5 or the ICD-11, such that it is rarely recognized by psychiatrists and seldom studied by researchers. Consequently, little is known regarding the etiology of this disorder. Blom et al. (2012) argue that BIID does not result from any specific physical or psychiatric comorbidity. They also note that other than surgery, no effective treatment or management strategies exist at present. Some conceptualize BIID as a congenital disorder. In fact, First (2005) noted that all but one of the 52 individuals with BIID he studied reported BIID onset during childhood.

Guimmarra et al. (2011) proposed a neurological model of BIID involving not only the rTPJ but also the insula (i.e., the brain region previously discussed for its role in interoception). These authors argue that BIID likely results from dysregulations at multiple levels of body processing (i.e., body representation, multisensory integration, agency, embodiment). We note the similarity between these bodily disturbances and those documented in schizophrenia. However, to our knowledge, no case studies of co-morbid BIID and schizophrenia exist, which might reflect an overwhelming overlap in presentation, or simply the lack of clinical attention given to body ownership disturbances. Regardless, current models of BIID again point to the rTPJ and the insula as brain regions that might be implicated in body ownership deficits.

Cotard's syndrome is characterized by nihilistic delusions (i.e., the belief that one is dead) and associated symptoms (i.e., anxious melancholia, insensitivity to pain, ideas of damnation; Debruyne et al., 2009). Though Cotard's delusion can target one's existence or life, it is most often associated with the body (86% of cases; Berrios & Luque, 1995). Cotard's delusion is considered a rare symptom observed across different clinical population rather than a discrete disorder (Berrios & Luque, 1995; Ramirez-Bermudez et al., 2010; Stompe & Schanda, 2013). There have been compelling case studies of Cotard's delusion in schizophrenia (e.g., Bott et al, 2016; Huacaya-Victoria, 2016). However, the incidence of Cotard's delusion in this population does not seem to be increased above the level found in the general population. In a study of 346 individuals with schizophrenia, Stompe and Schanda (2013) found that the prevalence of Cotard's delusion was less than 1%. A review of 479 psychiatric patients found no cases of Cotard's delusion in those diagnosed with schizophrenia (N=150; Ramirez-Bermudez, 2010).

Theoretical models of Cotard's delusion remain to be empirically validated. Currently, two models compete: the "one-stage" model, in which the delusion simply results from an abnormal perception, and the "two-stage" model in which the delusion occurs following the incorrect interpretation of an abnormal perception (Huarcaya-Victoria et al., 2016). Proponents of the two-stage model compare Cotard's delusion to *Capgras delusion* (i.e., the false belief that a loved one has been replaced by a physically identical imposter; Young et al., 1994). In fact, theoretical models of Capgras delusion posit that a lack of affective component of face recognition (i.e., abnormal perception) yields a false belief that that the person has been replaced by an imposter (i.e., incorrect interpretation). Similarly, Cotard's delusion can be understood as the incorrect interpretation that "I am dead" if "I feel nothing inside" (i.e., interoceptive deficit). In line with this conceptualization, Cotard's delusion has been linked to insular cortex atrophy, the brain region associated with interoceptive abilities (Chatterjee & Mitra, 2015).

Taken together, these studies point to the rTPJ and the insula as brain regions underlying (dis)embodiment. Notably, abnormalities in both these regions have been documented across the schizophrenia spectrum. As previously mentioned, abnormal insular structure and activity have been linked to interoceptive deficits in schizophrenia (Linnman et al., 2013; Palaniyappan et al., 2011). Furthermore, several studies documented abnormal activation patterns of the rTPJ in individuals with schizophrenia (Franck et al, 2002; Ganesan et al., 2005; Spence et al., 1997), and a study found that abnormally prolonged rTPJ activation was associated with bodily self-disturbances and schizotypy in the general population (Arzy et al., 2007). Given its placement on the cortical surface, the rTPJ might be a particularly interesting target for interventions using non-invasive neuromodulation (see Study 3).

Psychological and Environmental Factors

The diathesis-stress model of psychopathology posits that environmental stressors contribute to the development of mental illnesses. In this section, we review the effects of two environmental factors (i.e., trauma and loneliness) linked to disembodiment.

Trauma exposure has long been associated with dissociative experiences (e.g., Bremner & Marmar, 2002; Scaer, 2014; Spiegel, 1997). From an evolutionary perspective, dissociation can be seen as an adaptive repones to life-threatening situations in which neither fight nor flight responses are available (Barcha, 2004). This is particularly true for trauma that is experienced first-hand, during childhood (Schalinski & Teicher, 2015). Beyond the initial response to an acute danger, the dissociative response can be re-triggered by contextual cues (Schauer & Elbert, 2015). Persistent dissociative experiences have been shown to predict posttraumatic stress disorder (PTSD; Briere et al., 2005). The link between trauma and dissociations is evident by the inclusion of a dissociative subtype of PTSD in the DSM-V, characterized by symptoms of depersonalization (i.e., feeling detached from and/or the observer of one's own mental processes or body) and/or derealization (i.e., experiencing one's surroundings as unreal; APA, 2013). Dissociative Identity Disorder (DID), a controversial disorder which hallmark symptom is a disruption in identity (i.e., “discontinuity in the sense of self and the sense of agency”) is also believed to result from severe childhood trauma (APA, 2013, p. 292).

Increased rates of trauma exposure have been reliably documented in individuals with schizophrenia (Larsson et al., 2013; Lysaker et al., 2001; Mueser et al., 2004; Resnik et al., 2003). Trauma history has also been linked to schizotypal traits (Berenbaum, 1999). A growing body of literature further shows that trauma history might play a critical role in the development of psychosis (Isvoranu et al., 2016; Varese et al., 2012). Interestingly, recent work also points to the mediating role of self-disturbances in the relationship between trauma and psychotic-like experiences (Gawęda et al., 2018, 2019; Pionke-Ubych et al., 2021). Importantly, however, not all individuals with schizophrenia have a history of trauma. Some researchers have in fact argued for a subtype of schizophrenia characterized by trauma-related dissociative experiences (Sar et al., 2010). Thus, the etiology of bodily self-disturbances in individuals with psychosis who do not have a concurrent history of trauma remains to be clarified.

Loneliness (i.e., perceived social isolation) is an epidemic which effects on health are equivalent to smoking 15 cigarettes a day or meeting criteria for DSM-V Alcohol Use Disorder (Holt-Lunstad et al., 2015). The prevalence of loneliness is particularly elevated in the schizophrenia spectrum, with an estimated 80% of adults with psychosis endorsing loneliness in the past 12 months (Stain et al., 2012). Loneliness has been linked to a range of negative outcomes (Cacioppo & Hawkley, 2009). In particular, social isolation or defeat (i.e., being in an inferior or “outsider” position) has been linked to the onset or worsening of psychotic symptoms in vulnerable populations (de Soussa et al., 2015; Grassian, 1983; Hoffman, 2007; Jing et al., 2013; Selten et al. 2013). Analogous to the idea that sensory deprivation triggers perceptual aberrations, the Social Deafferentation hypothesis posits that social isolation leads to the internal creation of social agents, which underlies hallucination and delusions (Hoffman, 2007).

Based on evidence suggesting that social interactions scaffold the interpretation of our internal signals (Cioffi, 1991, Russell, 2003), Michael and Park (2016) experimentally tested the link between social isolation and anomalous bodily sensations. They found that individuals with schizophrenia were more susceptible to the Pinocchio Illusion (i.e., phantom nose elicitation), and that sensitivity to the illusion correlated with loneliness regardless of diagnosis (Michael & Park, 2016). In light of these results, the authors proposed an extension of the Social Deafferentation Hypothesis to include anomalous bodily sensations (Michael & Park, 2016). These findings directly highlight the link between loneliness and bodily disturbances in the schizophrenia spectrum. Additionally, the link between social functioning and embodiment is evident at the neural level, as the TPJ, which we have previously discussed for its involvement in bodily processing, is part of the social brain network (Wible, 2012).

In Autism Spectrum Disorders (ASD), which are characterized by social and communication deficits, the sense of self is also altered. In fact, the term "autism" is derived from the Greek word "autos," which means "self." When describing the core of the disorder, Kenner (1943) highlighted social isolation and a separation between the self and the other. Interestingly, the bodily disturbances observed in ASD counter those observed in the schizophrenia spectrum. For instance, individuals with ASD display a reduced sensitivity to the RHI while individuals with schizophrenia are more susceptible to the illusion (Crespi & Dinsdale, 2019). Similarly, ASD and schizophrenia are believed to lay at opposite ends of the peripersonal space continuum such that individuals with ASD possess a sharp body boundary, contrasting the weak/variable self-other boundary observed in schizophrenia (Noel et al., 2017), especially in social contexts (Lee et al., in press). Thus, Crespi and Dinsdale (2019) proposed a model of ASD and psychosis as diametrically opposite disorders of embodiment.

In sum, bodily disturbances in schizophrenia appear to be unique in both their nature and characteristics. The overlap between dissociative disorders and schizophrenia is evident in the original descriptions of dissociations (Janet, 1890) and schizophrenia (Bleuler, 1911), both described as a splitting of the psyche/mind (Putnam, 1989). And indeed, elevated rates of dissociative experiences are found in the schizophrenia spectrum (Renard et al., 2017). The recent bio-*pheno*-social model of schizophrenia acknowledges both shared and distinct symptoms in schizophrenia and dissociative disorders (Sass et al., 2018). According to this model, schizophrenia is characterized by both primary (i.e., trait-like, fundamental) and secondary (i.e., state-dependent, consequential) self-disturbances, while dissociations experienced in the context of other mental disorders are largely secondary (Sass et al., 2018). Thus, environmental factors (i.e., trauma, social defeat, loneliness) contribute to secondary, but not primary, dissociative experiences in schizophrenia (Sass et al., 2018).

OVERVIEW

Embodiment deficits were central to early theories of schizophrenia and remain at the core of phenomenological models of the disorder. Contemporary evidence confirms disturbances of the bodily self as central to the disorder and suggests that they might in fact be an early marker for schizophrenia risk. Thus, the study of embodiment in the schizophrenia spectrum might cast light on the nature and etiology of schizophrenia pathology and could yield valuable insight for treatment research. This dissertation is comprised of three studies that extend this line of research.

Though research points at the importance of interoception in creating a stable sense of embodied self, surprisingly few studies have investigated interoception in the schizophrenia spectrum. In **Study 1**, we assess interoceptive ability in individuals with schizophrenia (**Study 1A**) and in relation to schizotypy (**Study 1B**). Moreover, though anomalous emotional embodiment and body ownership deficits have been reliably documented in individuals with schizophrenia, these aspects of the embodied self have yet to be systematically studied in individuals with a latent liability for psychosis. In **Study 2**, we investigate bodily maps of emotions in relation to schizotypy. In **Study 3**, we use the Rubber Hand Illusion to investigate the link between schizotypy, self-reported bodily disturbances, and the sense of body ownership. In addition, based on neuroimaging evidence pointing at the role of the rTPJ on the sense of body ownership, Study 3 explores the effect of non-invasive neuromodulation of the rTPJ on the malleability of one's sense of body ownership.

CHAPTER II

Study 1. Interoception in Schizophrenia and Schizotypy

Garfinkel et al. (2015) make an empirically-driven distinction between (1) *interoceptive accuracy* (i.e., the objective performance on behavioral tasks assessing the ability of a participant to perceive their own internal signals), (2) *interoceptive sensibility* (the subjective evaluation of one's interceptive ability, measured via self-report questionnaires), and (3) *interoceptive awareness* (i.e., the metacognitive awareness of one's interoceptive ability, measured experimentally by comparing subjective ratings of confidence with objective performance on behavioral tasks).

To date, only two studies have experimentally measured interoception in schizophrenia. Both studies documented reduced interoceptive accuracy (measured by an individual's ability to accurately detect and count their heartbeat) in this population (Ardizzi et al., 2016; Koreki et al., 2021). These studies additionally reported a link between reduced interoceptive accuracy and the severity of positive symptoms (Ardizzi et al., 2016; Koreki et al., 2021). Koreki and colleagues (2021) also found differences in interoceptive sensibility between individuals with schizophrenia and control individuals. Specifically, using a self-report questionnaire, they found that though individuals with schizophrenia reported an increased ability to notice interoceptive signals, they also endorsed an increased tendency to ignore uncomfortable or painful sensations (Koreki et al., 2021). To our knowledge, the third dimension of interoception, interoceptive awareness, has never been measured in individuals with schizophrenia. Furthermore, the link between interoceptive functioning and schizotypy remains unexplored.

The general aim of this study is to investigate interoceptive functioning across the schizophrenia spectrum. In **Study 1A**, we compare a group of individuals with schizophrenia to a group of matched controls on interoceptive accuracy, awareness, and sensibility. In **Study 1B**, we explore the link between different dimensions of schizotypy (i.e., interpersonal, disorganized, cognitive) and interoceptive ability (i.e., accuracy, awareness, sensibility).

Study 1A. Interoception in Schizophrenia

In this study, we investigated the three dimensions in interoception (i.e., interoceptive accuracy, awareness, and sensibility) in a group of individuals with schizophrenia (SZ) and demographically matched individuals (CO). Based on previous research directly (Ardizzi et al., 2016; Koreki et al., 2021) and indirectly (Linnman et al., 2013; Palaniyappan et al., 2011; Wylie & Tregellas, 2010) documenting interoceptive deficits in schizophrenia, we anticipated that SZ and CO would differ on interoceptive ability. More specifically, consistent with the literature (Ardizzi et al., 2016; Koreki et al., 2021), we hypothesized that SZ would exhibit reduced interoceptive accuracy compared to CO, and that this deficit in interoceptive accuracy would be linked to the severity of positive symptoms. In line with the findings of Koreki et al. (2021), we also expected to find group differences in interoceptive sensibility. Given the lack of research exploring interoceptive awareness in schizophrenia to date, we did not have an a-priori hypothesis regarding this dimension of interoceptive functioning.

METHODS

Participants

Thirty individuals who met the DSM-5 criteria for schizophrenia or schizoaffective disorder (SZ) were recruited from an outpatient facility in Nashville, TN. Twenty-eight CO with no history of DSM-5 disorders were recruited from the same community by advertisements. Diagnoses were made using the Structured Clinical Interview for DSM-5- Research Version (First et al., 2015). Exclusion criteria for both groups were substance use or alcohol abuse within the past 6 months, brain injury, neurological disease, and IQ<70. In addition, potential CO reporting a family history of psychotic disorders were excluded from the study. Groups were matched on gender, age, and handedness. The Institutional Review Board of Vanderbilt University approved study protocols, and written informed consent was collected from each participant. Participants were compensated for their time at a rate of $20/hour. Demographic and clinical information for Study 1A participants is presented in Table 1.

Table 1. Demographic and clinical information for Study 1A participants.

	SZ (N = 30) Mean (SD)	CO (N = 28) Mean (SD)	Test statistic	*p*
M/F	16/14	14/14	$\chi^2 = 0$	$p=1$
Age	47.93 (10.21)	48.68 (8.2)	$t=0.31$	$p=0.76$
Handedness (R/L/Both)	24/5/1	26/2/0	$\chi^2 = 2.30$	$p=0.32$
Estimated IQ[a]*	101.96 (9.96)	108.61 (9.13)	$t=2.65$	$p=0.01$
BPRS	19.90 (9.74)	N/A	N/A	N/A
SAPS	24.37 (16.62)	N/A	N/A	N/A
SANS	38.47 (17.84)	N/A	N/A	N/A
CPZE dose (mg/day)[b]	533.68 (768.87)	N/A	N/A	N/A

* Significant difference between SZ and CO
[a] Estimated from the National Adult Reading Test, Revised (NART-R; Blair and Spreen, 1989).
[b] Antipsychotic dosage was converted to chlorpromazine equivalent (CPZE) (Andreasen et al., 2010).

Measures

Interoception Measures

Heartbeat Counting Task (HBCT; Schandry, 1981). The HBCT is the most widely used experimental task to measure interoceptive ability. It was shown to have good test–retest reliability (Tsakiris et al., 2011) and to highly correlate with other detection tasks (Knoll & Hodapp, 1992). The HBCT was used to measure interoceptive *accuracy* and *awareness*.

In this task, participants were instructed to sit with their hands on their lap, facing up to prevent facilitation of heartbeat detection. They were instructed to "count the number of times you think your heart beats from the time I say start to the time I say stop." They first completed a 22s practice trial and were given the opportunity to ask questions. Next, they completed four test trials of varying lengths (i.e., 33s, 25s, 41s, 17s). Meanwhile, a Bluetooth Polar H10 heartrate monitor (Polar Electro Öy, Kempele, Finland) was used to measure their actual number of heart beats. The sensor was attached to a strap that wrapped around the chest, below the pectoral line. To facilitate connection, the back of the strap was wet. Heart rate data was transmitted to a mobile device via Bluetooth using the Polar Beat App. After each trial, participants were asked "how many times did your heart beat?" and "how confident are you that your guess is correct, on a scale of zero to ten?".

Interceptive accuracy was computed using the following transformation:

$$\frac{1}{4} \Sigma \ (1-(|\text{recorded} - \text{counted}|) / \text{recorded})$$ (Schandry et al., 1981).

Higher scores represent less discrepancy between counted and recorded heartbeats, therefore indicating higher interoceptive accuracy.

Performance on the HBCT (i.e., interoceptive accuracy) can be influenced by a number of physiological and psychological factors (i.e., Knapp-Kline & Kline, 2005; Ring & Brener, 1996; Rouse et al., 1988). Thus, Body Mass Index (BMI), resting heart rate (i.e., average heart rate recorded during the HBCT), participant's knowledge of their resting heart rate (i.e., absolute difference between estimated and measured resting heart rate), and heart rate variability (HRV, measured as the root mean square of successive RR interval differences; Shaffer & Ginsberg, 2017), were assessed and included as covariates in the interoceptive accuracy analyses. In addition, one of the major criticisms of the HBCT is that participants may be estimating the number of seconds elapsed rather than counting their heartbeats. In line with other studies using this task (i.e., Ainley et al., 2014; Filippetti & Tsakiris, 2017), we therefore asked participant to estimate the lengths of four time intervals (i.e., 33s, 25s, 41s, 17s). Time perception accuracy was evaluated using a formula analogous to that used to estimate interoceptive accuracy (i.e., ¼ Σ (1-(|recorded –counted|) / recorded)) and also entered as a covariate in the subsequent analyses.

Interoceptive awareness was computed by calculating the Spearman correlation coefficient between interoceptive accuracy and self-reported confidence ratings across trials for each individual (Garfinkel et al., 2015). Interoceptive awareness scores therefore varied between -1 and 1, with higher score indicating greater correspondence between interoceptive accuracy and confidence ratings, therefore indicating higher interoceptive awareness.

Multidimensional Assessment of Interoceptive Awareness (MAIA; Mehling et al., 2012). The MAIA was used to assess *interoceptive sensibility*. The MAIA contains 32 statements rated by the participant on a six-point Likert scale where 0=never and 5=always. The MAIA assesses various aspects of interoceptive sensibility and yields eight subscales: 1) *Noticing* refers to one's awareness of their bodily sensations (e.g., "When I am tense I notice where the tension is located in my body"), 2) *Not-Distracting* measures one's tendency not to ignore sensations of discomfort or pain (e.g. “I do not notice (ignore) physical tension or discomfort until they become more severe”), 3) *Not-Worrying* assesses an individual’s tendency not to experience emotional distress in response to uncomfortable or painful bodily sensations (e.g. “When I feel physical pain, I become upset”), 4) *Attention Regulation* refers to one’s ability to sustain and control attention to bodily sensations (e.g. “I can pay attention to my breath without being distracted by things happening around me”), 5) *Emotional Awareness* refers to the awareness of the connection between one’s bodily sensations and their emotional states (e.g. “I notice how my body changes when I am angry”), 6) *Self-Regulation* measures one’s ability to regulate distress by paying attention to their body sensations (e.g. “When I feel overwhelmed I can find a calm place inside.”); 7) *Body Listening* assesses one’s tendency to use bodily sensations for insight and decision-making (e.g. “I listen for information from my body about my emotional state”), 8) *Trusting* measures one’s tendency to experience one’s own body as safe and trustworthy (e.g. “I am at home in my body.”). Ratings for items within a subscale are averaged, yielding a 0-5 score for each subscale, for each participant. Importantly, higher score indicates higher interoceptive sensibility across subscales. The MAIA has demonstrated good psychometric properties (Mehling et al., 2012) and is one of the most widely used instruments measuring interoceptive sensibility.

Clinical and Psychological Measures

Brief Psychiatric Rating Scale (BPRS, Version 4.0; Ventura et al., 1993). The BPRS is a clinical rating scale assessing a broad range of psychiatric (i.e., emotional, behavioral, psychotic) symptoms. Originally developed by Overall and Gorham in 1962, subsequent versions progressively extended the BPRS, and its administration manual and scoring guidelines became increasing more detailed to increase sensitivity to affective and psychotic disorders as well as reliability. In this study, we used the fourth version of the BPRS, which assesses 24 symptoms, each rated on a 1 (not present) to 7 (extremely severe) scale. The BPRS was administered to SZ by an advanced clinical graduate student or a trained research assistant.

Scale for the Assessment of Positive Symptoms (SAPS, Andreasen, 1984). The SAPS is a clinical rating scale designed to quantify levels of positive symptom severity in SZ. The scale is divided into four domains: Hallucinations, Delusions, Bizarre Behavior, and Positive Formal Thought Disorder, each containing five to twelve symptoms rated on a 0 (none) to 5 (severe) scale. The SAPS was administered to SZ by an advanced clinical graduate student or a trained research assistant.

Scale for the Assessment of Negative Symptoms (SANS, Andreasen, 1983). The SANS is a clinical rating scale designed to quantify levels of negative symptoms in SZ. The scale is divided into four domains: Affective Flattening, Alogia, Avolition/Apathy, Anhedonia/Asociality, and Attention, each containing two to six symptoms, rated on a 0 (none) to 5 (severe) scale. The SANS was administered to SZ by an advanced clinical graduate student or a trained research assistant.

20-Item Toronto Alexithymia Scale (TAS-20; Bagby et al., 1994). The TAS-20 is the most widely used instrument to measure alexithymia in research. Participants rate their level of agreement with 20 statements on a 5-point Likert scale. The TAS-20 has a three-factor structure: Difficulty Identifying Feelings (DIF; e.g., “I am often confused about what emotion I am feeling”), Difficulty Describing Feelings (DDF; e.g., “It is difficult for me to find the right words for my feelings”), and Externally-Oriented Thinking (EOT; e.g., “I prefer talking to people about their daily activities rather than their feelings”).

Positive and Negative Affect Schedule (PANAS, Watson et al., 1988). The PANAS is a 20-item self-report measure of current affect. The PANAS surveys ten positive (e.g., interested, excited) and ten negative (e.g., distressed, upset) emotions. Participants are instructed to rate the extent to which the feel each emotion on a 1 (i.e., "very slightly or not at all") to 5 (i.e., "extremely") Likert scale. A "positive affect" and a "negative affect" score is derived, each ranging from 10 to 50. Psychometric properties including reliability and validity were found to be satisfactory for the PANAS (Watson 1988).

Perceived Stress Scale (PSS, Cohen et al., 1983). The PSS is a 10-item self-report instrument that assesses the degree to which various situations affects one's feelings and level of stress. Participants are asked to rate each of the statements on a 5-point scale ranging from 0 (Never) to 4 (Very Often). Importantly, the PSS assesses appraisal of stressful life events rather than their mere occurrence.

UCLA Loneliness Scale (Version 3) (Russell, 1996). The UCLA loneliness scale is a 20-item self-report instrument assessing loneliness and perceived social isolation. Participants indicate the frequency with which they encounter several experiences on a scale 1 (Never) to 4 (Often) scale. The UCLA loneliness scale was found to have high internal consistency and test-retest reliability over a 1-year period (Russell, 1996).

Procedure

The order in which participants completed the HBCT, the MAIA, self-reported measures (i.e., demographic questionnaire, TAS-20, PANAS, PSS, UCLA loneliness scale), psychological assessments (i.e., NART) and clinical interviews (i.e., SAPS, SANS, BPRS; for SZ only) was randomized.

Data Analysis

The normality of each self-reported measure was first tested using the Shapiro-Wilk test, and group differences were assessed using *t*-tests or Wilcoxon Signed-Ranks tests accordingly.

Because diagnostic plots revealed the presence of outliers, a robust regression model with M estimator was used to assess the group difference in interoceptive accuracy. The model included group (SZ=1, CO=0), HBCT control variables (i.e., HR knowledge, resting HR, HRV, BMI, and time perception accuracy) and self-report variables (i.e., perceived stress, loneliness, alexithymia, affect) as predictors. Significance was assessed using a Wald test.

A Shapiro test revealed that the distribution of interoceptive awareness scores significantly deviated from normality (W=0.93, p=0.008). Thus, a Wilcoxon Signed-Ranks test was used to assess group difference in interoceptive awareness.

A MANOVA was used to examine group differences in interoceptive sensibility. Assumptions of linearity, multilinear normality, homogeneity of variance and covariance, multivariate outliers, and multicollinearity were checked and found not to be violated. Post-hoc univariate analyses were conducted to assess group differences in each of the eight dimensions of interoceptive sensibility (i.e., Noticing, Not Distracting, Not Worrying, Attention Regulation, Emotional Awareness, Self-Regulation, Body Listening, Trusting). Effect sizes were estimated using Partial Eta-Squared.

Finally, the relationship between interoceptive ability (i.e., interoceptive accuracy, awareness, sensitivity) and demographic (i.e., gender, age) and clinical variables (i.e., symptoms severity, medication dosage) was assessed using correlation analyses, Wilcoxon Signed-Ranks tests, *t*-tests, and MANCOVA.

RESULTS

Self-report measures

Significant group differences were found across most self-report psychological measures. In fact, SZ reported feeling more stressed (M_{sz}=18.83, *SDsz*=7.83, M_{co}=12.68, *SDco*=7.15, *t*=-3.13, *p*=0.003, *d*= -0.82) and more lonely (Median_{sz}= 42.5, Median_{co}= 31.5, *Z*=-2.34, *p*=0.02, *r*=-0.31) than CO. SZ also reported higher levels of alexithymia on all three TAS-20 subscales. Indeed, SZ reported higher Difficulty Describing Feelings (Median_{sz}= 12.5, Median_{co}= 9.0 *Z*=-3.49, *p*=0.0005, *r*=-0.46), Difficulty Identifying Feelings (Median_{sz}= 15.5, Median_{co}= 8.0, *Z*=-3.32, *p*=0.0009, *r*=-0.44), and Externally Oriented Thinking (M_{sz}=20.57, *SDsz*=74.75, M_{co}=17.68, *SDco*=4.02, *t*=-2.50, *p*=0.02, *d*= -0.65). Finally, SZ reported significantly lower levels of PANAS-positive affect (M_{sz}=33.63, *SDsz*=8.91, M_{co}=39.18, *SDco*=6.37, *t*=2.74, *p*=0.008, *d*= 0.71), though no group difference was found on self-reported levels of PANAS-negative affect *(Z*=-1.62, *p*=0.10).

Interoceptive Accuracy

A robust regression model revealed a significant deficit in interoceptive accuracy in SZ (*M*= 0.48, *SD*=0.25) compared to CO (*M*=0.73, *SD*= 0.19), after controlling for resting HR, HR knowledge, HRV, BMI, and time perception accuracy, *t*=-2.22, *p*=0.03. See **Fig. 4**.

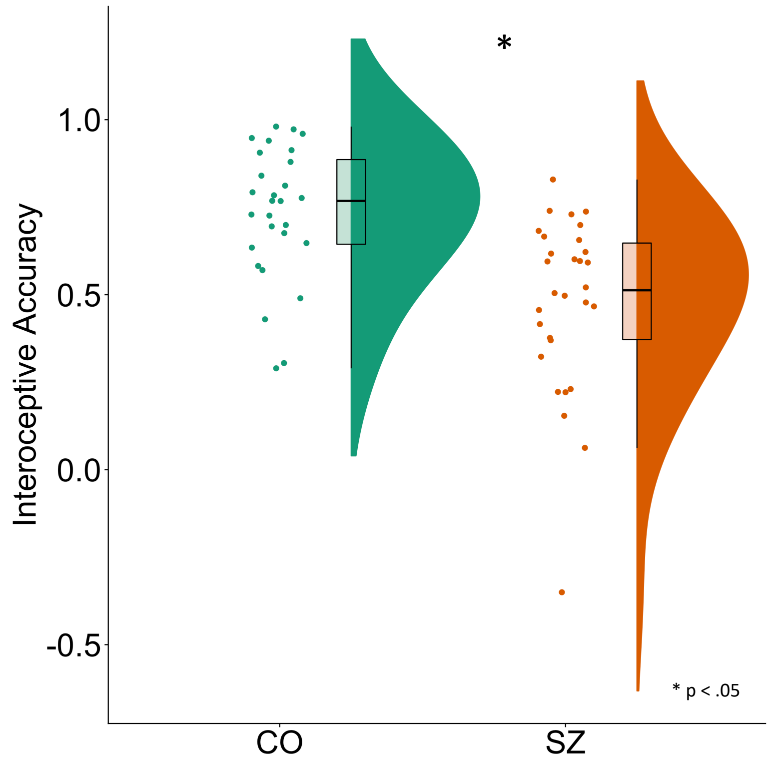

Fig. 4. Raincloud plots of interoceptive accuracy in SZ and CO

Time perception accuracy was found to significantly predict interoceptive accuracy, t=2.39, p=0.02. Notably, a trending group difference in time perception accuracy was found (Z=-1.9, p=0.054), suggesting that SZ (M=-0.67, SD= 7.44) might have difficulty with time perception compared to CO (M=0.58, SD= 1.18). Importantly, time perception was heterogenous in the SZ group, as evidenced by the large standard deviation of time perception accuracy scores in that group. In fact, though some SZ performed at a level comparable to that of CO, some performed particularly poorly. For instance, when asked to estimate a 17 second time interval, one of the SZ participants reported counting 1013 seconds. The results remained unchanged after removing this outlier from the analyses.

None of the other control (i.e., resting HR, HR knowledge, HRV, and BMI) or self-reported (i.e., stress, loneliness, alexithymia and current affect) variables were found to predict interoceptive accuracy (all *p*'s > 0.05). A significant group difference was found in HR knowledge, such that the difference between estimated and measured HR was greater in SZ (*M*=39.02, *SD*= 24.40) than CO (*M*=16.04, *SD*= 12.72), *Z*=-3.76, *p*=0.0002, suggesting a deficit in HR knowledge in SZ. SZ (*M*=33.47, *SD*= 7.92) were also found to have significantly higher BMI than CO (*M*=28.69, *SD*= 5.96), *Z*=-2.26, *p*=0.02. No group difference was found in resting HR or HRV.

Interoceptive Awareness

Interoceptive awareness was not found to significantly differ between SZ (*M*= 0.16, *SD*= 0.51) and CO (*M*= 0.21, *SD*= 0.51), *Z*= -0.49, *p*=0.62 (see **Fig. 5**).

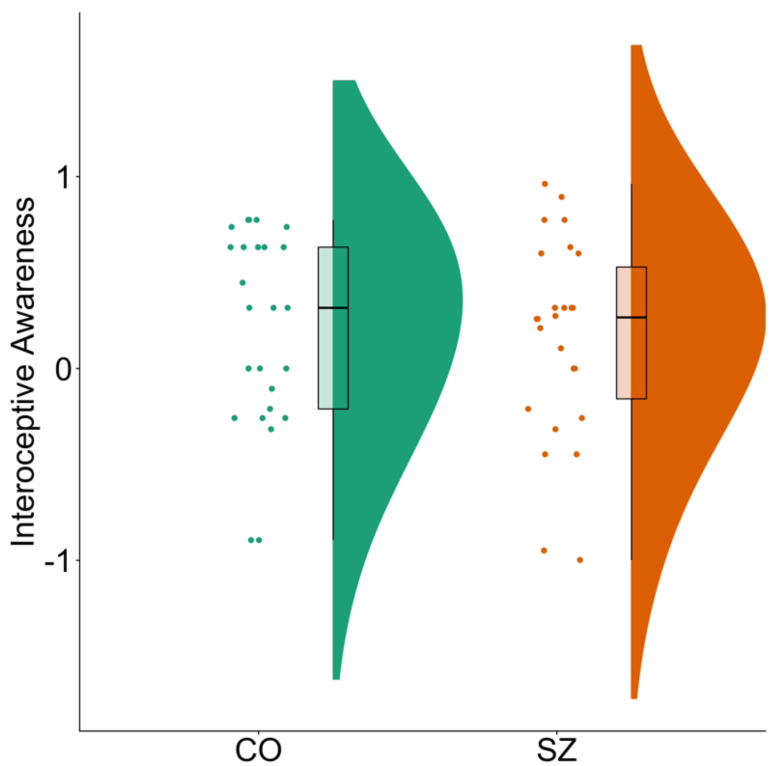

Fig. 5. Raincloud plots of interoceptive awareness in SZ and CO

Interoceptive Sensibility

A MANCOVA revealed a significant group difference in interoceptive sensibility, $F(8,49)=2.21$, $p=0.04$. Post-hoc univariate analyses showed that Attention Regulation, $F(1,56)=6.44$, p=0.01, $\eta^2= 0.10$, Not Worrying, $F(1,56)=3.97$, p=0.05, $\eta^2= 0.07$, and Trusting, $F(1,56)=6.56$, p=0.01, $\eta^2= 0.10$, were significantly lower in SZ than CO. Conversely, SZ scored significantly higher on Not Distracting than CO, $F(1,56)=4.75$, p=0.03, $\eta^2= 0.08$. SZ and CO did not significantly differ in Body Listening, Emotional Awareness, Noticing, and Self-Regulation (all p's > 0.05). See **Fig. 6.**

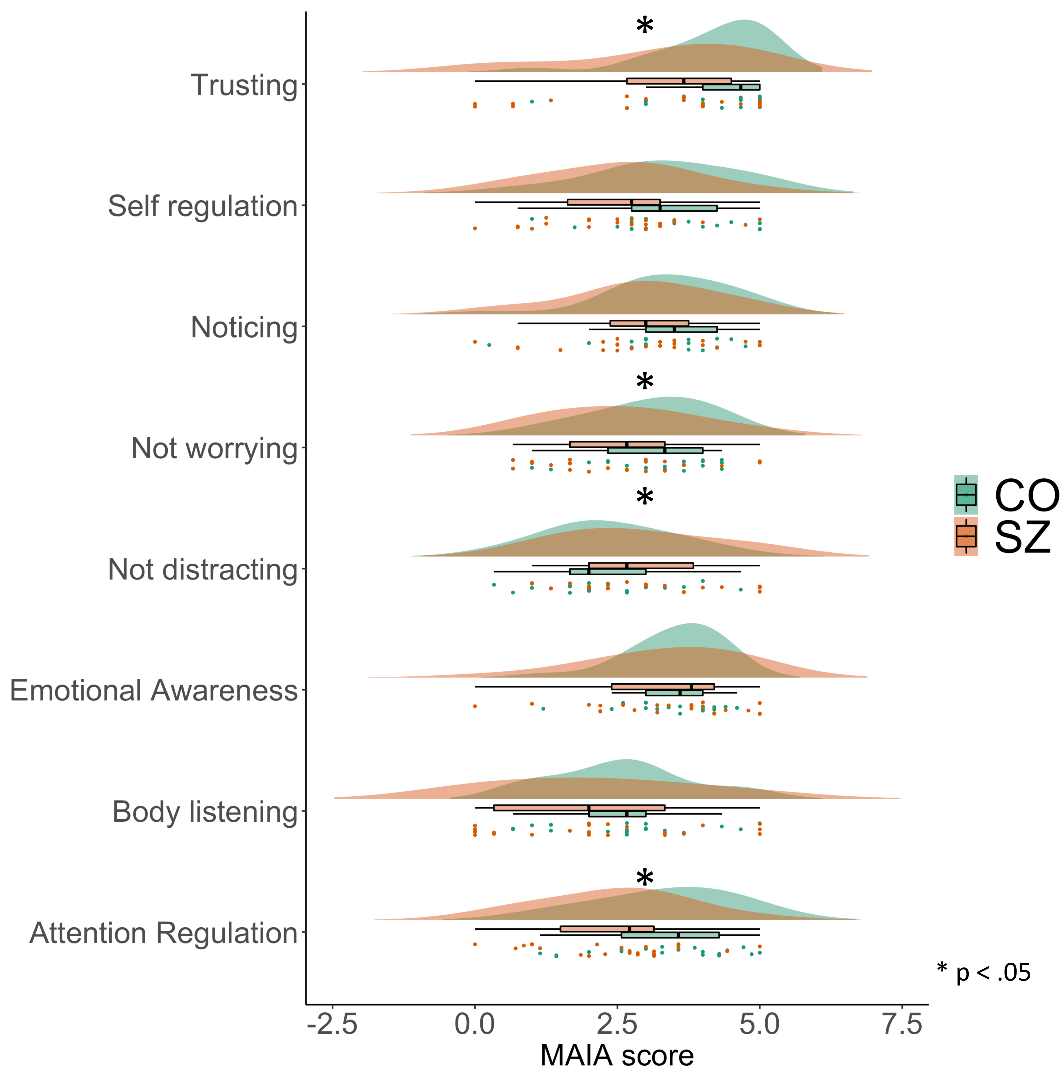

Fig. 6. Raincloud plots of interoceptive sensibility in SZ and CO

Interoceptive ability and demographic and clinical variable

Regression analyses revealed no link between symptom severity (i.e., overall psychiatric symptoms, positive symptoms, negative symptoms) and interoceptive ability (i.e., accuracy, awareness, sensibility) in SZ (all *p*'s > 0.05). Medication dosage was not correlated with interoceptive accuracy ($r(28)=-0.21$, $p=0.29$), though it was negatively correlated with interoceptive awareness ($r(28)=-0.44$, $p=0.04$). Following the method used by Koreki et al. (2021), we replicated these within-group analyses using a HR-adjusted measure of interoceptive accuracy (HR-adjusted Interoceptive Accuracy = 1 − |counted heartbeats – recorded heartbeats| / (counted heartbeats + recorded heartbeats) / 2); the results remained unchanged. A regression analysis revealed that the Emotional Awareness factor of the MAIA predicted antipsychotic medication dosage ($\beta=0.99$, $p=0.01$). No relationship was found between medication dosage and other aspects of interoceptive sensibility (all *p*'s > 0.05).

Spearman correlation analyses revealed that age was not significantly correlated with interoceptive accuracy ($r(56)=-0.01$, $p=0.94$), interoceptive awareness ($r(56)=-0.02$, $p=0.87$), or interoceptive sensibility (all *p*'s>0.10). Similarly, interoceptive accuracy ($Z=-0.22$, $p=0.82$), interoceptive awareness ($Z=-1.27$, $p=0.21$), and interoceptive sensibility ($F(8,49)=0.72$, $p=0.67$) did not significant differ between genders.

DISCUSSION

Our results indicate that SZ's performance on the HBCT was impaired compared to CO, suggesting poor interoceptive accuracy in this population. This finding is consistent with previous studies using the HBCT in individuals with schizophrenia. Across these studies, SZ's average interoceptive accuracy was estimated at 0.32 ± 0.34 (Koreki et al., 2021), 0.37 ± 0.63 (Ardizzi et al., 2016) and 0.48 ± 0.25 (present study). Though largely consistent, we note that SZ in our sample performed marginally better on the HBCT than the SZ in the previous two studies. This difference might be due to the fact that our sample exclusively included individuals with chronic schizophrenia treated on an outpatient basis, while Koreki et al.'s study (2021) included inpatient individuals. Interestingly, though interoceptive accuracy has been shown to decline with age (Khalsa et al., 2009) the older SZ in our study (age= 47.93 ± 10.21) were found to have higher interoceptive accuracy than the younger SZ in Ardizzi et al.'s study (age= 33.78 ± 6.33). Altogether, these findings suggest that interoceptive accuracy deficits are present throughout the course of schizophrenia illness, though they might be more severe in the early/acute stages.

Against our predictions, we did not find a link between interoceptive accuracy and the severity of any clusters of schizophrenia symptomatology. Though the two previous studies documented a link between interoceptive accuracy and overall positive symptoms (Ardizzi et al., 2016; Koreki et al., 2021), the results were inconsistent at the subscale level. In fact, Ardizzi et al. (2016) reported a link between interoceptive accuracy and grandiosity, while Koreki et al. (2021) noted that the severity of conceptual disorganization and hallucinations (but not grandiosity) predicted interoceptive deficits. Koreki et al. (2021) also found a link between negative symptoms (i.e., blunted affect, emotional and social withdrawal) and interoceptive accuracy in schizophrenia, Ardizzi et al. (2016) did not. We note that our study used the SAPS, SANS, and BPRS to measure the severity of symptoms while the previous two studies used the PANSS. Thus, it is possible the lack of link between interoceptive accuracy and symptoms severity in our study is due to a different in the instrument used. In sum, the evidence for a relationship between interoceptive accuracy deficits and schizophrenia symptomatology remains mixed and inconclusive at present.

Though the decreased interoceptive accuracy in SZ is not attributable to differences in felt emotions, the mechanism underlying this deficit remains to be elucidated. SZ reported feeling more stressed and more lonely, and experiencing higher levels of alexithymia and lower levels of positive affect compared to CO. However, these variables did not predict interoceptive accuracy. In other psychopathologies, interoceptive differences have been linked to perceptual or attentional abilities. For instance, Schauder et al. (2015) found that children with ASD have an increased ability to sustain attention to their heartbeat over longer time intervals. The mechanism (i.e., perceptual or attentional) underlying poor interoceptive accuracy in SZ remains to be elucidated.

We did not find a group difference in interoceptive awareness. Interoceptive awareness refers to the metacognitive awareness of one's performance on the HBCT. Thus, SZ's intact interoceptive awareness suggests insight into their low interoceptive accuracy. Importantly, medication dosage was negatively correlated with interoceptive awareness, indicating that antipsychotic medication might dampen insight into interoceptive deficits. To our knowledge, our study is the first to empirically explore interoceptive awareness in schizophrenia. Thus, our findings provide preliminary evidence of intact interceptive awareness in this population. We note that this finding is at odds with the metacognitive deficits broadly documented in schizophrenia (Lysaker & Dimaggio, 2014). Importantly, metacognitive deficits have been linked to impaired insight and poor psychosocial outcome (Lysaker et al., 2015; Lysaker et al., 2019). Thus, SZ's insight into their interoceptive deficits has important clinical implications as it might motivate treatment seeking, which could improve outcome.

In line with our expectations, our findings revealed a significant group difference in interoceptive sensibility. More specifically, we found that SZ reported difficulty sustaining attention to and trusting their bodily sensations, as well as an increased tendency to worry when experiencing pain or physical discomfort. Notably, SZ also reported an increased tendency not to distract themselves from bodily sensations of pain or discomfort. In other words, SZ are less likely than CO to ignore unpleasant bodily sensations, which suggests enhanced interoceptive functioning. No group differences were found in one's ability to notice or listen to one's bodily sensations, one's awareness of the connection between body sensations and emotional states or one's ability to regulate distress by attention to body sensations.

When considering our results in the context of prior empirical and phenomenological findings, gaps remain in our understanding of interoceptive sensibility in schizophrenia. First, we note important discrepancies between our findings and those of the only other study to date that empirically explored interoceptive sensibility in this population. Using the same instrument (i.e., MAIA), Koreki et al. (2021) found that SZ scored lower on Not Distracting (our results indicated the opposite effect), and higher on Noticing (we did not find a group difference on this subscale). It is possible that our sample size was too small to adequately capture group differences on subscales of the MAIA, which would explain the inconsistency between our results and previous ones. Additionally, phenomenological models of schizophrenia place hyperreflexivity (i.e., exaggerated self-awareness) at the center of the schizophrenia experience (Sass & Parnas, 2003). Hyperreflexivity refers to the increased monitoring of internal processes (e.g., thoughts, perceptions, movements) that normally occur unconsciously (Postmes et al., 2014). As a result, individuals with schizophrenia pay exaggerated attention to irrelevant, background internal stimuli (Sass & Parnas, 2003, 2007; Sass et al., 2013). Thus, one would expect SZ to report exaggerated interoceptive sensibility. In sum, differences in interoceptive sensibility exist in schizophrenia, though more research is needed to understand the specific aspects of interoceptive sensibility that might be disrupted—or enhanced—in this population.

Though we previously discussed interoception as a bottom-up process, recent models instead propose a predictive mechanism in which interoceptive experiences result from predictions regarding the expected state of the body given the internal signals (e.g., my stomach is growling, therefore I must be hungry; Barrett & Simmons, 2015). Beyond the objective (i.e., accuracy), metacognitive (i.e., awareness), and subjective (i.e., sensibility) experience of interoception, this view highlights the importance of the concordance between expected and observed bodily states. In empirical studies, this discrepancy has been operationalized as the difference between interoceptive sensibility and interoceptive accuracy, and called "Interoceptive Trait Prediction Error," (IPTE; Garfinkel et al., 2016; Young et al., 2017). IPTE is linked to anxiety (Paulus & Stein, 2006, 2010), severity of autistic traits (Garfinkel et al., 2016), abnormal skin sensations (Eccles et al., 2015), and emotional eating (Young et al., 2017). Paulus et al. (2019) in fact proposed an active inference model of interoceptive dysfunction in which interoceptive deficits stem from overtly precise priors (i.e., strong expectations) and context rigidity (i.e., little adjustment of expectations in the face of environmental changes). This model was used to explain interoceptive dysfunction in panic disorder, depression, somatic symptoms, anorexia nervosa, and anxiety, but no mention was made of schizophrenia, likely due to the scarcity of interoception research in the schizophrenia literature. To our knowledge, the role of prediction in interoception has never been examined in schizophrenia. In a post-hoc, exploratory analysis, we used the data collected in the present study to calculate IPTE in SZ and CO. We found no group difference in IPTE, $t(56)=-1.55$, $p=0.13$. More evidence is needed to understand the role of active inference in interoceptive dysfunction in this population.

Study 1B. Interoception and Schizotypy

In this study, we expand on Study 1A by investigating interoceptive functioning along the schizotypy spectrum to gain further insight on the etiology and nature of interoceptive dysfunction along the schizophrenia spectrum. By studying healthy individuals with a varying degree of psychometric liability for schizophrenia (i.e., schizotypy), we also eliminate some potential confounding variables related to schizophrenia illness or treatment (e.g., medication effects). To our knowledge, no study to date has investigated interoception in relation to schizotypy. However, the literature documents higher rates of alexithymia (Aaron et al., 2015), agency deficits (Asai & Tanno, 2007, 2008; Moore et al., 2020) and body ownership disturbances (Asai et al., 2011; Germine et al., 2013) in individuals with elevated schizotypal traits. Given the reliance of these aspects of embodied experience on one's perception of internal signals, it is possible that increased alexithymia and bodily disturbances in individuals with high schizotypy stem from interoceptive deficits in this population. Thus, we hypothesized that schizotypy would inversely predict interoceptive ability. Given the lack of previous research in this area, we did not formulate hypotheses regarding the links between specific dimensions of interoception or factors of schizotypy.

METHODS

Participants

109 college students were recruited from the Vanderbilt Psychology Research Subject Pool. Participants reporting substance use or alcohol abuse within the past 6 months, brain

injury, or neurological disease were not included in the study. All participants were English speakers and had normal or corrected-to-normal vision. Participants gave written informed consent, as approved by the Vanderbilt Institutional Review Board, and were granted course credit in compensation for their participation. Study 1B participants' demographic information is summarized in Table 2.

Table 2. Demographic and subclinical information for Study 1B participants.

	Participants (N=109) Mean (SD)
M/F	24/85
Age	19.43 (1.25)
Handedness (R/L)	98/10
Estimated IQ[a]	112.36 (5.10)
SPQ Interpersonal	2.58 (2.22)
SPQ Disorganized	1.86 (1.64)
SPQ Cognitive	2.26 (1.84)

[a] Estimated from the National Adult Reading Test, Revised (NART-R; Blair and Spreen, 1989).

Measures

Schizotypal Personality Questionnaire-Brief (SPQ-B; Raine & Benishay, 1995). The SPQ-B was used to assess schizotypy. The SPQ-B is a short self-report questionnaire containing 22 true/false items and yields three subscales: Cognitive/Perceptual, Interpersonal and Disorganization. Its psychometric properties were tested, and internal validity, test-retest reliability and criterion validity were all found to be satisfactory (Raine & Benishay, 1995).

The same measures as Study 1A were used to measure interoceptive functioning (i.e., HBCT, MAIA).

Procedure

The procedure for Study 1B was analogous to that of Study 1A: participants completed the HBCT, the MAIA, self-report measures (i.e., demographic questionnaire, SPQ-B) and cognitive assessment (i.e., NART) in a randomized order. We note that only a subset of participants (N=44) completed the MAIA.

Data Analysis

A hierarchical regression analysis was conducted to investigate the role of schizotypy in interoceptive accuracy. In the first model, only control variables (i.e., HR knowledge, resting HR, HRV, BMI, and time perception) were included as predictors. SPQ-B subscales (i.e., Interpersonal, Cognitive/Perceptual, Disorganized) were added to the second model, and the two models were compared using an ANOVA. Model assumptions (i.e., linearity, homogeneity of variance, normality and independence of residuals, influential values) were assessed and found satisfactory for both models.

A multiple linear regression model was originally used to assess the relationship between schizotypy dimensions and interoceptive awareness, but a Shapiro-Wilk test revealed that the assumption of normality of residuals was violated (W=0.97, p<0.0001). Therefore, Spearman correlations were instead used to assess the relationship between interoceptive awareness and schizotypy, and a Holm correction was applied.

In order to assess the relationship between interoceptive sensibility and schizotypy, a multivariate multiple regression was run. SPQ-B subscales (i.e., Interpersonal, Disorganized, Cognitive/Perceptual) were included as predictors and the eight MAIA dimensions (i.e., Noticing, Not Distracting, Not Worrying, Attention Regulation, Emotional Awareness, Self-Regulation, Body Listening, Trusting) as dependent variables. Assumptions were checked and found to be satisfactory.

Finally, gender differences in interoceptive ability were assessed using Mann-Whitney *U* tests (interoceptive accuracy and awareness) and MANOVA (interoceptive sensibility). The link between age and interoceptive ability was not evaluated given the limited range of ages (18-23) in this sample.

RESULTS

No link was found between schizotypy and interoceptive ability. In fact, a hierarchical regression analysis revealed that schizotypy did not significantly contribute to the regression model predicting interoceptive accuracy ($\Delta F = 0.18$, $p = 0.91$, See **Table 3**). No link was found between interoceptive awareness and Cognitive/Perceptual ($r(107)=-0.09$, $p=0.38$), Interpersonal ($r(107)=-0.20$, $p=0.12$), or Disorganized ($r(107)=-0.10$, $p=0.31$) schizotypy. Similarly, a multivariate multiple regression analysis revealed no link between schizotypy and interoceptive sensibility (*ps* > 0.5).

Table 3. Hierarchical regression models predicting interoceptive accuracy

Predictor variables	Model 1	Model 2
Resting heart rate	-0.27**	-0.28**
HR knowledge	0.021	0.02
HRV	0.09	0.10
BMI	0.06	0.07
Time perception accuracy	0.37***	0.38***
SPQ-B Interpersonal		0.08
SPQ-B Disorganized		-0.03
SPQ-B Cognitive/Perceptual		0.01
R^2	0.19	0.17
ΔR^2		-0.02
ΔF		0.18

**$p < .01$, ***$p < .001$

To explore possible non-linear relationships between schizotypy and interoceptive functioning scatterplots with Loess soothing lines were generated; no clear patterns were observed. Though scatterplots were generated for MAIA subscales, we only show plots averaging across interoceptive sensibility here (see **Fig. 7**).

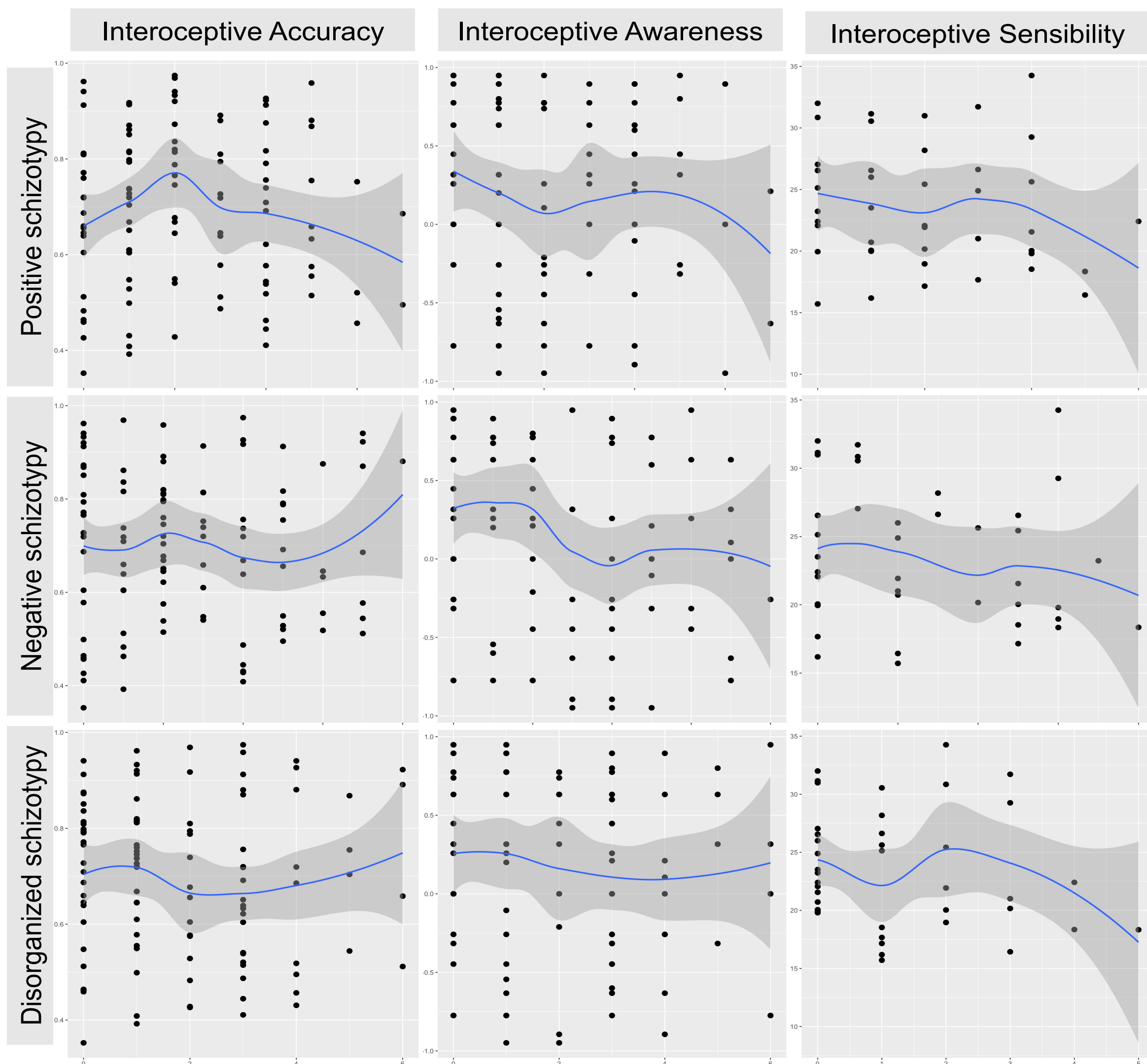

Fig. 7. Scatterplots of schizotypy factors and interoceptive ability. No non-linear relationships were observed between the variables. The interoceptive sensibility score is an average of a participants' scores on all eight subscales on the MAIA.

Interoceptive accuracy (Z=-1.67, *p*=0.09), interoceptive awareness (Z=-0.23, *p*=0.81), and interoceptive sensibility ($F(8,35)=1.82$, *p*=0.11) did not significantly differ across genders.

DISCUSSION

For the first time, Study 1B investigated interoceptive functioning in relation to schizotypy. Contrary to our predictions, our results revealed no link between schizotypy and interoceptive ability. In fact, interoceptive accuracy, awareness, and sensibility do not systematically vary across any of the schizotypy dimensions. It is possible that these null results explain the lack of available literature investigating interoception and schizotypy. We note that the nature of our sample (i.e., healthy undergraduates) might have under-represented the higher end of the schizotypy spectrum, which limits the interpretation of our results. In fact, our findings indicate that in the general population interceptive functioning is independent from schizotypy, though this might not be true in help-seeking individuals.

STUDY 1 GENERAL DISCUSSION

Our work provides new insight into various aspects of interoceptive functioning in schizophrenia. Study 1A adds to a recent body of literature documenting low interoceptive accuracy in this population (Ardizzi et al., 2016; Koreki et al., 2021), and suggests that interoceptive dysfunction might be more pronounced in the early/acute stages of schizophrenia illness. Consistent with prior literature (Koreki et al., 2021), our results also highlighted differences in the subjective experience of interception (i.e., interoceptive sensibility) in schizophrenia, though the specific aspects of interoceptive sensibility affected remain to be clarified. More research is also needed to reconcile empirical findings with phenomenological models of schizophrenia, which suggest heightened interoceptive sensibility (i.e., hyperreflexivity) in this population. Lastly, for the first time, our study documented intact interoceptive awareness in SZ, which bears important clinical implications as insight into one's interoceptive limitations might promote treatment engagement.

In fact, various psychological, physiological, and behavioral interventions aimed at strengthening the mind-body connection exist and might be beneficial to individuals with schizophrenia. For instance, Mindful Awareness in Body-Oriented Therapy (MABT) was shown to improve interoceptive processing (Price & Hoover, 2018). Another study found that an 8-week body-scan practice significantly improved interoceptive functioning (Fischer et al., 2017). In biofeedback, electrical sensors are used to increase awareness and control over one's bodily functions (e.g., heart rate; Meyerholz et al., 2019). Bioelectronic medicine, which uses electrical stimulation to modulate the activity of targeted brain regions, has also been proposed as a candidate for interoceptive enhancements (Bonaz et al., 2021). Other experimental behavioral interventions, including the practice of power posing (Weineck et al., 2019) and physical exercise (Wallman-Jones et al., in press) have been shown to improve interoceptive functioning. Increasing the attention to the self by using a photo, words, or a mirror also seems to improve interoception (Ainley et al., 2012; 2013). In a recent review paper discussing interventions and manipulations of interoception, Weng et al. (2021) argue that the practice of slow breathing, either directly or indirectly via neuromodulation of the vagal nerve or meditation practice, might be particularly effective in training interoceptive ability. The authors further suggest that clinicians should integrate biological and psychological methods to benefit from possible additive effects (Weng et al., 2021).

Study 1B casts new light on interoceptive functioning in the schizophrenia spectrum. Contrary to our expectations, we found no link between schizotypy and interoceptive functioning. Though our results indicate that schizotypy and interoceptive functioning are independent in the general population, this might not be true in help-seeking/prodromal populations. In fact, a recent paper documented abnormal interoceptive sensibility in youth with psychotic-like experiences (Barbato et al., in press). More specifically, this study found that individuals at high risk for psychosis scored lower on Not Distracting, Not Worrying, Attention Regulation and Trusting, though they scored higher on Emotional Awareness and Body Listening. We note that these results are largely consistent with the findings of Study 1A which documented differences in Not Distracting, Not Worrying, Attention Regulation and Trusting in SZ. Thus, it is possible that interoceptive dysfunction emerges closer to the psychosis onset, during the prodromal stage. Only a minority of individuals with high schizotypy will develop a psychotic illness (e.g., Debbané et al., 2015) and as previously mentioned, these prodromal individuals would be under-represented in our non help-seeking sample. We posit that interoceptive deficits are unrelated to schizotypy in the general population but that they may emerge during the prodromal stage preceding the onset of psychosis. However, this hypothesis needs to be tested in longitudinal studies.

The main limitation of this study is our reliance on the HBCT to measure interoceptive accuracy and awareness. The HBCT has been criticized for its methodological shortcomings (e.g., Reed et al., 1990; Zamariola et al., 2018). As an alternative, the Heartbeat Discrimination Task requires participants to gauge the synchrony of their heartbeat with an external auditory stimulus (Brener & Kluviste, 1988). However, as Ardizzi et al. (2016) point out, the documented multisensory integration deficits in schizophrenia make this task a poor candidate for measuring interoceptive ability in this population. As noted by Kleckner and colleagues (2015), the HBCT is feasible and accessible, and remains the gold standard behavioral task of measuring interoception. The current study attempted to address some of these methodological limitations by measuring various physiological and psychological variables and including them as covariates in the analyses.

Overall, our findings suggest that individuals with schizophrenia perceive their internal signals with low accuracy and are aware of this deficit. Some subjective aspects of interoceptive experiences also appear to be dampened or heightened in schizophrenia. These differences in interoceptive dysfunction are note observed in individuals with elevated schizotypy, which might suggest that interoceptive dysfunctions are specific to schizophrenia illness such that they emerge during the prodromal stage.

CHAPTER III

Study 2. Effects of Schizotypy on Bodily Maps of Emotions

In a previous study, we found evidence for anomalous emotional embodiment in individuals with schizophrenia (Torregrossa et al., 2019b). More specifically, we found that individuals with schizophrenia reported less differentiated and less congruent (e.g., deactivation for high arousal emotions) bodily sensations of emotions. Additionally, the results of a similarity analysis indicated a specific alteration of embodiment of low arousal emotions in this population. Lastly, findings suggested that the nature of bodily sensations of emotions (i.e., activation or deactivation) was less clearly defined in schizophrenia, though there was no group difference in the intensity of reported embodied emotions (Torregrossa et al., 2019b).

In the present study, we follow the same procedure with a modified data analysis scheme (to account for the dimensional nature of our dataset) to explore emotional embodiment across the schizotypy spectrum. This study aims to answer the following questions: 1) Does schizotypy predict characteristics (i.e., diffusion, size, clarity, intensity) of embodied emotions? 2) Do individuals with higher schizotypy report less congruent bodily sensations of emotions? 3) Is the link between schizotypy and emotional embodiment specific to low arousal emotions?

We hypothesized that the bodily maps of emotions generated by our sample would be consistent with those of previous studies assessing embodied emotions in the general population (e.g., Numenmaa et al., 2014; Volynets et al., 2019). Based on the results of Torregrossa et al. (2019b), we hypothesized that the diffusion, size, and clarity (i.e., activation vs deactivation) of embodied emotions would be proportional to schizotypy, especially for low arousal emotions. We did not predict to find a link between schizotypy and the intensity (i.e., strength) of emotional embodiment. Our second hypothesis is that schizotypy will predict incongruent bodily sensation of emotions (e.g., bodily activation for low arousal emotions). The lack of previous research in this area prevented us from making hypotheses about specific dimensions of schizotypy (i.e., positive, negative, disorganized), though our analyses considered them separately.

METHODS

Participants

419 participants were recruited through the Vanderbilt University Psychology Subject Pool. Participants reporting substance use or alcohol abuse within the past 6 months, brain injury, or neurological disease were not included in the study. All participants were English speakers and had normal or corrected-to-normal vision. Participants gave written informed consent, as approved by the Vanderbilt Institutional Review Board, and were granted course credit in compensation for their participation. Demographic information is presented in **Table 4**.

Table 4. Demographic information for Study 2 participants.

	Participants (N=419)
Gender (M/F/other)	103/312/1
Age	19.50 (1.22)
Handedness (R/L)	377/40
Race/Ethnicity	
Black	35

Asian	91
Hispanic	13
Multiracial	41
White	227
Other	12

Measures

Emotional Embodiment. The EmBODY task (Nummenmaa et al., 2014) was used to assess embodied emotions. EmBODY (**Fig. 8**) is a computerized body mapping tool requiring participants to color the bodily regions where they feel a change in activity while experiencing a given emotion. Specifically, EmBODY presents participants with two body outlines and an emotion word, and instructs them to color the bodily regions they feel activating (left body outline) and deactivating (right body outline) in the context of an emotion. Five basic emotions (anger, fear, disgust, happiness, and sadness), six non-basic emotions (anxiety, love, depression, pride, shame, and jealousy), and one neutral state were used in this study. Nummenmaa et al. (2014) previously found that emotion words and emotion elicitation resulted in similar bodily maps, emotion words were therefore used in this study to reduce the burden on participants. The words were presented one at a time in a randomized order, and the participants were provided with a list specifying the definition of each emotion word.

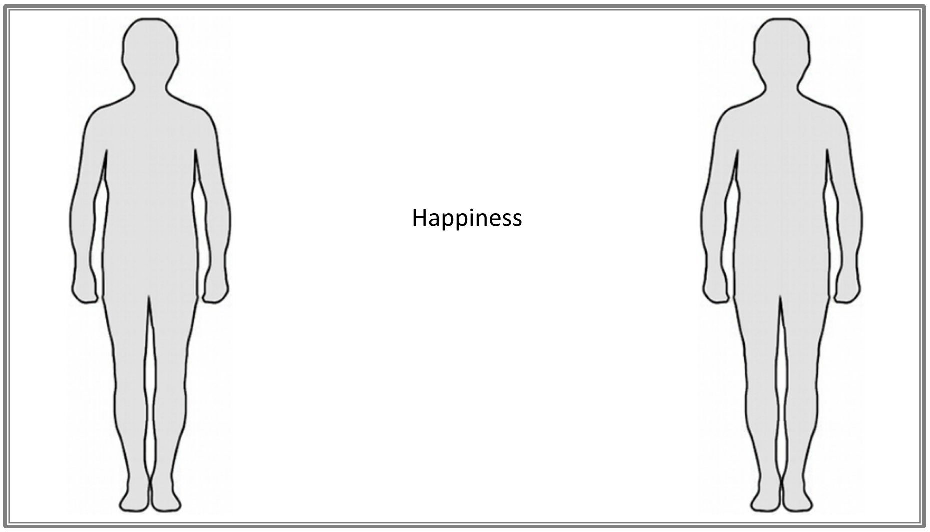

Fig. 8. EmBODY task. Participants use the computer mouse to color where on their body they feel an increase (left) or decrease (right) in activity while experiencing a given emotion (e.g., happiness).

Schizotypy. Schizotypy was assessed using the Schizotypal Personality Questionnaire (SPQ, Raine, 1991) and the Schizotypal Personality Questionnaire-Brief (SPQ-B; Raine & Benishay, 1995). The SPQ is a 74-item questionnaire designed to assess schizotypal traits based on DSM-III Schizotypal Personality Disorder criteria (APA, 1980). Responses are binary such that items rated as "true" are scored 1, and items rated as "false" receive a score of 0. The SPQ is the most widely used tool to assess schizotypy in research settings and has been shown to have excellent psychometric properties (e.g., Chapman et al., 1995; Wuthrich & Bates, 2005). It yields nine subscales: Ideas of Reference, Excessive Social Anxiety, Odd Beliefs/Magical Thinking, Unusual Perceptual Experiences, Odd/Eccentric Behavior, No Close Friends, Odd Speech, Constricted Affect, and Suspiciousness. A factor analysis revealed that these subscales best fit a three-factor model of schizotypy: Cognitive/Perceptual deficits, Interpersonal deficits, and Disorganization. The SPQ-B is an abbreviated version of the SPQ, described in Study 1B.

In our sample, 153 participants completed the SPQ and 266 completed the SPQ-B. In order to combine these two sub-samples, a factor analysis was conducted to reduce the dimensionality of the SPQ dataset to three factors (i.e., cognitive/perceptual, interpersonal, disorganized), mirroring the SPQ-B dataset. Scores were then converted into Z-scores such that each participant had a Z-score for each of the three schizotypy dimensions.

Data Analysis

Data Preprocessing and Visualization

Statistical analyses were implemented in MATLAB r2016a (www.mathworks.com) and R (Version 3.5.1, R Core Team, 2018). In the EmBODY task, painting was dynamic such that repeated or extended painting over the same region increased the intensity of the coloring. Paint intensity at each pixel thus ranged from 0 (no paint) to 100 (fully saturated), representing the strength of the colored bodily sensation. The diameter of the painting tool was 12 pixels. Preprocessing consisted of manually screening for anomalous responding (i.e., writings, lack of painting) and smoothing the data using a Gaussian disk to remove spatial dependencies created by the mouse clicks during painting. Bodily maps of emotions were generated for the whole sample using the method outlined by Numenmaa et al., 2014. Briefly, the activation and deactivation reported by a participant for a given emotion were combined into a single map, and mass univariate *t*-tests were used to compare the activation/deactivation of each pixel against zero. A False Discovery Rate (FDR) correction with α=0.05 was applied to account for multiple comparisons. T values were used to generate maps where pixel coloration represents statistically significant bodily sensation in the context of an emotion. In these bodily maps of emotions, warm colors (i.e., red) represent bodily activation while cold colors (i.e., blue) represent bodily deactivation.

Quantification of the Characteristics of Embodied Emotions

In order to address our specific research questions regarding the characteristics (i.e., diffusion, size, intensity, clarity and congruency) of emotional embodiment across the schizotypy spectrum, we extracted different metrics from the EmBODY data. These methods were adapted from previous body mapping studies (Galvez-Pol et al., 2021; Lloyd et al., 2021; Numenmaa et al., 2014; Sachs et al., 2019; Torregrossa et al., 2019b) and/or novel (i.e., diffusion metric).

To quantify the *diffusion* of embodied emotions an individual's body map for a given emotion was divided into 5 ROIs (i.e., arms, legs, head, abdomen, and chest) and diffusion scores were calculated for each. A diffusion score represents the average Manhattan distance (i.e., sum of the distances along each axis) between two colored pixels within an ROI. For instance, the Manhattan distance between colored pixel 1 at (x_1, y_1) and colored pixel 2 at (x_2, y_2) would be $|x_1 - x_2| + |y_1 - y_2|$. As such, a high diffusion score indicates a spread-out bodily sensation of emotion, while a low diffusion score represents a precisely defined embodied emotion. Given the nested nature of our dataset, linear mixed effect analyses with random intercepts for each participant, emotion, and ROI were used to assess the effect of schizotypy on the diffusion of the bodily maps using the *lme4* package (Bates et al., 2014). To estimate *p* values, we used a Satterthwaite approximation of degrees of freedom (Satterthwaite, 1941) and performed *t* tests with *lmerTest* (Kuznetsova et al., 2017). We note that the absence of coloring within an ROI resulted in a diffusion score of 0 (25% of observations), which biased the dataset. To address this, we conducted a new analysis excluding zero scores; the results remained unchanged. Lastly, we note that the diffusion metric is a novel method developed by our group to to quantify the spread of bodily sensations of emotions.

To assess the *size* of bodily sensations, we computed the proportion of the body colored for each emotion (Galvez-Pol et al., 2021; Lloyd et al., 2021). To do so, we divided the number of nonzero pixels (i.e., colored pixels) by the total number of pixels (50,364) for each participant, for each emotion. We note that this measurement does not take into consideration the intensity value of a pixel, but simply whether or not it was colored (i.e., 1 or 0). The proportion of body colored is conceptually close, though not analogous to, the diffusion metric previously described. In fact, by considering ROIs separately, the diffusion score represents the spread of a given bodily sensation. As such, a low diffusion score represents a precisely located bodily sensation (e.g., activation in the heart) while a low proportion of body colored represents a small bodily sensation which could be highly localized (e.g., activation in the heart only) or not (e.g., several dots of activation/deactivation across the body). Due to assumption violations for a linear regression model, the relationship between the size of embodied sensations of emotions and schizotypy was assessed using Spearman correlations, and a Holm correction was applied.

The *intensity* of the reported bodily sensations of emotions was estimated by summing the intensity values (ranging from 0 to 100 depending on click-duration) of colored pixels per participant, per emotion. For the overall analysis, we averaged across emotions such that each participant had one intensity score estimating the overall strength of their emotional embodiment. We first attempted to assess the link between schizotypy and the strength of emotional embodiment using a linear regression model, but diagnostic tests indicated that two assumptions (i.e., linearity and nature of the distribution of residuals) of the model were violated. Thus, the relationship between schizotypy and size of embodied emotions was assessed using Spearman correlations with a Holm correction.

To investigate the *clarity* of embodied emotions, we computed the number of “mixed pixels” (i.e., pixels colored for both activation and deactivation by a given participant for the same emotion; Torregrossa et al., 2019b; Sachs et al., 2019). To account for the count nature of the variable, its overdispersion, and excess zeros (i.e., most pixels were either not colored or colored only for activation or deactivation), the link between schizotypy and mixed pixels was assessed using a zero-inflated negative binomial regression in the *pscl* package (Jackman et al., 2020; Zeileis et al., 2008). Exponentiated coefficients were calculated to estimate odds ratios.

In order to investigate the *congruency* of reported bodily sensations of emotions in relation to schizotypy, the strength (i.e., intensity) of activation and deactivation reported for low and high arousal emotions was assessed as a function of schizotypy. It is widely accepted that arousal/activation and valence are the two dimensions underlying the subjective experience of emotions (e.g., Colibazzi et al., 2010; Lang et al., 1993; Posner et al., 2005). By asking participants to report the activation and deactivation experienced in the context of different emotional experiences, the EmBODY task directly prompts for arousal (Hartman et al., 2021). We therefore used the hierarchical cluster analysis conducted by the original group to categorize emotions into low and high arousal groups. Numenmaa and colleagues (2014) found that the bodily sensations of emotions formed five clusters: at one extreme laid a cluster of low arousal emotions (i.e., depression and sadness), while “positive” (i.e., happiness, love, and pride) and “negative” (i.e., anger and fear) high arousal emotions formed the two furthest clusters (see **Fig. 9**). Notably, low arousal emotions are consistently experienced as bodily deactivation (i.e., blue), while high arousal emotions are reliably experienced as bodily activation (i.e., red) in previous body mapping experiments (Numenmaa et al., 2014; Volynets et al., 2019) as well as in the current study (see **Fig. 10**). Thus, in our study, depression and sadness formed the low arousal group, while the high arousal group consisted of happiness, love, pride, anger and fear. The emotions that fell in the two middle clusters (i.e., shame, disgust, and jealousy), as well as the neutral state were discarded from this analysis.

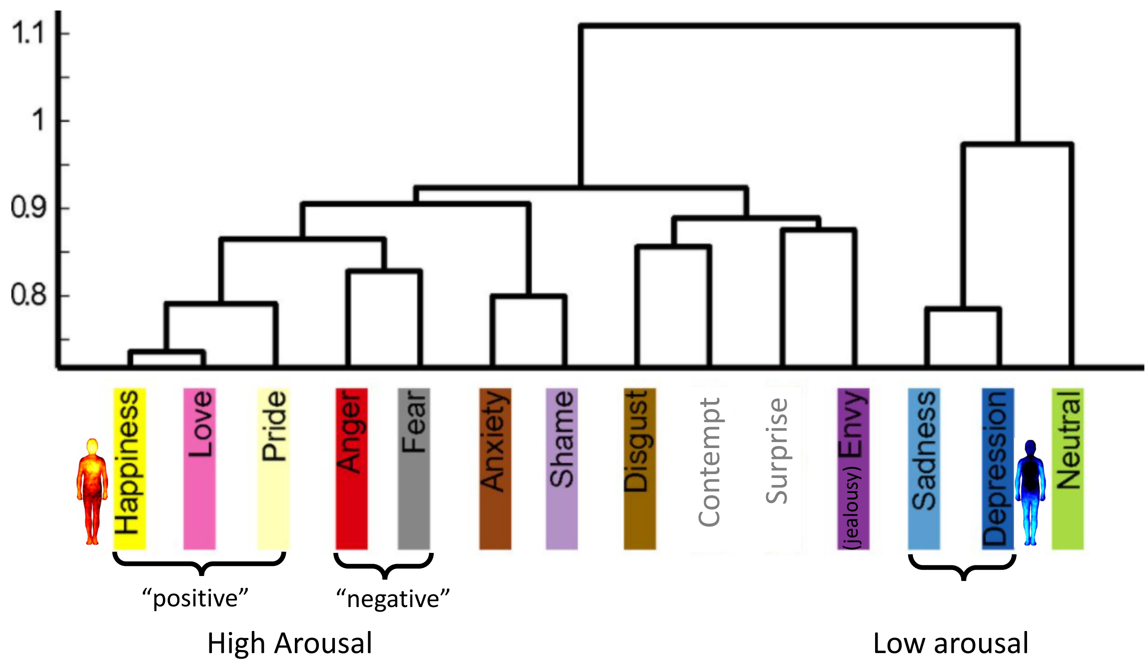

Fig. 9. Adapted from Nummenmaa et al. (2014). Hierarchical structure of the similarity between the bodily sensation of emotions. Sadness and depression formed a cluster that was clearly separated from all the other emotions (i.e., low arousal). Furthest from this low arousal cluster was a cluster of "positive" high arousal emotions (happiness, love, and pride) and a cluster of "negative" high arousal emotions (anger and fear). Low arousal emotions are experienced as bodily deactivation (i.e., blue in the map of depression) while high arousal emotions are embodied as bodily activation (i.e., red in the map of happiness). The two central clusters included anxiety, shame, disgust, and jealousy/envy as well as two emotions not included in the present study (i.e., contempt and surprise; shown in grey). The neutral state was distinct from all other categories. This cluster analysis was used to form the low arousal (sadness and depression) and the high arousal (happiness, love, pride, anger and fear) groups used in our study.

In our analyses, we conceptualized activation reported in the context of a high arousal emotion (i.e., happiness, love, pride, anger, fear) and deactivation reported in the context of a low arousal emotion (i.e., depression, sadness) as *congruent* bodily sensations of emotions, while activation reported in the context of a low arousal emotion and deactivation reported in the context of a high arousal emotions are examples of *incongruent* bodily sensations of emotions.

Again, violations of assumptions prevented the use of multivariate linear regressions to test whether schizotypy predicted the strength of congruent (i.e., activation for high arousal emotions and deactivation for low arousal emotions) and incongruent (i.e., deactivation in high arousal emotions and activation in low arousal emotions) bodily sensations of emotions. Instead, we used Spearman correlations with a Holm correction to assess the relationship between schizotypy dimensions and reported congruent/incongruent bodily sensation of emotions.

RESULTS

Fig. 10 shows the bodily maps of emotions of our sample. Emotions were associated with distinct bodily patterns of activation (red) and deactivation (blue) that are in accordance with previous cross-cultural results (Nummenmaa et al., 2014; Volynets et al., 2019). We note that the emotions categorized as low arousal in subsequent analyses (i.e., sadness and depression) are experienced as bodily deactivation while high arousal emotions (i.e., happiness, love, pride, anger and fear) are experienced as bodily activation. In contrast, the emotions that were excluded from the high/low arousal analysis (i.e., anxiety, shame, disgust, and jealousy) tend to be embodied a mix of activation and deactivation.

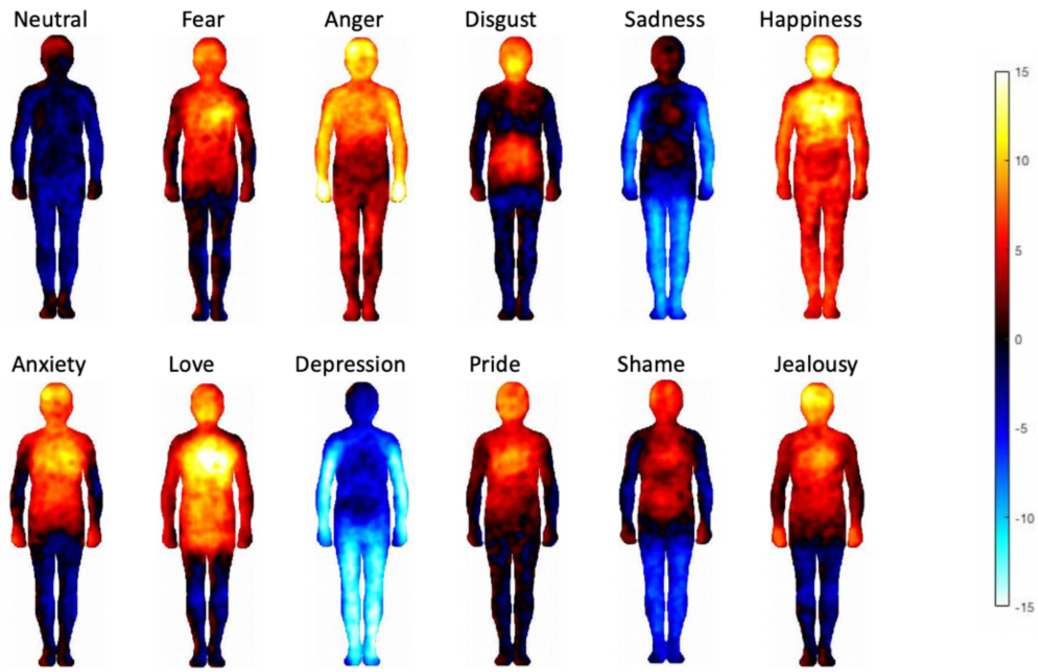

Fig. 10. Bodily maps of emotions. The bodily regions whose activation was increased are depicted by warm colors and the bodily regions whose deactivation was increased are depicted by cool colors. The color bar indicates the t-statistic range.

A mixed-effect analysis revealed no link between any of the schizotypy factors and the diffusion of bodily sensations of emotions (all *p's* >0.5). Similarly, no link was found between any of the schizotypy dimensions and the proportion of the body colored (all *p's* >0.5). This remained true when grouping emotions into low (i.e., depression and sadness) and high (i.e., happiness, love, pride, anger and fear) arousal. Thus, against our expectation, schizotypy did not predict the diffusion or size of embodied emotions.

A zero-inflated negative binomial regression revealed no effect of schizotypy on the presence (inflated model) or number (count model) of mixed pixels (all *p's* > 0.5). However, when investigating high and low arousal emotions separately, we found a link between Cognitive/Perceptual (i.e., positive) schizotypy and zero inflation (Z=-2.58, p=0.01). More specifically, the baseline odd of having no mixed pixels was 1.57 for low arousal emotions. This odd was decreased by 0.73 for each one-unit increase in positive schizotypy, suggesting that positive schizotypy predicted the presence of mixed pixels. Not link was found between schizotypy and the number (i.e., count) of mixed pixels in low arousal emotions, or the presence or number of mixed pixels in high arousal emotions.

A positive correlation was found between Cognitive/Perceptual (i.e. positive) schizotypy and the intensity of bodily sensations of emotions ($r(417)=0.13$, $p=0.02$). Interpersonal ($r(417)=0.10$, $p=0.10$) and Disorganized ($r(417)=0.09$, $p=0.10$) schizotypy did not significantly correlate with the intensity of painting. When investigating high and low arousal separately, we found that Cognitive/Perceptual ($r(417)=0.15$, $p=0.006$), Interpersonal ($r(417)=0.11$, $p=0.04$) and Disorganized ($r(417)=0.11$, $p=0.04$) schizotypy all predicted the intensity of low arousal emotions. In contrast, none of the schizotypy dimensions predicted the intensity of high arousal emotions (all *p's* > 0.5).

Correlation analyses further revealed a link between schizotypy and incongruent bodily sensation of emotions (see **Table 5.**) Specifically, we found that Cognitive/Perceptual schizotypy correlated with both the amount of deactivation reported in the context of high arousal emotions ($r(417)=0.14$, $p=0.01$) and the amount of activation reported in the context of low arousal emotions ($r(417)=0.12$, $p=0.05$). A link was also found between Interpersonal schizotypy and the amount of deactivation reported in the context of high arousal emotions ($r(417)=0.12$, $p=0.04$). No relationship was found between schizotypy dimensions and the amount of congruent bodily sensation of emotions (i.e., activation for high arousal emotions or deactivation for low arousal emotions) reported (all *p*'s>0.05).

Table 5. Correlations between schizotypy dimensions and congruent/incongruent bodily sensations of emotions

	Congruent		Incongruent	
	High Arousal Activation	Low Arousal Deactivation	High Arousal Deactivation	Low Arousal Activation
SPQ Interpersonal	0.06	0.06	0.12*	0.08
SPQ Cognitive/Perceptual	0.08	0.08	0.14**	0.12*
SPQ Disorganized	0.07	0.09	0.07	0.04

**p*< .05, ***p* < .01

DISCUSSION

Our results indicate that schizotypy, especially the positive (Cognitive/Perceptual) factor, predicts some differences in emotional embodiment. Against our expectations, schizotypy did not predict the spread (i.e., diffusion), or size (i.e., proportion of the body colored) of embodied emotions. However, positive schizotypy correlated with an increased intensity of bodily sensations of emotions, and all schizotypy dimensions predicted the strength of low arousal emotions though no link was found between schizotypy and the intensity of high arousal emotional embodiment. Positive schizotypy also predicted the presence of mixed pixels for low arousal emotions. In line with our hypothesis, we found that schizotypy predicted incongruent bodily sensations of emotions. Specifically, positive schizotypy predicted both bodily deactivation felt in the context of a high arousal emotion and bodily activation during a low arousal emotions. Negative (Interpersonal) schizotypy also predicted activation during low arousal emotions. In sum, individuals with higher positive schizotypy reported experiencing embodied emotions with higher intensity and lowed clarity (i.e., more mixed pixels), and endorsed more incongruent bodily sensations of emotions (the latter was also true for those with high negative schizotypy). As expected, these differences were particularly notable for low arousal emotions.

The nature or impact of the emotional embodiment differences related to schizotypy remains to be investigated. In fact, given the results of Study 1B, which found no link between schizotypy and interoceptive functioning, we do not believe that the increased intensity of bodily sensation reported by individuals with high positive schizotypy results from a heightened awareness or attention to bodily signals in this population. We also contrast this finding with that of a study that found decreased intensity of embodied emotions in individuals with alexithymia (Lloyd et al., 2021). It is therefore possible that the increased intensity of embodied emotions experienced by individuals with high positive schizotypy facilitates emotion identification. However, our results also indicated that individuals with high schizotypy experience heighted levels of incongruent (e.g., activation in the context of a low arousal emotion, or deactivation in the context if a high arousal emotion) and blurred (i.e., activation and deactivation being experienced simultaneously in a given bodily region) bodily sensations of emotions, which could in turn lead to incorrect emotion identification. Therefore, the functional impact of emotional embodiment differences along the schizotypy spectrum remains to be investigated.

In comparing the present results to those of a previous study investigating emotional embodiment in people with schizophrenia (Torregrossa et al., 2019b), we note key parallels and highlight differences. Torregrossa et al. (2019b) found that individuals with schizophrenia reported more deactivation in the context of high arousal emotions, the present study revealed the same tendency in individuals high schizotypy. Similarly, in line with the higher number of mixed pixels recorded in individuals with schizophrenia (Torregrossa et al., 2019b), the present study documented a link between positive schizotypy and the presence of mixed pixels for low arousal emotions. We also note that the emotional embodiment difference observed along the schizotypy spectrum were particularly pronounced for low arousal emotions, which echoes the specific alteration of embodiment of low arousal emotions in schizophrenia (Torregrossa et al., 2019b). On the other hand, though Torregrossa et al. (2019b) found no difference in the intensity (*Note*. Intensity is referred to as "magnitude" in Torregrossa et al.; 2019b) of embodied emotions reported by individuals with schizophrenia and control participants, the present study found a link between positive schizotypy and the intensity of bodily sensations of emotions. Additionally, though Torregrossa et al. (2019b) did not compute the diffusion or size (i.e., proportion of the body colored) of the embodied emotions in their sample, their topographical maps suggested that individuals with schizophrenia endorsed bodily sensations of emotions that were more spread out than controls'. In the present study, we found no link between schizotypy and the diffusion or size of emotional embodiment.

These discrepancies make it difficult to assess whether the differences in emotional embodiment found in individuals with elevated positive schizotypy represent the emergence of anomalous bodily sensations of emotions documented in schizophrenia (Torregrossa et al., 2019b). In fact, though most individuals with high schizotypy will not go on to develop a psychotic illness, the literature suggests that a minority of them will (e.g., Debbané et al., 2015). A longitudinal design will be needed to determine whether differences in emotional embodiment in young adults with elevated schizotypy represent an early marker for risk for psychosis. Studies investigating emotional embodiment across the psychotic spectrum (i.e., in prodromal individuals and people experiencing the first episode of psychosis) are also needed to clarify the developmental trajectory of anomalous emotional embodiment in the schizophrenia spectrum.

Our work bears some limitations. First, differences in methodology prevent important comparisons between our work and previous body mapping studies. For instance, as previously mentioned, Torregrossa et al. (2019b) did not compute the proportion of the body colored or diffusion of the bodily sensations of emotions. However, Torregrossa et al. (2019b) used a Linear Discriminant Analysis (LDA) to test whether different emotions were associated with statistically different bodily sensations in schizophrenia, and found a reduced classification accuracy in schizophrenia compared to CO. The dimensional nature of our dataset prevented the use of LDA to assess the independence of embodied emotion in relation to schizotypy. Additionally, given the nature of our sample (i.e., undergraduates), it is likely that the distribution of schizotypy scores is positively skewed such that the higher end of spectrum is under-represented. Our decision to investigate the schizotypy spectrum dimensionally (i.e., general population) also prevents us from drawing definitive conclusions about the link between differences in emotional embodiment in people with high schizotypy and those documented in individuals with schizophrenia (Torregrossa et al., 2019b). Lastly, we did not measure alexithymia or other aspect of emotional or social functioning, which limits the interpretations of our results regarding the impact of the observed difference in embodiment emotions along the schizotypy spectrum.

In sum, Study 2 linked, for the first time, differences in emotional embodiment and schizotypy. We found that individuals with elevated positive schizotypy experience the bodily sensation of their emotions with greater intensity but less clarity (for low arousal emotions). We also found that both positive and negative schizotypy predicted incongruent bodily sensations of emotions (e.g., bodily activation felt in the context of a low arousal emotion). Importantly, some aspects of emotional embodiment (i.e., the diffusion and size of bodily sensations) did not systematically vary as a function of schizotypy. More work is needed to understand the implications of these results in terms of emotional and social functioning as well as with regard to psychosis-risk.

CHAPTER IV

Study 3. Neuromodulation of Body Ownership on Relation to Schizotypy

The literature consistently documents body ownership disturbances in the schizophrenia spectrum. Though the increased sensitivity to the RHI is well documented in schizophrenia, only three studies have investigated the RHI in relation to schizotypy (Asai et al., 2011, Germine et al., 2013; Thakkar et al, 2011). They found a link between positive schizotypy and sensitivity to the RHI. Thakkar et al. (2011) also found a positive relationship between RHI sensitivity and negative schizotypy. Our first aim is to replicate these results by investigating RHI sensitivity in relation to schizotypy in a large sample. For the first time, we also investigate the link between RHI sensitivity and self-reported bodily disturbances. A second, more exploratory, aim of this study is to alter individual sensitivity to the RHI using neuromodulation.

At the neural level, the sense of body ownership has been reliably linked to the activity of the right tempoparietal junction (rTPJ). Specifically, neuroimaging studies have highlighted the role of the rTPJ in maintaining a coherent sense of one's body separate from external objects (Tsakiris et al., 2008) as well as integrating vestibular, visual, and tactile information (Blanke, 2012). In a seminal study, Blanke and colleagues (2005) recorded rTPJ activity while healthy volunteers imagined a change of perspective consistent with and out-of-body experience. Blanke et al. (2005) also identified the rTPJ as the seizure focus in the case study of an epileptic individual reporting out-of-body experiences during epileptic episodes. Studies investigating asomatognosia (i.e., neurological disorders characterized by a lack of ownership over a specific limb) were also critical in discovering the role of the rTPJ in our sense of body ownership

(Feinberg et al., 2010; Vallar & Ronchi, 2009). And Guimmarra et al. (2011) proposed a neurological model of Body Integrity Identity Disorder (BIID) involving the rTPJ and the insula (i.e., the brain known for its involvement in interoception).

A few studies have documented anomalous rTPJ activity in the schizophrenia spectrum. For instance, a study found that abnormally prolonged rTPJ activation was associated with bodily self-disturbances and schizotypy scores in the general population (Arzy et al., 2007). Other neuroimaging studies documented abnormal activation patterns of the rTPJ in individuals with schizophrenia (Franck et al, 2002; Ganesan et al., 2005; Spence et al., 1997). This body of literature suggests that the rTPJ might be a key component of body ownership disturbances in schizophrenia. Thus, the second aim of this study is to manipulate rTPJ activity to experimentally modulate one's sense of body ownership. To this end, we use a non-invasive method (i.e., transcranial Direct Current Stimulation; tDCS) in conjunction with the RHI to explore the effects of rTPJ activity modulation on body ownership.

TDCS is a neuromodulation technique that has been widely used to investigate brain function. TDCS offers many advantages over other neurostimulation techniques. In fact, it is non-invasive, safe, painless, and well tolerated (Stagg & Nische, 2011). In addition, the effects of tDCS are polarity-specific (i.e., anodal stimulation enhances cortical excitability while cathodal stimulation suppresses it) and relatively short-lived, allowing for safe experimental manipulations. On a practical level, tDCS equipment is cheap and easy to use, which explains the recent popularity of the technique amongst researchers (Thair et al., 2017).

TDCS has been shown to have beneficial effects for a variety of clinical disorders such as depression (e.g., Boggio et al., 2008), addiction (e.g., Fregni et al., 2008), and autism spectrum disorders (e.g., Schneider & Hopp, 2011). In the last decade, tDCS has also been used as an experimental intervention technique to alleviate symptoms of schizophrenia. For instance, tDCS was shown to reduce auditory hallucinations (Agarwal et al., 2013) and ameliorate negative symptoms (Gomes et al., 2015). Empirical evidence also suggests that tDCS might be useful to improve various cognitive processes such as insight (Bose et al., 2014), corollary discharge (Nawani et al., 2014), or cognitive performance (Hoy et al., 2014) in individuals with schizophrenia. In this study, we use tDCS to investigate the effects of rTPJ activity modulation on an individual's sense of body ownership, as measured by the RHI.

Based on past results (Asai et al., 2011; Germine et al., 2013; Thakkar et al., 2011), we hypothesized that we would find a relationship between schizotypy and RHI sensitivity. More specifically, we anticipated that individuals with higher positive schizotypy would be more prone to the RHI. Regarding our second aim (i.e., manipulating rTPJ activity to experimentally modulate one's sense of body ownership), based on the findings of from Olaf Blanke's laboratory (Blanke et al., 2005) we anticipated that anodal stimulation (i.e., activation) on the rTPJ would increase individual sensitivity to the RHI, while cathodal stimulation would reduce it.

METHODS

Participants

Ninety-seven undergraduate students participated in Study 3. Participants were recruited through the Vanderbilt Psychology Research Subject Pool system. Inclusion criteria stipulated that participants were aged 18 or older and had no prior history of neurological or psychiatric disorder or current drug use. In order to capture the full spectrum of schizotypy, undergraduate students in an Introduction to Psychology class were screened using the following three questions: 1. Have you ever had the experience of being separated from your body (during wake time)? 2. Do you see things that others can't or don't see? and 3. Have you ever felt that someone was playing with your mind? Potential participants who responded "yes" to any of these questions were contacted by the research team and invited to participate in the study. Participants were randomized to one of three tDCS conditions (i.e., anodal, cathodal, sham; more details provided subsequently). The Vanderbilt Institutional Review board approved study protocol and written consent was obtained from each participant. Participants received course credit for their participation. Participants demographic information is summarized in **Table 6.**

Table 6. Demographic information for Study 3 participants.

	Anodal (N=34)	Cathodal (N=30)	Sham (N=32)	Group comparison
Gender (F/M/unknown)	21/11/2	19/10/1	21/10/1	$p = 0.98$
Age	20.47 (1.29)	20.24 (0.95)	20.48 (1.31)	$p = 0.69$
Handedness[a]	81.20 (42.39)	90.19 (24.48)	68.22 (58.31)	$p = 0.16$
Race/Ethnicity				$p = 0.78$
Black	7	3	4	
Asian	11	12	8	
Hispanic	0	1	0	
Multiracial	4	2	5	
White	10	10	14	
Unknown	2	2	1	
Schizotypy[b]				
Positive	7.86 (4.57)	7.93 (5.00)	8.13 (6.21)	$p = 0.98$
Negative	7.31 (4.70)	7.76 (4.30)	6.87 (4.33)	$p = 0.74$
Disorganized	5.94 (3.24)	5.01 (3.66)	5.68 (2.94)	$p = 0.58$

Note. One of the participants was not assigned to a tDCS condition and therefore does not appear in this table. This participant was only included in the analysis exploring the link between baseline RHI sensitivity and schizotypy/self-reported bodily self-experiences.

[a] Estimated using the Edinburgh Handedness Inventory (Oldfield, 1971). Scores range from -100 (left-handed) to 100 (right-handed).
[b] Measured using the SPQ (Raine, 1991).

Measures

Rubber Hand Illusion

Materials. Participants sat in front of a two-chamber box (one opaque and one transparent). They placed their hand in the opaque chamber while a rubber hand was placed in the transparent one such that they could see the rubber hand but not their own hand. A neutral density filter was placed over the clear chamber to de-emphasize the color of the rubber hand. A cape was placed around the participant to cover their arms. During the manipulation, the experimenter synchronously brushed the rubber hand and the participant's hand using two identical paintbrushes (see **Fig. 11**).

Fig. 11. Reprinted from Thakkar et el. (2011). Rubber Hand Illusion setup.

Procedure. The participant was installed according to the experimental setup shown in **Fig. 11**. Prior to the experimental manipulation, six measurements of perceived index finger location of participant's hand (hidden in the opaque chamber) were taken. For each measurement, a ruler was placed on top of the box, and participants were asked to indicate their perceived index finger position by naming a number on the ruler. Different rulers, each offset by a random length, were used to prevent participants from re-using their previous estimation. Following pre-stimulation measurements, the experimenter simultaneously brushed the index finger of the rubber hand and that of the participant's hand with a paintbrush at approximately one stroke per second for four minutes. The participant was instructed to look at the rubber hand the whole time the experimenter was brushing, and to report any sensations they might experience. Following stimulation, six additional measurements of the participant's perceived index finger location of the hidden hand were taken. Finally, the subject was asked to fill out a self-report questionnaire developed by the RHI's original group (Botvinik & Cohen, 1998).

Measurement. The proprioceptive drift (i.e., objective measure of RHI sensitivity) was measured by calculating the difference between the perceived position of the participant's hand before and after the tactile stimulation. A positive proprioceptive drift indicates that the perception of one's own hand has shifted towards the rubber hand as a result of the manipulation, suggesting a sense of ownership over the rubber hand while the participant's own hand becomes disembodied. The subjective experience of the RHI was quantified by summing participants' responses to the self-report questionnaire, which instructed them to rate the occurrence of nine subjective experiences of the RHI (e.g., "I felt as if the rubber hand was my hand") on a 7-point Likert scale ranging from -3 (strongly disagree) to 3 (strongly agree).

Transcranial Direct Current Stimulation Procedure

We used tDCS to noninvasively manipulate cortical brain activity by passing a weak electrical current through electrodes placed on the scalp. Specifically, participant received electrical activation, deactivation, or no stimulation over the rTPJ, depending on the experimental condition they were assigned to.

Participants were first fitted with an elastic cap (Electro-Cap International) containing holes corresponding to the 10-20 EEG system (TransCranial Technologies). The cap was used to identify the stimulation site consistent with published studies that have used tDCS for rTPJ stimulation (Santiesteban et al., 2012; Sowden et al., 2015; Ye et al., 2015). TDCS was administered using a battery driven, constant current stimulator (MindAlive Inc., Alberta, Canada) and a pair of conductive rubber electrodes (active: 19.25 cm^2, reference: 52 cm^2). The electrodes were placed over sponges soaked in salt water and each was held in place with an elastic headband. The active electrode was placed over the rTPJ (site CP6 of the 10-20 system) and the inactive electrode was placed on the center on the right cheek to avoid any confounding effects from other brain regions. Specifically, the reference electrode was placed 3cm from the lip corner (cheilion), diagonally along an imaginary line connecting the cheilion to the ipsilateral lateral tip of the mandibular condyle of the lower jaw. In the active conditions (i.e., anodal, cathodal), current was applied at an intensity of 2.0 mA for 20 minutes. The sham condition followed the same protocol as the active conditions, except the stimulator was only turned on for 30 seconds at the beginning and 30 seconds at the end of the 20-minute period. This allowed the stimulator to ramp up, resulting in the same physical sensations (e.g., tingling, itching) as those reported with active tDCS. **Fig. 12** illustrates the tDCS set-up for each condition.

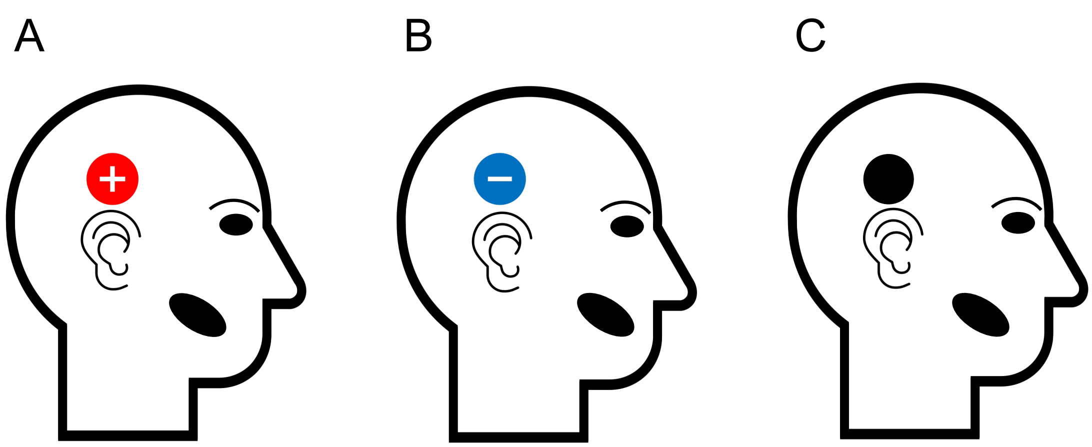

Fig. 12. TDCS setup for each experimental condition. Participants were randomly assigned to a condition. **A.** In the anodal condition, the rTPJ is activated (i.e., anodal electrode on CP6). **B.** In the cathodal condition, the rTPJ is deactivated (i.e., cathodal electrode on CP6). **C.** In the sham condition, an electrode is placed on CP6, but the stimulator is turned off after 30 seconds (i.e., the activity of the rTPJ is not modulated). In all conditions, the reference electrode is placed on the right cheek.

Self-Report Measures

Schizotypal Personality Questionnaire (SPQ, Raine, 1991). The SPQ was used to assess schizotypy (see Study 2 for a description of the SPQ). Based on Davidson et al. (2016), the nine SPQ subscales were combined to form the three schizotypy factors as follows: Cognitive/Perceptual (i.e., Ideas of Reference, Odd Beliefs/Magical Thinking, Unusual Perceptual Experiences, and Suspiciousness), Interpersonal (i.e., Excessive Social Anxiety, No close Friends, and Constricted Affect), and Disorganization (Odd/Eccentric Behavior, and Odd Speech).

Perceptual Aberration Scale (PAS; Chapman, et al., 1978). The PAS is a 35 true/false items scale designed to measure perceptual disturbances, especially those related to the body. The PAS in fact measures five types of anomalous bodily experiences: (1) unclear body boundaries, (2) feelings of unreality or estrangement of body, (3) feelings of deterioration of one's body parts, (4) perceptions of the change of size of one's body parts, and (5) changes in the appearance of the body. It yields good to excellent reliability and is designed for use in both healthy and clinical populations (Chapman et al., 1978). In our study, the PAS we used to measure bodily disturbances.

Multi-Modality Unusual Sensory Experiences Questionnaire (MUSEQ; Mitchell et al., 2017). The MUSEQ is a 43-item self-report instrument assessing unusual sensory experiences across six modalities (i.e., auditory, visual, olfactory, gustatory, bodily sensations, sensed presence). Participants are asked to rate the frequency of each unusual experiences on a 5-point Likert scale ranging from "Never (never happened)" to "Frequently (at least monthly)." A subscale score is calculated for each modality. The MUSEQ has been shown to have good reliability and construct validity, and to successfully discriminate non-clinical and clinical groups

(Mitchell et al., 2017). Thus, the MUSEQ is a useful and reliable tool for measuring a variety of unusual sensory experiences in relation to schizotypy. In this study, we used the Bodily Sensations (BS) and Sensed Presence (SP) scales of the MUSEQ as measures of bodily disturbances.

Experimental Design and Procedure

The experiment in this study uses a within- and between-subjects design, with group determined by type of stimulation received (i.e., anodal cathodal, sham). Participants were randomly assigned to a group and were blind to group assignment. This randomization procedure was used to prevent potential confounds. Groups did not differ in demographic characteristics (see **Table 6**). All study procedures were the same between the three groups.

At the beginning of the session, participants completed self-report measures assessing unusual bodily experiences (i.e., PAS and MUSEQ) to avoid potential tDCS effects in responding. The RHI was then administered to get a baseline measure of a participant's sensitivity to the illusion (i.e., RHI PRE). Participants then received 20 min of active (i.e., anodal or cathodal) or sham tDCS over the rTPJ, depending on group assignment. During tDCS, participants completed non-body related self-report measures (i.e., SPQ, demographic information). At the end of the tDCS procedure, participants filled out a tDCS safety questionnaire inquiring about their experience. Immediately after tDCS, participants completed the RHI again (i.e., RHI POST). The RHI takes approximately 15 minutes to complete, which is well within the time window in which tDCS effects have been shown to last (Reinhart & Woodman, 2014). **Fig. 13** summarizes the study procedure.

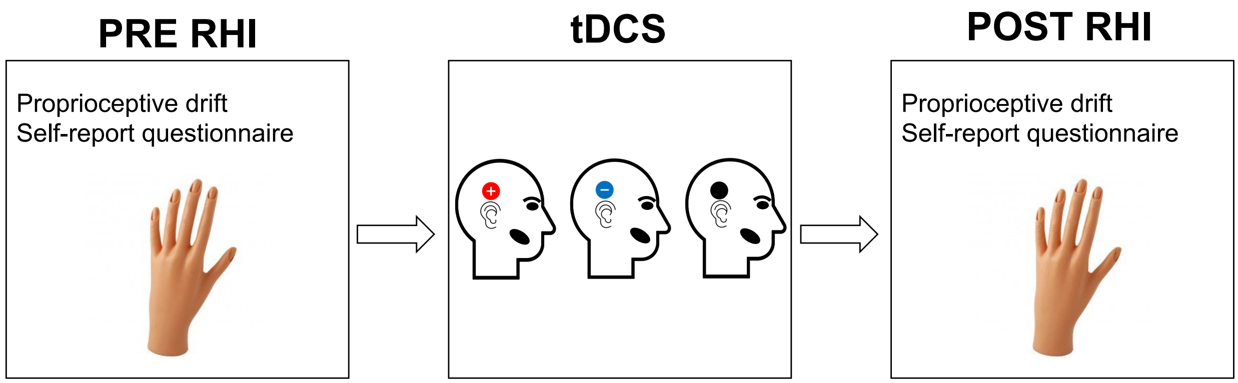

Fig. 13. Study 3 protocol. Participants were randomized to one of three tDCS conditions such that they received electrical activation (i.e., anodal), deactivation (i.e., cathodal), or no stimulation (i.e., sham) to the rTPJ. They completed the RHI pre and post tDCS.

Data Analysis

Schizotypy, self-reported bodily-self-disturbances, and RHI sensitivity

Linear regressions were used to investigate the link between schizotypy and RHI sensitivity at baseline. Two models were used to assess the objective (i.e., proprioceptive drift) and subjective (i.e., self-report) sensitivity to the illusion separately. In the first model, the three dimensions of schizotypy (i.e., Cognitive/Perceptual, Interpersonal, Disorganized) were used as predictors, and proprioceptive drift as the outcome measure. The second model included the same predictors, but the subjective experience of the illusion was used as the outcome measure instead. Pairwise *t*-tests with Bonferroni corrections were used for post-hoc analyses as needed. Additionally, ordinal logistic regressions were used to investigate the link between schizotypy and specific items endorsed on the self-report questionnaire, and linear regressions were used to investigate the effect of specific SPQ subscales on RHI sensitivity.

A composite "bodily disturbance" score was created for each participant by summing the scaled values of the MUSEQ Bodily Sensation (BS), Sensed Presence (SP), and the PAS. Spearman correlations were used to assess the link between bodily disturbances and (1) RHI questionnaire score and (2) proprioceptive drift.

Effect of rTPJ tDCS on RHI sensitivity

Repeated-measures ANOVAs were used to assess the role of rTPJ modulation on RHI sensitivity. In these analyses, the effect of group (i.e., anodal, cathodal, sham), time (i.e., PRE- or POST- tDCS) and their interaction on RHI sensitivity were evaluated. The objective (i.e., proprioceptive drift) and subjective (i.e., questionnaire) measures of RHI sensitivity were investigated separately. Repeated-measures analyses were used to account for individual variability in RHI sensitivity and tDCS response.

Three participants were excluded from these analyses because they did not complete the tDCS procedure due to technical issues (N=2) or undesirable side effects (N=1). The sample size for these analyses was therefore 94 (Anodal N=33, Cathodal N=29, Sham N=32). Given the importance of brain laterality in neurostimulation, analyses were replicated after excluding N=7 left-handed participants, resulting in Anodal N=31, Cathodal N=28, Sham N=28. The results remained unchanged after excluding left-handed participants; we therefore report the full-sample results.

RESULTS

Schizotypy, bodily-self-disturbances, and RHI sensitivity

A linear regression indicated that Cognitive/Perceptual schizotypy predicts subjective sensitivity to the RHI (b=0.09, t= 3.20, p=0.001). This suggests that elevated positive (i.e., Cognitive/Perceptual) schizotypy predicts a higher subjective experience of the illusion. No link was found between Interpersonal or Disorganized schizotypy and RHI questionnaire score (p's >

0.05). Furthermore, no link was found between schizotypy and proprioceptive drift (all *p*'s > 0.05). **Fig. 14** summarizes these results.

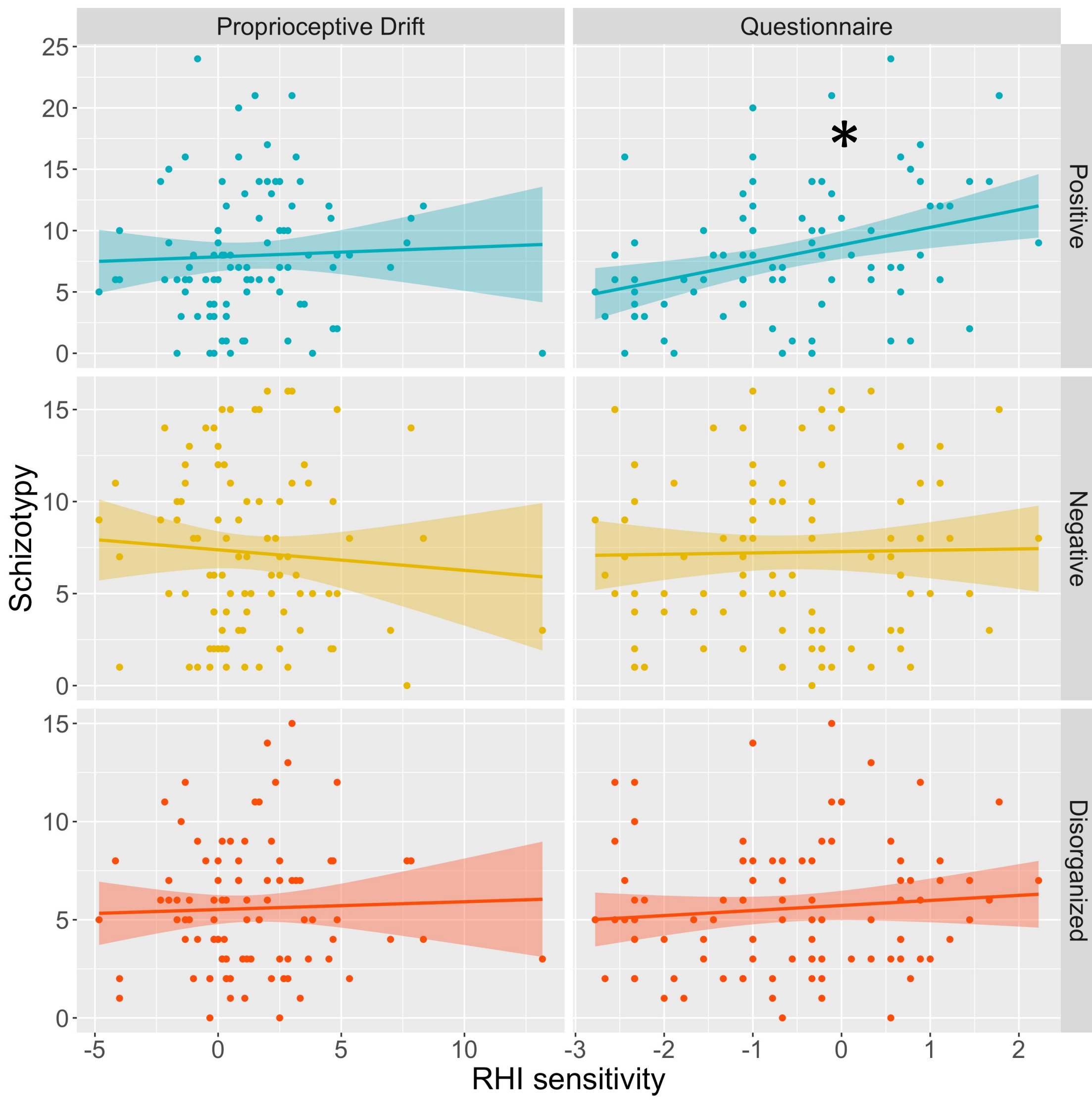

Fig. 14. Link between schizotypy and RHI sensitivity at baseline. Positive (i.e., Cognitive/Perceptual) schizotypy was found to predict the subjective experience of the illusion. Negative (i.e., Interpersonal) and Disorganized schizotypy were not found to predict RHI sensitivity. No link was found between schizotypy and the objective measure of RHI sensitivity (i.e., proprioceptive drift).

When examining the nine SPQ subscales (Ideas of Reference, Excessive Social Anxiety, Odd Beliefs/Magical Thinking, Unusual Perceptual Experiences, Odd/Eccentric Behavior, No Close Friends, Odd Speech, Constricted Affect, and Suspiciousness), only Odd Beliefs/Magical Thinking (within the Cognitive/Perceptual factor) was found to predict the strength of the subjective experience of the illusion (b=0.25, t= 2.11, p=0.04). Notably, Constricted Affect (within the Interpersonal factor) was found to predict a smaller proprioceptive drift (b= -0.62, t= -2.17, p=0.04).

We then used ordinal logistic regressions to investigate the role of schizotypy on the endorsement of specific items of the RHI questionnaire. Briefly, Cognitive/Perceptual schizotypy was found to predict the strength of endorsement of five of the nine items. In contrast, an inverse relationship was found between Interpersonal schizotypy and one of the items. These results are presented in **Table 7** in terms of odds ratio. An odds ratio significantly higher than one indicates an increase in endorsement (e.g., from *strongly disagree* to *disagree*, or from *agree* to *strongly agree*) with every one unit increase in schizotypy. For instance, a one unit increase in Negative (i.e., Interpersonal) schizotypy significantly decreased the odds of agreement with RHI questionnaire item 1 by 11% [i.e., (1 -0.89) x 100%]. On the other hand, for every one unit increase in Positive (i.e., Cognitive/Perceptual) schizotypy, the odds of agreement with RHI questionnaire item 4 is multiplied by 1.11 (increased by 11%).

Table 7. Odds ratios of RHI questionnaire item endorsement based on schizotypy factors

	Schizotypy		
RHI questionnaire item	Positive	Negative	Disorganized
1. It seemed as if I were feeling the touch of the paintbrush where I saw the rubber hand	1.05	0.89*	1.13
2. It seemed as though the touch I felt was caused by the paintbrush ouching the rubber hand	1.03	1.00	1.01
3. It felt as if the rubber hand was my hand	1.08	0.95	0.99
4. It felt as if my real hand was drifting towards the rubber hand	1.11**	1.03	0.96
5. It felt as if I might have more than one right hand	1.12*	0.95	0.98
6. It felt as if the touch I was feeling came from somewhere between my own hand and the rubber hand	1.09*	0.98	1.01
7. It felt as if my real hand was turning ‘rubbery’	1.12*	0.97	1.02
8. It appeared visually as if the rubber hand was drifting towards my hand	1.11*	0.98	0.95
9. The rubber hand began to resemble my own hand in terms of shape, skin tone, freckles, or some other visual feature	1.08	1.10	0.89

*p< .05, **p < .01

Correlation analyses revealed a significant link between bodily disturbances and RHI sensitivity measured both subjectively (r=0.21, p=0.04) and objectively (r=0.23, p=0.02; **Fig 15**). At the item level, we found that the severity of bodily disturbances predicted the strength of endorsement of items 4 “It felt as if my real hand was drifting towards the rubber hand” (r=0.20, p=0.05), 6 “It felt as if the touch I was feeling came from somewhere between my own hand and the rubber hand” (r=0.28, p=0.006) and 9 “The rubber hand began to resemble my own hand in terms of shape, skin tone, freckles, or some other visual feature” (r=0.23, p=0.03).

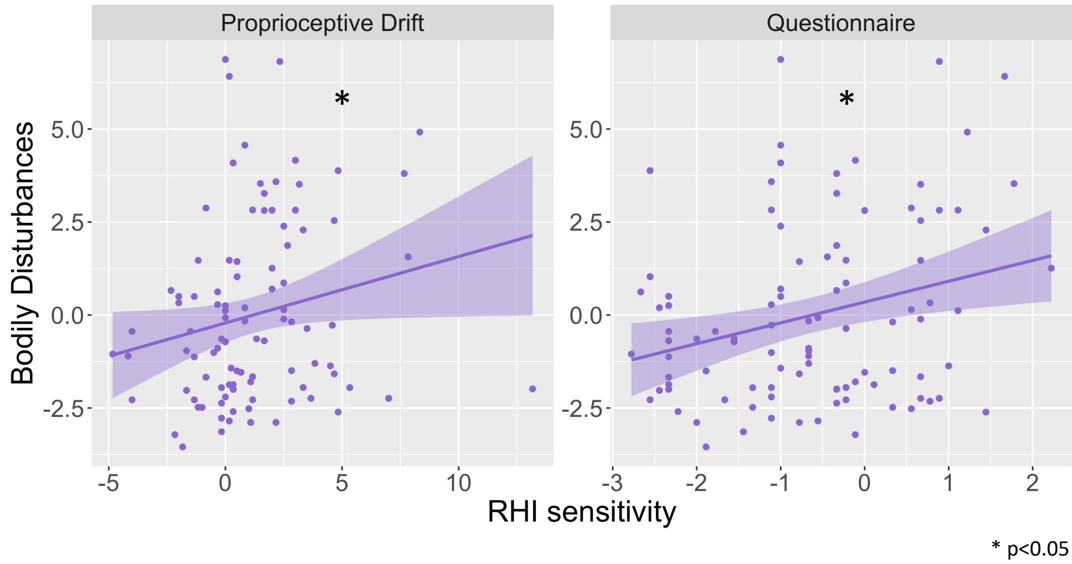

Fig. 15. Link between bodily disturbances and RHI sensitivity at baseline. Bodily disturbances were calculated by summing the scaled scores of MUSEQ BS, MUSEQ SP and PAS.

No gender effect was found in RHI sensitivity measured objectively (p=0.25) or subjectively (p=0.88).

Effect of rTPJ tDCS on RHI sensitivity

A repeated measures ANOVA revealed a main effect of group on the subjective experience of the illusion, $F(2,91)=4.31$, p=0.02, such that participants in the sham (M=1.11, SD=2.83, p=0.0005) and cathodal (M=1.01, SD=2.25, p=0.02) conditions endorsed RHI questionnaire items at higher rates than those in the anodal group (M=0.65, SD=2.50) across timepoints (i.e., PRE and POST). No main effect of time was found on the strength of the subjective experience of the illusion, $F(1,91)=1.07$, p=0.31. The interaction between time and group was not significant, indicating that the subjective sensitivity to the RHI was not differentially affected by tDCS conditions.

A second analysis revealed a main effect of time on objective sensitivity to the RHI such that the proprioceptive drift significantly decreased from PRE (M=1.21, SD=2.82) to POST (M=0.61, SD=2.20), $F(1,91)=5.56$, $p=0.02$. No main effect of group was found ($F(2,91)=0.38$, $p=0.68$), suggesting that average proprioceptive drift did not differ in the anodal, cathodal, and sham conditions. The interaction between time and group was not significant ($F(2,91)=0.85$, $p=0.76$), indicating that the objective sensitivity to the RHI was not differentially affected by tDCS conditions.

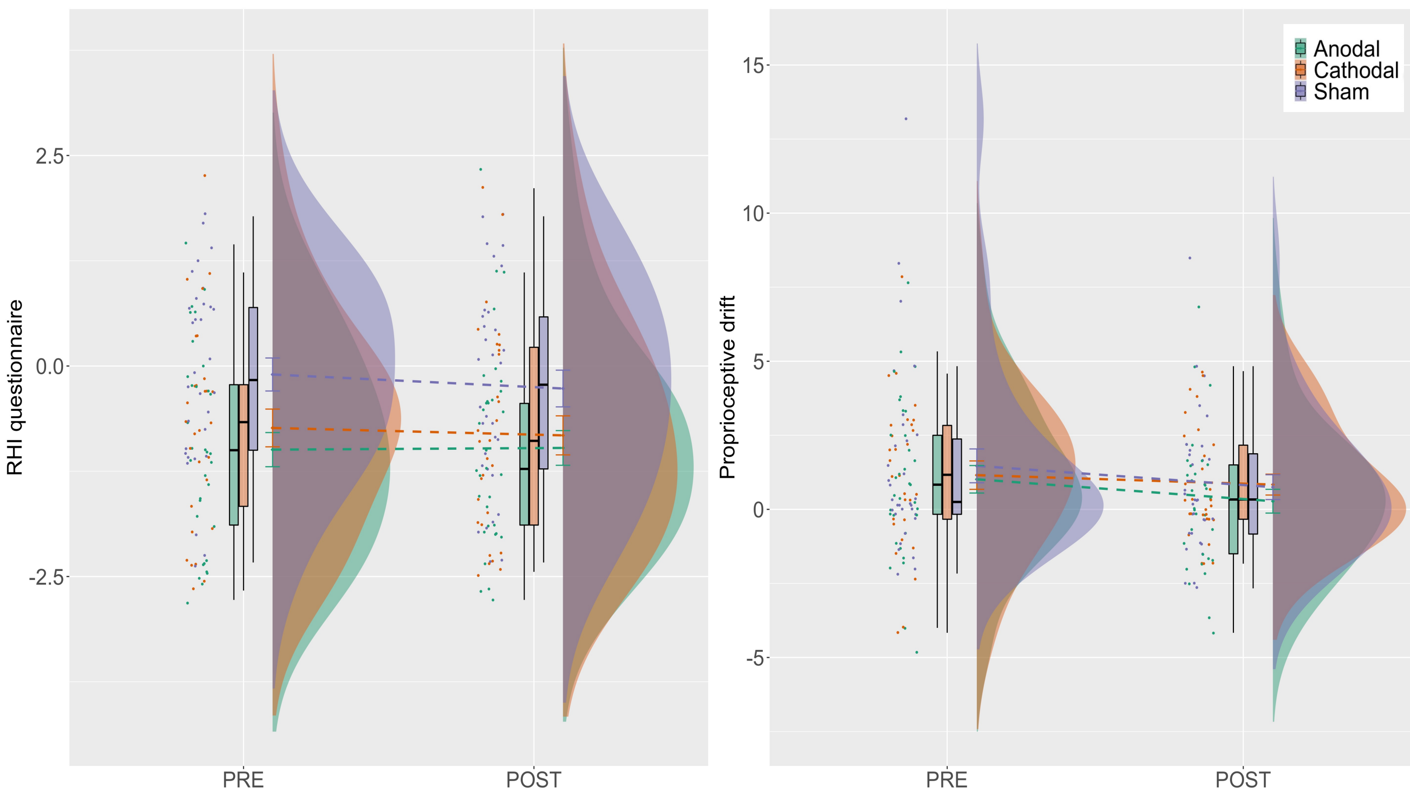

Fig. 16. Rain cloud plots of RHI sensitivity (left: subjective, right: objective) PRE and POST tDCS in each of the three experimental conditions (i.e., anodal, cathodal, sham). A main effect of group was found on the subjective experience of the illusion (i.e., RHI questionnaire). A main effect of time was found on the objective experience of the illusion (i.e., proprioceptive drift). The time by group interaction was not found to be significant for either measure of the illusion.

Given the variability in individual sensitivity to the RHI, we repeated these analyses on the subset of participants who experienced the illusion at baseline (i.e., "RHI responders"). This subset was created by selecting people who had a positive proprioceptive drift (i.e., 95% CI of proprioceptive drift across the six measurements was positive and did not cross zero, N=52), OR those who endorsed (i.e., reported some level of agreement with) at least three of the nine questionnaire items (N=63) at baseline. This resulted in a subset of N=73 participant who experienced the RHI objectively, subjectively, or both, at baseline (Anodal N=21, Cathodal N=24, Sham N=28). In this subsample, the main effect of time was significant for both the objective ($F(1,70)=12.93$, $p=0.0006$) and subjective ($F(1,70)=7.56$, $p=0.008$) experience of the illusion. There was no main effect of group on either the objective ($F(2,70)=0.04$, $p=0.96$) or subjective ($F(2,70)=2.47$, $p=0.09$) experience of the illusion. Importantly, the interaction between time and group remained insignificant for both the proprioceptive drift ($F(2,70)=2.18$, $p=0.12$) and the RHI questionnaire ($F(2,70)=0.34$, $p=0.72$, which suggests that even in RHI responders, tDCS activation (anodal) or deactivation (cathodal) of the rTPJ did not differentially affect individual sensitivity to the RHI.

Lastly, we compared the groups on their endorsement of items on the tDCS experience questionnaire. The groups did not differ on their endorsement of five of the six items (**Fig. 17**). Participants in the sham group reported an *increased* difficulty concentrating relative to the two active groups (i.e., anodal and cathodal). Notably, 59% of participants in the sham condition, 69% in the anodal condition and 83% in the cathodal condition reported experiencing "sensations like pain, tingling, itching, or burning under the electrodes during or after stimulation," the difference in group endorsement for that item was not significant. In sum, these results indicate that the blinding procedure was successful such that participants in the sham condition believed that they were receiving active stimulation.

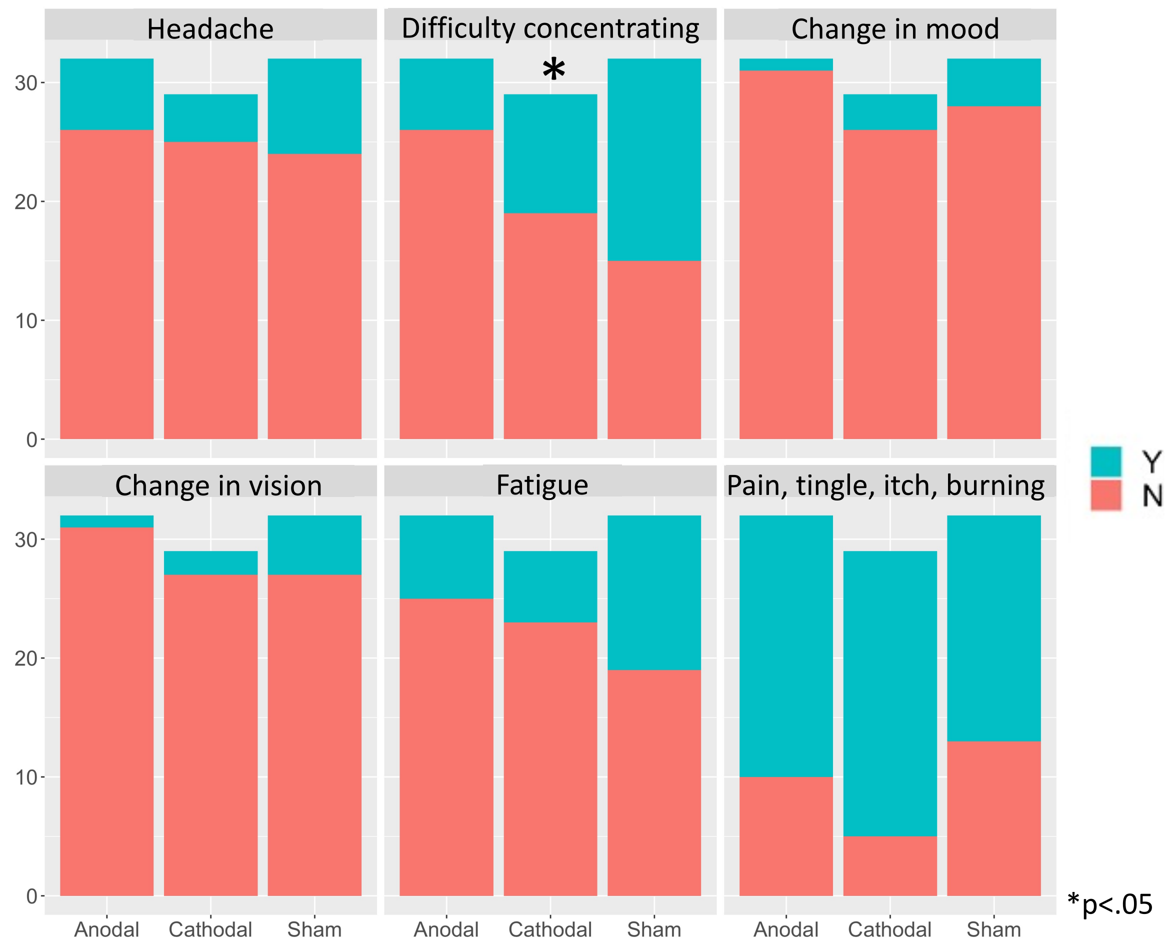

Fig. 17. TDCS questionnaire endorsement (Yes/No) per group. A difference between the sham and anodal/cathodal groups was observed only for one item, for which participants in the sham condition endorsed experiencing difficulty concentrating at a higher rate than participants in the two active conditions.

DISCUSSION

First, our results confirm the specific link between positive schizotypy and the subjective experience of the RHI previously documented. Consistent with previous studies, we found that positive schizotypy predicted the strength of the subjective experience of the illusion (Asai et al., 2011; Germine et al., 2013; Thakkar et al., 2011). We note that Asai et al. (2011) also found a link between positive schizotypy and proprioceptive drift, though this finding was not replicated in our study or others (Thakkar et al., 2011; Germine et al., 2013). In sum, our study confirms the specific link between positive schizotypy and the subjective experience of the RHI in the largest sample to date.

Our results also suggest a protective role of negative schizotypy on the susceptibility to the illusion. In fact, Constricted Affect (which loads onto the Interpersonal/negative schizotypy factor of the SPQ) predicted a smaller proprioceptive drift and negative schizotypy was associated with lower odds of agreement with the first RHI questionnaire item ("It seemed as if I were feeling the touch of the paintbrush where I saw the rubber hand"). These findings however contrast with those of Thakkar et al. (2011) who documented a positive relationship between negative schizotypy and RHI sensitivity in N=21 control participants. We note the parallel between this novel finding and that of delayed RHI sensitivity in ASD (Cascio et al., 2012). In fact, Interpersonal schizotypy is associated with autistic features in the general population (Dinsdale et al., 2013), and children with ASD were shown to experience the illusion only after 6 minutes of brushing. In our study, the tactile stimulation occurred for 4 minutes and we did not record time to onset of the illusion. Thus, it is possible that, analogous to autistic traits, negative schizotypy delays the experience of the illusion. In short, our findings suggest that negative schizotypy, like autistic features, predict decreased RHI, though this is uncorroborated by previous studies and therefore remains to be replicated.

Our study is the first to document a link between self-reported bodily self-disturbances and sensitivity to the RHI, thereby bridging the gap between empirical and phenomenological research. We found that bodily disturbances (measured using the PAS, MUSEQ SP and MUSEQ BS) correlated with RHI sensitivity measured both objectively and subjectively. This novel finding is particularly important as it begins two bridge two areas of research that have been historically separated: (1) the quantification of phenomenological experiences via self-report measures and (2) the assessment of experimentally induced bodily disturbances. These two types of assessment answer fundamentally different questions such that self-report instruments aim at understanding and quantifying the holistic experience of anomalous sense of body ownership while experimental tasks aim at isolating the mechanisms underlying body ownership disturbances. To date, research in these two areas remains largely disconnected, resulting in a lack of consensus in the conceptualization of body ownership. By showing that self-reported bodily disturbances correlate with the RHI, we begin bridging this gap. Our results suggest that the phenomenological experience of body ownership disturbances captured in self-report instruments and the malleability of one's sense of body ownership measured by the RHI are, in fact, related.

In the second, more exploratory part of our study, we attempted to experimentally manipulate individual sensitivity to the RHI using tDCS. Contrary to our expectations, we did not find evidence suggesting that rTPJ activation (i.e., anodal) or deactivation (i.e., cathodal) differentially affected sensitivity to the RHI measured objectively or subjectively. In contrast, we found a uniform decrease in RHI sensitivity from PRE to POST, suggesting a habituation effect after repeated induction of the RHI. This finding is inconsistent with a previous study documenting a learning effect of the RHI such that control individuals experienced the illusion quicker and more strongly over repeated trials (Lev-Ari et al., 2015). In that study, the experimenters preformed the RHI trials on different days over a 2-week period. In contrast, we performed the two RHI trials (i.e., PRE and POST) within the same 1.5-hour testing session. Thus, it is possible that our trials were too close in time for learning to occur. Our finding instead suggests that in the short-term, repeated RHI trials might lead to habituation such that the sensitivity to the illusion is temporarily inhibited. A temporary reduction of RHI sensitivity could explain our null results.

The heterogeneity in sensitivity to the RHI in the general population might have also contributed to the lack of measurable effect of rTPJ modulation on RHI sensitivity in our study. In fact, only 55% of our participants had a reliably positive proprioceptive drift at baseline, and only 67% endorsed at least three out of nine of the subjective experiences surveyed in the RHI questionnaire. This heterogeneity in individual sensitivity to the RHI is consistent with other studies. For instance, after pre-testing 54 potential participants to assess RHI sensitivity, Sciortino and Kayser (2021) retained only 24 (i.e., 44%) RHI responders in their recent study. Thus, only about half of the general population experiences the RHI. This variability in RHI sensitivity might have been particularly problematic in our study given that tDCS can have differential effects depending on individual characteristics. For instance, in a visual working memory paradigm, only low performers benefitted from tDCS stimulation of the posterior parietal cortex (Hsu et al., 2014). Thus, it is possible that only a subgroup of individuals respond to rTPJ stimulation, but our sample was too heterogenous to capture this isolated effect. In an attempt to address this issue, we replicated the between-group analyses after excluding RHI non-responders. However, our results remained unchanged, which might be due to the reduced sample size of these follow-up analyses, resulting in low power. Future research aiming at manipulating individual sensitivity to the RHI might benefit from pre-testing potential participants to select a reliable subset of RHI responders and testing them following tDCS on a different day to avoid the potential short-term habituation to the RHI.

Another important consideration in understanding our null results is that of the specific role of the rTPJ in the sense of body ownership. In a Transcranial Magnetic Stimulation (TMS) study, Tsakiris et al. (2008) showed that the rTPJ was responsible for the comparison between incoming sensory stimuli (i.e., seeing the rubber hand being brushed) and the mental representation of the body (i.e., what does my hand look like) to ensure a match between the to-be-embodied object and the internal model of the body. In fact, after disrupting rTPJ activity, Tsakiris et al. (2008) found that participants could experience ownership over a neutral, non-hand-like object, suggesting that the rTPJ ensures the distinction between body and non-body objects. Our use of the traditional setup of the RHI (i.e., a rubber hand) prevented us from capturing differences in one's ability to embody non-body objects as a result of rTPJ stimulation. Thus, it is possible that tDCS over the rTPJ did indeed affect one's sense of body ownership, but our experimental design was ill-equipped to capture this specific disruption (i.e., reduced contribution of the body model).

We also note the limitation of the reductionist approach we (in line with other experimental psychologists) used to study body ownership. Tsakiris (2010) proposed a neurocognitive model of body ownership which emphasizes the interaction between multisensory input and internal models. This model involves a network of brain regions whose contributions interact to create the phenomenological sense of body ownership. For instance, the parietal and premotor cortices underlie body-related multisensory integration, and the right insular lobe gives rise to the subjective experience of the RHI (Tsakiris, 2010). Thus, the rTPJ is only one node of a network of brain regions giving rise to the sense of body ownership. By targeting a single region, we neglected to consider the phenomenon as a whole, which is a common limitation to the empirical study of self-disturbances. Future research might benefit from a multi-methods approach considering all aspects of, and mechanisms underlying, body ownership.

In sum, in the first part of this study, we replicated the finding of positive schizotypy predicting an increased sensitivity to the subjective experience of the RHI and found evidence suggesting that negative schizotypy could, in contrast, protect against individual sensibility to the illusion. Our baseline analysis also revealed a significant relationship between self-reported bodily disturbances and both the subjective and objective experience of the RHI, thereby beginning to bridge the gap between phenomenological and experimental psychology. In the second, more exploratory part of our study, we failed to find a causal relationship between experimental modulation of rTPJ activity and individual sensitivity to the RHI. This null result might be explained by experimental limitations.

CHAPTER V

General Discussion

SUMMARY

Though disembodiment has long been considered central to schizophrenia, current conceptualizations of the disorder ignore bodily self-disturbances, rather focusing on positive and negative symptoms (APA, 2013). By favoring clinical reliability over construct validity, contemporary psychiatry has not only lost the core of the disorder, but also hindered treatment progress. In fact, current treatment guidelines for schizophrenia recommend second-generation antipsychotic medication to target positive symptoms and psychosocial interventions to address negative symptoms (NICE, 2014). However, one to two thirds of patients show an inadequate response to medication (e.g., Kane et al., 1988, Samara et al., 2019), and the efficacy of psychosocial treatments remains limited (Jauhar et al., 2019; Jones et al., 2018; McKenna et al., 2019).

Given the limitations of current treatments for schizophrenia, research efforts have recently shifted to focus on early identification of individuals at risk for psychosis and the development of prevention programs to reduce the burden associated with the disorder. Individuals with high schizotypy have been reliably found to exhibit sub-threshold symptoms (i.e., cognitive, perceptual and behavioral anomalies, as well as bodily disturbances) that can be used to predict risk for transition to a schizophrenia-spectrum disorder (Barrantes-Vidal et al., 2013; Kwapil et al., 2013). However, mirroring the current conceptualization of schizophrenia, common instruments used to assess risk for psychosis exclusively rely on psychotic-like experiences, especially auditory hallucinations and delusions, rather than bodily disturbances. For instance, the Structured Interview for Psychosis-Risk Syndromes (SIPS; McGlashan et al., 2001) surveys positive, negative, disorganized, and general symptoms, but only positive symptoms are considered in determining psychosis-risk status. Bodily disturbances, which have been documented in prodromal individuals and shown to predict transition in at-risk populations (Nelson et al., 2008; Nelson et al., 2012), are not yet used to assess risk. This might be due to remaining gaps in the literature documenting embodiment deficits in the schizophrenia spectrum. The research program in this dissertation addressed these gaps by investigating several aspects of the bodily self (i.e., interoception, emotional embodiment, body ownership) in individuals with schizophrenia in relation to schizotypy.

Given the role of interoception in embodiment and the lack of empirical research systematically investigating interoceptive ability across the schizophrenia spectrum, in **Study 1** we empirically measured the three dimensions of interoception in individuals with schizophrenia (**1A**) and in schizotypy (**1B**). We found that individuals with schizophrenia have low interoceptive accuracy and report differences in the subjective experience of their interoceptive experiences (i.e., interoceptive sensibility). For the first time, our work revealed intact interoceptive awareness in individuals with schizophrenia. Against our expectations, we found no link between schizotypy and interoceptive functioning in the general population, which suggests that changes in interoception may only arise with the onset of psychosis. These result reveal interoceptive dysfunction as a particularly appealing target for early intervention in prodromal populations. Furthermore, individuals with schizophrenia appear to be aware of their interoceptive deficits (i.e., intact interoceptive awareness), which might promote treatment seeking behavior and encourage treatment engagement.

In **Study 2**, we used a topographical mapping tool to investigate emotional embodiment in relation to schizotypy. We found that individuals with high positive schizotypy experience embodied emotions with higher intensity but lower clarity, and endorse more incongruent bodily sensations of emotions. In line with the anomalous emotional embodiment documented in individuals with schizophrenia (Torregrossa et al., 2019b), we found that these differences were particularly notable for low arousal emotions. The functional impact of these emotional embodiment differences remains unclear and longitudinal work is needed to link them to the anomalous bodily sensations of emotions documented in schizophrenia.

In **Study 3** we investigated body ownership in relation to schizotypy and explored the effectiveness of rTPJ modulation in altering one's sense of body ownership. We confirmed the link between positive schizotypy and the subjective experience of the RHI and found a protective role of negative schizotypy against RHI sensitivity. Our study also empirically linked, for the first time, the phenomenological experience of bodily disturbances (i.e., measured using self-report questionnaires) and the experimentally measured sense of body ownership. In the second part of this study, we failed to find an effect of rTPJ modulation on individual sensitivity to the illusion. In interpreting these null results, we highlighted the limitations of the reductionist approach experimental psychologists apply to the study of self-disorders (i.e., isolating one mechanism thus failing to consider the phenomenological experience as a whole).

Together, these findings suggest that some mild bodily disturbances (i.e., anomalous emotional embodiment and impaired body ownership), analogous to those observed in schizophrenia, exist in individuals with elevated schizotypy. This is consistent with the body of literature already linking agency deficits to schizotypy (Asai & Tanno, 2007; Asai & Tanno, 2008; Moore et al., 2020). Importantly, interoceptive functioning does not systematically vary with schizotypy, such that interoceptive dysfunction might be a marker of prodromal onset in the schizophrenia course of illness.

FUTURE DIRECTIONS

An important question that remains to be answered is whether bodily disturbances discriminate individuals with high schizotypy who will transition to a schizophrenia-spectrum illness from those who will not. Though bodily-self disturbances were shown to predict transition to a schizophrenia-spectrum illness in prodromal youths (Nelson et al., 2012), the specific aspects of the bodily self affected remained unknown, and it was unclear if these disturbances preceded the prodrome. This dissertation addressed these questions by empirically investigating different aspects of embodiment (i.e., interoception, emotional embodiment, and body ownership) in relation to schizotypy. Our results show that in the general population, interoception is not linked to schizotypy but individuals with high schizotypy do exhibit mild anomalies in emotional embodiment and body ownership. This could suggest that interoceptive dysfunction only develops in the minority of individuals with high schizotypy who will develop a schizophrenia-spectrum illness whereas emotional embodiment and body ownership systematically vary across the schizotypy spectrum regardless of risk status. However, longitudinal designs are needed to test this hypothesis. In sum, future research should investigate whether early bodily disturbances differentiate those who transition from those who do not.

The mechanisms underlying embodiment differences in those with high schizotypy also remain unknown. The null results in Study 1B (i.e., no link between schizotypy and interoception) suggest that the early bodily disturbances documented in schizotypy in other studies (i.e., Study 2: emotional embodiment, Study 3: body ownership) do not stem from interoceptive dysfunction. As such, the mechanisms underlying embodiment differences related to schizoptypy remain to be uncovered. Given the variety of factors linked to disembodiment in schizophrenia (i.e., exteroceptive and interoceptive sensory processing, multisensory integration, internal models, prediction), a number of candidates exist for future research to explore (e.g., Klaver & Dijkerman, 2016; Postmes et al., 2014; Tsakiris, 2010).

Though this dissertation largely focused on bottom-up aspects of bodily disturbances, top-down contributions are also crucial to the self-experience. For instance, recent predictive models of interoception posit that interoceptive experiences result from predictions regarding the expected state of the body given the internal signals (e.g., my stomach is growling, therefore I must be hungry; Barrett & Simmons, 2015). In line with this predictive model of interoception, Seth (2013) argues that both emotional experiences and body ownership result from interoceptive inference. More specifically, affective experiences are thought to result from active inferences regarding the cause of interoceptive signals (e.g., I predict that my elevated heart rate results from my upcoming dissertation defense, which makes me feel nervous). In alexithymia, the predictive representation of the bodily sensations of emotions is therefore believed to be weakened (Bonaz et al., 2021). Seth (2013) also highlights the role of interoceptive prediction in our sense of body ownership such that body ownership results from predictive multisensory integration of exteroceptive and interoceptive signals (Seth, 2013). This is consistent with the neurocognitive model of body ownership proposed by Tsakiris (2010), which posits that incoming sensory information is compared to internal models of the body before an object/body part can be considered “mine.” Thus, future work should also consider the role of top-down processes (e.g., interoceptive prediction) in bodily-self disturbances in the schizophrenia spectrum.

Lastly, we encourage empirical research to continue bridging the gap between experimental and phenomenological accounts of bodily disturbances. We argue that though distinct, the various components of the bodily self (i.e., body ownership, agency, first person perspective, self-location) work in conjunction to yield a holistic sense of the self. This view is consistent with neuroimaging evidence suggesting different neural pathways for different aspects of self-experience (Serino et al., 2013) and makes intuitive sense as various aspects of the bodily self are easily distinguishable at the phenomenological level (e.g., I own a body ≠ I am the initiator of my actions ≠ I see the world through my eyes). This view is also in line with clinical observations of phenomena like out-of-body experiences and the Alien Hand Syndrome. To continue gaining insight into the holistic experience of the bodily self and its disturbances, we encourage experimental psychologists to explore different aspects of the self-experience in conjunction rather than in isolation. To this end, future experimental studies should empirically measure various aspects of the bodily self (i.e., body ownership, self-location, agency, first person perspective) in the same cohort. We also note that though useful to elucidate the nature and trajectory of disembodiment in schizophrenia, isolating the mechanisms underlying different aspects of the bodily self might not yet be well suited to clinically target the holistic experience of self-disorders, as evidenced by our unsuccessful attempt at altering one’s sense of body ownership using rTPJ neuromodulation in Study 3.

CLINICAL CONSIDERATIONS

Body-based Interventions

Given the central role of bodily disturbances in schizophrenia phenomenology, body-based interventions might be particularly relevant in this population. A recent review revealed a robust effect of a variety of body-centered interventions on both physical and psychological symptoms across a variety of clinical populations (Tarsha et al., 2020). Movement (i.e., dance, emotional freedom technique, yoga, body awareness therapy) and non-movement (i.e., massage therapy, functional relaxation, reflexology, acupuncture, rolfing) body interventions were indeed found to decrease stress, pain, and mental health symptoms (e.g., depression, anxiety) across a variety of psychological conditions. We briefly review the application of these interventions to the treatment of schizophrenia.

Dance/movement therapy (DMT) is the "the psychotherapeutic use of movement to promote emotional, social, cognitive, and physical integration of the individual, for the purpose of improving health and well-being" (ADTA, 2018). A recent review reported consistent beneficial effects of DMT on psychological outcomes across different diagnoses (Koch et al., 2019). Studies specifically investigating the efficacy of DMT as a treatment for schizophrenia found that the intervention decreased anger and depression, and improved negative symptoms in this population (Lee et al., 2015; Martin et al., 2016). DMT was also found to improve psychological well-being (Pohmann et al., 2017) and promote functional remission (Gökcen et al., 2021) in individuals with schizophrenia.

Exercise programs have long been considered an effective treatment for a variety of symptoms of schizophrenia (for reviews see: Biddle, 1999; Girdler et al., 2019; Gorczynski &

Faulkner, 2010). In a large-scale meta-analysis, exercise was found to improve clinical symptoms (i.e., positive, negative, and general), quality of life and global functioning while decreasing depression in individuals with schizophrenia (Dauwan et al., 2013). The literature also reliably documents a beneficial effect of aerobic exercise on cognition (Firth et al., 2017; Kimhy et al; 2015). In a randomized-controlled trial (RCT), physical exercise and Tai-chi were found to improve clinical symptoms, memory, and motor coordination in schizophrenia (Ho et al., 2016). In light of the wealth of evidence for the beneficial effects of exercise in schizophrenia, Yung and Firth (2017) argue that exercise should be an integral part of schizophrenia treatment routinely used in conjunction to medication and psychotherapy.

Yoga has also been shown to improve schizophrenia symptomatology. Two Cochrane reviews investigated the efficacy of yoga on several metrics of mental health (i.e., symptoms, social functioning, quality of life) in schizophrenia. The first one found moderate evidence in favor of yoga over standard care for schizophrenia (Broderick et al., 2015), the second found no clear evidence for the advantage of yoga versus other non-standard interventions (i.e., aerobic exercise) in treating schizophrenia (Broderick et al., 2017). Other reviews found moderate evidence for short-term effects of yoga on quality of life (Cramer et al., 2013) and a robust effect of yoga on improvement of long-term memory (Dauwan et al., 2013). A recent RCT suggests that yoga might be useful in reducing negative symptoms of schizophrenia when used as an add-on to standard care (Rao et al., 2021).

Body psychotherapy is a type of therapy that combines elements of psychodynamic theory, DMT, and techniques designed to address body image disturbances (Röhricht, 2009). A RCT documented a significant improvement of negative symptoms that lasted for up to four months following 20 sessions of body psychotherapy (Röhricht & Priebe, 2006). In contrast, Priebe et al. (2016) found no consistent evidence for the effect of body psychotherapy on negative symptoms of schizophrenia. However, a re-analysis of the data revealed an important gender effect such that body psychotherapy reduced negative symptoms in women, but not men, with schizophrenia (Savill et al., 2017).

Basic Body Awareness Therapy (BBAT) is rooted in Tai-chi tradition and uses body movement to improve the sense of body ownership and the tolerance for a range of sensory and affective sensations. BBAT was shown to improve self-efficacy, coping, and sleep in patients treated on an outpatient basis (Gyllensten et al., 2003). Though BBAT was originally introduced in a doctoral thesis focused on schizophrenia rehabilitation (Roxendal, 1985), surprisingly few studies have explored the efficacy of BBAT in schizophrenia treatment. A qualitative analysis identified four categories in which individuals with schizophrenia reported improvement following BBAT: affect regulation, body awareness and self-esteem, social functioning, and cognition (Hedlund, 2010).

In sum, body-based interventions were consistently shown to improve a variety of schizophrenia symptoms. Across body-based interventions, the effects on negative symptoms seems to be the most robust. According to NICE, art therapy (e.g., DMT) is in fact the only type of intervention that reliably reduces negative symptoms in schizophrenia (NICE, 2014). Surprisingly, the vast majority of studies investigating body-based interventions in schizophrenia did not assess the effect of their intervention on embodiment. The study exploring the effect of BBAT (i.e., a type of psychotherapy specifically designed to improve embodiment) in schizophrenia is a notable exception (Hedlund, 2010).

Postmes et al. (2014) proposed a model of schizophrenia as a self-disorder due to perceptual incoherence. The authors suggest that individuals with schizophrenia might therefore benefit from interventions aimed at improving sensory processing (Postmes et al., 2014). We argue that body-based interventions, which have already been shown to improve cognition, clinical symptoms, and psychosocial outcome in schizophrenia, might be particularly well suited to target bodily disturbances, though this remains to be empirically tested. Some also argue that traditional behavioral interventions, such as behavioral activation, might also be efficient in targeting bodily-self disturbances in schizophrenia (Tschacher et al., 2017).

Psychotherapy Considerations

We also urge therapists to consider self-disturbances in their treatment plan and delivery. In a recent article, we suggested targeting the core phenomenological features of psychotic illnesses in sessions by 1. Focusing on the form/structure of cognitions rather than their content 2. Valuing implicit and nonverbal intersubjectivity (e.g., encouraging community-based activities) and 3. Increasing the sense of self-presence using body-oriented strategies (Nelson, Torregrossa et al., 2020). We also encouraged clinicians to address the self-other relationship to improve social disconnection and loneliness, and suggested the use of novel techniques (i.e., virtual reality, bio- or neuro-feedback) to increase therapeutic gains (Nelson et al., 2020).

Other phenomenologically oriented researchers and clinicians have offered guidelines for the treatment of schizophrenia as a disorder of the self. Against the CBT principle of “reality testing” which assumes a common “reality” shared by the clinician and their client, phenomenologists encourage clinicians to accept their client’s experiences as real rather than attempting to correct them, which reportedly could enhance therapeutic gain and alliance

(Humpston & Broome, 2020; Irarrázaval, 2013). Practically, Humpston and Broom (2020) urge clinicians to "listen more carefully with an open mind" while focusing on psychoeducation. Stanghellini and Lysaker (2006) further posit that reflecting the client's experience (e.g., "it's scary") back using the second-person perspective (e.g., "*you* are scared") will help them develop a sense of subjectivity (i.e., first person perspective), which will in turns help them navigate the social world. Lysaker et al., (2011) argue that metacognitive interventions promote the development of self-reflection. These considerations are particularly important not only because self-disorders are central to the schizophrenia experience, but also because they directly impact the therapeutic encounter. In fact, disembodiment compromises synchrony, which plays a large role in the therapeutic relationship and alliance (Tschacher et al., 2017).

CONCLUSION

To conclude, this dissertation examined the role of the bodily self in the phenomenology of the schizophrenia spectrum. Across three studies, we showed that though *dis*embodiment is at the core of the schizophrenia experience, the role of bodily disturbances in schizotypy is more ambiguous. In fact, while a link was identified between positive schizotypy and mild embodiment differences (i.e., bodily sensations of emotions, body ownership), none were observed between schizotypy and interoceptive functioning. Our findings also suggest a potentially protective role of negative schizotypy against body ownership disturbances, though this remains to be confirmed.

Close to three decades ago, Chapman et al. (1994) found that bodily aberrations predicted schizophrenia onset. This dissertation begins to elucidate the specific aspects of embodiment that might be relevant to predicting psychosis risk. Our findings suggest that some aspects of emotional embodiment and body ownership might be endophenotypes of schizophrenia (i.e., shared by all those who carry a latent liability for schizophrenia) while interoceptive dysfunction might selectively affect those who have a schizophrenia spectrum illness. In line with the categorical model of schizotypy, this would suggest that some aspects of schizophrenia liability are not continuous in the general population (i.e., interoceptive ability does not systematically vary with risk for psychosis, but interoceptive dysfunction emerge as a biomarker for those with manifest schizophrenia spectrum characteristics). Studies examining interoceptive functioning in clinical-high risk populations (i.e., help-seeking prodromal individuals) will be needed to determine whether interoceptive dysfunction develops prior to schizophrenic illness. Such a finding would suggest that risk assessment measures for schizophrenia spectrum disorders need to be revised to include, or focus on, bodily disturbances to more accurately identify youths at risk for psychosis. Lastly, it is important to note that the continuum model of the schizophrenia spectrum and a more categorical framework are not mutually exclusive. Furthermore, both models are theoretically and clinically valuable for understanding the nature of psychosis.

We hope that this work will inspire more research on the nature and etiology of self-disorders in the schizophrenia spectrum. In the meantime, we encourage clinicians to incorporate the phenomenology of the illness into their case conceptualizations and treatment plans, perhaps by employing body-based interventions to target the embodiment deficits that are so central to their client's everyday experiences.

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