



Review article

Neuroimaging the consciousness of self: Review, and conceptual-methodological framework



Paul Frewen^{a,*}, Matthias L. Schroeter^b, Giuseppe Riva^{c,d}, Pietro Cipresso^{c,d}, Beth Fairfield^e, Caterina Padulo^e, Andrew Haddon Kemp^f, Lena Palaniyappan^g, Mayowa Owolabi^h, Kwabena Kusi-Mensahⁱ, Maryna Polyakova^j, Nick Fehertoi^k, Wendy D'Andrea^k, Leroy Lowe^l, Georg Northoff^m

^a Departments of Psychiatry, Psychology and Neuroscience at the University of Western Ontario, London, Ontario, Canada

^b Neurology Department, Max Planck Institute for Human Cognitive and Brain Sciences & Clinic for Cognitive Neurology, University Hospital Leipzig, Germany

^c Applied Technology for Neuro-Psychology Lab., Istituto Auxologico Italiano, 20145, Milan, Italy

^d Center for Communication Psychology, Università Cattolica del Sacro Cuore, 20123, Milan, Italy

^e Department of Psychological, Health and Territorial Sciences, University of Chieti, Italy

^f Psychology, Swansea University, Swansea, Wales, United Kingdom

^g Robarts Research Institute and Department of Psychiatry, University of Western Ontario, London, Ontario, Canada

^h Department of Medicine, College of Medicine, University of Ibadan, Ibadan, Oyo State, Nigeria

ⁱ Department of Psychiatry, Komfo Anokye Teaching Hospital, Kumasi, Ghana

^j Neurology Department, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

^k The New School for Social Research, New York, NY, United States

^l Neuroqualia (NGO), Truro, Nova Scotia, Canada

^m Mind, Brain Imaging and Neuroethics Research Unit, University of Ottawa Institute of Mental Health Research, Royal Ottawa Mental Health Centre, Canada

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ABSTRACT

We review neuroimaging research investigating self-referential processing (SRP), that is, how we respond to stimuli that reference ourselves, prefaced by a lexical-thematic analysis of words indicative of “self-feelings”. We consider SRP as occurring verbally (V-SRP) and non-verbally (NV-SRP), both in the controlled, “top-down” form of *introspective* and *interoceptive* tasks, respectively, as well as in the “bottom-up” spontaneous or automatic form of “mind wandering” and “body wandering” that occurs during resting state. Our review leads us to outline a conceptual and methodological framework for future SRP research that we briefly apply toward understanding certain psychological and neurological disorders symptomatically associated with abnormal SRP. Our discussion is partly guided by William James’ original writings on the consciousness of self.

1. Introduction

How do I feel? In asking yourself this question you may note that the syntactic structure of “I feel X” statements intrinsically implicates first-person self-referential processing, that is, feelings seem to inherently refer to a self *that* feels. Moreover, most of the words that will logically and grammatically fit the “I feel X” syntax will equally fit an “I am X” structure (e.g., “I feel happy” and “I am happy”). Thus, it appears that “feelings” and SRP tend to go hand in hand in both conscious subjective experience and the language we use to communicate our experiences to each other.

This essay reviews functional neuroimaging (functional magnetic resonance imaging [fMRI], electroencephalographic [EEG] and non-

invasive brain stimulation [NIBS]) research investigating self-referential processing (SRP), that is, how we respond to stimuli that reference ourselves, including a focus on the relevance of SRP for affective neuroscience, that is, for understanding “self-feelings”. We conduct a qualitative review that is prefaced by a lexical-thematic analysis of words indicative of self-feelings (Siddharthan et al., 2018) and makes some additional observations using automated keyword-based meta-analyses (Yarkoni et al., 2011) and resting-state functional connectivity (RSFC) analyses (Yeo et al., 2011) using the neurosynth.org database. These exercises lead us to outline a new conceptual and methodological framework that we hope could help guide future SRP research.

In brief, our review is anchored by two psychological principles. First, broadly speaking, we posit that there are at least two natural

* Corresponding author.

E-mail address: pfrewen@uwo.ca (P. Frewen).

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kinds of SRP, specifically, SRP as it occurs in the “mind”, that is, via the *verbal* modality (V-SRP), and SRP as it occurs in the “body”, that is, via the *nonverbal* (NV-SRP) modality; some readers may prefer the terms “semantic” vs. “somatic” SRP, respectively, which we will also use interchangeably. Regarding NV-SRP, we will also differentiate between internal (or “inner”) vs. external (or “outer”) bodily self-consciousness (BSC). Secondly, we will posit that SRP of each kind occurs largely independently (in parallel) via “bottom-up” pathways. However, we will also posit that each kind of SRP can become the object of “top-down” attention via executive control processes. Much of our conceptual framework finds explicit precedent in the Jamesian (James, 1890) tradition on understanding self-feelings and the consciousness of self, to which we make explicit reference in several sections.

The organization of this essay is as follows. First, we consider a consensus definition of “feelings” (Siddharthan et al., 2018) and its specific application to “self-feelings”, including the results of our lexical-thematic analysis and its comparison with the writings of William James (James, 1890) on the same subject. This discussion leads us to the notion that SRP might occur either primarily verbally (V-SRP) or non-verbally (NV-SRP) as referring to semantic vs. somatic stimuli or “self-objects”. Second, we overview human neuroimaging (fMRI and EEG) studies and non-invasive brain stimulation (NIBS) studies that have investigated “top-down” V-SRP and NV-SRP tasks in the form of *introspection* and *interoception*, respectively, where the study conducted by Araujo and Damasio and their colleagues (Araujo et al., 2015) is discussed at length as a particularly good example. Third, we overview human neuroimaging and NIBS studies that have investigated “bottom-up” V-SRP and NV-SRP occurring during the “mind-wandering” and “body-wandering” that frequently occurs during “resting state”. Fourth, we consider the role of executive control in SRP, not only during task-focused attention and central executive processing as constitutive of an “agentic self” but also as focused toward resting state, the latter likened to the practice of mindfulness meditation as the workings of an “observing self”. Fifth, we outline a conceptual framework for understanding SRP in its verbal (V-SRP) and non-verbal (NV-SRP) forms with reference to an “attentional spotlight” within the “theatre of consciousness” metaphor (Baars, 1989, 1999) and a methodological framework based on the comparison of brain regions of interest (ROIs) identified through conjunction analyses that compares response occurring during task-focused SRP, SRP occurring during resting state, and response occurring during non-SRP tasks, extrapolating from the excellent study conducted by Davey and colleagues (Davey et al., 2016, 2015). Finally, we briefly apply this framework towards classifying certain psychological and neurological disorders that are symptomatically associated with abnormal SRP. In so doing we seek to contribute an integrative conceptual and methodological approach to understanding SRP and self-feelings that is generally in keeping with the Jamesian view on the consciousness of self.¹

¹Our review is being undertaken as part of the ‘The Human Affectome Project’ (henceforth, simply the “project”), an initiative organized in 2016 by a non-profit organization called “Neuroqualia” aiming to produce a series of overarching reviews that can summarize much of what is currently known about affective neuroscience while simultaneously exploring the language that we use to convey our feelings. The project is comprised of twelve teams that are organized into a taskforce that is focused on the development of a comprehensive and integrated model of affect that can serve as a common focal point for affective research in the future. To that end, our team was specifically tasked to review the neuroscience research related to “the self” and the language that people use to express feelings that relate to the self, including consideration of a lexical-thematic analysis of self-feeling words. We were further asked to consider whether or not the feelings that people convey in language might inform the way we approach self-related neuroscience research. We were also asked to identify the relationships that exist between the self and the other areas of affective research within this special issue (i.e., Physiological, Social, Anticipatory, Actions, Attention, Motivation, Anger, Fear, Sadness, Happiness,

2. Self-related feelings in mind and body: a lexical-thematic analysis referencing William James’ psychological principles on the consciousness of self

Lay intuition would suggest that in attending toward ourselves, that is, engaging in self-referential processing (SRP), at any given moment we will primarily emphasize either our “mental” or our “bodily” based sense of self. Indeed this differentiation between SRP into a verbal-semantic form versus a nonverbal-somatic form has long precedent in philosophy, psychology, and neuroscience. For example, among the best known philosophical treatises on self and consciousness, Rene Descartes, in his *Meditations*, presumed to find proof of his own existence exclusively in verbal SRP: *cogito ergo sum* (I think, therefore I am) was for him “so certain and of such evidence that no ground of doubt, however extravagant, could be alleged by the sceptics capable of shaking it”. Further, Descartes differentiated verbal SRP from nonverbal SRP: “that *I*, that is to say, the mind by which I am what I am, is wholly distinct from the body, and is even more easily known than the latter”. Further, although the extreme metaphysical interpretation of Descartes’ dualism that our minds (or subjective consciousness) might potentially exist entirely independent of our bodies holds little sway among most present day cognitive neuroscientists, the more restricted interpretation that the neural representations constitutive of the *experience* of mind vs. body might be rather different remains empirically defensible, as will be detailed herein.

Nearly equally well known, William James (James, 1890) investigated the nature of SRP in the tenth chapter of his *Principles of Psychology* which he titled “Consciousness of Self”. James distinguished a “spiritual self” (which was essentially psychological in nature; i.e., verbal) from a “material self” (which was physical in nature; i.e., nonverbal). He described “The body [as] the innermost part of the *material Self* in each of us” (p. 292) while, regarding the spiritual self, he noted: “our considering the spiritual self at all is a reflective process, is the result of our abandoning the outward-looking point of view, and of our having become able to think of subjectivity as such, to *think ourselves as thinkers*” (p. 296, italics original). However, contrary to Descartes’ position, James believed that we know ourselves most fundamentally through *feelings* rather than thought: “For this central part of the Self is *felt*... it is at any rate no *mere ens rationis*, cognized only in an intellectual way, and no *mere* summation of memories or *mere* sound of a word in our ears. It is something with which we also have direct sensible acquaintance... when it is found, it is *felt*; just as the body is *felt*...” (p. 298–299, italics original).

Referring to the kinds of self-feelings we might become aware of, James (1890) provided a parsimonious framework in distinguishing between a mere two affective valence-based categories, essentially positive self-feelings in comparison with negative self-feelings that he termed “*self-complacency*” and “*self-dissatisfaction*”, respectively (p. 305). He considered that: “Language has synonyms enough for both primary feelings. Thus pride, conceit, vanity, self-esteem, arrogance, vain, glory, on the one hand; and on the other modesty, humility, confusion, diffidence, shame, mortification, contrition, the sense of obloquy and personal despair.” He concluded that “these two opposite classes of affection seem to be direct and elementary endowments of our nature” (p. 306) suggesting that he conceived of self-feelings as natural kinds and biologically based. Moreover, he emphasized that self-feelings can express not only as brief states but also as more enduring traits: “there is a certain average tone of self-feeling which each one of us carries about with him, and which is independent of the

(footnote continued)

and Hedonics) and to summarize future research needs. We agree with the advisory board of the project that no treatise concerning the neuroscience of subjective feelings can be complete in absence of discussing the role of self-referential processing and self-feelings.

objective reasons we may have for satisfaction or discontent” (p. 306). This suggests that he believed a constitutional predisposition toward certain self-feelings might form the basis of personality structures and vulnerability to affective disorders. Additionally, he considered that most will be aware of the valence of the feelings with which they regard themselves, a matter that interestingly he seems to attribute primarily to NV-SRP rather than V-SRP: “And in fact we ourselves know how the barometer of our self-esteem and confidence rises and falls from one day to another through causes that seem to be visceral and organic rather than rational” (p. 307). While such a quotation might apply just as easily to general emotional states that have no particular reference to the self other than the fact that a person experiencing an emotion can always attribute that emotion to him or herself, its use in James’ psychological principles on consciousness of self suggests a particular relevance for understanding self-feelings. He also supposed that positive and negative self-feelings class among the basic emotions, having a characteristic behavioural and physiological expression: “The emotions themselves of self-satisfaction and abasement are of a unique sort, each as worthy to be classed as a primitive emotional species as are, for example, rage or pain. Each has its own peculiar physiognomical expression.” (p. 307). In this case, he presupposed the relevance of an affective neuroscience approach to better understand self-feelings. Finally, he considered the social and moral implications of self-feelings. Considering the former he related that: “Our *social self-seeking* is carried on directly through our amateness and friendliness, our desire to please and attract notice and admiration, our emulation and jealousy, our love of glory, influence, and power” (p. 308, italics original). In comparison, regarding the latter he described: “It is only the search of the redeemed inward nature, the spotlessness from sin, whether here or hereafter, that can count as *spiritual self-seeking* pure and undefiled” (p. 309, italics added).

Our thematic and lexical analysis of “feeling” words determined to be thematically descriptive of “self” as a theoretical construct tended also to naturally differentiate into words that were self-referential primarily either in reference to psychological versus physical-bodily substrates (Siddharthan et al., 2018) that were of either generally positive or negative valence. Using a formal definition of feelings as a starting point (Siddharthan et al., 2018), a linguistic analysis was undertaken and ultimately proposed nine broad categories of feelings (i.e., Physiological or Bodily states, Attraction and Repulsion, Attention, Social, Actions and Prospects, Hedonics, Anger, General Wellbeing, and Other). In the creation of the nine lexical categories, “self” was initially referenced explicitly but was ultimately merged with ‘other’ categories because it was difficult to enumerate all aspects of the self that feelings could pertain to and, also, because the “other” category was otherwise rarely used. This result is not only suggestive that “self-feelings” could represent a unique category of feelings, as also speculated by James, but also that the category could potentially be rather large and difficult to delineate, suggesting that SRP might figure more or less in the foreground or at least in the background during the experience of most or even all feelings states. In any case, the lexical analysis led to the result that self-feelings were found in the “other” category which was defined as follows:

“If none of the above categories apply, but nonetheless, the sentence “I feel X[ed]” is plausible for the given word sense. This category includes feelings related to appraisals of the self with respect to categories such as: size (e.g. big, etc.), weight (e.g. fat, etc.), age (e.g. old, etc.), gender (e.g. masculine, etc.), fitness (e.g. unfit, etc.), intelligence (e.g. smart, etc.), attractiveness (e.g. beautiful, etc.), dress and adornment (e.g. fashionable, etc.), uniqueness (e.g. unremarkable, etc.), general normality (e.g. weird, etc.), self-esteem (e.g. self-loathing, etc.), identity and belonging (e.g. Buddhist, American).”

As one can peruse, many of the words in the lexical-thematic analysis (see Supplemental Materials for a full listing) primarily addressed self-feelings in the verbal modality (i.e., “mind”). Verbal self-feelings

broadly emphasized themes of competence, autonomy, relatedness (social) and the like as consistent with established motivational theories in psychology (Ryan and Deci, 2000), and the words overlapped greatly with James’ positive and negative valence categories of “*self-complacency*” and “*self-dissatisfaction*”, respectively (reviewed previously). Further, there also seemed to be some overlap between SRP and other-referential processing (ORP) within the word list, in other words, feelings that reference others, or the self in relation to others, for example, words referencing *normality* and *uniqueness* in relation to social norms. Further relating to ORP, many of the terms related to social interactions, including *authenticity* (e.g., genuine), *sociability* (e.g., open), *refinement/manners* (e.g., refined, rude), *humour* (e.g., comical), *seriousness*, (e.g., serious), *truthfulness* (e.g., honest), *reliability* (e.g., steady), *morality-ethics* (e.g., trustworthy), *benevolence* (e.g., generous), *humility* (e.g., humble), *communications* (e.g., understandable), and *visibility* (e.g., visible, obscured). Within this set of feelings related to social interactions, the self-feelings related to morality-ethics and truthfulness are consistent with the contemporary category of “self-conscious emotions” also referred to as “moral emotions” including guilt, shame, embarrassment and pride (Tangney et al., 2007) and consistent with James’ concept of “spiritual self-seeking”. Additional social terms related to an array of group affiliations, such as *religion* (e.g. Christian), *social class* (e.g., noble, ignoble), *nation* (e.g., nationalistic), and *others* (e.g., socialistic), broadly referencing the principle of *belongingness*, all of which are self-appraisals that appear consistent with James’ concept of “social self-seeking”. As a result of these considerations, comparison of the neural correlates of SRP versus ORP is also taken up later in this essay.

A key point to note from the present framework, however, is that the aforementioned self-feelings, in this evaluation, do not make any obvious, direct reference to a felt sense of the physical body, but rather appear to primarily involve a form of V-SRP. This is so, in our view, even as we suppose that each should entail some pleasurable or displeasurable bodily marker of arousal as a feeling, given the consensus definition of *feelings* to which we ascribe (Siddharthan et al., 2018). However, in stark comparison, other words in the lexical-thematic analysis seemed primarily to address nonverbal self-feelings, that is, directly referencing bodily characteristics and the physical feeling of them. Examples of these included the need for one’s body to be perceived as of a certain *size or shape* (e.g., large, small), *strength* (e.g., strong, weak), *gender* (e.g., masculine, feminine), *attractiveness* (e.g., pretty, ugly), *cleanliness* (e.g., clean, dirty), *clothing/adornments* (ornamented, bare), as well as references to *personal resources* (e.g., flush, poor) and a *sense of place* (e.g., domestic, rootless). Thus, collectively, this set of self-feelings seemed to more directly reference NV-SRP. Nevertheless, we consider both sets of needs to be broadly rooted in identity-based concerns, hence the appropriateness of designating them under a broader rubric of “self-feelings”.

3. Introspection vs. interoception: self-referential processing in the verbal-semantic vs. nonverbal-somatic modalities

Whereas our lexical-thematic analysis lent credence to the intuitive notion that our verbal (“mind”) versus non-verbal (“bodily”) sense of ourselves can be distinguished in conscious “self-feeling” states, these differing experiences of ourselves can also be contrasted by neuroimaging experiments requiring participants to perform tasks involving either *introspection* or *interoception*. In one of the few such experiments utilizing a within-subjects design, Araujo and Damasio and their colleagues (Araujo et al., 2015) directed participants’ self-focused attention toward “core” bodily processes (in our parlance, NV-SRP) by asking them questions requiring “interoception” (e.g., “Do you feel hungry?”), emphasizing internal sensations or interior bodily self-consciousness [BSC] or “exteroception” (e.g., “Are your legs wet?”), emphasizing external sensations or exterior BSC; notice that both questions directly occasion explicit reference to BSC and for present

Verbal Self-Referential Processing (V-SRP, “Introspection”) vs. Non-verbal SRP (NV-SRP, “Interoception”) in Araujo et al. (2015)

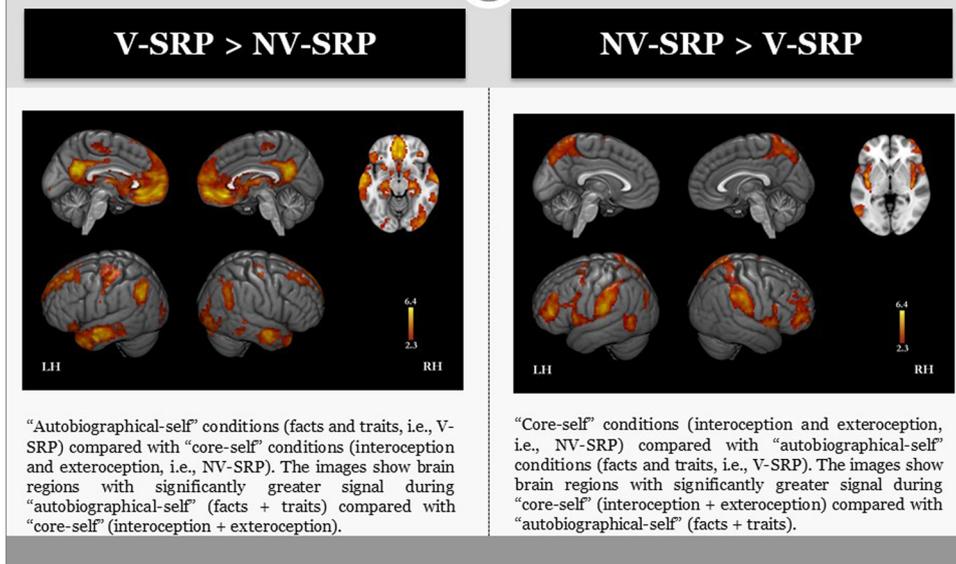


Fig. 1. Title: Verbal self-referential processing (V-SRP) vs. non-verbal self-referential processing (NV-SRP) in Araujo et al. (2015).

Caption: Supplementary findings comparing the main effects of V-SRP (“autobiographical-self” conditions) and NV-SRP (“core self”) in Araujo et al. (2015). V-SRP was associated with greater response in the posterior cingulate cortex (PCC), medial prefrontal cortex (MPFC), temporal poles, and posterior inferior parietal lobe (IPL). NV-SRP was associated with greater response in the posterior medial superior parietal lobe (P-MSPL), anterior temporoparietal junction (supramarginal gyrus, A-TPJ), insula, frontal operculum, and middle frontal gyrus.

purposes need not yet be distinguished. In contrast, “autobiographical-narrative” processing (V-SRP) was primed by asking participants questions about personality traits (e.g., “Does the word *‘honest’* describe you?”) or about their biographical history (e.g., “Are you a student?”); notice that neither of the latter questions explicitly or intrinsically refer to BSC but rather require self-focused attention at a more conceptually abstract or semantic level of representation.

Strikingly, Araujo et al. (2015) found that “core” NV-SRP was more strongly associated with response in bilateral insula, medial superior parietal lobe (M-SPL), and bilateral anterior temporal parietal junction (A-TPJ; supramarginal gyrus), whereas priming of “autobiographical-narrative” V-SRP was more strongly associated with response in medial prefrontal cortex (MPFC), posterior cingulate (PCC) and medial posterior or ventral precuneus (V-PRC), bilateral posterior temporal parietal junction (P-TPJ; angular gyrus), and bilateral temporal poles (see Fig. 1). Araujo et al. thus revealed a marked division of labour within the brain for representing SRP within verbal (V-SRP, “semantic”) vs. nonverbal (NV-SRP, “somatic”) modalities, among the most striking and reliable of which entailed differences within the MPFC, medial parietal cortex (PCC and PRC vs. M-SPL), mediolateral temporal cortex (temporal poles vs. insula), and temporoparietal junction (posterior [P-TPJ] vs. anterior [A-TPJ]), respectively (see Fig. 1).

Despite this, it is important to acknowledge that, when a person introspects about, for example, whether or not a trait adjective applies to themselves, it is likely that non-verbal somatic qualia (what James [1890] might call ‘visceral and organic’) inform the judgement, and that, alternatively, when making judgements about one’s bodily state, verbal-semantic categories are likely used to parse interoceptive data. From the perspective of predictive processing (i.e., active and interoceptive inference) response to these kinds of questions are generally regarded as hypotheses that best explain exteroceptive and interoceptive sensations. In other words, various declarations such as “I am hungry” vs. “I am honest” are viewed as the best explanation for the sensory evidence at hand, wherein this evidence can obtain primarily from the semantic or somatic domains but will typically be influenced by both representations, the latter either primarily emphasizing the exteroceptive sense of the outer body or the interoceptive sense of the inner body. Crucially, this means that SRP is – on a predictive

processing or Bayesian brain view – inherently conceptual *and* multimodal. In short, on this view, existential self-referential descriptions seem to transcend any particular sensory modality, becoming high-level (sometimes emotionally valenced) constructs. In this context, it should be noted that in Araujo and Damasio and colleagues’ study (Araujo et al., 2015), V-SRP, specifically in the case of response to “facts” (in comparison with “traits”), and NV-SRP, specifically in the case of response to “interoception” (in comparison with “exteroception”), exhibited a common response in the ventromedial prefrontal cortex (V-MPFC) whereas, critically, a response common to all four conditions in comparison with rest occurred in the dorsomedial prefrontal cortex (D-MPFC). The latter finding, in particular, suggests that the D-MPFC may operate at an integrative level of SRP beyond verbal-semantic vs. nonverbal-somatic differentiation, a key point that we will return to later. Generally these congruencies in response also suggest some degree of overlap in the brain bases underlying SRP across verbal and non-verbal foci, as well as between different (interoceptive vs. exteroceptive) foci in BSC, points to which we will also return later.

Unfortunately, the study by Araujo et al. (2015) is among only a few that has directly compared SRP in the verbal-semantic (V-SRP) versus nonverbal-somatic (NV-SRP) modalities using a within-subjects design. Instead, these two tasks are typically investigated by different researchers in different studies as will be reviewed below. A future meta-analysis directly contrasting the results of neuroimaging studies of introspection (V-SRP) versus interoception (NV-SRP) would therefore be useful to assess the representativeness of their findings. As a precursor to a formal direct comparison, we utilized the neurosynth database (Yarkoni et al., 2011) (www.neurosynth.org) to illustrate response occurring during studies involving introspection (V-SRP; with the search term “self referential”, $n = 166$ studies) and interoception (NV-SRP; with the search term “interoceptive”, $n = 81$ studies), with results depicted comparatively in Fig. 2 (see Supplementary Figs. 1 and 2 for larger rendering of each individual brain mapping). The association test maps for “self-referential” are displayed for each 10 mm transverse slice in green to the left of the association test maps for “interoceptive” which are plotted in red, while for both maps blue colouring illustrates the results of the respective uniformity test maps. Uniformity test maps illustrate voxels that are consistently activated in studies that include

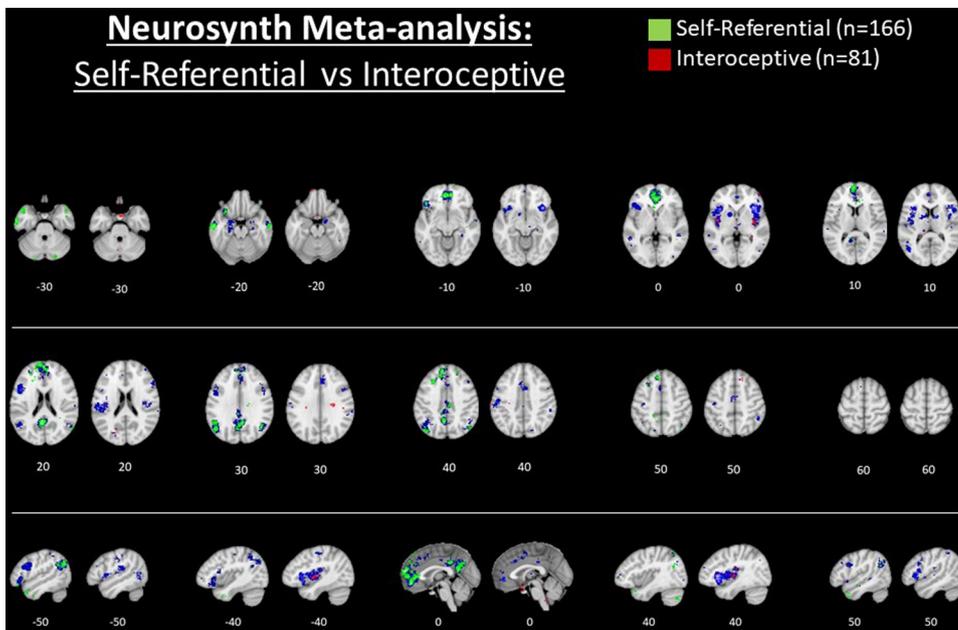


Fig. 2. Title: Automated meta-analysis of the search term “self referential” vs. “interoceptive” via neurosynth.org.

Caption: Results for the association test map for “self referential” ($n = 166$ studies) are shown in green (left) and for “interoceptive” ($n = 81$ studies) in red (at right) for each transverse slice. In comparison, results for the respective uniformity test maps are shown in blue. Only positive results are depicted. Results are FDR corrected to $p < .01$. Please see supplementary file for further description.

the given terms in their abstracts while association test maps illustrate voxels that are selectively activated by the given terms, that is, in comparison with studies that do not report the term (see supplementary materials for additional technical details regarding the use of the neurosynth database as implemented herein). Later, we will suggest that the comparison of the uniformity and association test maps proves crucial to a figure-ground representational framework that differentiates top-down SRP from bottom-up SRP. But for now, it is equally important to acknowledge that such results are limited due to analysis of text-based correspondence between the search terms and the published literature comprising this database which, unfortunately, creates a hazard that results will merely amplify trends in associating regions with certain themes, serving only to confirm a bias that certain brain regions play key roles in SRP, rather than the case that SRP may actually be implemented in distributed network interactions less likely to appear in abstracts and activation tables. We would like to confirm here that we suspect that such broad and integrative psychological functions as V-SRP and NV-SRP would require the operation of distributed neural networks rather than only a localist brain topography.

Whilst acknowledging such limitations, our automated meta-analyses tended to validate the differences observed between V-SRP and NV-SRP found in the aforementioned experiment by Araujo and Damasio and their colleagues (Araujo et al., 2015) and several formal meta-analyses that will be reviewed later. In particular, V-SRP was prominently associated with response in the frontal pole (or middle MPFC [M-MPFC]) extending to the perigenual anterior cingulate cortex (P-ACC) (compare $Z = 0$ to $+20$), as well as in the V-MPFC (see $Z = -10$), PCC, the bilateral posterior temporoparietal junction (P-TPJ, $z = 30$) and posterior inferior parietal lobe (P-IPL, $z = 40$) (but more strongly especially for the left hemisphere), the PRC, and the temporal poles. In comparison, NV-SRP was limited almost exclusively to response in the middle-insula (M-Ins) and posterior-insula (P-Ins) (see $Z = 0$), although response was also observed within the very inferior V-MPFC within the so-called affective or limbic network (see $Z = -30$) and in the right dorsal anterior insula and frontal operculum (DA-Ins, see $X = 40$). In summary, our automated meta-analyses conducted via neurosynth also tended to suggest differences between the brain bases underlying introspection (V-SRP) and interoception (NV-SRP). We turn now to a more elaborated review of the literature examining top-down introspective tasks, that is, SRP in the verbal “semantic” modality (V-SRP), followed by a review of the literature examining top-down

interoceptive tasks, that is, SRP in the non-verbal “somatic” modality (NV-SRP), including discussion of the results of prior formal meta-analyses that have been conducted for each kind of task.

4. Introspection: top-down verbal SRP

As used herein, “introspective” tasks are those that take the form of explicitly asking participants to silently read trait adjectives in order to evaluate whether the adjectives are self-descriptive or not; these tasks have generally been termed *self-referential processing* (SRP) tasks since the publication of an early influential review (Northoff et al., 2006). The kinds of adjectives used overlap the kinds of words we identified in our lexical analysis; positive and negative words that grammatically fit an “I am...X” statement but which the research participant may or may not adopt as self-descriptive and thus veritably true. Collectively answering such questions requires a search of internal autobiographical representations (i.e., memory, rather than of stimuli in the external environment) presumably of either a primarily semantic or episodic nature. In comparison, control tasks have typically involved judging whether the adjectives are descriptive of other persons of varying personal familiarity and relational closeness to the participant (e.g., parent, friend, famous person, stranger, herein termed other-referential processing [ORP]) or involved passive lexical or phonetic judgments (e.g., counting of syllables). Requiring a person to evaluate whether a verbal stimulus is self-referential or not is thus by definition an example of SRP in the verbal modality, that is, V-SRP as used herein. Moreover, such introspective tasks are of obvious relevance to a neuroscientific understanding of SRP. Note however that the task involves assessment of the self-descriptiveness of the words (i.e., “Are you X?”) rather than to self-feelings directly (“Do you feel X?”), a point to which we will return later (e.g., Farb et al., 2007).

An extensive literature has formed the basis of multiple meta-analyses confirming that V-SRP tends to be reliably mediated by response within dorsal medial prefrontal cortex (D-MPFC), anterior or middle medial prefrontal cortex (M-MPFC; i.e., frontal pole), ventral medial prefrontal cortex (V-MPFC), medial parietal cortex (including the posterior cingulate cortex (PCC) and precuneus (PRC)), lateral inferior parietal lobe (IPL) or the posterior temporoparietal junction (P-TPJ), and anterior medial temporal cortex (including the insula, amygdala, and hippocampus), and anterior and middle lateral temporal cortex (including the temporal poles), generally in agreement with the

automated meta-analysis we conducted herein using neurosynth (see Fig. 2 and Supplementary Fig. 1). Further, from the outset, response to visually-presented verbal self-referential stimuli has to be distinguished from the visual self-recognition of non-verbal stimuli such as recognizing one's face in a mirror. A meta-analysis indeed showed response overlap between V-SRP (self-evaluation of traits) and visual self-face recognition limited to the dorsal ACC (D-ACC) and left inferior frontal gyrus extending to the left insula, suggesting that visual self-recognition tasks engage distinct forms of SRP than do typical V-SRP tasks (Hu et al., 2016). As compared to V-SRP, visual self-recognition was also associated with greater response within inferior frontal gyrus, superior occipital gyrus, fusiform gyrus, and postcentral gyrus, all in the right hemisphere, all areas that have not been previously highlighted as bases for V-SRP, whereas V-SRP was associated with greater response within the perigenual ACC (P-ACC) and V-MPFC, the latter discussed as a particularly reliable node of response during V-SRP (Hu et al., 2016).

A longstanding question for introspective verbal trait evaluation studies has been whether response during V-SRP vs. V-ORP (self vs. other) can be dissociated in the brain, where ORP involves ascertaining the descriptiveness of words not to the self but rather for other people. This interest is also relevant to the results of our lexical analysis, described earlier, that considered certain self-feelings as descriptions of oneself in relation to others. While most individual studies and earlier meta-analyses generally found similar responses for SRP and ORP (e.g., Gillihan and Farah, 2005; Legrand and Ruby, 2009), more recent reviews suggest a greater response for SRP than for ORP may occur in M-MPFC (Araujo et al., 2013; Denny et al., 2012; Qin et al., 2012), whereas a greater response for ORP than for SRP may occur in medial posterior cortex, specifically the PCC (Qin et al., 2012) and PRC (Araujo et al., 2013) or both regions (Murray et al., 2015, 2012). Moreover, SRP may produce greater response in left medial temporal cortex (anterior and middle insula and temporal pole), whereas ORP may produce greater response within D-MPFC and the temporoparietal junction (TPJ); (Denny et al., 2012; Murray et al., 2015, 2012). V-SRP as compared with ORP was also associated with response in the bilateral middle-frontal gyri, bilateral TPJ and left PRC in the previously discussed meta-analysis of Hu and colleagues (Hu et al., 2016). Moreover, a study using dynamic causal modeling (DCM) demonstrated that SRP elicited preferential activation of the rostral-perigenual anterior cingulate cortex (P-ACC) and V-MPFC, while ORP engaged PCC and PRC (Soch et al., 2017). This study further showed that during ORP information flow to regions involved in SRP was inhibited, while the reverse was true during SRP, leading the authors to conclude that their findings may represent an efficient mechanism for stimulus-specific switching between SRP and ORP (Soch et al., 2017).

To further elaborate the results of studies comparing SRP and ORP we also utilized the neurosynth database to illustrate response occurring during ORP (here, with the search term “social cognition”, $n = 220$ studies) in comparison with the aforementioned results conducted for V-SRP, depicted in Fig. 3 (see also Supplementary Fig. 3). Comparing results for V-SRP and with ORP, in partial agreement with the prior analyses, whereas response during V-SRP is seen within the P-TPJ and P-IPL proper (i.e., angular gyrus), these effects are absent for ORP (compare parietal responses at $Z = 30-40$) where instead the results situated response during ORP more so in the superior temporal gyrus rather than the IPL/TPJ (compare posterior responses at $Z = 10-20$); to our knowledge, such differences have not been emphasized in previous reviews of the SRP vs. ORP literature. Further, regarding the midline parietal cortex, whereas common responses tend to be seen for the ventral PCC and PRC, unique responses tend to be seen for V-SRP in the dorsal PCC (D-PCC), while unique responses tend to be seen for ORP in the posterior mid-cingulate, also findings that to our knowledge have not been emphasized by previous reviews (e.g., compare medial central vs. parietal response at $Z = 30-40$). Within the PCC, that common responses are seen for V-SRP and ORP in the V-PCC whereas only V-SRP shows response for the D-PCC may also be meaningful given differences

between the RSFC of the V-PCC vs. D-PCC as will be detailed later. Finally, regarding response in the MPFC, findings suggest a greater response in the frontal pole (M-MPFC) for V-SRP (e.g., compare medial anterior response at $Z = 0$ and $Z = -10$), but a greater response for ORP may occur not only in the anterior superior D-MPFC (e.g., compare anterior response at $Z = +30$) but also in the inferior V-MPFC (e.g., compare anterior response at $Z = -20$). This differentiation along the inferior to superior axis within the MPFC is consistent with results suggesting that at least a three-fold inferior-to-superior parcellation exists for the MPFC into ventral-orbital (V-MPFC), middle-anterior (M-MPFC, i.e., frontal pole), and dorsal-superior (D-MPFC) regions (e.g., Andrews-Hanna et al., 2010; de la Vega et al., 2016; Frewen et al., 2017). These findings notwithstanding, although it afforded the best choice among the alternatives available, it needs to be acknowledged that this automated meta-analysis is limited due to the use of the keyword terms “social cognition” probably not being the best way to assess the neural correlates of ORP in comparison with V-SRP, because most of the social cognition tasks assess theory of mind, judging others' intentions, facial expressions, and non-verbal communication, rather than ORP as generally takes place as a comparison condition in V-SRP tasks. These results must therefore be treated with caution, and we recommend an updated formal meta-analysis comparing response during V-SRP vs. ORP be conducted in the future. Moreover, the distinctiveness of SRP from ORP very likely depends on how the “self” vs. “other” (or “non-self”) are defined; notice that each of these constructs is defined in reference to and thereby entails the other. For example, research suggests that how the self is defined varies by culture. Whereas people raised in individualistic cultures tend to define “self” in reference to single persons (“me”), collectivistic cultures are more likely to define “self” with reference to multiple persons (“we”), for example, by family, race-ethnicity, geographic region, or sociopolitical views, thus further defining in-groups (“us”) versus out-groups (“them”) (Molenberghs, 2013). Neuroimaging studies suggest more similar responses to SRP may occur for persons from collectivistic cultures to stimuli referring to the individual self vs. a family member, for example, although results are heterogeneous and nuanced (Chen et al., 2015, 2013; Chiao et al., 2010; Han et al., 2016; Harada et al., 2010; Ng et al., 2010). Further, although some culture features are stable across time, other cultural aspects are dynamic (e.g., generations, lifespan, situations), and a major source of cultural change within a sociocultural environment is the human tendency to emigrate (Chiao and Ambady, 2007; Chiao et al., 2010; Manning, 2005). Chen et al. (2015) stated that self-construal changes during the process of acculturation in recent immigrants to another culture are reflected in the relative engagement of brain structures implicated in V-SRP (i.e., MPFC and PCC) when judging traits regarding oneself or a close other (e.g., family member (Han et al., 2016; Northoff et al., 2006; Oyserman and Lee, 2008). Finally, an electrophysiological study (Knyazev et al., 2012) found that enhanced alpha activity within the DMN predicted spontaneous self-referential thoughts, with greater alpha activity in the posterior network in Russian and in the anterior network in Taiwanese participants, leading the authors to speculate that spontaneous self-referential thoughts may be accompanied by enhanced alpha activity in the posterior DMN hub when these thoughts are not on complex social relationships that are generally associated with positive emotions, while mental simulations of complex social relationships, which are frequently associated with negative emotions, may engage the MPFC to a greater extent. One might conclude that more complex ORP entailing negative emotions may prevail in more individualistic individuals, whereas less complex ORP associated with positive emotions may be more representative of collectivistic persons.

A better understanding of cognitive V-SRP is important to affective neuroscience because persons may adopt positive or negative valence descriptions of both themselves and others (Fossati et al., 2003; Moran et al., 2006; van der Crujnsen et al., 2017), in turn associated with a propensity toward positive or negative affect, as observed for the notion

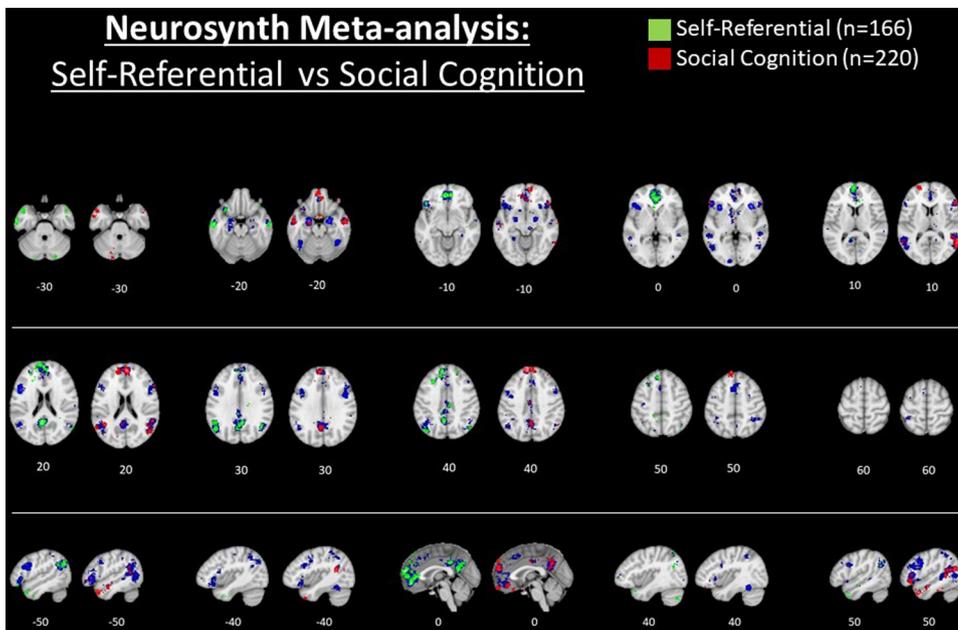


Fig. 3. Title: Automated meta-analysis of the search term “self referential” vs. “social cognition” via neurosynth.org.

Caption: Results for the association test map for “self referential” (n = 166 studies) are shown in green (left) and for “social cognition” (n = 220 studies) in red (at right) for each transverse slice. In comparison, results for the respective uniformity test maps are shown in blue. Only positive results are depicted. Results are FDR corrected to $p < .01$. Please see supplementary file for further description.

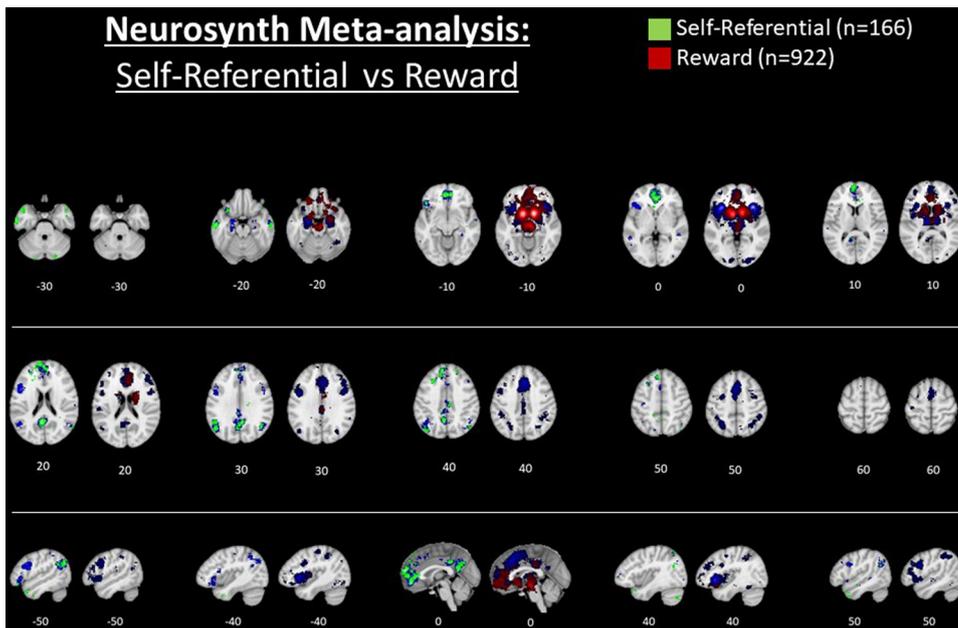


Fig. 4. Title: Automated meta-analysis of the search term “self referential” vs. “reward” via neurosynth.org.

Caption: Results for the association test map for “self referential” (n = 166 studies) are shown in green (left) and for “reward” (n = 922 studies) in red (at right) for each transverse slice. In comparison, results for the respective uniformity test maps are shown in blue. Only positive results are depicted. Results are FDR corrected to $p < .01$. Please see supplementary file for further description.

of self-feelings described by James (1890). In this respect it is important to note that many of the brain bases observed to be involved in V-SRP overlap with reward circuitry, specifically, as involving a shared response within V-MPFC and the ventral striatum, leading some investigators to consider whether SRP might entail nothing other than reward processing (Enzi et al., 2009; Northoff and Hayes, 2011). Under this view, SRP may be intrinsically rewarding. However, de la Vega et al.’s meta-analysis suggested that the previously reviewed three-fold inferior to superior parcellation within MPFC into V-MPFC, M-MPFC, and D-MPFC has likely functional significance for valenced SRP, whereby V-MPFC exhibits preferential response during decision-making and reward paradigms, while D-MPFC exhibits preferential response during social perspective-taking paradigms such as theory of mind and the experience of social emotions during which participants are required to evaluate not only their own but also others’ likely response to stimuli (Frewen et al., 2011). Beyond this, we utilized the neurosynth database to illustrate response occurring during reward (here, with the

search term “reward”, n = 922 studies), with the results depicted in Fig. 4 (and Supplementary Fig. 4). Again, comparing the brain maps depicted for “self-referential” vs. “reward” one can see that, in replication of prior findings, response overlap between V-SRP and reward paradigms does appear to occur in the V-MPFC, although very inferior orbitofrontal response during reward was not seen during V-SRP (i.e., compare medial frontal response at Z = -20). In comparison, while prominent during V-SRP, there appears to be an absence of response during reward in posterior nodes such as the PCC, PRC, or the IPL, during which instead a response during reward was uniquely seen to occur in the posterior mid-cingulate similar to that seen during ORP (compare medial central vs. parietal response at Z = 30). Moreover, entirely absent in the meta-analysis of V-SRP, there were very prominent responses during reward processing in the ventral ACC, thalamus, and striatum.

Moreover, acknowledging the response overlap in the V-MPFC seen here, even still, a study by Yankouskaya and colleagues further suggests

that, even within the V-MPFC, V-SRP and reward processing may be neuroanatomically dissociable, whereby V-SRP and reward processing may be differentially associated with anterior and posterior response within the V-MPFC, respectively (Yankouskaya et al., 2017). Moreover, this compelling research found that V-SRP and reward processing could be dissociated in relation to the functional connectivity of the posterior V-MPFC. Specifically, during V-SRP response, the posterior V-MPFC was more strongly correlated to the M-MPFC (frontal pole), whereas during reward processing, the posterior V-MPFC was more strongly correlated to the left inferior and middle temporal lobes, with these different functional connectivity patterns further predictive of behavioural performance during the task (Yankouskaya et al., 2017). This research indicates yet further neuroanatomical subspecialization within the V-MPFC that differentiates V-SRP from reward processing, although the study did not examine explicit valenced SRP, tempering conclusions (Yankouskaya et al., 2017). Furthermore, neither V-SRP nor reward processing were associated with D-MPFC in this passive response study (Yankouskaya et al., 2017). In sum, these findings suggest a possible yet more specific role for the anterior V-MPFC in emotionally-valenced, motivationally-relevant SRP, while the D-MPFC may be preferentially engaged by reflective tasks that subjectively disengage or detach from affectively motivated V-SRP, for example, to allow for ORP (e.g., as in social cognition, such as theory of mind and empathy tasks) and self-monitoring. In this model, a more specific role for the M-MPFC however remains unclear, although M-MPFC may be involved in comparably more affectively neutral V-SRP, a point to which we return later.

Referring to studies investigating affectively valenced SRP, a common confound has been that psychological healthy participants will evaluate positive traits as more self-descriptive than negative ones, that is, the self-positivity bias in self-esteem (Mezulis et al., 2004), making it difficult to investigate negatively-valenced V-SRP, although neuroscience research into the nature of self-esteem has had some scrutiny (e.g. Chavez and Heatherton, 2015; Eisenberger et al., 2011; Frewen et al., 2013; Nowicka et al., 2018; Oikawa et al., 2012; Pan et al., 2016; van Schie et al., 2018; Yang et al., 2012, 2014b). One approach has been simply to require participants to passively view positive and negative words that were rated for SRP earlier, but the relevance to SRP of response during the subsequent presentation can be unclear following this design (Yang et al., 2014a). Another method that has been tried is to present negative words under the presumption that one's peers have indicated they are descriptive of the participant and inquire of the participant's agreement with their ratings; even here, however, those with higher self-esteem are unlikely to endorse the peers' ratings, interpretation of which is further complicated by a confounding of SRP with ORP using this design (e.g., (Yang et al., 2016)). Finally, alternative approaches include associatively conditioning SRP (and ORP) with positivity or negativity on different trials. For example, Frewen and colleagues developed the Visual-Verbal Self-Other Referential Processing Task (VV-SORP-T; (Frewen and Lundberg, 2012; Frewen et al., 2013) during which participants rehearse "I am..." before reading valenced words while viewing a face-only photograph of themselves on SRP trials, while rehearsing "He is..." or "She is..." before reading the same words and viewing pictures of another person on ORP trials, thus associating SRP or ORP with positivity (e.g., "I am...smart") or negativity (e.g., "I am...stupid") on different trials depending on word valence. An advantage of this design for the study of SRP as it relates to affective neuroscience is that the researchers were able to engender self-feelings of relatively high intensity during both SRP and ORP (e.g., guilt, envy, pity), especially among women reporting lower trait self-esteem, which is not usually observed in response to other standard V-SRP tasks (Frewen and Lundberg, 2012; Frewen et al., 2013). Moreover, on average, only positive SRP was associated with response within V-MPFC, whereas negative SRP was associated with response in D-MPFC, possibly indicative of the fact that positive SRP was rewarding, associated with positive affect, and few participants endorsed negative words as self-descriptive, engendering an unnatural affective response

that may have been akin to ORP and sometimes associated with dysphoria, anxiety, anger, and other negative feelings (Frewen et al., 2013) (see also (Kim et al., 2016)). However, those with lower self-esteem were more likely to show response within V-MPFC and V-ACC during negative SRP, while those with higher self-esteem and those who reported experiencing more positive affect during the task were especially likely to show response within V-MPFC and M-MPFC during positive SRP, respectively (Frewen et al., 2013). Collectively the results of Frewen et al. (2013) thus implicate V-MPFC in introspective V-SRP of valenced stimuli, both positive and negative. Another unique paradigm directly comparing SRP with processing of valence was adopted by Phan et al. (2004) whereby pictures were rated regarding their valence during certain trials and for self-reference during others, allowing a task-by-event-rating interactive design. The authors found that whereas the V-MPFC was active during SRP independent of the determined self-relevance of the pictures, perhaps indicative of emotional processing of the intrinsic valence of the pictures, the M-MPFC and D-MPFC were most active during SRP when the pictures were actually determined to be self-relevant by individual participants. The results of various paradigms are therefore suggestive of a stronger role for the V-MPFC in valenced SRP or "self-feelings" whereas M-MPFC and D-MPFC may play more significant roles for less affectively significant forms of V-SRP.

In order to compare response occurring during V-SRP with emotional processing more broadly, we conducted another automated meta-analysis via the neurosynth database to illustrate response occurring during emotional valence (here, with the search term "valence", $n = 361$ studies), with the latter results depicted in Fig. 5 (and Supplementary Fig. 5). Once again, we see response overlap between V-SRP and valence tasks in the MPFC, possibly with unique response during valenced tasks in the very inferior orbitofrontal cortex as was seen for "reward" (e.g., compare medial anterior response at $Z = -30$). Interestingly, however, there again appears to be little response attributable to valence in either the PCC/PRC or IPL/PTJ, which were prominently noted during V-SRP (compare posterior response at $Z = 30$ and $Z = 40$). Together with the absence of responses during "reward" processing in the PCC or IPL/TPJ (Fig. 4), these results tend to favour an interpretation of response occurring in the IPL/TPJ as more indicative of V-SRP than emotional processing per se. By comparison, a prominent response for "valence" uniquely appears in the bilateral amygdala (e.g., $Z = -20$), the ventral ACC (e.g., $Z = -10$, $X = 0$), and the right anterior insula extending into the right ventrolateral prefrontal cortex (e.g., $Z = 0$, $X = 40$; Fig. 5) in comparison to V-SRP.

The studies reviewed thus far have emphasized the spatial neuroanatomy of V-SRP as investigated by fMRI, but have not addressed the neural correlates of SRP in the temporal neuroelectrophysiological domain such as are better identified by EEG or MEG (Knyazev, 2013). Knyazev comprehensively reviewed earlier EEG literature to show that alpha-band (8–12 Hz) oscillations tend to desynchronize during active periods of V-SRP within posterior midline cortex (PCC, PRC) relative to rest; delta-theta oscillations in midline frontal cortex may also demonstrate this pattern although no spatiotemporal components could be identified within the alpha domain that correlate with default mode network masks or SRP task design (Knyazev et al., 2011). By contrast, posterior PCC-PRC alpha oscillations demonstrate the opposite pattern during eyes-closed resting state where they are found to synchronize rather than desynchronize as is well known, an effect that is positively correlated with the experience of self-referential mind-wandering, discussed in greater detail later (Knyazev, 2013; Knyazev et al., 2011). Knyazev and colleagues also identified two posterior PCC-PRC alpha oscillators during both an SRP task and resting state. During resting state, within the alpha domain a dorsal PRC component could be differentiated from a ventral PCC component. By contrast, during task-driven V-SRP, a ventral-dorsal PCC-PRC alpha component could be differentiated from an anterior-superior component restricted to the PRC. These findings again suggest a subparcellation of function within the PCC-PRC may exist that is expressed in the alpha frequency domain

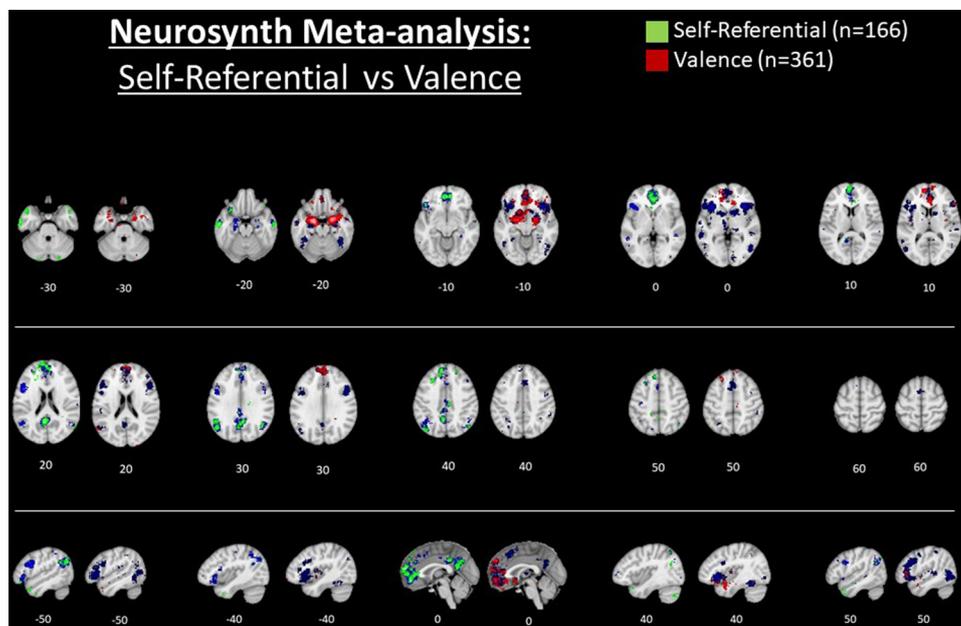


Fig. 5. Title: Automated meta-analysis of the search term “self referential” vs. “valence” via neurosynth.org.

Caption: Results for the association test map for “self referential” ($n = 166$ studies) are shown in green (left) and for “valence” ($n = 361$ studies) in red (at right) for each transverse slice. In comparison, results for the respective uniformity test maps are shown in blue. Only positive results are depicted. Results are FDR corrected to $p < .01$. Please see supplementary file for further description.

during V-SRP that has so far not yet been specified in fMRI studies specifically during V-SRP (as opposed to resting state), considerations to which we will return later in analyses of RSFC. Indeed such a neuroanatomical subparcellation has been identified in fMRI studies of RSFC which will be reviewed subsequently, and has already been discussed as it may relate to V-SRP in comparison with NV-SRP in reference to the fMRI findings of Damasio and colleagues (Araujo et al., 2015).

Beyond consideration of event-related oscillations, studies of event-related potentials have also revealed SRP in the time-domain of neuroelectrophysiological responses. For example, while the P300 component typically differentiates SRP from ORP (Knyazev, 2013), research has also shown that the averaged amplitude of the preceding P2 component is higher for self-relevant information than for moderately self-relevant, minimally self-relevant, and non-self-relevant information (Fan et al., 2013), and these findings were reported along with similar findings for the later N2 and P3 components. Further, since identifying the P300 component as important for distinguishing between self- and others-related information (Knyazev, 2013), it has also been shown that this component is modulated by the degree of importance of self-related content with respects to ethnicity, nationality, sex, relational roles in family, occupation and age identity (Xu et al., 2017), such that higher importance of self-related content was associated with larger P300 amplitude. Interestingly however, the P200 and N200 components were also modulated by importance, leading the authors to conclude that importance captures attention more quickly at earlier time-points and is processed more deeply at later timepoints, reflecting later cognitive evaluation. However, other research has shown (Walla and Herbert, 2015) that while personal pronouns including ‘my’, ‘his’ and ‘you’ are distinguished from the non-personal pronoun, ‘a’, early in the time-course (around 250 ms over the left parieto-temporal area), it is only later in the time-course that the self-related possessive pronoun, “my”, differs from the processing of all other personal and non-personal pronouns (around 350 ms post-stimulus over the left frontal cortical area). These findings were interpreted according to multiple aspect theory (Walla et al., 2008, 2007), which proposes distinguishing between a low-level processing stage that involves distinguishing between personal and non-personal pronouns, and a later-stage of processing involved in distinguishing between the personal self from others. Finally, research on EEG bandwidths using EEG and MRS (Bai et al., 2016) demonstrated that perception of self-related pictorial stimuli from the International Affective Picture System was associated with

elevated power in the low alpha frequency range (8–9 Hz) – reflecting activity in the thalamo-cortical network (Klimesch, 1999; Lopes da Silva et al., 1980) – in combination with increased negativity between 150–400 ms, interpreted as reflecting the subjective component associated with the processing of self-related stimuli. This study also reported that pre-stimulus alpha power and resting state concentration of glutamate in the P-ACC may actually mediate judgements that stimuli are highly related to the self, where the authors concluded that that these findings may reflect the neuro-biochemical mechanisms for the generation of whether pictorial stimuli are self-relevant.

The causal significance of different brain regions for SRP nevertheless remains difficult to establish on the basis of varying response to experimental stimuli or task-related conditions alone, and researchers are now also turning to neuromodulation studies utilizing non-invasive brain stimulation (NIBS) as including transcranial direct current stimulation (tDCS) and repetitive transcranial magnetic stimulation (rTMS) in order to attribute causal significance of different brain regions for SRP, most frequently targeting neuromodulation of the MPFC. Lou et al. (2004, 2010) failed to establish a causal role for MPFC in V-SRP by using single-pulse TMS during a reaction time and accuracy recognition test conducted five minutes after a standard V-SRP in comparison with a ORP task, although the researchers found that stimulation of the bilateral IPL/TPJ suppressed the self-reference effect in memory when conducted 160 ms or more post-stimulus onset (Lou et al., 2010); limitations of the studies however included the fact that TMS was administered only during the subsequent memory task rather than during ongoing V-SRP (i.e., encoding) and the lack of inclusion of a sham or control condition. As a follow up study, Luber et al. (2012) therefore recruited 27 new participants who completed the same tasks but received no TMS stimulation and, moreover, the researchers sought to examine whether effects might vary by word valence. Interesting, the reanalysis now showed that only TMS of the MPFC suppressed the self-enhancement effect for attributing more positive words to the self versus others in a time-specific manner about 160 ms post-stimulus onset, that is, whereby MPFC stimulation caused participants to assign more desirable words to their best friends over themselves; with regards to the parietal cortex, no self-enhancement effect was found. Comparing their prior report with these subsequent results, the authors therefore concluded that MPFC and parietal nodes may play different roles during SRP, with the MPFC thought to be more responsible for self-evaluative processing while the parietal cortex may be more responsible for the retrieval of self-relevant associations across valence

types.

By contrast, De Pisapia and colleagues (2018) were the first to examine fMRI of valenced V-SRP and ORP as an outcome following 1 Hz (deactivating) rTMS over the M-MPFC using a within-subjects (repeated measures) sham-controlled design. Behavioural results suggested that, following true rTMS in comparison with sham treatment, reaction times were slowed for negative valenced processing across both V-SRP and ORP. Coinciding with this, D-PCC was found to be the only brain region exhibiting higher response during negative valence processing following rTMS than following sham intervention. Other brain regions, however, including the MPFC, L-IPL and anterior temporal cortex, exhibited interactions as a function of valence and SRP vs. ORP. Interestingly, only following active rTMS was the M-MPFC more strongly activated during SRP than ORP, independent of valence. Finally, both the left angular gyrus and left anterior temporal cortex were modulated by active rTMS such that response was increased following negative SRP in comparison with sham stimulation. The authors concluded that, given effects were observed primarily as a function of the valence of the words, their results favored a more pronounced role of MPFC in “affective coding rather than in self-other distinctions” (De Pisapia et al., 2018), which appears consistent with the results reported by Lou et al. (2010). Moreover, they considered whether the M-MPFC plays a role in top-down modulation of negative affect during SRP-ORP such that: “In our experiment, the virtual lesion of MPFC, a key component of this supervisory mechanism, could be interpreted as inducing in the participants a stronger effort specifically in the task to evaluate whether negative adjectives (e.g., childish, unpleasant, spoiled) were appropriate in describing them or a pre-specified close person” (De Pisapia et al., 2018). Limitations of the study, however, likely include fatigue resulting of the length of conducting four rTMS treatments followed by four fMRI scans, where carry over effects between interventions and scans could not be addressed.

In summary, introspective studies investigating response during task-driven V-SRP tend to reliably activate anterior cortical midline (D-MPFC, M-MPFC, V-MPFC, pACC), posterior cortical midline (PCC, PRC), lateral inferior parietal lobe [IPL]), the medial temporal lobe (insula, amygdala, and hippocampus), and anterior and middle lateral temporal cortex (including the temporal poles). EEG studies further suggest that alpha oscillations may play a significant role for V-SRP, and event-related responses to specific self-referential stimuli have also been identified within the first few hundred milliseconds following stimulus onset of self-referential words and the first-person pronouns. Further, specificity of response within some of these areas has been identified on the basis of whether the response occurs more so for SRP than ORP, and as a function of the affective valence of the words evaluated. Comparing brain maps across V-SRP, ORP, reward, and valence, a striking commonality can in fact be found in the MPFC, varying however in its ventral, middle, and dorsal aspects (V-MPFC, M-MPFC, D-MPFC), where more emotional processing consistent with response during reward and valence studies implicate the V-MPFC that also responds during V-SRP as possibly indicative of “self-feelings” (that is, affectively significant as opposed to “neutral” V-SRP). By comparison, there appears to be less common variance in the PCC, PRC and IPL/TPJ for the more blantly emotional processing tasks, that is, “reward” and “valence”, instead found distinctly during V-SRP and ORP although with certain additional distinctions; moreover, the neurosynth maps suggest that IPL/TPJ response may in fact be more robust for V-SRP, while response during ORP was seen in more inferior regions, that is, posterior aspects of the superior temporal gyrus. NIBS studies further suggest that valenced V-SRP may be mediated by ventral anterior regions (V-MPFC, M-MPFC), whereas the parietal cortex may play a more dominant role in less valenced forms of V-SRP or memory retrieval processes relevant to SRP. The significance of these contrasts will be taken up again later, but for now we turn to consideration of SRP in an alternate and what we consider to be non-verbal form: *interoception*.

5. Interoception: top-down non-verbal SRP

In contrast to introspective V-SRP tasks, which we have taken to mean evaluation of a verbal stimulus regarding its self-descriptiveness in relation to semantic and episodic autobiographical memory indicative of the experience of self-referential *thoughts*, we understand interoceptive NV-SRP tasks primarily to engage an internal, somatic, *bodily-felt* experience of SRP, that is, bodily self-consciousness (BSC). As an example, the most researched interoceptive task is undoubtedly the heart-beat detection task, whereby participants estimate the pacing of their recorded heart beats (Schandry, 1981). Schulz’s (2016) meta-analysis of nine cardiac interoceptive accuracy studies revealed the involvement of the bilateral posterior and middle insula when participants’ attention is tuned to an awareness of their own heart-beat as a non-verbal, bodily-felt self-stimulus, together with a marked right hemispheric dominance in response within claustrum, precentral gyrus, and MPFC. Moreover, the relevance of such findings for an affective neuroscience of self-feelings was buttressed by Adolph and colleagues who demonstrated in another meta-analysis that bilateral anterior insula is activated during interoception of heart-beat detection as a response common to other tasks engaging emotional processing and social cognition via conjunction analyses (Adolfi et al., 2017). In partial agreement, our analysis via the neurosynth database discussed earlier also showed that interoception tasks tend to robustly activate the bilateral middle and posterior insula, as well as the right anterior insula, although the latter was generally not activated more reliably than other tasks, that is, showing only in the uniformity map. In comparison, MPFC response was seen only in very inferior slices in the orbitofrontal regions at $Z = -20$ and $Z = -30$ of the affective-limbic network (Fig. 2, and Supplementary Fig. 2). Moreover, a tDCS study of interest to the current framework showed that interoceptive accuracy of heartbeat detection improved across practice sessions despite sham NIBS but failed to improve after true anodal stimulation of both left and right insula where the cathode was placed over the contralateral frontal pole (Sagliano et al., 2019). This study may indicate insula stimulation together with deactivation of the MPFC disturbs NV-SRP, although the relative influence of MPFC vs. insula for this outcome remains unclear; utilizing both sites may in fact impact their functional connectivity.

In summary, the role of the insula in interoception and BSC has received much attention, especially as conceptually integrated by Craig and his colleagues (Craig, 2009) (Craig, 2003, 2010, 2011). On this view, the insula may be responsible for monitoring, aggregating, and integrating afferent visceral, sensory, and hedonic signals from the interior of the body to create bodily-emotional moments in time that accumulate to create a global sense of “me-ness” and “now-ness”, one basis in BSC for a “sentient self” (Herbert and Pollatos, 2012). From this perspective, interoception has been conceptualized as being more than only a “perception of the body from within” (Ciaunica and Fotopoulou, 2017) (p.16) but rather constituting a “self-feeling”, a “non-conceptual somatic form of knowledge” (Balconi, 2010) (p60). Seth (Seth, 2013; Seth and Critchley, 2013) also hypothesized a model of interoceptive inference that suggests that top-down predictions of bodily-emotional experience are weighed against bottom-up prediction errors such that one can infer how much weight to give their interoceptive cues relative to proprioceptive or exteroceptive cues. The model proposed by Seth has found support in studies that have analyzed the discrepancy between objective interoceptive accuracy and subjective interoceptive sensitivity (see (Critchley and Garfinkel, 2017; Garfinkel et al., 2015, 2016)). This work collectively has therefore strongly implicated the insula in partly mediating certain interoceptive forms of NV-SRP.

Even still, the precise definition of what exactly constitutes a sense of interoception has changed over the years, creating some recent confusion. While the term used to refer to a purely physiological sense of the interior body stemming primarily from afferent autonomic nervous system signals, recently a more inclusive definition has come into favour that pertains to the phenomenological sense of an integrated,

multisensory body state including the viscera, muscles, and even skin (Ceunen et al., 2016; Evrard et al., 2014). In our view, however, this more inclusive definition traverses important conceptual boundaries, for example Araujo and Damasio and their colleagues' distinction between interoceptive vs. exteroceptive NV-SRP as operationalized by answering questions such as “Do you feel hungry?” vs. “Are your legs wet?” that was discussed earlier (Araujo et al., 2015). Moreover, in support of the distinction, Araujo et al. showed in direct contrasts that interoceptive NV-SRP led to greater response than exteroceptive NV-SRP within MPFC (including V-MPFC, M-MPFC, D-MPFC), PCC (including V-PCC and D-PCC), temporal poles, insula, postcentral gyrus, and anterior aspects of the IPL/TPJ, thus exhibiting striking parallels with the very same regions differentiating introspection (V-SRP) from interoception (NV-SRP) discussed earlier, perhaps implicating more similar processes between introspection and interoception than might be apparent otherwise, and differentiating both from processes underlying exteroceptive forms of BSC. In comparison, exteroceptive forms of NV-SRP led to greater response than interoceptive NV-SRP in the superior PRC and the superior parietal lobe (SPL) in their study, as well as in the dorsolateral prefrontal cortex (Araujo et al., 2015). Moreover, interestingly, only interoceptive and not exteroceptive NV-SRP activated the anterior insula more so than did V-SRP (introspection), whereas both forms of NV-SRP led to greater response within the posterior insula when compared with V-SRP (Araujo et al., 2015). It therefore appears that conceptually distinguishing between interoceptive and exteroceptive NV-SRP remains important.

Indeed an equally voluminous literature has examined the exteroceptive processing of the self-body under the concept of BSC through the experimental use of multisensory bodily illusions (e.g., reviews by (Blanke et al., 2015, 2009; Riva, 2018; Tsakiris, 2017)). From this perspective, subjective experience of selfhood, “self-experience”, is always localized within a body, experienced as one's own, wherefrom the self perceives the world, that is, from a given position in space (de Vignemont, 2018d). As a consequence of this bodily localized NV-SRP, scenarios can be experimentally contrived wherein visual-perceptual NV-SRP appears incongruent with tactile (proprioceptive) NV-SRP, creating an experience of conflict, either in reference only to a specific body part (e.g., the location of one's hand in the so-called “rubber hand illusion”) or for the body as a whole (i.e., as has been studied using virtual reality technology to provoke the sense of “full body illusions”). Neuroimaging studies of these manipulations have demonstrated integration of bodily signals in different structures of the brain (Blanke, 2012; Noppeney and Lee, 2018; Riva, 2018) specifically, the premotor, posterior parietal, temporoparietal, and extrastriate cortices, involving primary sensory and higher-order association areas. Noticeably absent from this list are therefore the insula, MPFC, and ACC responses that have figured more prominently in studies of interoceptive processing of cardiac signals (Schulz, 2016; Adolphi et al., 2017), suggesting that a simplistic conceptual expansion of the term “interoception” to include integrated visual and tactile NV-SRP may indeed be misguided. In so far as these studies require simultaneously internally-referenced (i.e., proprioceptive) and externally-referenced (i.e., visual) NV-SRP, that is, self-object stimuli, it is difficult to consider these forms of NV-SRP to be merely “interoceptive” in nature. In our opinion, the idea that different brain systems may mediate internally (interoceptive) vs. externally (exteroceptive) bodily-focused NV-SRP must therefore be retained.

Nevertheless, the idea of an expanded conception of “interoception” to include NV-SRP of the whole body may find some resolve in an integrative, hierarchical model put forth by Park and Blanke (Park and Blanke, 2019a) (see also (Seth and Tsakiris, 2018)). Their review primarily of studies of multisensory-evoked full-body illusions suggests that interoceptive signals from the autonomic nervous system, on the one hand, and exteroceptive (proprioceptive and vestibular) representations from the periphery, on the other, may be integrated in the peripheral nervous system at the level of the torso. Moreover, at the

level of the brain, the authors posit that key nodes unique for the interoceptive system include the insula and premotor cortex, whereas key nodes unique for the exteroceptive system include the PCC and the TPJ (see (Park and Blanke, 2019a)). However, the authors further posit that a node that overlaps both systems thus facilitating their co-modulation likely includes the intraparietal sulcus. The authors also review several studies revealing integrative NV-SRP across the interoceptive and exteroceptive domains, whereby for example individual differences in interoceptive (cardiac) sensitivity predict susceptibility to the rubber hand illusion (e.g., (Tsakiris et al., 2011)) and the reverse, that exteroceptively induced illusory body perception alters interoceptive accuracy (e.g., (Filippetti and Tsakiris, 2017)). Furthermore, contiguous cardiac signaling during experience of the exteroceptive full-body illusion increased participants' susceptibility to the illusion. Moreover, beyond a focus on the heart, other interoceptive signals such as those of respiration have also been shown to modulate and be modulated by exteroceptive visual and tactile NV-SRP (e.g., (Adler et al., 2014)). These studies and others reviewed by Park and Blanke (Park and Blanke, 2019a) therefore strongly suggest potentials for a level of interaction and integration between NV-SRP in the interoceptive and exteroceptive domains may underlie BSC. Consistent with the notion of a hierarchical integration of different forms of NV-SRP, Moseley and colleagues also suggest that different body maps are integrated in the “body matrix,” a coarse supramodal multi-sensory representation of the body and the space around it (Gallace and Spence, 2014; Moseley et al., 2012; Riva, 2018). As underlined by Moseley and colleagues (Moseley et al., 2012) “the body matrix integrates these constructs by proposing a direct interrelationship between cognitive representations, such as ownership over a body part, and homeostatic function, such as thermoregulation.” (p. 43). Specifically, the connections between the insular cortex and the posterior parietal cortex allow the body matrix to integrate somatotopic and peripersonal sensory data with body-centred spatial sensory data and an object-centred body image from vision and memory. Further, Riva (Riva, 2018) similarly suggested the existence of six different representations of the body that are progressively integrated: “our bodily experience is constructed from early development through the continuous integration of sensory and cultural data from six different representations of the body, i.e., the Sentient Body (Minimal Selfhood), the Spatial Body (Self Location), the Active Body (Agency), the Personal Body (Whole Body Ownership – Me); the Objectified Body (Objectified Self – Mine), and the Social Body (Body Satisfaction – Ideal Me).” (Riva, 2018) (p. 241).

As so far discussed, however, BSC has only been described as a perceptual experience, which misses its intentional aspect, that is, as a means of coordinating movement and action. Riva (2018) however goes further to suggest that the development of more advanced body maps allows NV-SRP to enact a more advanced level of intentionality (Riva and Waterworth, 2014; Riva et al., 2004, 2011; Waterworth et al., 2010). What's further, the reflections of different authors (Bara et al., 2011; Ciaramidaro et al., 2007; Pacherie, 2008; Searle, 1983) suggest a possible structure of human intentionality that includes six levels of intentions for which satisfactory conditions are mapped using the six different body representations reviewed before (Riva, 2018). Specifically, this framework includes simple undirected motor intentions, private and social proximal intentions, and private, social and collaborative distal intentions, forming an intentional cascade (Pacherie, 2006, 2008) in which higher intentions generate lower intentions. Moreover, Mylopoulos and Pacherie (Mylopoulos and Pacherie, 2017) suggested that the link between these intentions and the different body representations is achieved through motor schemas wherein intentions, through different bodily maps, gate the representation of the range of potential motor acts, giving sense to objects in the world thereby allowing their identification as potential targets for one's own actions or others' actions (Maranesi et al., 2014). Moreover, whereas most studies have used only correlational neuroimaging designs, Tsakiris et al. (2008) used a NIBS framework to uncover the potentially causal role of

the right TPJ for NV-SRP in a rTMS study. Using a within-subjects design, ten participants completed the rubber hand illusion while undergoing true TMS over the right TPJ, TMS over the vertex, and in a no TMS condition. When stimulated 350 ms after visual-tactile stimulation on the middle finger, TMS over the right TPJ reduced proprioceptive drifts when viewing the rubber hand, but significantly increased drifts when viewing a neutral household tool (a kitchen spoon). Such a result also suggests that the right TPJ may play a role not only in BSC but also in intentionality (e.g., hand-motor action). In turn, altered functioning of the right TPJ may also blur the boundary between self-perceived bodily stimuli and non-corporeal stimuli.

However, this dynamic, fluid process of constant negotiation and renegotiation between the interoceptive and exteroceptive senses of self should normally take place without our conscious awareness in the absence of a grievous mismatch between top-down prediction and bottom-up sensory feedback. We should therefore emphasize the rather contrived and unnatural way that most studies bring about the experience of altered and unexpected exteroceptive NV-SRP to the foreground of BSC, that is, requiring visual and tactile stimulations to be grossly discrepant as in the rubber hand illusion. Thus other than during similarly affectively salient experiences of distress, phenomenologically, our bodies, as the modalities of NV-SRP, are usually thought to remain experientially transparent, in the *background* rather than the *foreground* of conscious experience, both in respect of the interior body (e.g., cardiac signal) and the exterior body (e.g., tactile feeling of one's hand) (Gallagher, 2017). This “transparency” of the body has indeed been described by the philosopher Havi Carel (Carel, 2016) as a sense of ‘bodily certainty,’ a “kind of taken-for-grantedness—unreflective, disinterested” (p.90) that operates in the background of our immersion in the world. It therefore seems that it is normally only at times of distress that the body may be experienced as an explicit object of awareness and (often negative) appraisal, resulting in one's “attention [being] withdrawn from the world and focused on her body” (Carel, 2016) (p.92). During emotional arousal a kind of “bodily doubt” is thus thrust upon individuals seemingly without their consent, as seems also to take place during multisensory bodily illusion studies. It may therefore be that NV-SRP taking place in the “background” vs. “foreground” of awareness, and during intentional vs. unintentionally provoked circumstances, could afford qualitatively different forms of BSC, a matter we turn to next in review of SRP taking place more so in the background of awareness, during resting state.

In summary, tasks involving interoception, the prototype example being intentional awareness of one's heartbeats, have tended to highlight, in particular, response in the insula cortex, both its posterior and anterior aspects, as a form of NV-SRP, as well as in the ACC and to some extent the V-MPFC. Beyond this interior view of NV-SRP, complex brain systems have also been studied in mediating our exteroceptive BSC as a multisensory experience of NV-SRP including the viscera, muscles, and even skin via the premotor, posterior parietal, temporoparietal, and extrastriate cortices, involving primary sensory and higher-order association areas, where response within the right TPJ/IPL has received considerable attention. Further, recent research is now investigating whether and how such interoceptive and exteroceptive forms of NV-SRP might in turn be integrated at yet higher levels of representation (e.g., (Park and Blanke, 2019a)), and considering the role of such integrative NV-SRP in agency and intentionality (e.g., (Riva, 2018)). Unfortunately, however, there has been surprisingly little discussion as to how each of these forms of NV-SRP might relate to V-SRP, and we hope the current essay will stimulate research in this area. We now turn to a discussion of both V-SRP and NV-SRP as it occurs during less focused, task-driven processes, that is, as it occurs generally in the background, during resting state.

6. Resting state: bottom-up mind- and body-wandering

The neuroimaging studies of active V-SRP (interoception) and NV-

SRP (interoception, and exteroceptive BSC) reviewed thus far have been for the most part predicated on a stimulus-response paradigm wherein tasks explicitly requiring SRP are compared to various control conditions including baseline periods of non-interest termed “rest”. Returning to the study by Araujo and Damasio et al. (Araujo et al., 2015), for example, its experimental design might lead one to suspect that V-SRP and NV-SRP were each merely “turned on” by the top-down task questions, only to be turned off again during the resting period. Although this task-based neuroimaging literature has been fundamental to our understanding of the brain bases of the consciousness of self, researchers are also increasingly recognizing that V-SRP and NV-SRP also likely occurs spontaneously in “bottom-up” fashion, that is, passively during periods of wakeful “rest” or “resting state”, during which participants are typically instructed to allow their minds to wander to their various self-referential concerns.

This interest in the brain processes underlying periods of passive wakeful rest has a good rationale, given that psychological studies estimate that such experiences of “mind wandering” are endemic to human consciousness, where as much as 30–50 % of reportable conscious activity may concern contents that are unrelated to one's immediate sensory environment or activities (Killingsworth and Gilbert, 2010). Moreover, in the interest of understanding how the brain creates affective feelings, the amount with which people's minds wander appears to predict negative affect, particularly when thoughts focus on past social concerns (ORP) as opposed to future personal ones (SRP) (Ruby et al., 2013) and depending on the valence of such thought (Andrews-Hanna et al., 2013). As a consequence of such research, the contents and processes underlying mind-wandering states have become an area of significant research interest (Callard et al., 2013; Christoff et al., 2016; Smallwood and Schooler, 2015). Moreover, although research has more often emphasized the deleterious outcomes of mind-wandering for cognitive performance, it is also clear that spontaneous thought - particularly as it occurs during periods of wakeful rest - can serve adaptive functions, for example, in future planning and creative problem solving (Andrews-Hanna et al., 2013; Christoff et al., 2016; Leszczynski et al., 2017; Mooneyham and Schooler, 2013; Smallwood, 2013a; Smallwood and Andrews-Hanna, 2013).

Research suggests that the brain regions known to be especially active during resting states seem to exhibit the greatest overlap with those identified during task-driven V-SRP (“introspection”) as already discussed, as opposed to those identified for NV-SRP (“interoception”) and exteroceptive BSC, particularly for the M-MPFC and PCC (Qin et al., 2012); but see (Babo-Rebelo et al., 2016) and Fox et al. (2015) discussed below. In particular, meta-analytic conjunction analyses have showed that V-SRP and resting-state studies exhibit overlapping response in the M-MPFC, P-ACC, and V-PCC at the border of the V-PRC (Qin et al., 2012). Nevertheless, some specific responses for V-SRP in comparison with passive mind-wandering during resting-state were also identified, whereby V-SRP exhibited a greater response within M-MPFC than did passive resting state (mind wandering), while resting state was associated with greater response in L-IPL in the meta-analysis (Qin et al., 2012). We conducted yet another automated meta-analysis via neurosynth.org along these lines which tends to validate the aforementioned findings, shown in Fig. 6 (Supplementary Fig. 6). Here, however, there was a comparable absence of response in M-MPFC for resting state specifically at $z = 0$, and in fact a lesser response in more anterior aspects of the MPFC proper during resting state, where instead response is seen more so in anterior P-ACC within area 32 (see $x = 0$). Further, whereas resting state exhibits response within the insula cortex in the uniformity maps, this is not seen for V-SRP as has previously been emphasized (see e.g., $z = 0-20$, and $x = \pm 40$). Additionally, there appears to be a more prominent response within the right TPJ/IPL for resting state as compared to V-SRP (see $z = 30$ and particularly $z = 40$; also $x = 50$).

Considering these results in comparison with those previously described for NV-SRP, we might extrapolate that participants are more

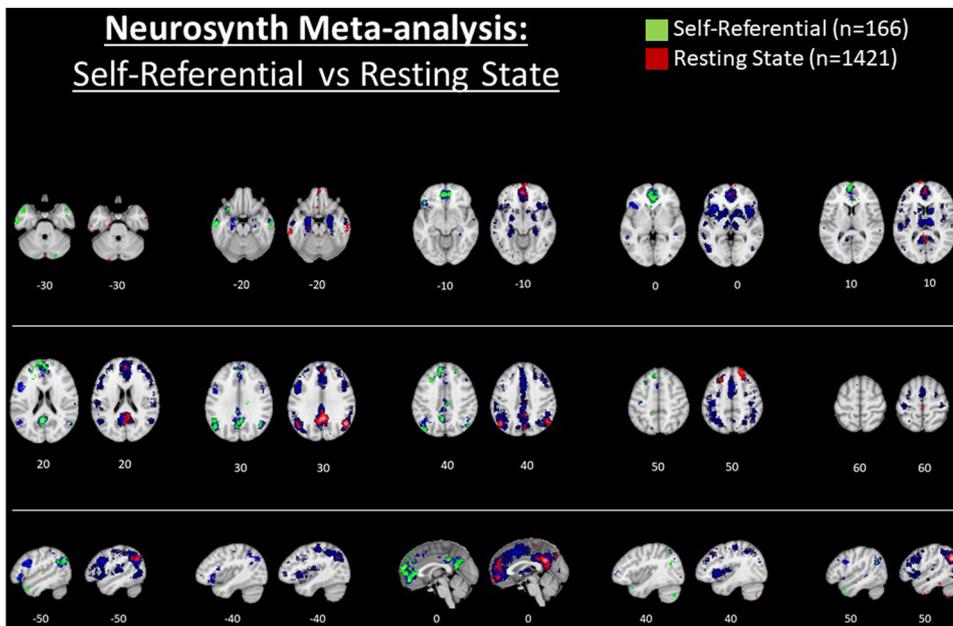


Fig. 6. Title: Automated meta-analysis of the search term “self referential” vs. “resting state” via neurosynth.org.

Caption: Results for the association test map for “self referential” (n = 166 studies) are shown in green (left) and for “resting state” (n = 1421 studies) in red (at right) for each transverse slice. In comparison, results for the respective uniformity test maps are shown in blue. Only positive results are depicted. Results are FDR corrected to $p < .01$. Please see supplementary file for further description.

frequently “in their minds” than “in their bodies” during resting state scans, that is, they may be more engaged in V-SRP rather than NV-SRP, although the more unique response during resting state in the right TPJ/IPL could also be consistent with NV-SRP and the representation of BSC during resting state. Moreover, the greater apparent correspondence between resting state and V-SRP that is often emphasized, in comparison with NV-SRP, may partly reflect inherently biased instructions routinely given to participants to “allow their *minds* to wander” during resting-state scans, rather than to attend primarily toward bodily sensation. In fact, research suggests that, despite its name, verbal thought may in fact *not* be the predominant experience during “mind wandering” states. Rather, research suggests that verbal mentation may only comprise about 30–40 % of the conscious contents of “mind wandering” occurring naturally in the resting state, while visual and somatosensory awareness (the latter, as equivalent to our use of the term “body-wandering” as a form of NV-SRP) may together comprise as much as 50 % of the conscious contents occurring during resting state (Delamillieure et al., 2010). This is also true of meditation practice where spontaneous conscious experiences arise as a distraction from focused attention to respiratory sensation not only in the form of “thoughts” (e.g., planning, memory) but also in the form of other bodily sensations (e.g., physical discomfort such as neck or back ache; (Frewen et al., 2010). Indeed mindfulness practices, seemingly in contradiction to their name, typically have as one of their primary goals reorienting dispositional attention away from V-SRP toward NV-SRP and BSC, for example, toward respiratory sensation or a semi-structured somatic awareness exercise called “body scan meditation”. Such body-oriented mindfulness meditation tasks can be considered a form of intentional and variably organized “body-wandering”, a term we utilize here as an analog to the use of “mind-wandering” in conventional literature but taking as its primary object NV-SRP and BSC rather than the verbal stream of thought. It will be of interest to determine whether mind- vs. body-focused resting state scans would yield differences in active brain regions in a future study (Farb et al., 2015). Indeed neuroimaging research is now suggesting the complexity of the resting state and its function not only in V-SRP but also in NV-SRP. For example, (Fox et al., 2015) showed in a meta-analysis that mind-wandering and related spontaneous thought processes not only recruit MPFC and parietal structures but also recruit response in ACC, insula, temporopolar cortex, secondary somatosensory cortex, and lingual gyrus, areas typically more often associated with BSC and NV-SRP.

Returning to James (James, 1890), these considerations also find precedent in his psychological principles in so far as he attributed the conscious feeling of self-awareness to a *bodily feeling within the stream of thought*, in other words, a sort-of body-mind integration. Describing first the stream of thought, he wrote: “I am aware of a constant play of furtherances and hindrances in my thinking, of checks and releases, tendencies which run with desire, and tendencies which run the other way.” This description of the stream of thought seems akin to what is conventionally referred to as *mind-wandering* in current cognitive neuroscience and would appear to emphasize verbal mentation or V-SRP. However, for James, upon attending to the process of mind-wandering, he purports to find an integrated bodily-motor representation: “*Whenever my introspective glance succeeds in turning round quickly enough to catch one of these manifestations of spontaneity in the act, all it can ever feel distinctly is some bodily process, for the most part taking place within the head.*” (italics original). More specifically, he relates that, “In attending to either an idea or a sensation belonging to a particular sense-sphere, the movement is the adjustment of the sense-organ, felt as it occurs.” For example, referring to visualization or visual imagery, he reflected “I cannot think in visual terms, for example, without feeling a fluctuating play of pressures, convergences, divergences, and accommodations in my eyeballs.” Moreover, referring to the verbal stream of thought, he concluded: “*the ‘Self of selves,’ when carefully examined, is found to consist mainly of the collection of these peculiar motions in the head or between the head and throat*” (italics original). Thus as a predecessor of an embodied approach to understanding SRP, he believed that “*our entire feeling of spiritual activity, or what commonly passes by that name, is really a feeling of bodily activities whose exact nature is by most men overlooked.*” (italics original).

Also consistent with a form of body-mind integration occurring during resting state, a study by (Babo-Rebello et al., 2016) also emphasizes the likely role of the default mode network, observed during resting state, in the integration of bodily-based signals (NV-SRP) into V-SRP. In their study, participants were instructed to fixate a visual screen and allow their minds to wander until prompted by an on-screen instruction to divulge the contents of their conscious experience, with the timing determined randomly. More specifically, influenced by William James’ (James, 1890) conceptualization regarding consciousness of self, participants were instructed to indicate at those very moments whether their thoughts were in the form of first-person (egocentric) or third-person (allocentric) perspective and either concerned SRP or ORP in

content. Throughout the duration of the experiment, magnetoencephalography (MEG) recorded heart-evoked potentials such that the researchers could examine whether the contents of consciousness varied by the co-occurrence of the prompt relative to the participants' heart beats that were also recorded. The authors found that approximately 300 msec after a T peak in the cardiac rhythm, spontaneous first-person SRP (in comparison to third-person non-SRP) was associated with greater response over medial posterior sensors with a source location consistent with the left V-PRC. In comparison, about 100–170msec following a T peak, spontaneous SRP in comparison to non-SRP was associated with increased response in medial frontal sensors localized to the V-MPFC. There were no differences, however, as a function of the valence or temporal contents of consciousness. Moreover, this correlated neural activity to participants' heart beats could not be trivially explained by cardiac artifacts given the time windows measured, nor psychophysiological arousal effected by SRP, given that no correlations with heart rate or its variability were found. Broadly speaking, the authors therefore concluded that “our results reveal a direct link between selfhood and neural response to heartbeats... our findings indicate that the two seeming distinct roles of the DN [default network], in self-related cognition on the one hand, and in the monitoring of bodily signal for autonomic function regulation, on the other, are functionally coupled” (p. 7837). The study also illustrates the correspondence between brain activity observed during resting state and the particular contents of a person's conscious experience, dependent on the coordinated activity of the heart. More studies of the HEP as it may relate to both V-SRP and NV-SRP are needed in the future (Park and Blanke, 2019b). Critically, we will return to the notion of first-person (egocentric) vs. third-person (allocentric) perspective in a subsequent section as a means of further differentiating roles for the M-MPFC (and V-MPFC) in comparison with the D-MPFC.

Other studies have also yielded individual differences in the typical contents of a person's conscious awareness when it wanders including between a focus on V-SRP in comparison with NV-SRP (Delamillieure et al., 2010; Gorgolewski et al., 2014; Hurlburt et al., 2015). For example, a study by Smallwood and colleagues found that resting-state connectivity between the left temporal pole and the PCC was predictive of both future- and past-oriented mind wandering and negative intrusive thoughts occurring during a cognitive task, while connectivity between the hippocampus and PCC was predictive of the detail of such thoughts. These findings emphasize the PCC as a point of convergence or correlation within the brain systems mediating spontaneous V-SRP that may be integral to determining the content of the stream of thought; similar results were found for the V-MPFC at a more liberal level of statistical analysis (Smallwood, 2013b). The results also confirm previously known dense interconnectivity of the PCC (e.g., (van den Heuvel and Sporns, 2011)) but suggest this interconnectivity likely at least partly populates the contents of SRP, which may vary across persons in emphasizing V-SRP over NV-SRP or vice versa. Regardless of its contents, these results suggest that whereas the default mode network and resting state were first discovered simply in relation to a reduction in activity in response to high-load cognitive tasks (i.e., the so-called task-positive vs. task-negative networks) (Raichle, 2001, 2015; Raichle and Snyder, 2007), such brain and behavioral states must now be understood as serving specific adaptive functions including endogenous SRP in various forms (Buckner et al., 2008).

Moreover, beyond correlational designs alone, researchers have also shown that NIBS can modulate the tendency toward mind wandering during resting state, suggesting a causal role for different brain regions in SRP during the subjective state of mind wandering. For example, (Bertossi et al., 2017) showed that the tendency to mind wander decreased among men (but not among women) after cathodal tDCS stimulation applied to the V-MPFC as compared to sham treatment or tDCS applied to occipital cortex. Moreover, mind wandering exhibited a decreased tendency toward SRP (relative to ORP) over time in men especially following cathodal V-MPFC tDCS. However, such results may

not be specific, as an increase in mind wandering can be evoked through tDCS at other placements including for the dorsolateral prefrontal cortex (Axelrod et al., 2015, 2018) (but see (Boayue et al., 2019)) while a decrease was seen after anodal (vs. cathodal) stimulation of the R-IPL associated with reduced effective connectivity of the R-IPL (and M-MPFC) to the PCC (Kajimura et al., 2015; Kajimura and Nomura, 2015). Further (Eldaief et al., 2011) impacted DMN connectivity at rest by utilizing rTMS over the L-IPL, where 20 Hz (activating) rTMS decreased functional connectivity with PCC, V-MPFC, and R-IPL, whereas 1 Hz (deactivating) rTMS had no appreciable effect on L-IPL functional connectivity with these ROIs but instead increased correlations with the hippocampus; unfortunately, whether there were any psychological effects of the intervention for SRP (e.g., mind wandering) was not reported.

To provide a preliminary conclusion, it appears that neuroimaging studies of the resting state are also suggestive of similarities and differences with SRP whether in the verbal or non-verbal modalities. However, the observations we have so far made along these lines have been limited only to qualitative visual comparison of the different maps, and so we also conducted a conjunction analysis, the results of which is featured in Fig. 7 (technical description is included in the supplementary materials). The conjunction mapping tends to validate the aforementioned different regions of interest (ROIs) for both V-SRP, NV-SRP, resting state, and the various comparator conditions previously discussed (“social cognition”, “reward”, “valence”). With a focus on response overlapping with “self referential” tasks we see that conjunction analyses reveal the most consistent activation across tasks coheres in the V-MPFC and M-MPFC. However, at the left of this figure, various regions of interest are also plotted in yellow on the neurosynth results for “self referential” that will become the subject of the foregoing discussion, that is, that different subregions in various ROIs for SRP are important to distinguish based on studies of resting state functional connectivity.

7. Subparcellation of regions of interest to SRP by resting state functional connectivity

Beyond comparisons between top-down SRP studies and tendencies toward bottom-up or spontaneous SRP that occurs in mind wandering during resting state, studies of resting state have also primarily been used to uncover functional connectivity networks and subspecialization of various regions of interest to both V-SRP and NV-SRP as have been discussed previously, specifically, for the PCC, PRC, IPL, insula, ACC, and MPFC. Beginning with the medial posterior cortex, at least a four-fold parcellation between ventral posterior cingulate cortex (V-PCC), dorsal posterior cingulate cortex (D-PCC), retrosplenial cortex (RSC), and precuneus (PRC) has been differentiated during resting state (Bzdok et al., 2015). Moreover, these distinctive nodes were found to exhibit differential functional connectivity with the MPFC and other ROIs to SRP. Specifically, Bzdok et al.'s resting-state functional connectivity analysis (Bzdok et al., 2015) showed that V-PCC exhibited the greatest correlated activity with V-MPFC, whereas D-PCC exhibited the greatest correlated activity with D-MPFC. Further, whereas the V-PCC correlated more strongly than the D-PCC with the TPJ in its posterior aspects (P-TPJ), the reverse was true for its anterior aspects (A-TPJ). Comparably, activity in RSC correlated primarily to limbic regions. This three-fold differentiation of the PCC in its patterns of functional connectivity was also revealed by Yu et al. (Yu et al., 2011) who also examined response within the ACC, discussed below. Further, the PRC correlated more strongly than the PCC subregions only with the medial superior parietal lobe (MSPL) in this study. However, what was referred to as the PRC exhibited a subparcellation into as many as 8 clusters in another study (Zhang and Li, 2012), although here some differences arise in labeling what constitutes the PRC in comparison with the Bzdok et al. study (Bzdok et al., 2015), wherein the authors also clearly include the medial superior parietal lobe (MSPL) and also appear to

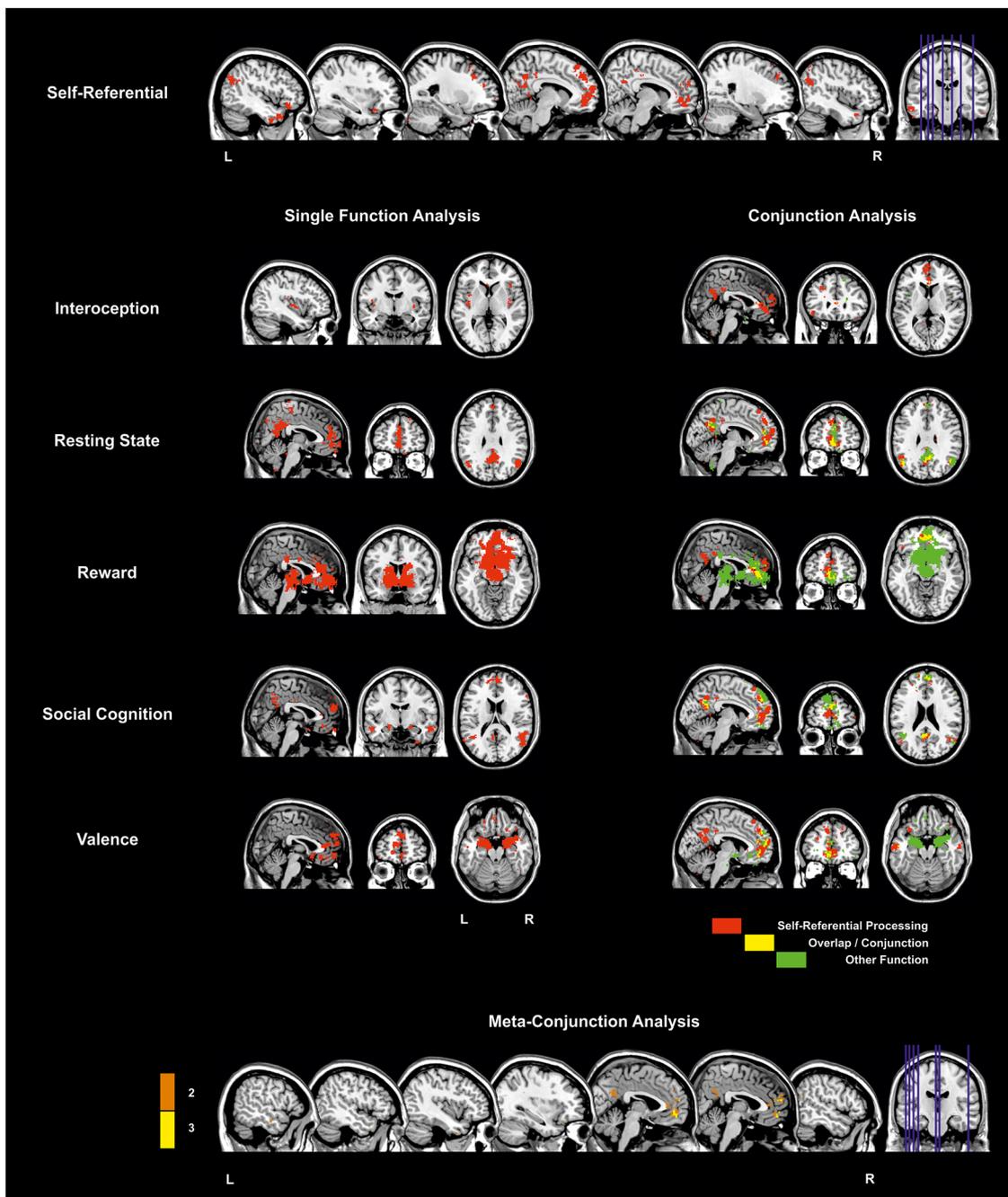


Fig. 7. Title: Conjunction analyses comparing meta-analyses of the search term “self referential” with other terms via neurosynth.org. Caption: At right, results for the association test map for “self referential” are shown in red, the other search terms are shown in green, and the conjunctive overlap in yellow. At bottom right, “meta-conjunction analyses” show maps where “self referential” overlaps with minimally one other search term in orange and minimally two other search terms in yellow. At left, the results for “self referential” are enlarged to depict the association test map in red and uniformity test map in blue, overlaid upon which are yellow circles depicting the approximate location of various ROIs as described in the text and forming the basis of resting state functional connectivity analyses, the results of which are described in subsequent figures. Only positive results are depicted. Results are FDR corrected to $p < .01$. Please see supplementary file for further description.

include posterior aspects of what was referred to as the V-PCC by Bzdok et al. With this approach, Zhang and Li illustrate that the more posterior aspects of the MSPL (their clusters 1–3, cluster 2 and 3 describing the MSPL anteriorly and posteriorly, respectively, and cluster 1 the SPL in its more lateral aspects) in fact exhibits *negative* connectivity with the primary nodes of the DMN, insula, and temporal lobes, while the anterior-ventral PRC proper bordering the V-PCC (clusters 5–8) does reveal positive connectivity with the MPFC and lateral IPL whilst also being negatively functionally correlated with activity in the insula.

Moreover, only their cluster 8, appearing posterior to but possibly inclusive of posterior aspects of the V-PCC, exhibited positive connectivity with the D-MPFC. Further, only the most superior and anterior aspects of the MSPL (cluster 4) exhibited positive connectivity with the insula, somatosensory cortex, and motor cortex. In summary, medial parietal functional connectivity during resting state, when participants typically are variably engaged in some form of “mind-” and/or “body-wandering”, appears to exhibit differential functional connectivity patterns depending on whether seeds are placed in anterior-vs.-

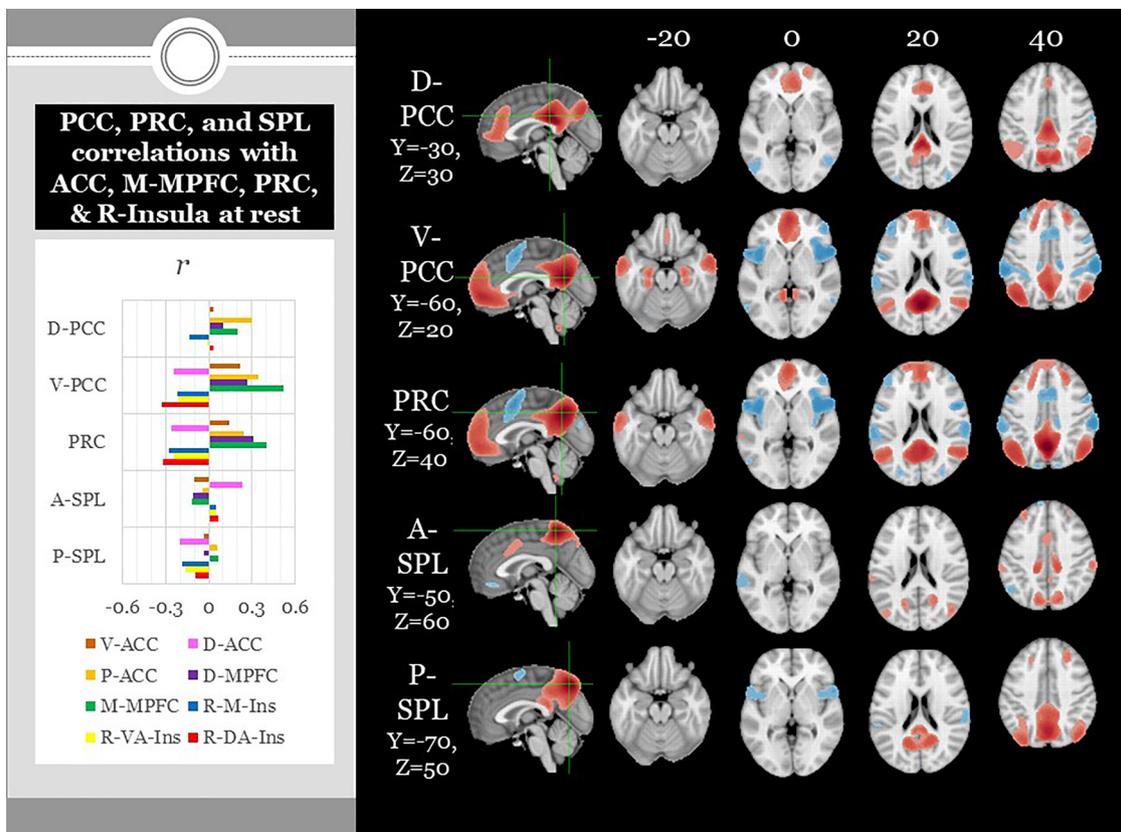


Fig. 8. Title: Resting state functional connectivity analysis examining D-PCC, V-PCC, PRC, and medial SPL seed regions with ACC, M-MPFC, PRC, & right insula. Caption: RSFC analyses were conducted using the online neurosynth.org database comprised of resting state scans collected from $n = 1000$ young adults. Seed voxels are shown at $x = 0$ at the cross hairs in the axial slices, with Y and Z coordinates given. Red depicts a positive correlation of minimally $r > 0.20$ while blue depicts a negative correlation of minimally $r < -0.20$. Obtained correlations with selected ROIs are plotted at left as indicated. Please see supplementary materials for further description including MNI coordinates for seed regions and dependent variables (ROIs).

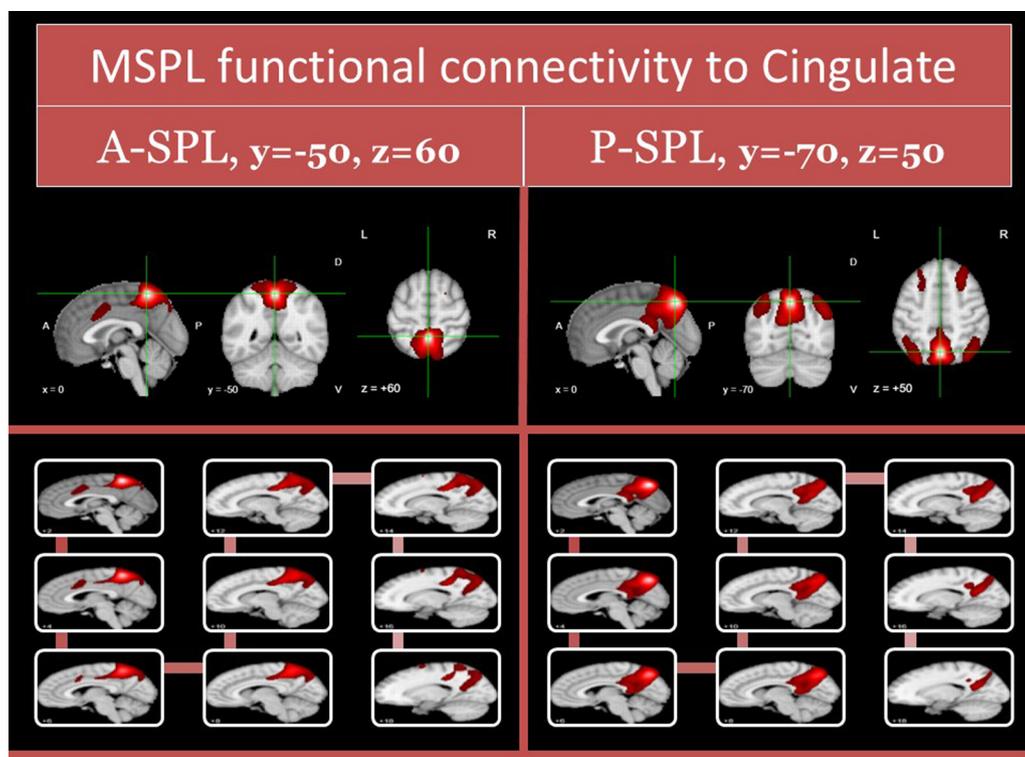


Fig. 9. Title: Resting state functional connectivity analysis examining anterior vs. posterior medial superior parietal lobe seeds. Caption: RSFC analyses were conducted using the online neurosynth.org database comprised of resting state scans collected from $n = 1000$ young adults. Only positive correlations are shown in red which depicts minimally $r > 0.20$. The seed regions are depicted at cross hairs at the given coordinates. Correlation maps are shown up to $x = 16$ at 2 mm intervals (right hemisphere). Similar results can be seen for the left hemisphere (not shown). Please see supplementary materials and main text for further description.

posterior and superior-vs.-inferior seed regions, possibly reflective of different neuroanatomical pathways of functional connectivity that may be differentially involved in V-SRP vs. NV-SRP.

For purposes of illustration in the present review, we sought to replicate some of these differential patterns in correlation maps using the neurosynth $n = 1000$ resting state functional connectivity (RSFC) database (Yeo et al., 2011), particularly exploring patterns of PCC and medial parietal connectivity to ROIs in the MPFC, ACC, and insula as especially pertinent to the current review of V-SRP and NV-SRP discussed so far (see Fig. 8). Referring first to a seed placed just anterior to the subparietal sulcus for the D-PCC, we see that it exhibits positive connectivity posteriorly and medially to the posterior medial SPL, laterally to the bilateral IPL, and anteriorly to the perigenual ACC (P-ACC) and dorsal ACC (D-ACC) in areas 24 and 32; no significant correlations however can be seen with the MPFC (in areas 9–12) or insula. Referring to the V-PCC and PRC, many similarities in the maps are notable and that differentiate it from the D-PCC, revealing positive connectivity throughout the PCC, MPFC, ACC, bilateral temporal poles, and bilateral P-TPJ and P-IPL, whereas negative connectivity can be seen with the bilateral A-TPJ, anterior and middle insula bilaterally, and the D-ACC and premotor cortex. Further, comparing the V-PCC versus PRC maps, a unique positive correlation was found with the hippocampus only for the V-PCC. Finally referring to the MSPL, anterior (A-MSPL) vs. posterior (P-MSPL) seeds further revealed prominent differences. A posterior seed placed at the posterior limits of the MSPL in a location consistent with the peak activation for the contrast of NV-SRP with V-SRP in the study conducted by (Araujo et al., 2015), hereafter termed P-MSPL, shows positive connectivity with the bilateral P-IPL in the absence of prominent connectivity with the P-TPJ, and negative connectivity with the A-TPJ and middle insula, in addition to non-significant negative connectivity with the D-ACC ($r < .20$); no connectivity with the MPFC or temporal poles however can be seen. In comparison, an anterior seed placed just posterior to the marginal cingulate sulcus, hereafter termed A-MSPL, instead shows positive connectivity with the D-ACC and negative connectivity with the V-MPFC. Moreover especially as can be seen at the cortical midline ($x = 0$) the figure suggests an altogether lack of correlation between the A-MSPL and the PCC. Indeed this lack of connectivity can be further visualized laterally up to $x = \pm 16$ wherein the correlation maps suggest that the A-MSPL seed might follow a dorsal functional connectivity pathway anterior to the subparietal sulcus medially and laterally, while also following a second ventral pathway posterior to it along the parietooccipital fissure only laterally but not medially, revealing a striking horseshoe shape medially but a shoe shape laterally on the correlation map (see Fig. 9). The apparent outcome of this may thereby be for the A-MSPL to evidence null correlations with the posterior D-PCC underlying the subparietal sulcus and instead seemingly to correlate more so in the direction of the mid-cingulate (Fig. 9). By comparison, the correlation map in Fig. 9 suggests that the posterior seed (P-MSPL) might correlate only in the direction of the ventral path toward the subparietal sulcus and along the fissure toward both the V-PCC and D-PCC. These findings are consistent with and indeed highly reminiscent of Leech, Kamourieh, Beckmann, and Sharp's (Leech et al., 2011) fractionation of the default mode network during cognitive control tasks into ventral and dorsal aspects, where the dorsal PCC was seen to play a more significant role in cognitive control.

Moving from the medial to the lateral parietal lobe, it is possible that similarly distinctive anterior-dorsal vs. posterior-ventral sub-nodes within ROIs may underpin different forms of SRP. Specifically, RSFC within the temporoparietal junction (TPJ) as also related to SRP exhibits distinct patterns within subclusters wherein researchers have identified at least a three-fold subparcellation of the TPJ into the anterior and posterior TPJ (A-TPJ, P-TPJ) versus the dorsal inferior parietal lobe (D-IPL) proper (Mars et al., 2012). In particular, whereas the D-IPL correlated with response within lateral SPL, cerebellum, the D-MPFC, DLPCF, and frontal eye fields, consistent with involvement in

a frontoparietal control network, the P-TPJ correlated with response in the primary nodes of the DMN and overlapping ROIs known to underpin V-SRP, whereas the A-TPJ correlated primarily with response in the insula, ventral frontal cortex, D-ACC, and postcentral gyrus, more consistent with regions known to underpin NV-SRP and a ventral attention network as has been discussed previously. The IPL itself, however, exhibits yet further subparcellation into at least five or more distinctive areas, introducing even further complexity (Mars et al., 2011). For the purposes of illustration herein, we also sought to replicate these results using the neurosynth $n = 1000$ RSFC database (see Fig. 10). Note here though that to obtain bilaterally similar maps for the A-TPJ, however, the seed had to be placed 10 mm anteriorly in the left hemisphere as compared to the right suggesting possibly the impact of the placement of the auditory association cortex in the dominant hemisphere. We found that the contralateral P-TPJ seeds were correlated $r = .51$, while the A-TPJ seeds were only correlated $r = .33$, a difference that may further reflect the positioning of the auditory cortex. In contrast, the ipsilateral P-TPJ and A-TPJ seeds were correlated $r = -.21$ in the right hemisphere, but only $r = -.13$ in the left, again perhaps indicative of the necessary differential seeding on the axial plane. Regarding correlations with the MPFC, PCC-PRC, and insula ROIs, a clear double dissociation was replicated whereby the P-TPJ exhibits positive correlations with the MPFC and PCC-PRC and negative correlations with the insula, D-ACC and premotor cortex, whereas essentially the opposite is found for the A-TPJ. However, it is important to note that while the positive correlations exhibited by the bilateral P-TPJ with regions of the DMN are strong, often $r > .50$, the negative correlations exhibited by the bilateral A-TPJ are weaker and typically not $r < -.30$. This same dissociation in correlation magnitude can be seen for the differential correlations with the insula seeds: stronger negative correlations tended to be exhibited for the bilateral P-TPJ, often $r < -.20$, whereas weaker positive correlations were shown for the bilateral A-TPJ, often not $r > .20$. Moreover, no obvious laterality effects could be discerned in previously discussed ROIs to SRP although a positive correlation with the ipsilateral middle temporal gyrus is prominent for the left P-TPJ while not for the right P-TPJ, and a positive correlation with the ipsilateral superior temporal gyrus is prominent for the right A-TPJ while not for the left A-TPJ. Moreover, very similar results can be yielded for posterior seeds placed 10 mm superiorly in case of a placement more consistent with the IPL proper (results not shown). Accordingly, these illustrations agree with the notion that the anterior vs. posterior TPJ/IPL might play different roles of relevance to SRP, whereby the posterior ROIs exhibit RSFC maps more consistent with V-SRP and inclusion in the default mode network whereas the positive correlation with the insula revealed for the anterior ROIs might suggest a possible role in NV-SRP consistent with involvement in a ventral attention network. These differential RSFC maps are revealed even more clearly in Fig. 11 as a point of emphasis to show the anterior seed seems to exhibit a correlation path by way of the lateral fissure toward the temporal operculum and posterior insula, whereas the posterior seed seems to correlate superiorly and posteriorly to the superior parietal lobe and ultimately the V-PCC/PRC. Further, in so far as both the P-TPJ seeds in the current analysis and PCC-PRC seeds in the prior analysis evidence RSFC with the MPFC, the question arises how the posterior regions might interact in correlation with the MPFC. To evidence this we also calculated a mediation analysis from the observed correlations using the simple formula that the indirect path c' is equivalent to the correlation for the direct path c minus the product of paths a and b in a three nodal analysis (Fig. 12). This calculation predicts that RSFC between the bilateral P-TPJ/IPL and M-MPFC will be rendered null after taking into account the RSFC shared with the V-PCC/PRC ($r(c) = .39$, $r(c') = .07$), in other words, that the V-PCC/PRC nearly fully mediates the RSFC that the P-TPJ/IPL exhibits with the M-MPFC, further emphasizing the medial posterior cortex as a probable point of convergence or "hub" within the default mode network. Moreover, the V-PCC/PRC appears to strongly albeit not fully mediate

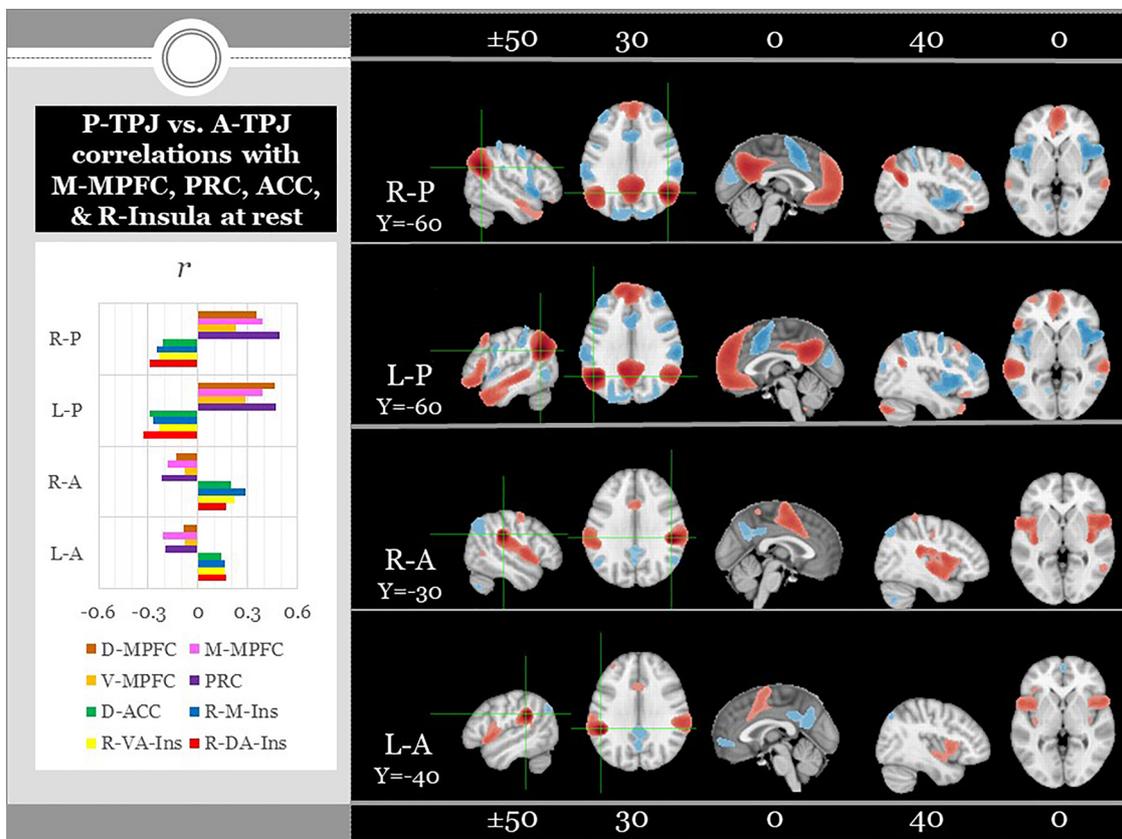


Fig. 10. Title: Resting state functional connectivity analysis examining bilateral anterior and posterior TPJ/IPL seed regions with M-MPFC, PRC, ACC, & right insula. Caption: RSFC analyses were conducted using the online neurosynth.org database comprised of resting state scans collected from n = 1000 young adults. Seed voxels are shown at x = ± 50 at the cross hairs in the axial slices, with Y and Z coordinates given. Red depicts a positive correlation of minimally $r > 0.20$ while blue depicts a negative correlation of minimally $r < -0.20$. Obtained correlations with selected ROIs are plotted at left as indicated. Please see supplementary materials for further description including MNI coordinates for seed regions and dependent variables (ROIs).

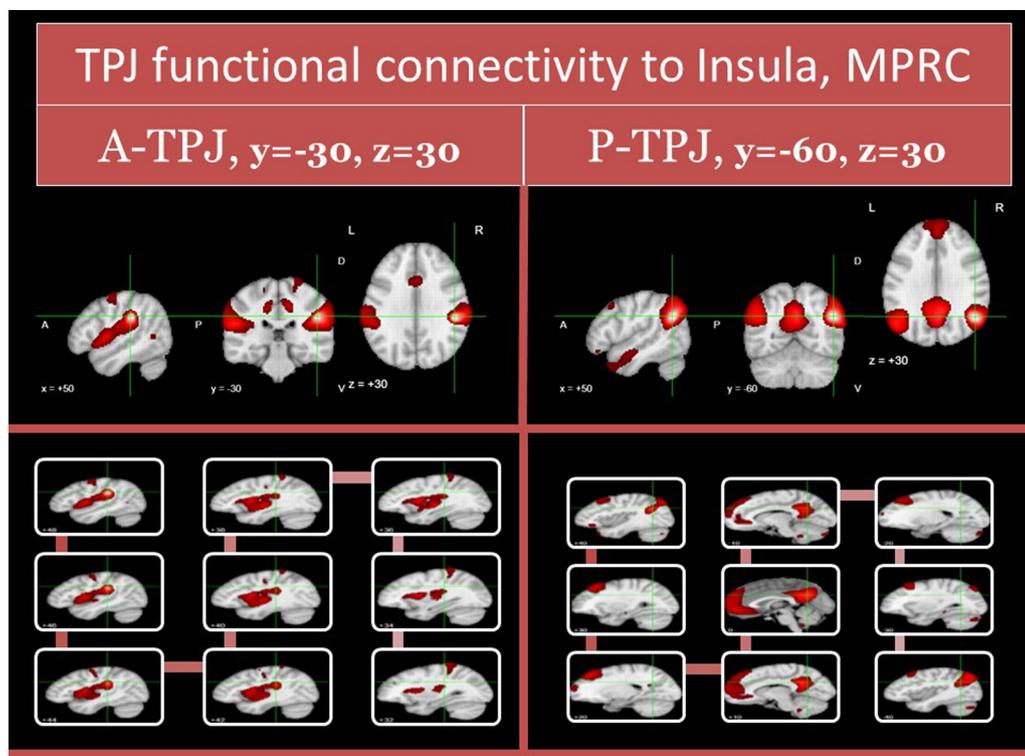


Fig. 11. Title: Resting state functional connectivity analysis examining right anterior vs. posterior temporoparietal junction seeds. Caption: RSFC analyses were conducted using the online neurosynth.org database comprised of resting state scans collected from n = 1000 young adults. Only positive correlations are shown in red which depicts minimally $r > 0.20$. The seed regions are depicted at cross hairs at the given coordinates. For the A-TPJ in left panel correlation maps are shown up to x = 32 at 2 mm intervals, whereas for the P-TPJ in right panel correlation maps are shown from +40 (right hemisphere) to -40 (left hemisphere) at 10 mm intervals. Please see supplementary materials and main text for further description.

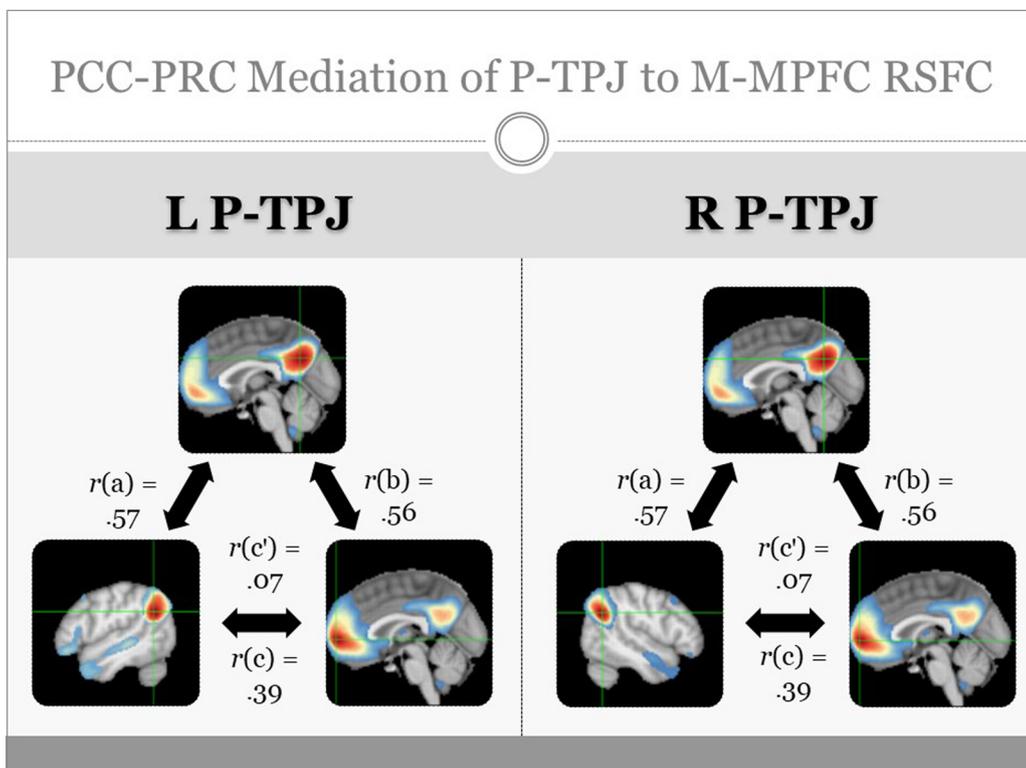


Fig. 12. Title: PCC-PRC mediation of P-TPJ to M-MPFC resting state functional connectivity.

Caption: RSFC analyses were conducted using the online neurosynth.org database comprised of resting state scans collected from $n = 1000$ young adults. Seed voxels are shown at the cross hairs in the axial slices. The correlation $r(c')$ was calculated using the formula that the indirect path c' is equivalent to the correlation for the direct path c minus the product of paths a and b in a three nodal analysis. Left panel depicts results for the left P-TPJ and the right panel depicts results for the right P-TPJ, although identical statistics are found in the two hemispheres. Moreover, the V-PCC/PRC appears to strongly albeit not fully mediate the RSFC exhibited between the bilateral P-TPJ seeds themselves, where the same calculations give $r(c) = 0.51$, $r(c') = .19$ (not shown in figure). Please see text for further description.

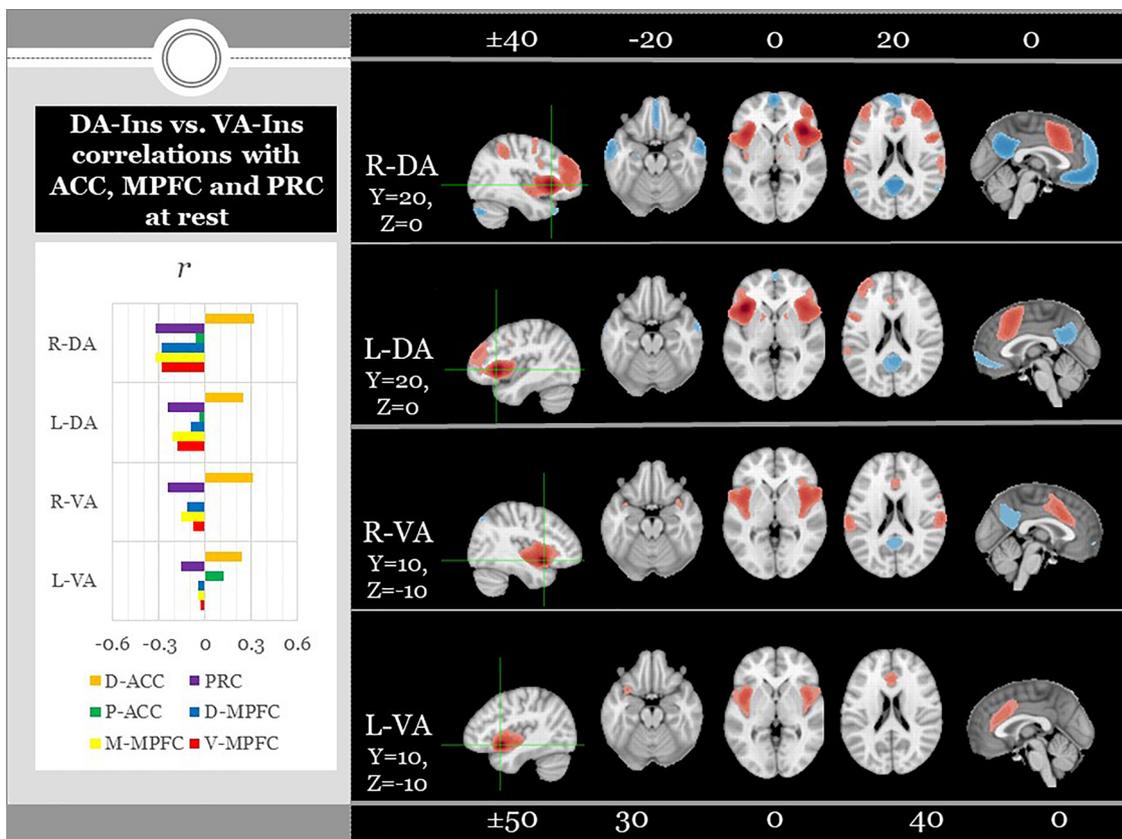


Fig. 13. Title: Resting state functional connectivity analysis examining bilateral dorsal and ventral anterior insula seed regions with M-MPFC, ACC, and PRC. Caption: RSFC analyses were conducted using the online neurosynth.org database comprised of resting state scans collected from $n = 1000$ young adults. Seed voxels are shown at $x = \pm 40$ at the cross hairs in the axial slices, with Y and Z coordinates given. Red depicts a positive correlation of minimally $r > 0.20$ while blue depicts a negative correlation of minimally $r < -0.20$. Obtained correlations with selected ROIs are plotted at left as indicated. Please see supplementary materials for further description including MNI coordinates for seed regions and dependent variables (ROIs).

the RSFC exhibited between the bilateral P-TPJ seeds themselves, where the same calculations give $r(c) = .51$, $r(c) = .19$.

Turning to the functional connectivity of subregions of the insula cortex, several studies reveal dissociable RSFC patterns primarily with the frontocingulate cortex during resting state. Taylor and colleagues first differentiated insula connectivity via resting-state fMRI in humans into three subregions, namely anterior (A-Ins), middle (M-Ins), and posterior (P-Ins), wherein A-Ins correlated more strongly than other insula subregions with response within P-ACC and anterior D-ACC, whereas M-Ins and P-Ins correlated only with posterior aspects of the D-ACC (Taylor et al., 2009). However, Deen and colleagues subsequently found that functional connectivity within the A-Ins could be further parcellated into the ventral A-Ins (VA-Ins) versus the dorsal A-Ins (DA-Ins), each of which also exhibited differential connectivity with ACC and mid-cingulate that were further differentiable from that of the P-Ins (Deen et al., 2011); see also (Cauda et al., 2011). Specifically, VA-Ins exhibited a largely unique connectivity with the P-ACC, while the P-Ins exhibited a largely unique connectivity with the mid-cingulate. By comparison, all insula subregions exhibited connectivity with the D-ACC, although the strongest connectivity was exhibited by the DA-Ins. The authors therefore concluded that their results demonstrate a dorsal-ventral gradient that “indicate the presence of two closely linked but dissociable networks of anterior insular and cingulate regions: a dorsal network primarily involved in cognitive control and a ventral network more involved in emotional experience”. Moreover, Deen and colleagues revealed that only the P-Ins exhibited connectivity with primary and secondary motor and somatosensory cortex in the lateral hemispheres, while only the P-Ins and DA-Ins (but not the VA-Ins) exhibited connectivity with the TPJ. Peng and colleagues have also revealed that all insula subregions tend to correlate negatively with response within PCC (Peng et al., 2018). Collectively these findings again are strongly suggestive of differential ventral-to-ventral and dorsal-to-dorsal

pathways of functional connectivity linking the insula with the cingulate cortex, and further the VA-Ins with the TPJ, and finally with all insula subregions correlating negatively with the PCC.

Owing to the theoretical significance of the anterior insula to interoception and NV-SRP, again, for the purposes of illustration herein, we sought to replicate some of the results described by Deen et al. differentiating between the dorsal anterior insula (DA-Ins) vs. ventral anterior insula (VA-Ins) using the neurosynth $n = 1000$ RSFC database, with a particular interest in ascertaining whether their might be any laterality effects in correlation with ROIs for SRP specifically with the MPFC, ACC, and PRC; results are presented in Fig. 13. Referring to the correlations between the insula seed regions themselves, the contralateral DA-Ins seeds correlated $r = .50$, while the contralateral VA-Ins seeds correlated only $r = .21$, suggesting greater laterality for the VA-Ins relative to the DA-Ins. Meanwhile, the ipsilateral seed regions correlated $r = .28$ in the right hemisphere, and $r = .20$ in the left, supportive of distinguishing possible different roles for these ROIs within both hemispheres. Perusal of the figure further reveals that the DA-Ins and VA-Ins tended to differentiate in patterns of RSFC with the noted ROIs. First referring to similarities, it appears that all seed regions correlate positively with the D-ACC but are not strongly correlated with the P-ACC. Comparing the DA-Ins bilaterally to the VA-Ins bilaterally, we see that negative correlations with regions of the default mode network are clearly more prominent for the DA-Ins seeds. Finally, considering laterality effects, we see that correlations appear about twice as strong for the right insula seeds than for the left seeds. In summary, these results agree with the importance of differentiating between the dorsal and ventral aspects of the bilateral anterior insula with regard to its connectivity with other ROIs to SRP, potentially implicating the seed regions differentially in V-SRP vs. NV-SRP, respectively, as well as the two hemispheres differentially in NV-SRP with an apparent possible right hemisphere dominance. Particularly in so far

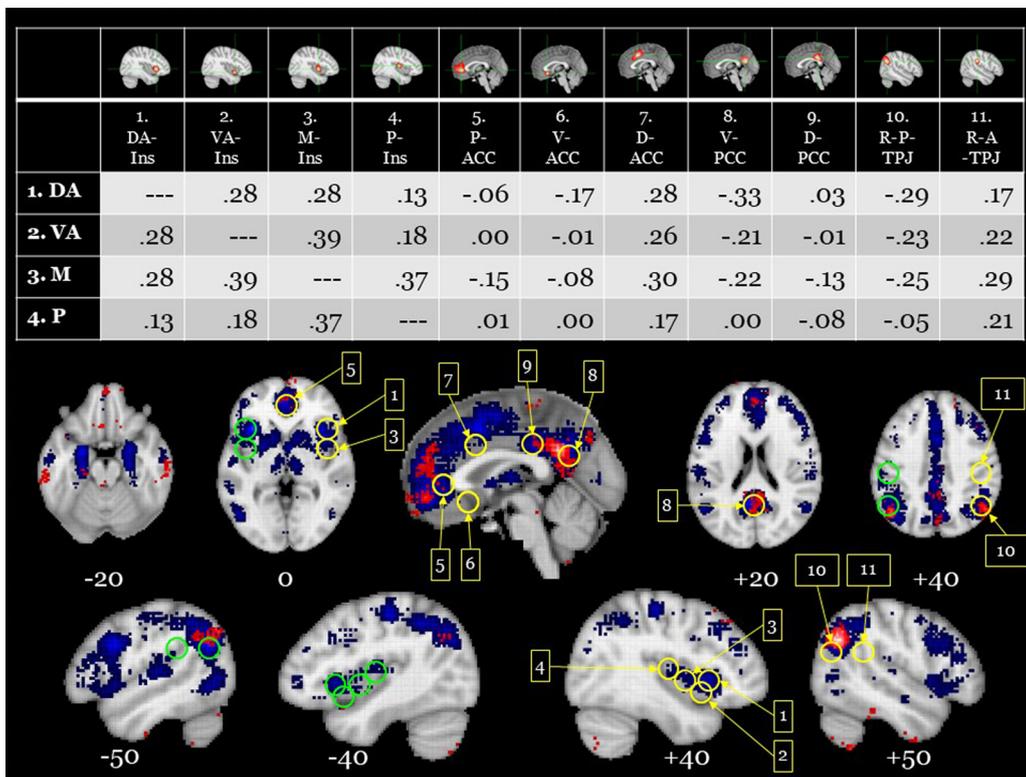


Fig. 14. Title: Correlational results of resting state functional connectivity analysis examining dorsal anterior, ventral anterior, middle, and posterior insula seed regions with various ROIs in comparison with plots of the “resting state” automated meta-analysis using neurosynth.org.

Caption: At top, the correlation table reports the results of RSFC analyses which were conducted using the online neurosynth.org database comprised of resting state scans collected from $n = 1000$ young adults. The table reports effect sizes obtained between each of four seed regions (rows) and the other ROIs indicated (columns). Cross hairs for the seed regions are indicated. At bottom, results for the association and uniformity test maps for “resting state” ($n = 1421$ studies) are shown in red and blue, respectively, and the approximate location of the ROIs specified in the table are shown and labelled with yellow circles at the cortical midline and for the right hemisphere (green circles are shown for the respective left hemisphere ROIs, but data is not shown). Only positive results are depicted for these maps, and results are FDR corrected to $p < .01$. Please see supplementary file for further description including MNI coordinates for seed regions and dependent variables (ROIs).

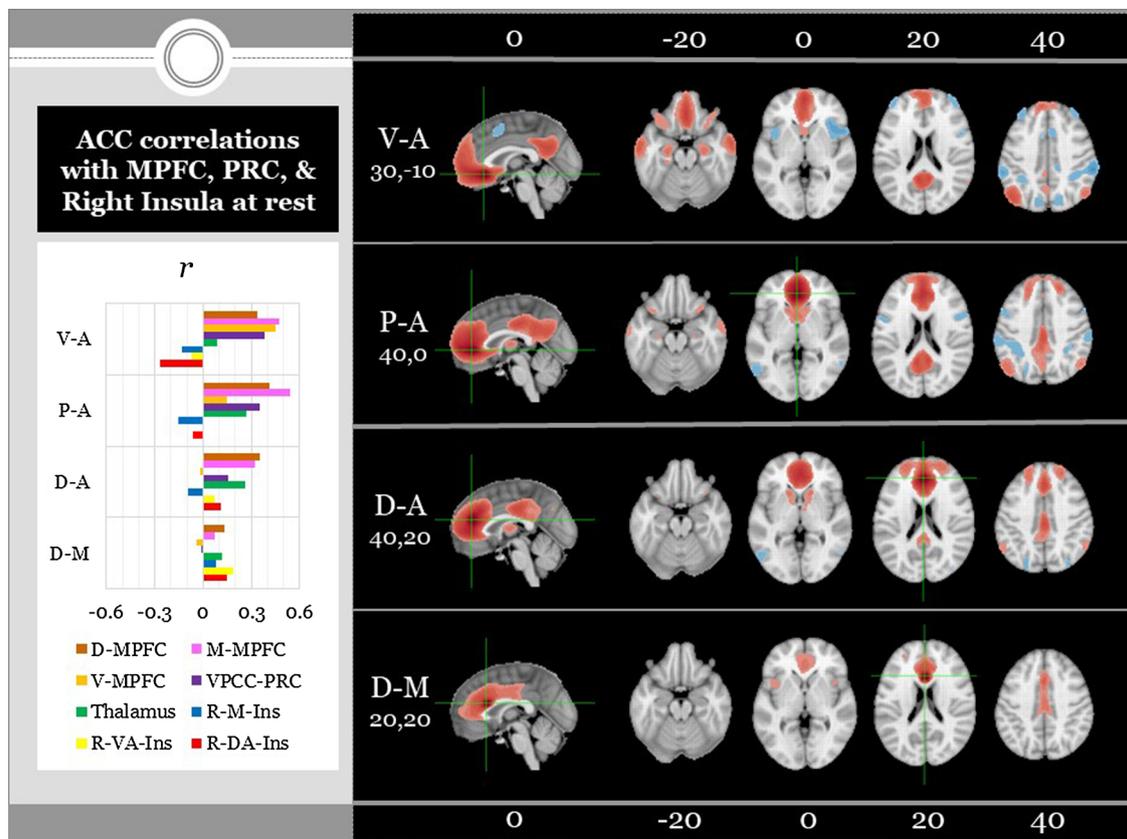


Fig. 15. Title: Resting state functional connectivity analysis examining ventral, perigenual, dorsal anterior, and dorsal middle anterior cingulate seed regions with M-MPFC, PRC, dorsomedial thalamus and insula.

Caption: RSFC analyses were conducted using the online neurosynth.org database comprised of resting state scans collected from $n = 1000$ young adults. Seed voxels are shown at $x = 0$ at the cross hairs in the axial slices, with Y and Z coordinates given. Red depicts a positive correlation of minimally $r > 0.20$ while blue depicts a negative correlation of minimally $r < -0.20$. Obtained correlations with selected ROIs are plotted at left as indicated. Please see supplementary materials for further description including MNI coordinates for seed regions and dependent variables (ROIs).

as the right insula is considered a key ROI within the extant literature on NV-SRP and interoception, a more quantitative rendering of these results, in addition to those in comparison for the middle and posterior insula, is also included as Fig. 14, which tables the correlations exhibited between each right insula seed and between the insula seeds and various ROIs in the cingulate and ipsilateral TPJ. At the bottom of Fig. 14, for comparison purposes, the neurosynth automated meta-analysis for “resting state” are again shown for the same ROIs.

Whereas prior functional connectivity studies have tended not to reveal strong correlated activity between the insula and MPFC but rather between the insula and cingulate cortex, the ACC is also long known to exhibit differential functional connectivity with the MPFC by way of a similar dorsal-ventral gradient (Margulies et al., 2007). Within the ACC, Margulies et al. identified differential functional connectivity for the ventral ACC (V-ACC; their inferior areas i8 and i9) which showed positive correlated activity primarily with both the V-MPFC and M-MPFC, but interestingly negative connectivity with the IPL/TPJ. In comparison, P-ACC (their superior areas s6-s7) showed positive correlated activity primarily with both the D-MPFC and M-MPFC, and positive connectivity with the IPL. Moreover, effectively identical results were replicated by Yu et al. (2011). These results are therefore also consistent with differential ventral-to-ventral and dorsal-to-dorsal pathways of functional connectivity linking the ACC with the MPFC and differentially with the IPL, further providing an indirect correlation between the insula and MPFC by way of the ACC. Moreover, both studies (Margulies et al., 2007; Yu et al., 2011) reveal the D-ACC (i.e., superior areas s4-s5 in (Margulies et al., 2007)) to be more strongly correlated with the D-MPFC than with the M-MPFC or V-MPFC, while

the D-ACC and mid-cingulate was found to correlate negatively with response in the M-MPFC and V-MPFC, whilst being positively correlated with response in the IPL. We further sought to replicate certain of these results for purposes of illustration herein via use of the neurosynth $n = 1000$ RSFC database, where results are depicted in Fig. 15. The figure reveals that it is the V-ACC alone that strongly correlates negatively with the DA-Insula, while a seed placed in the dorsal middle cingulate evidences a positive correlation with the middle insula. Beyond that, the V-ACC was the only ACC seed examined to reveal correlations with the hippocampus, while both the P-ACC and D-ACC reveal correlations with the dorsomedial thalamus. Further, the V-ACC tends to exhibit correlations with the V-PCC but not the D-PCC, the D-ACC tends to show correlations with the D-PCC but not the V-PCC, while the P-ACC shows correlations with both the V-PCC and D-PCC. Finally, the dorsal mid-cingulate seed exhibited neither correlations with the V-PCC or D-PCC. Replicating the prior studies, these analyses strongly show dissociable RSFC patterns among different subregions of the ACC.

In comparison, we were surprised not to find a similarly systematic seed-based RSFC study to review of the differential functional connectivity that may be exhibited by the previously mentioned threefold parcellation of the MPFC into D-MPFC, M-MPFC, and V-MPFC (e.g., (Andrews-Hanna et al., 2010; de la Vega et al., 2016; Frewen et al., 2017)) and so also constructed one for purposes of illustration in the present review using neurosynth (Yeo et al., 2011). We placed a seed for the frontal pole (M-MPFC) at MNI coordinates 0, 60, 0 and a seed for the D-MPFC 20 mm superior. We then placed two additional seeds 20 mm from these coordinates posteriorly on the inferior diagonal for the V-MPFC and on the superior diagonal for a second D-MPFC seed (D-

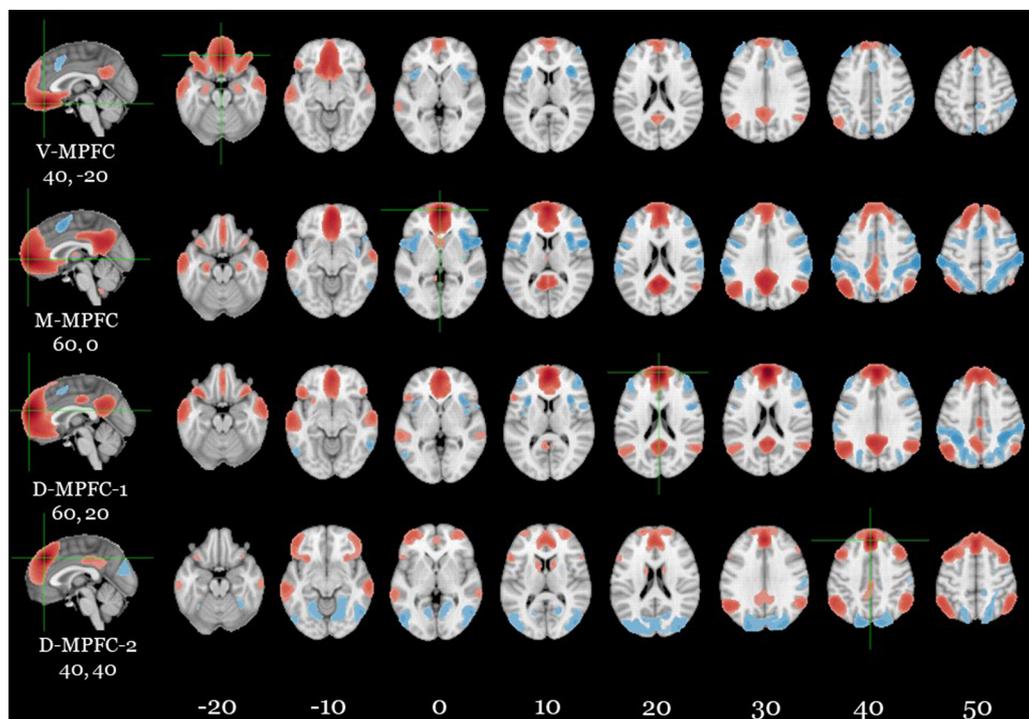


Fig. 16. Title: Resting state functional connectivity analysis examining V-MPFC, M-MPFC and two D-MPFC seed regions.

Caption: RSFC analyses were conducted using the online neurosynth.org database comprised of resting state scans collected from $n = 1000$ young adults. Seed voxels are shown at $x = 0$ at the cross hairs in the axial and respective transverse slices, with Y and Z coordinates given. Red depicts a positive correlation of minimally $r > 0.20$ while blue depicts a negative correlation of minimally $r < -0.20$. Please see supplementary materials for further description including MNI coordinates for seed regions and dependent variables (ROIs).

MPFC-2) more consistent with area 8 (frontal eye fields) as a comparator seed for the first D-MPFC seed for reasons that will become clearer later. The seeds yielded both quantitatively and qualitatively distinctive RSFC maps as can be seen in Fig. 16. The V-MPFC, M-MPFC, and D-MPFC-1 were consistent in showing positive correlations with the temporal poles (see $-20 \leq z \leq -10$) and negative correlations with

the DA-Ins and M-Ins ($0 \leq z \leq 10$) and DLPFC ($20 \leq z \leq 40$). But only the V-MPFC and M-MPFC were found to correlate positively with the hippocampus ($z = -20$), and only the M-MPFC and D-MPFC-1 were found to correlate positively with the P-ACC, D-MPFC, and D-PCC ($0 \leq z \leq 40$) and D-IPL ($z = 40$) while negatively with the P-MSPL ($z = 50$). Comparably, only the M-MPFC showed a negative correlation with the

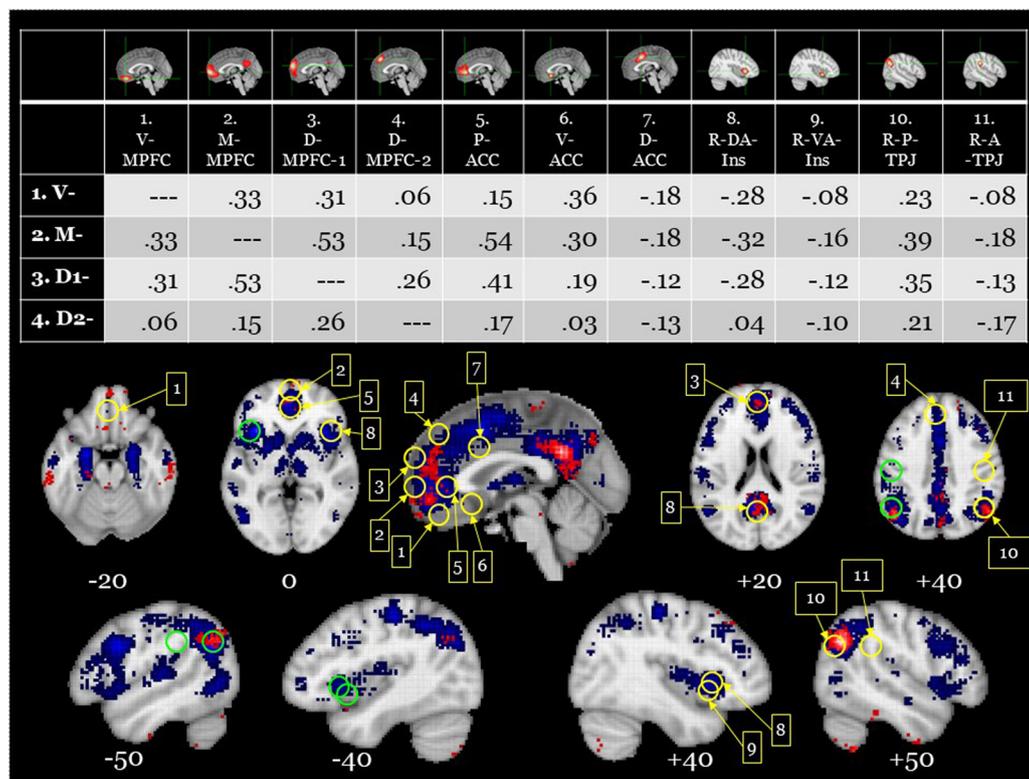


Fig. 17. Title: Correlational results of resting state functional connectivity analysis examining V-MPFC and M-MPFC and two D-MPFC seed regions with various ROIs in comparison with plots of the “resting state” automated meta-analysis using neurosynth.org.

Caption: At top, the correlation table reports the results of RSFC analyses which were conducted using the online neurosynth.org database comprised of resting state scans collected from $n = 1000$ young adults. The table reports effect sizes obtained between each of four seed regions (rows) and the other ROIs indicated (columns). Cross hairs for the seed regions are indicated. At bottom, results for the association and uniformity test maps for “resting state” ($n = 1421$ studies) are shown in red and blue, respectively, and the approximate location of the ROIs are shown and labelled with yellow circles at the cortical midline and for the right hemisphere (green circles are shown for the respective left hemisphere ROIs, but data is not shown). Only positive results are depicted for these maps, and results are FDR corrected to $p < .01$. Please see supplementary file for further description including MNI coordinates for seed regions and dependent variables (ROIs).

Summary of ROIs and RSFC pathways underlying the Consciousness of Self

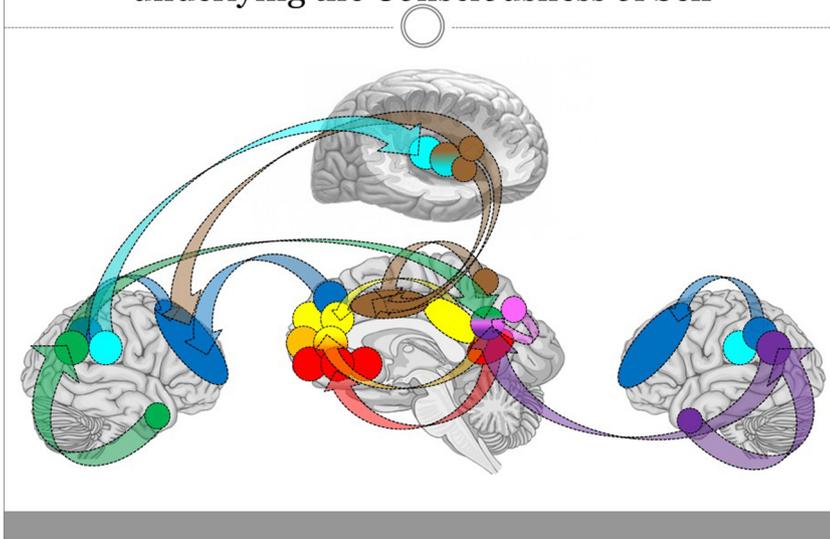


Fig. 18. Title: Summary of hypothesized ROIs and RSFC pathways underlying the consciousness of self.

Caption: Shown in single-coloured circles are various regions of interest (ROIs) involved in neuroimaging studies of SRP. Resting state functional connectivity (RSFC) between ROIs is depicted by coloured arrows. Multi-coloured circles are used to reflect hubs, that is, points of high between-ROI correlations. Three such hubs are depicted: the PCC-PRC, M-Insula, and P-ACC.

A-TPJ ($z = 30$) (supramarginal gyrus). A very different pattern of results is seen for the second more superior D-MPFC seed, which fails to demonstrate significant positive correlations with the V-MPFC ($-20 \leq z \leq 0$), which is the only seed to reveal positive correlations with the ventrolateral PFC extending to the VA-Ins, exhibits prominent correlations with the extent of area 8, and exhibits prominent negative correlations with the occipital cortex. In so far as the MPFC is considered a key ROI to V-SRP, Fig. 17 includes a table of obtained correlations between each of these seed regions and ROIs for the DA-Ins and VA-Ins, and P-TPJ and A-TPJ, to enable quantitative comparisons, while the approximate location of these ROIs are again plotted on the neurosynth automated task-based meta-analysis for “resting state” at the bottom of the figure for purposes of comparison. Regarding the latter, in the frontal ROIs, it is noticeable that the activations are seen more strongly in the ACC in area 32 rather between the P-ACC (area 24) and M-MPFC proper (area 10). Comparably, the response for the meta-analysis of “self referential” discussed earlier does include response in the most anterior frontopolar cortex (area 10) (see Fig. 7). These findings could suggest that on-task “top-down” SRP may engage the anterior frontopolar cortex proper (areas 9 and 10) more so than “bottom-up” SRP as it occurs during resting state principally within the P-ACC (area 32).

Taking these resting-state studies into summary, it appears that RSFC among virtually all of the aforementioned ROIs previously associated with SRP might exhibit dorsal versus ventral and anterior versus posterior neuroanatomical principles, perhaps typified by their involvement in different neural networks that are a significant focus of current investigation. Specifically, the ROIs identified are suggestive of their involvement in the operation of the dorsal attention (DAN) vs. ventral attention networks (VAN) as well as the frontoparietal control (FPCN) versus limbic-affective networks (AN), respectively (Yeo et al., 2011), describing dorsal vs. ventral pathways involved in SRP. These networks, in turn, may regulate and are regulated in turn by a “middle” network, the default mode network (DMN), which in comparison with the previously mentioned neural networks has the most established involvement in SRP based on task-based neuroimaging. For example, referring to the IPL, the TPJ was differentiated into its anterior (A-TPJ) vs. posterior (P-TPJ) aspects, where the A-TPJ belongs to the VAN, while the P-TPJ inclusive of the posterior aspects of the D-IPL proper belong to the DMN. Comparably, the anterior aspects of the D-IPL are known to belong to the FPCN while the P-SPL belongs to the DAN and the A-SPL belongs to the VAN. Further, the V-MPFC and D-MPFC-2 seeds as defined herein represent nodes attributable to the FPCN and

AN networks, respectively, whereas both the M-MPFC and the D-MPFC-1 seeds as defined herein are established nodes of the DMN. Therefore these dorsal versus ventral and anterior versus posterior neuroanatomical principles seem integral to understanding different aspects of SRP. Moreover, the D-MPFC-1 exhibits some overlap with both the ventral and dorsal streams, having the highest average correlation across the four MPFC seeds at rest in the current RSFC analyses. Thus while the M-MPFC may appear to belong to the DMN, the D-MPFC would also seem to provide a source of connectivity with the FPCN, and between the latter and the AN as represented by the V-MPFC. These findings underscore the relevance of investigating SRP at both local-regional and distributed-network levels of analysis. An attempt to illustrate many of these pathways is made in Fig. 18, which emphasizes three points of high convergence (that is, high RSFC or “hubs”) as important to SRP: the V-PCC/PRC, P-ACC, and middle insula. This principal of differentiating between (localized) dorsal vs. ventral ROIs in SRP was broadly anticipated by (Schmitz and Johnson, 2007) but is hereby elaborated in greater detail with regard to ROI subspecialization, as nodes of neural networks, and based not only in stimulus evoked response but rather extended to the analysis of functional connectivity including that occurring during resting state.

Whereas the previously cited literature identifies some of the neural correlates of “mind-wandering” and “body-wandering” as it occurs essentially “on-task”, during resting state, it will also be important to investigate the neural bases of mind- and body-wandering when it occurs “off task”, as a form of distraction from other non-SRP tasks at hand. The latter experiences implicate faults of cognitive control networks such as the FPCN, which are increasingly being studied in their application to SRP, validating the exploratory placement of a second more posterior D-MPFC seed within the FPCN in the frontal eye fields in the aforementioned RSFC analyses. It is to this essential literature that we turn to next.

8. “Off-task” SRP as a distraction: the role of top-down attentional control

We have so far seen that V-SRP and NV-SRP are frequently not only active when participants are explicitly instructed to complete introspective and interoceptive tasks, respectively, but may also be experienced passively, although strictly speaking still in an “on-task” fashion, during resting state scans in which participants are likewise instructed to allow their minds to wander to their various self-

referential concerns. Such mind (and body) wandering, however, may occur not only during lengthy blocks of relative cognitive inactivity, such as during “resting state”, but also during comparably briefer periods of relative cognitive inactivity, for example, during the restful waiting that occurs between the presentation of different experimental stimuli during psychological tasks (interstimulus interval [ISI]).

Indeed Northhoff and colleagues’ “rest-stimulus interaction” (Northhoff et al., 2010) theoretical framework serves to remind us that it is likely that V-SRP and NV-SRP are each continuously active, even including during supposedly inactive periods of “rest” during the ISI. Moreover, response to task-prompted stimulation of either modality is likely to be significantly influenced by the status of both systems prior to stimulus onset. As one example, Meyer and Lieberman showed that greater M-MPFC response during resting state prior to stimulus presentation (i.e., during the ISI) facilitated task performance on a subsequent V-SRP trial, such that increased M-MPFC response during the seconds preceding V-SRP was associated with faster response time; a similar effect was found for the D-MPFC for ORP (Meyer and Lieberman, 2018). In another example, researchers showed that increased activity within the right TPJ and right temporal pole two seconds preceding the onset of white noise predicted the tendency for a person to report hearing their own name in the white noise in comparison with another person’s name (names were masked by the white noise and not actually accurately detectable above chance level) (Qin et al., 2016). Studies such as these illustrate the rest-stimulus interaction concept which describes how endogenous (baseline) activity preceding stimulus presentation must be understood as modulating stimulus-evoked activity prior to its presentation, and further how stimulus-evoked activity, in turn, should modulate the endogenous activity that follows during the next ISI (Northhoff et al., 2010). In other words, the state of my brain in response to a future stimulus not yet presented is partly predictable by the current state of my brain, where in the given examples such preceding states tended to be facilitative of future SRP and performance in SRP tasks. In these cases then, the rest-stimulus interaction framework provides a theoretical explanation of automaticity of response to subsequent self-referential stimuli; self-referential stimuli will be afforded a processing advantage in so far as during the ISI participants are engaged in SRP as a default state, thus already engaging these brain systems prior to stimulus presentation, providing a measure of readiness to respond.

In this vein, it is important to distinguish resting state studies, wherein participants’ task is simply to allow their minds to wander, from such mind wandering as it occurs during other non-SRP tasks, perhaps as such representing a distraction from the task and associated with a decrement in performance in responding to non-self-referential stimuli (Christoff et al., 2016). Essentially, contrast of these states differentiates between on-task vs. off-task mind wandering. As we have considered before, during resting state, mind-wandering is *on-task*: although resting states are characteristically low-load tasks, where little if any response is required of participants, nevertheless in these tasks, participants are simply instructed that their minds are free to associate as they will, in the Freudian sense, with their stream of consciousness open and unobstructed, in the Jamesian sense, and so doing so must technically be considered *on-task*. For conceptual clarity, on-task mind wandering during resting state as such must necessarily be contrasted with *off-task* mind wandering during performance of other non-SRP tasks, where spontaneous SRP occurs off-task as a non-intentioned intrusion (Smallwood, 2013b).

Regarding the potentially intrusive nature of SRP, Sui and Humphreys (Humphreys and Sui, 2016; Sui and Humphreys, 2015) describe how self-referential stimuli, both verbal (e.g., own name) and non-verbal (e.g., own face), tend to be perceptually salient, thus for all intents and purposes exhibiting an automatic attention capturing effect that can be facilitative, in the case of tasks involving SRP and requiring response to the intrinsically self-referential stimuli, but distracting and disruptive when the self-referential nature of these stimuli is not

relevant to performance in a non-SRP task. For example, when participants’ task is simply to attend to various simple objects (e.g., circle, square, triangle), associatively pairing one stimulus to the self offers a future processing advantage for that stimulus, but a relative decrement accordingly for processing of the remaining stimuli (e.g., (Sui et al., 2012)). Interestingly, processing these non-self-associated stimuli over the self-associated stimuli then later requires greater cognitive effort, from an attentional control perspective, which their research suggests is effected by the FPCN, within which they focus on both its dorsolateral prefrontal cortex (DLPFC) and (left) intra-parietal sulcus nodes (Sui et al., 2015, 2013) (Corbetta and Shulman, 2002). But Humphreys and Sui (Humphreys and Sui, 2016) also describe how top-down attentional control networks can also be recruited in the service of SRP, through modulation of the MPFC; here, however, their research regarding response to trials in which SRP represents a distraction shows a negative correlation between DLPFC response and V-MPFC, rather instead suggesting inhibition (Sui et al., 2013).

In summary, work such as that reviewed by Humphreys and Sui (Humphreys and Sui, 2016) clarifies the importance of understanding SRP as it occurs automatically, in the “background” as it were, such as during lengthy blocks of “resting state”, shorter ISI, and as a function of the processing prioritized for intrinsically self-referential stimuli and previously neutral stimuli that have been associatively conditioned to be self-referential. These findings suggest that SRP potentially occurs spontaneously, requiring little cognitive effort or attention, in a “bottom-up” fashion as it were. We would suggest that in so far as self-referential stimuli are emotionally salient, bottom-up processing may occur via ventral processing pathways (e.g., V-PCC and V-MPFC) implicating the ventral attention (VAN) and limbic-affective networks (AN) that disrupt the otherwise comparably neutral socioemotional contexts in which we normally find ourselves, and in which DMN is characteristically implicated by name. Their work, however, shows that such automatic forms of SRP can also be overridden by attentional control networks such as the FPCN at times when it proves distracting. In so doing, they illustrate how a cognitive control network might be recruited in “supervisory” fashion, to discourage bottom-up SRP when it is not helpful to the task at hand, but rather is proving distracting. However, such work has so far emphasized the lateral aspects of the superior frontal cortex (DLPFC) as compared to its medial aspects (D-MPFC). Given that self-referential stimuli are thought already to be given a processing advantage through associative-automatic processes, how might attentional control networks such as the FPCN facilitate rather than only disrupt bottom-up SRP in a top-down fashion? This question is taken up in the next section.

9. Top-down regulation: observing and executive SRP

The previous section considered the role of cognitive control networks in regulating attention away from bottom-up SRP when it distracts from task requirements, emphasizing the role of the DLPFC. However, although less often emphasized within the literature, it needs to be recognized that the FPCN not only includes the DLPFC as is usually discussed but also the D-MPFC. In fact, the D-MPFC is one of the more reliably identified nodes of the network across participants, maybe even more so than is the DLPFC across participants (Marek and Dosenbach, 2018). Moreover, involvement of different aspects of the D-MPFC in both the FPCN and the DMN may make this area of the brain a particularly significant ROI for integrating cognitive control processes into SRP and affect regulation. Further, whereas DLPFC tends to deactivate during resting state, D-MPFC may tend to remain active (Fox et al., 2015). This finding is suggestive of a potential role for D-MPFC in regulating not only high-load external task-focused cognitive attention but also in the modulation of the kinds of low-load internally- or self-focused attention that tends to occur during resting state, whether verbally (V-SRP) or non-verbally (NV-SRP, as BSC). What role might D-MPFC play as a higher-order, top-down ROI during lower-load

internally-focused attention tasks?

Buhle et al. (Buhle et al., 2014) meta-analysed fMRI studies of the cognitive reappraisal of emotion as a task involving attention to and modulation of emotional experience and found that the D-MPFC was among the brain regions exhibiting a greater response during cognitive reappraisal of emotional responses as compared with natural, uninterrupted emotional responding; other regions included the middle and inferior frontal gyri, the SPL, and the middle temporal gyrus, but prominently *excluded* any indication of V-MPFC involvement in cognitively reappraising one's emotional response. Similar to our differentiation between D-MPFC and V-MPFC patterns of functional connectivity during resting state, this meta-analysis suggests that the two MPFC regions are differentially involved during emotion regulation, wherein the authors were led to conclude that the “dmPFC may support semantic and self-reflective processes relevant to elaborating the affective meaning of stimuli or perceiving one's affective state” (p. 2984) but that, while “the implementation of reappraisal consistently activated domain-general cognitive control regions, including dmPFC, dlPFC, vlPFC, and posterior parietal lobe... reappraisal does not rely on vmPFC-mediated emotional control” (p. 2987). Moreover, during the up-regulation of positive emotional responses, Koush et al. (2019) even found that the D-MPFC was negatively correlated with the V-MPFC in an effective connectivity study, while being largely independent during passive viewing of emotional stimuli. However, it will be important in the future to carefully differentiate more inferior-anterior aspects of the D-MPFC in area 9 from more superior-posterior aspects (e.g., area 8). For example, Buhle et al. report D-MPFC in very superior coordinates of $z > 60$, seemingly unlikely to be consistent with placement in area 9 and instead suggesting placement either in area 8 or even 6, the latter of which is instead correlated positively with the DA-Insula at rest, implicating yet another distinctive RSFC topography beyond the scope of analysis herein.

Although cognitive reappraisal tends to invoke verbal strategies as means to regulate emotional responding, another way that the D-MPFC might regulate emotionality is by way of modulating perspective taking during SRP, including in emotional contexts (e.g., (Kalisch et al., 2005)). In a direct comparison of different emotion regulation strategies, it was only the use of emotional “detachment”, instructed to participants as a kind of manipulation of first person egocentric to third-person observer or allocentric perspective, specifically, to “look at the following picture directly but try to take the position of a non-involved observer, thinking about the present picture in a neutral way” ((Dorfel et al., 2014), p. 300) that activated D-MPFC as well as the right IPL/TPJ; this was in contrast to cognitive reappraisal which was instructed as “to reinterpret the picture so that it no longer elicits a negative response” (p. 300). The notion of “detachment” or “distancing” was defined in the experiment as “taking the perspective of an uninvolved observer in order to reduce the subjective relevance of stimuli. It relies upon the (explicit) generation of a self-image distanced from the experienced scene and the potentially overwhelming emotions” ((Dorfel et al., 2014), p. 299; see also (Kalisch et al., 2005)). For example, it has long been known from work by Ruby and Decety ((Ruby and Decety, 2001, 2003, 2004)) across motor, conceptual, and emotional experiential domains that taking a third-person perspective (i.e., adopting the perspective of another person or third-person observer) versus taking the natural first person perspective activates the D-MPFC and right IPL/TPJ, although in their study of perspective taking during emotional processing they also emphasize a role for the V-MPFC (Ruby and Decety, 2004), consistent with the more general role of the V-MPFC in valenced SRP and emotional processing. Their findings concerning D-MPFC however also agree with the general finding that ORP may activate the D-MPFC more so than does V-SRP as was discussed earlier, such that ORP involves taking the third-person perspective as in theory of mind or mentalizing tasks. Finally, the right P-TPJ/IPL was found to be specifically involved during third-person perspective taking in emotional contexts, whereas a more anterior region (A-TPJ/IPL) was

found to be more involved during third-person perspective taking in a neutral (non-emotional) context.

Another meta-analysis by Bzdok et al. (Bzdok et al., 2013, 2012) indeed confirms a role for the D-MPFC in perspective taking whereas the V-MPFC was found to be more activated by reward-related tasks, leading the authors to conclude that, while the V-MPFC is predominantly involved in bottom-up affective processes of approach vs. avoidance and evaluative processing, the D-MPFC may be more engaged by top-down, meta-cognitive processing of social and emotional experience, perhaps associated with a greater sense of detachment, from the allocentric or observer perspective. Thus the authors' finding that the D-MPFC along with the PRC is conjunctively involved in social cognition, emotion, and processing during resting state suggests that it also “might play an interestingly dual role in being part of and shaping bottom-up processes, while at other times also contributing to the top-down regulation of social behavior by means of introspective processes. In other words, it may serve as an interface between neural networks which subserve internally as compared to externally directed cognition” ((Schilbach et al., 2012), p. 7). In comparison, the V-MPFC has been particularly associated with emotionally-valenced SRP, suggestive of a level of emotional identification and the first-person perspective, while the M-MPFC has also been associated with the first-person perspective but in a way that may be more independent of emotional arousal and thus more active in the context of baseline affective neutrality or “resting state”. It thus needs to be emphasized that the typical or default orientation is the first-person one, and therefore the M-MPFC, PCC-PRC and P-TPJ/IPL can be thought of as being associated to the ego-centric level of representation including during resting state (e.g., (Vogeley and Fink, 2003)). However, the modulation of such experience into a third-person allocentric representation may entail additional or different processes within many of these same brain regions as well as engaging SRP more dorsally within the MPFC, perhaps akin to a neurobiomarker of an “observing self” (e.g., (Baars et al., 2003)), that is, a less identified or egocentric self-representation.

Moreover, this “decentering” from the natural or default-mode of egocentricity is of much current interest, for example, as a means of understanding the effects of mindfulness meditation. During mindfulness meditation both V-SRP and NV-SRP is supposedly viewed from a less egocentric perspective, for example, wherein thoughts and feelings are no longer considered “owned” as “my thoughts” or “my feelings” but are instead “just thoughts”, “just feelings”, emphasizing the Buddhist principle of *annata* or “non-self” (Golubickis et al., 2016)(Holzel et al., 2011; Kerr et al., 2011; Kross, 2009; Shapiro et al., 2006). Farb et al. (Farb et al., 2007) provide an example whereby, particularly among practiced meditators, during a V-SRP task involving presentation of personality trait words, a ruminative “narrative” evaluation of the trait words (i.e., “judging what is occurring, trying to figure out what that trait word means to the participant, whether it describes the participant, and allowing oneself to become caught up in a given train of thought”, p. 315) was more strongly mediated by the V-MPFC and M-MPFC, PCC, middle temporal cortex and hippocampus, with a tendency toward greater left-hemisphere involvement, whereas an “experiential” evaluation of one's response to presentation of the same words (i.e., “sensing what is occurring in one's thoughts, feelings and body state, without purpose or goal”, p. 314–315), indicative of “decentering” or an “observing self” as described herein, was associated with greater response within the posterior insula, supramarginal gyrus, and ventrolateral prefrontal cortex, with a tendency toward greater right-hemisphere involvement. Although this study contrasted these two forms of SRP in response to the visual presentation of trait words, the task might have been undertaken as oriented toward ongoing spontaneous self-referential experience occurring during the resting state, perhaps in so doing providing a basis for defining and differentiating the actual task of mindfulness mediation as understood herein, that is, as taking a third-person perspective toward phenomenological experiences that normally occur in first-person perspective during resting

state. In other words, we understand mindfulness meditation as the task of actively self-monitoring the activities of ongoing passive V-SRP as it passes along the stream of consciousness (mind wandering) as well as ongoing passive NV-SRP (body wandering) in a subjectively detached, decentered, and allocentric orientation.

Similar to the open self-monitoring orientation toward experience practiced during mindfulness meditation, neurofeedback can also be understood as a practice of decentering or of an “observing self”. In contrast to NIBS studies, where neuromodulation is under the control of an external device, neurofeedback (NFB) represents another means of potentially modulating ROIs of interest to SRP with downstream psychological effects, but comparably one that is theoretically assumed to be more under the voluntary control of the participant. Specifically, neurofeedback is an intervention by which real-time recording of a measure of a participant’s brain activity (e.g., EEG or fMRI) is provided to them, typically in the form of a visual or auditory signal, in response to which the participant attempts to learn to self-regulate the measured state of their own nervous system, for example, by self-modulation of their degree of attention and/or arousal (e.g., (Demos et al., 2005)). This sort of a conscious allocentric form of self-focused attention would provide a operational task for an “observing self” *par excellence*, entailing observing and attempting to willfully manipulate aspects of oneself that are by definition rendered into a third-person metric, for example, as a number or graph on a screen. As an example, using either fMRI (Garrison et al., 2013a, b) or high density EEG (van Lutterveld et al., 2017) previous researchers measured PCC response during V-SRP as a baseline and then instructed participants to reduce their PCC activity relative to that first-person self-referential baseline, based on findings that highly practiced meditators exhibit relatively little activity in regions of the default-mode network during meditation, including for the MPFC and PCC (Brewer et al., 2011; Tang et al., 2015); stronger coupling is also observed between the PCC, dorsal ACC and dorsolateral PFC at baseline and during meditation conditions in practiced meditators suggesting greater cognitive control over ROIs governing V-SRP in meditators relative to controls (Brewer et al., 2011; Tang et al., 2015). The NFB studies found that voluntarily reducing PCC activity was associated with an increased meditation-related experience of “effortless awareness”, defined as a state of mindful concentration whereby sensory experience is observed with a sense of contentment, devoid of any effort to change it, consistent with the decentered activity of an “observing self” as described herein (Garrison et al., 2013a). These findings are also consistent with results showing that down-regulation of the amplitude of EEG alpha oscillations recorded from midline posterior cortex (Pz electrode site) is possible in healthy volunteers via EEG-NFB, and correlated with the subjective experience of mind-wandering, as well as to blood-oxygenation effects observed by fMRI within the medial parietal lobe (i.e., PRC; (Ros et al., 2013)). Moreover, a meta-analysis of MRI-NFB shows that, independent of what particular region of the brain represents the target of training, and even independent of the directional effect (i.e., increased or decreased amplitude) that is targeted, amplitude tends to be reduced in PCC and PRC during the practice of NFB (Emmert et al., 2016). Such findings implicate reduced activity within midline posterior cortex (PCC, PRC) in both the cause and effect of attempted self-regulation of central neurophysiological state with a potential downstream effect on SRP and self-feelings. Metaphorically, NFB might be akin to a dialing down of certain aspects of ongoing V-SRP and NV-SRP possibly mediated by PCC-PRC activity in favour of attending toward and attempting to modulate an externalized measure of internalized selfhood. In association with the relative decrease in PCC-PRC, other brain regions that were found to be involved in MRI-NFB included amplitude increases in insula, motor cortex, dorsolateral and ventrolateral prefrontal cortex, ACC, temporoparietal cortex, and temporooccipital cortex, while additional decreases in amplitude were observed in bilateral temporal cortex and right parietal lobe (Emmert et al., 2016). Interestingly then, increases were also seen for many of the same regions identified by Farb

et al. (Farb et al., 2007) for the task of “experiential evaluation”, a task considered here to emulate the “decentered” orientation of third-person perspective, and were also consistent with the activities of brain regions involved in interoceptive NV-SRP as described herein. Taken together, these findings also strongly suggest NFB as a possible intervention for modulating SRP that may be akin to effecting the operation of an allocentric “observing self”.

Moreover, the notion that what might be unique concerning SRP lies primarily with the first-person perspective rather than the contents of consciousness is consistent with James’ (1890) distinction between the self as “me” (self-as-object or “contents”) vs. “I” (self-as-subject or “perspective”) (see also Legrand and Ruby, 2009). Concerning affective experience and “self-feelings”, we would suggest that attributing the agentic “I” or self-as-subject activity more so to the D-MPFC rather than the M-MPFC is consistent with the meta-analytic findings of Kober et al. (Kober et al., 2008) who showed that the D-MPFC is one of the most frequently activated regions of the brain during emotional processing, and also one of the most consistently co-active with core non-cortical emotional processing regions, including being the only frontal region to correlate with activity within the periaqueductal gray and the hypothalamus, also suggesting a role for the D-MPFC in higher-order modulation of affect. In fact these findings led Kober et al. to conclude that, “coupled with evidence that dmPFC activity is often found when people evaluate the significance of situational context for the self or others, these results suggest a uniquely important role for dmPFC in the perception and experience of emotion” (p. 1022). The D-MPFC may therefore provide one basis for taking a decentered and deidentified (allocentric) perspective during SRP and emotional processing, either in the service of downregulating negative emotions, upregulating positive ones, or simply to facilitate a kind of decentered open monitoring toward self-referential stimuli as they arise either verbally, in “thought”, or non-verbally, in the interior or exterior of the body, an experience we consider to be akin to the practice of mindfulness meditation and neurofeedback as previously noted. The modulation of attention by means of allocentric third-person perspective may thus allow an orientation toward affective experience including self-feelings in a way that is more decentered, that is, less egocentric.

This “observing self” representation, however, is considered here to be relatively passive in its behavioural orientation, as for example occurs in mindfulness meditation and neurofeedback. This representation must therefore be differentiated, in turn, from aspects of SRP that are more active in nature. Regarding the latter, we would ascribe these more active “agentic” aspects of the self to the yet more superior aspects of D-MPFC in area 8, that is, the frontal eye fields, part of the central executive network together with the DLPFC as was described in the previous section. As of the present writing we can conceive of no better place for theoretically representing this more active source of (at least visual) self-engagement either with the outer world, as in looking outward, versus the inner world, as in looking inward. We would therefore like to distinguish these differing areas within the D-MPFC as mediating representations primarily of the activity of an “observing self” versus a cognitive control system consistent with an “executive self”, respectively. Referring to the involvement of the frontal eye fields in the FPCN, this indeed reminds of James’ (1890) phenomenological account that, looking inward to the operations of “the self”, he finds in part the operation of his eyes: “I cannot think in visual terms, for example, without feeling a fluctuating play of pressures, convergences, divergences, and accommodations in my eyeballs.” Moreover, we speculate that the function of both of these D-MPFC nodes may feel like the subject who is “doing” the attending, that is, may be coupled to the subjective experience of agency but in different (passive vs. active) contexts. We thereby recommend greater study of the possible role of eye movements and gaze in SRP for the future.

But in seeking to address self-feelings as a particular interest of affective neuroscience, we are also particularly interested in SRP that is correlated with the experience of affective “self-feelings”, be they

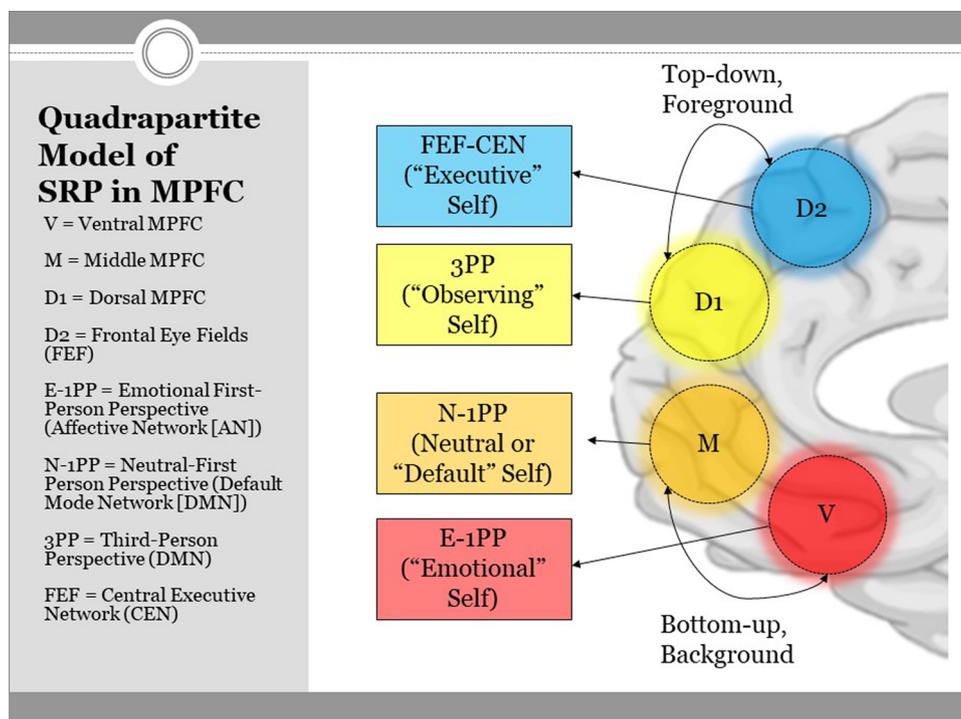


Fig. 19. Title: Quadrapartite model of SRP in MPFC.

Caption: Different levels or functions of SRP are attributed to different ROIs within the MPFC as part of different neural networks as indicated. Please see text for further description.

positive (pleasurable) or negative (aversive). Here, however, it will be important to differentiate between bottom-up and top-down processes. On the one hand, the D-MPFC was reviewed by Kober et al. (Kober et al., 2008) to have a “uniquely important role in the perception and experience of emotion”, perhaps implicating top-down processing. But in contrast to that, conjunction analyses conducted herein rather implicate greater overlap between SRP and both “valence” and “reward” in the V-MPFC, wherein our “meta-conjunction analysis” in fact shows no response overlap for multiple tasks in the D-MPFC (Fig. 7). Accordingly, during SRP, we attribute V-MPFC to emotionally motivated SRP of salient self-referential objects of either kind (semantic or somatic), be they desirable (signally approach) or undesirable (signally avoid), that is, also of either valence. Further, we speculate that in so far as such SRP is held to be emotionally motivated or arousing of either valence, it should naturally occur in first-person (i.e., ego-centric) perspective. By contrast, we speculate that processing within the M-MPFC may be attributable to SRP of comparably affectively neutral content, indicative of its greater involvement in the resting or default state, titled as such in so far as it is supposedly by definition a state of low arousal or an emotionally neutral state. This is further in keeping with our observations regarding neurosynth automated meta-analytic findings indicating that “resting state” may be less reliably associated with activation in the V-MPFC (area 11) as compared with the frontopolar cortex proper (M-MPFC, area 10 and the inferior aspect of area 9). In this case, however, we also speculate that, in so far as these areas are strongly represented in the so-called “default state” (DMN), they should also be considered to partly underpin the first-person (i.e., egocentric) perspective, given that this orientation toward subjective experience is also the natural or “default” state in humans. We thus attribute the M-MPFC to first-person (egocentric) SRP of comparably neutral stimuli or in affectively neutral contexts. Interestingly then, the corollary is also instructive: orienting toward subjective experience from an allocentric third-person perspective must itself represent a deviation from the default state of first-person perspective, thereby being a task requiring some level of top-down control. This attentional manipulation could be

understood as the product of the more dorsal aspects of D-MPFC being directed toward self-referential stimuli (e.g., as during mindfulness meditation) which should then exhibit different patterns of RSFC to the M-MPFC, as was indeed revealed in analyses illustrated herein. Finally, even yet more superior aspects of the D-MPFC in the frontal eye fields may be part of a central executive network more active in cognitive control.

Fig. 19 depicts this localized inferior to superior neuroanatomical framework for conceptualizing these different forms of SRP, effectively a quadrapartite model of the MPFC. The function of bottom-up emotional first-person perspective is attributed to the V-MPFC (in red), while bottom-up neutral first-person perspective is attributed to the M-MPFC (in orange). Comparably, top-down third-person perspective is attributed to the D-MPFC in area 9 (in yellow), considered a representation of an “observing self”. By contrast, top-down central executive control, as for example in coordinating and executing eye movements, is attributed to an “executive” self-representation in yet more dorsal aspects of the D-MPFC within area 8 (in blue). We emphasize that given the V-MPFC and M-MPFC nodes are considered to mediate bottom-up processes, their roles in emotional vs. neutral SRP is here understood to be *intrinsic*; they will be differentially engaged by the intrinsic properties of stimuli as salient to the self or not. Notice, however, that SRP taking place in third-person perspective is held to be a top-down process *by definition*. Therefore, attention directed allocentrically should be independent of the intrinsically arousing versus neutral properties of stimuli. In fact, as has been reviewed, allocentric attention directed toward stimuli that are inherently salient for SRP may tend to nullify their emotional significance as was reviewed in the tasks of cognitive reappraisal and detachment-decentering, where V-MPFC was also found to *not* be involved in such processes. Moreover, we described how allocentric attention directed toward comparably neutral stimuli occurring during resting state could provide a neuropsychological mechanism by which one can openly monitor the ongoing stream of consciousness as in mindfulness meditation practices or their neural correlates as in neurofeedback. While maintaining

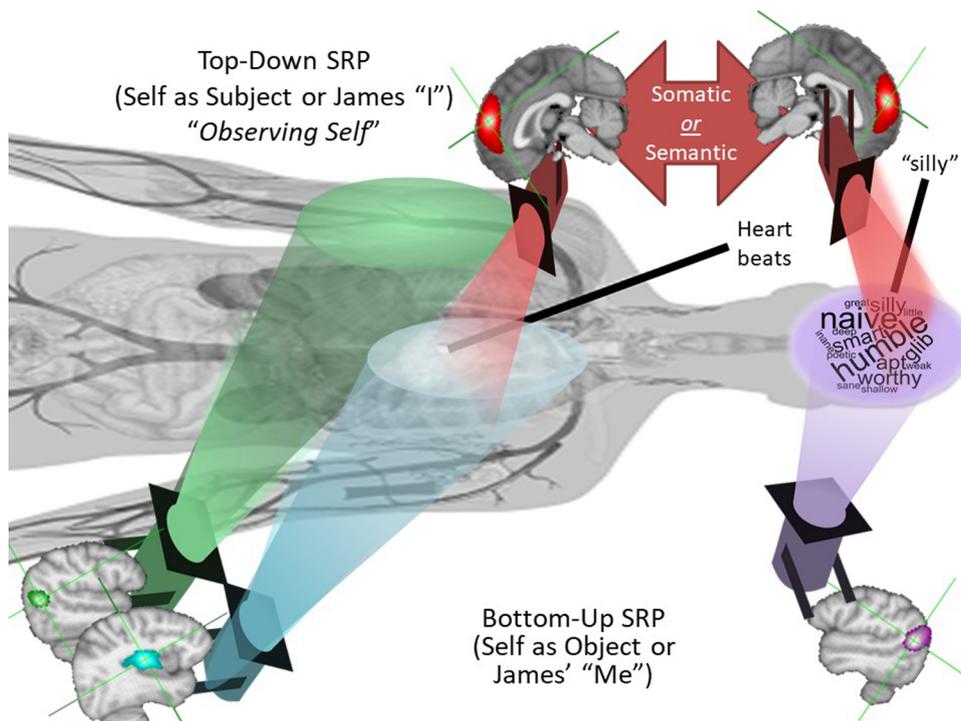


Fig. 20. Title: Attentional spotlights in the theatre of consciousness of self.

Caption: Three "bottom-up" spotlights depict automatic V-SRP in L-IPL (purple), interoceptive NV-SRP in the posterior insula (aqua), and exteroceptive NV-SRP in the R-IPL (green). Top-down SRP in the form of attentional control and an "observing self" are depicted as the function of D-MPFC (red) which can be directed either at the contents or operations of V-SRP (e.g., the thought that one is "silly") or NV-SRP (e.g., heart beats). Please see text for further description.

awareness of such stimuli, but with a sense of experiential detachment from the contents of self-referential thoughts and bodily sensations, one may thereby execute the operations of an "observing self", or by refocusing attention away from SRP as a kind of distraction one executes the operations of an "executive self"; both operations are consistent with an experience of agency as top-down processes. These concepts figure crucially in the conceptual analogy that follows, that is, description of SRP as taking place either in the foreground or background of awareness, as akin to the center vs. outskirts of a theatre stage.

10. SRP in the foreground versus background

We have so far reviewed research investigating active, "on-task" SRP in the verbal (V-SRP) introspective and non-verbal (NV-SRP) interoceptive modalities, as well as what we regard to be much more passive, low-load (albeit "on-task") V-SRP and NV-SRP as potentially occurring during resting state scans during which participants are generally instructed simply to allow their minds to wander. The latter "on-task" mind wandering has also been contrasted with mind wandering when it occurs "off-task" and represents a distraction from task requirements whatever they may be, for example, during exteroception, where attending to external, non-self-referential stimuli is the predominant task requirement, as opposed to the internal attention that is more characteristic of most SRP tasks (Lieberman, 2007a,b). Further, we considered the possible neural correlates of an "observing self" as the orientation toward SRP in third-person allocentric perspective as compared to the default position of first-person egocentric perspective, including as this takes place during resting state, a subjective experience we consider analogous to mindfulness meditation and that may also be partly involved in neurofeedback and other forms of biofeedback. Finally, we considered representations that could execute a more active self-engagement with the surrounding world through the functions of a central executive network, that is, with a focus on yet more dorsal aspects of the D-MPFC in the frontal eye fields.

Before we operationalize these constructs further as they could be measured in task-based neuroimaging studies as compared to their representation in the resting state, we will borrow some familiar metaphors to further illustrate the concepts, specifically, coming from the

study of visual attention (i.e., the "attentional spotlight" (Posner et al., 1980)) and a model of conscious working memory (i.e., the "theatre" metaphor as understood from the global workspace perspective, Baars, 1989, 1999). Regarding the concept of an "attentional spotlight", this metaphor dominated early studies in visual attention where information in a subregion of the greater visual field is thought to be prioritized for more intensive processing (figure) relative to a fuller visual display (ground). This notion also generally accords with the analogy that various sensory- or cognitive-domain specific processes converge as if different actors on a theatre floor, but where an attentional spotlight, itself held to be operating under executive control (akin to the director of the play), shines more brightly upon certain spaces and stimuli, processes that then become conscious contents, thereby also creating a figure-ground relation in a global workspace or "theatre of consciousness". Based on our literature review as so far described, we speculate that to understand SRP one requires the use of at least four such "spotlights" (see Fig. 20), three of which are "always on" but are set at "dim" (aqua blue, green, and purple in Fig. 20) whereas the fourth, which is often "off", is characteristically bright when turned "on" (shown in red in Fig. 20). The three dim spotlights are intended to stand for bottom-up, broadly-focused SRP, usually more or less taking place unconsciously, "in the dark" as it were, in respect of Baar's (1997) theatre metaphor. These processes are thought to be continuously active, performing endogenous monitoring functions, including during resting state. By contrast, the fourth "brighter spotlight" is considered to operate in a top-down fashion, exemplifying executive control processes.

In particular, we speculate that at least two dim "bottom-up" spotlights are necessary to account for background NV-SRP or BSC and another dim spotlight is required to account for background V-SRP. Firstly, concerning NV-SRP, Park & Blanke (Park and Blanke, 2019a) provide a strong case for distinguishing between NV-SRP in the interoceptive ("inner body") versus so-called exteroceptive ("outer body") senses of BSC, which we depict using aqua and green spotlights in Fig. 20, respectively, intended to depict the presumed right-hemisphere dominance in the P-TPJ and insula to each process, respectively. However, we speculate that this distinction between interoceptive vs. exteroceptive NV-SRP might also hold in relation to the involvement of

the anterior vs. posterior TPJ in NV-SRP and BSC as analysed herein. Here, the P-TPJ (approximating the angular gyrus, and more typically the location discussed for the TPJ if not further specified) is thought by Park and Blanke primarily to underpin exteroceptive BSC in the right hemisphere; notably this region is found to correlate strongly with the more dorsal IPL proper and therefore other ROIs attributable to the DMN, as well as to correlate negatively with the insula, as was replicated in RSFC analyses conducted herein. However, the ipsilateral A-TPJ (approximating the supramarginal gyrus), which is not explicitly discussed in the Park and Blanke's framework, may be more so involved in interoceptive monitoring where it is positively correlated with response in the insula and the D-ACC in the VAN but only weakly negatively correlated with the MPFC, again as shown in the RSFC analyses conducted herein. As more research however has considered a role for the insula directly in mediating interoceptive BSC, it is the insula rather than the A-TPJ that is depicted in Fig. 20 accordingly.

Further, we speculate that a third spotlight facilitating ongoing endogenous V-SRP should also be specified, depicted purple in Fig. 20. In keeping with a parietal focus, an adequate placement for this node would appear to include the P-TPJ/IPL but rather in the left hemisphere. Whereas the right P-TPJ/IPL has been strongly linked to BSC, the left P-TPJ/IPL while not the right has tended to more often be identified in V-SRP studies (e.g., in the critical study by Davey et al., 2016, discussed in detail subsequently). Therefore, whereas both the right and left P-TPJ/IPL figure prominently in the resting state and are considered part of the DMN, this divergence of results might implicate the left P-TPJ/IPL more so in underpinning V-SRP during the resting state, while the contralateral right P-TPJ/IPL may underpin exteroceptive NV-SRP or outer BSC during the resting state. Therefore, although we primarily emphasize ventral-dorsal and anterior-posterior neuroanatomical principles of organization as underlying different aspects of SRP, this may represent an instance where laterality differentiates V-SRP from NV-SRP on the sagittal plane. Nevertheless, as just noted, the bilateral P-TPJ/IPL is active during resting state, perhaps providing a means of understanding how the resting and “default mode” state could involve not only “mind-wandering” in the verbal modality but also “body-wandering” in the nonverbal modality. In summary, we speculate that the aforementioned three spotlights function in a bottom-up way largely independent of attention, being “always on”, processing different self-referential contents as “objects” or stimuli involuntarily in an ongoing, spontaneous, and more or less independent fashion in parallel, including during resting state: *interoceptive* self-referential stimuli (aqua spotlight, e.g., heartbeat, breathing rate), *exteroceptive-proprioceptive* self-referential stimuli (green spotlight, e.g., body position or location), and *introspective* self-referential stimuli (purple spotlight, i.e., James' so-called “stream of thought”). In the metaphor of a theatre of consciousness, these processes are akin to the various supporting actors on stage that are generally outside the main spotlight; from a figure-ground perspective, these processes would represent the “ground” of SRP.

However, these somatic versus semantic forms of SRP may become the automatic objects of attention (i.e., figure from ground) via bottom-up processes in the case where endogenous SRP identifies salient self-as-object needs, that is, deviations from a homeostatic equilibrium, for example, hunger, in the case of NV-SRP in the interoceptive sense, an unanticipated mismatch between tactile and visual perception of a body part, in the case of NV-SRP in the proprioceptive sense, or a psychological-level threat, for example, a “worry”, in the case of V-SRP. These results presumably will be mediated through operations of the VAN involving the D-ACC and anterior insula mediated alerting mechanisms, consistent with the fact that M-MPFC and V-MPFC were otherwise both shown to exhibit negative correlations with the D-ACC and DA-Insula during resting state in analyses presented herein, suggesting tonic inhibition. Indeed the notion that attentional gating and tonic inhibition may play a salient role in these background processes is consistent with a Bayesian framework generally pertaining to a process of optimising

the precision of sensory information and thus target-selection for further enhanced processing (e.g., (Feldman and Friston, 2010)). As a model to demote ongoing endogenous self-referential stimuli into the background of awareness, bottom-up self-referential stimuli may be attenuated through a mechanism that reduces their sensory precision, thus avoiding unnecessary attention (e.g., Blakemore et al., 2000). As a corollary, this means that at rest, sensory inputs that are propagated with reduced precision are likely to be tagged as self-originating, that is, self-contents or “self-as-object” stimuli, of less immediate concern. However, among the broad array of sensory inputs at any given time, a relative increase in precision may be afforded to a certain input via ventral attention selection processes subserving attentional control in motivational (i.e. drive to act) contexts as has been described by others (e.g., (Pezzulo et al., 2018)). From this perspective, these ventral attentional pathways should be more active during periods of greater emotional arousal of either valence, signalling conflict or some unexpected effect of a “surprising” nature within the background V-SRP and NV-SRP that must then take priority, otherwise being under tonic inhibition during the resting state. In summary, this account of the bottom-up bringing forth of background SRP to foreground attentional salience is intended to be consistent with generative precision-based computational mechanisms with a focus in ventral attention systems.

In comparison to these bottom-up background processes, the D-MPFC and the frontoparietal control network (FPCN), better known for its role in top-down cognitive control, can be opted for use in consciously focused SRP of either kind of self-referential content in a domain general fashion, that is, toward either V-SRP or NV-SRP, such as in the case of conscious introspective vs. interoceptive tasks. In comparison with the sequestering away of attention by bottom-up unconscious SRP of salient self-as-object features, we are therefore suggesting that this spotlight functions at a level akin with conscious working memory and attentional control in the FPCN. This is consistent with the distinction between ventral attention networks known for attending toward unexpected and surprising salient cognitive and emotional conflicts versus dorsal networks that are better known for their role in initiating and adjusting cognitive control on a flexible trial-by-trial basis (e.g., (Dosenbach et al., 2008)). Even still, whereas the DLPFC is typically emphasized as a key node for the FPCN and indeed seems particularly relevant when attention must be turned *outward*, that is, *away from* self-referential objects to adequately perform non-SRP tasks, we speculate that when attention is consciously and intentionally turned inwardly toward self-referential stimuli during SRP, such as during mindfulness meditation, a better placement for a primary node for this network may be the D-MPFC in area 9 which exhibits RSFC not only with area 10 in the DMN but also area 8 in the FPCN. Critically, as has already been emphasized in the previous section, the latter is known as the frontal eye-fields, recognized to partly coordinate eye-movements which may indeed be involved in the “inward-looking” visual orientation that seems to take place during focused SRP, that is, as the activity of an “observing self”.

In summary, referring first to task-driven SRP, we explicated *introspection* as a *self- (or inwardly-) focused attention* V-SRP task wherein the top-down attentional spotlight is directed focally toward specific verbal self-as-object contents (or “thoughts”) within the ongoing stream of consciousness, thus bringing to the fore V-SRP that would otherwise be taking place primarily in the background. In such instances, evaluating the degree of self-reference of the stimulus (e.g., of an adjective such as “intelligent”) is akin to taking it as figure against the background store of all ongoing V-SRP, where we speculate the left TPJ/IPL may be critical. By contrast, we explicate *interoception* as a *self-focused attention* NV-SRP task wherein top-down attention is directed focally toward specific non-verbal self-as-object stimuli such as the beating of one's heart or the feeling of one's torso or extremities, partly represented by different “spotlights” in the predominantly right insula and right TPJ/IPL, respectively. In such instances, a specific physiological measure (e.g., heart beats) is taken as the figure against the

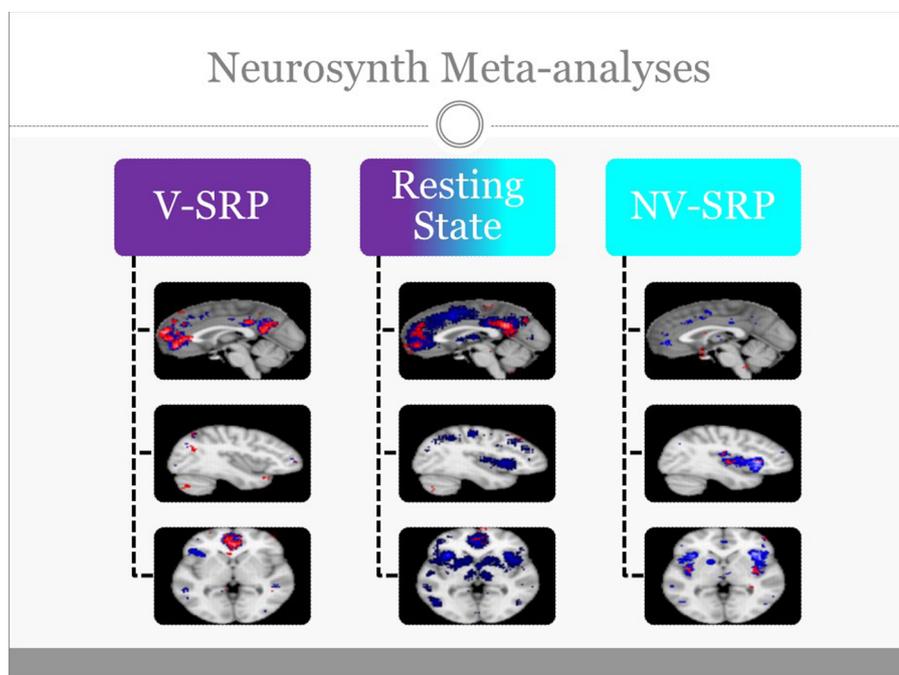


Fig. 21. Title: Resting state as a state of relative convergence for V-SRP and NV-SRP.

Caption: Neurosynth.org automated meta-analytic results for the association test maps are shown in red for “self referential” ($n = 166$ studies) in the left panel, for “resting state” ($n = 1421$ studies) in the middle panel, and for “interoceptive” ($n = 81$ studies) in the right panel. Slices are shown for MNI coordinates $x = 0$, $x = +40$, and $Z = 0$ in rows top to bottom, respectively. Results for the respective uniformity test maps are shown in blue. Only positive results are depicted. Results are FDR corrected to $p < .01$. Please see supplementary file for further description. The figure is constructed to illustrate the hypothesis that the resting state exemplifies a state of possible convergence between V-SRP (e.g., introspection) and NV-SRP (e.g., interoception) when considering the combined results of the association and uniformity test maps.

greater background of all potentially conscious bodily states. Besides these controlled SRP tasks, we have also considered usually characteristically less controlled forms of introspective V-SRP and interoceptive NV-SRP as they operate endogenously in the background of awareness during resting state. Here, during resting state, participants are frequently not only aware of their verbal “thoughts” but also become aware of bodily sensations, wherein the resting state might be likened not only to “mind-wandering” but also to “body-wandering”.

In this way, the resting state may itself be considered a kind of point of “convergence” as a subjective state, for example, between V-SRP and NV-SRP, where neither are necessarily strongly taken as “figure” or “ground” at all times, but rather that both may feature in either relative position at different times. This concept is illustrated in Fig. 21, where cortical midline and right insula ROIs are depicted for the previously described neurosynth automated meta-analyses for the search terms “self-referential” (i.e., V-SRP in purple at left), for “interoceptive” (i.e., NV-SRP in aqua at right), and for “resting state” as a possible state of “convergence” between V-SRP and NV-SRP in the middle. Here, it can be seen that the meta-analysis for “resting state” exhibits greater overlap in the association (red) maps with V-SRP at the cortical midline, but exhibits considerable overlap in the uniformity (blue) maps with NV-SRP in the insula. One might interpret such results as suggesting that the resting state is more strongly associated with V-SRP in a relative foreground position in this figure, but NV-SRP is also represented in the position of a relative background. One may thus consider the association versus uniformity test maps as indicative of the figure vs. ground representations, respectively. In other words, analysis of uniformity maps also seems crucial as a basis of developing hypotheses about both the resting state but also task-focused SRP in so far as these maps are suggestive of ROIs involved in various tasks irrespective of whether or not they are *more* involved in the tasks in comparison with other tasks. Within this scheme, concerning roles for V-SRP and NV-SRP, we therefore consider that both V-SRP and NV-SRP are potentially the primary cause not only of more salient self-feelings, which are taken by definition to be integrated mind-body states in the position of “figure”, but also as relative contributions to the “ground” resting state. Nevertheless, it seems fair to argue that during most phenomenological states *either* V-SRP (“the mind”) or NV-SRP (“the body”) will be experienced in the dominant position of figure, more so in the spotlight of the theatre of self-consciousness, with the remaining

modality referenced less focally in the background, thus representing a balance or ratio of emphasis within the background, which would be consistent with the negative RSFC that was found between certain aspects of the MPFC and insula, for example, described herein. The ground representation is thus conceptualized as an integrative multimodal representation in so far as it would receive continuous inputs from V-SRP and NV-SRP and not necessarily be specific to either, but rather represent the balance of their input at any given moment. In agreement, Northoff (Northoff, 2018) states: “Since interoceptive, exteroceptive, and neural stimuli are all integrated and bound together within the brain’s spontaneous activity, there are no exclusively somatically or perceptually guided thoughts, nor solely self-generated thoughts. Instead, the contents of our thoughts are supramodal and domain independent and can therefore be traced to the balance between interoceptive, exteroceptive, and neural stimuli. Rather than considering each type of stimulus independent of the others, it is rather a matter of their balance and the degree to which one predominates over the others.” (Northoff, 2018) (p.9). Further consistent with the concept of a relative “balance” of V-SRP vs. NV-SRP input or presence into the ground representation, Tsakiris has suggested that interoception transpires not only as explicit sensations that are consciously attended to but rather as a transparent, pre-reflective background state that individuals with higher interoceptive accuracy may be registering more often, as well as more frequently relative to other forms of sensory perception, in background experience (i.e., resting state) (Tsakiris, 2017). Thus, Fig. 21 can be considered itself to exhibit a figure-ground relationship whereby endogenous SRP of different unimodal (i.e., V-SRP, NV-SRP) kinds converge and become integrated as multimodal representations in the endogenous activity transpiring during resting state. This framework thus suggests “ground” representations must be in multimodal or association cortex or, in the modern parlance of graph theory, hubs. As we have stated earlier in reference to Fig. 18, we envision three such hubs to include the V-PCC/PRC, the P-ACC, and the middle insula, all prominent in relative activity within the literatures investigating V-SRP, NV-SRP, and resting state, as can be seen in Fig. 20. These three ROIs are envisioned here as underpinning higher order (multimodal) SRP.

Moreover, critically the “theatre” metaphor reveals something about the nature of the relationship between SRP as it occurs during task-focused introspection and interoception vs. when these processes

occur during rest: we speculate that the latter will be mediated by bottom-up endogenous processes, whereas the former should additionally recruit top-down processes, that is, another “spotlight”. This characterization therefore predicts that that this additional spotlight, that of top-down attentional control, will normally be less active or “bright” during the aimless mind-wandering and body-wandering usually taking place during resting state in comparison with task-focused introspection and interoception. However, the operation of this spotlight could be more so turned “on” during the kinds of allocentric forms of self-focused attention that can take place during mindfulness meditation and neurofeedback especially among practiced meditators as was discussed in the previous section, during which participants self-monitor via a third-person decentered perspective. Based on literature reviewed for example by Qin et al. (2012) and the framework developed here, it is thus tempting to think about the multi-modal ground state as being partly represented in the midline posterior regions, that is, the PCC and PRC, as depicted in Fig. 18, which are known to be among the most highly interconnected network hubs in the human brain, whereas unimodal V-SRP and NV-SRP would be rather found in the lateral regions (parietal and insula). As we have already said, the various subnodes of MPFC and ACC would also be considered multi-modal in so far as they receive projections from the PCC-PRC as measured by RSFC. What then might be the difference between the posterior and anterior cortical midline structures in SRP?

We suggest that the medial posterior (cingulate, parietal) regions may primarily represent the “ground” representation, whereas the medial anterior (frontal, cingulate) regions may instead represent the “figure” representation. In essence, we speculate that representations within the PCC-PRC may be *brought forward* into the figure position or “spotlight” in the anterior regions (i.e., MPFC, ACC, insula), either via ventral pathways more so involved in bottom-up processes or via dorsal pathways more so involved in top-down processes. From this perspective, we can consider what is consciously processed, within the “spotlight” in the position of figure, as what will be most likely correlated to the *contents* of self-consciousness at any given moment. In contrast, what remains outside the spotlight, in the background and unconsciously processed, will not be considered “self” to the same degree. This distinction between what is experienced as “self” contents as compared with what is not also finds precedent in the writings of James (1890) who, somewhat awkwardly, appropriated the terms “consciousness” vs. “sciousness” to each of these functions, respectively: “It would follow that *all* that is experienced is, strictly considered, *objective*; [but] that this Objective falls asunder into two contrasted parts, one realized as ‘Self,’ the other as ‘not-Self;’ ...Instead, then, of the stream of thought being one of *con*-sciousness... it might be better called a stream of *Sciousness* pure and simple, thinking objects of some of which it makes what it calls a ‘Me,’ and only aware of its ‘pure’ Self in an abstract, hypothetic or conceptual way. Each ‘section’ of the stream would then be a bit of sciousness or knowledge of this sort, including and contemplating its ‘me’ and its ‘not-me’ as objects which work out their drama together”. Further consistent with the notion that the posterior nodes may take the position of ground while the anterior ones take the position of figure, Crick and Koch (Koch and Crick, 2001) write that “it is useful to think of the front or higher/executive part of the cortex as looking at and interacting with the back, or sensory part.” In this case, we are therefore led to speculate that processing within the anterior regions might be akin to the figure or contents of self-consciousness whereas the posterior regions might rather represent the (unconscious) background in a figure-ground representation akin to a “spotlight” in a theatre of self-consciousness. A similar distinction may also be evident in the posterior-middle versus anterior insula, as was also depicted in Fig. 18.

One way to understand such a relation is to think about the anterior regions as primarily serving a supervisory function that is largely inhibitory in nature, while the posterior regions provide continuous positive input. Just this kind of relation was indeed found by Davey and

colleagues in a dynamic causal modelling study that is one way of estimating the influence one brain region exerts over another, technically known as effective connectivity (Davey et al., 2016, 2017). In contrast to functional connectivity which describes only the statistical correlations or dependencies between neuronal responses in different parts of the brain and is a data feature that speaks to some form of coupling, effective connectivity is the directed coupling that mediates functional connectivity. Specifically, Davey and colleagues applied dynamical causal modeling of fMRI toward understanding major depression among adolescents (Davey et al., 2017, 2016), where V-SRP was operationalized as conjunctively those brain regions for which activity was not only greater during explicit V-SRP than for rest, but also greater during rest than for a low-load external attention task. Only three brain regions exhibited this complex contingency: the M-MPFC (frontal pole), the PCC, approximating more specifically the dorsal PCC (D-PCC), and the left IPL/TPJ. Dynamic causal modeling suggested that the PCC exerted a primary positive influence over activity within the other two nodes, which variably provided negative feedback to the PCC; further, only in depressed adolescents was negative feedback by the M-MPFC to the L-IPL also found to be statistically significant, implying that in the healthy brain M-MPFC and L-IPL functional connectivity may rather be mediated by the PCC, as was also found in the mediation calculations conducted herein referring to RSFC. Concerning their observation of the differential positive vs. negative effective connectivity exhibited between the PCC and MPFC, respectively, the authors wrote: “The system can be hypothesized to function as a network in which complex phenomena, such as self-representations, are dynamically accessible via PCC and IPL activity, and which are gated into conscious awareness by activity in the MPFC, as influenced by changing internal and external demands.” (Davey et al., 2016), p. 396).

Critically, the authors thus attribute the MPFC to an inhibitory *gating* function, a theoretical notion that also finds precedent in James’ principles (James, 1890). Specifically, returning to James’ considerations regarding the stream of thought, we find that he considered a certain “section” of the stream to hold particular significance for an understanding of SRP: “If the stream as a whole is identified with the Self far more than any outward thing, a *certain portion of the stream abstracted from the rest* is so identified in an altogether peculiar degree, and is felt by all men as a sort of innermost centre within the circle, of sanctuary within the citadel, constituted by the subjective life as a whole.” (p. 297, italics original). Of particular relevance, this “portion” of the stream of consciousness, “subtracted from the rest”, is experienced as if *aware* and *agentic*: “Probably all men would describe it in much the same way up to a certain point. They would call it the *active* element in all consciousness; saying that whatever qualities a man’s feelings may possess, or whatever content his thought may include, there is a spiritual something in him which seems to *go out* to meet these qualities and contents, whilst they seem to *come in* to be received by it.” (p. 297, italics original). Moreover, critically, James’ also likewise attributes this portion of the stream as serving a *gating* function: “It is what welcomes or rejects. It presides over the perception of sensations, and by giving or withholding its assent it influences the movements they tend to arouse.” (p. 297–298). Similarly, further along he writes: “It is as if all that visited the mind had to stand an entrance-examination, and just show its face so as to be either approved or sent back. These primary reactions are like the opening or the closing of the door. In the midst of psychic change they are the permanent core of turnings-towards and turnings-from, of yieldings and arrests...” (p. 302).

Once again, the effective connectivity identified by Davey and colleagues between the PCC and M-MPFC is therefore suggested as a potential candidate mechanism for the gating function, akin to the PCC continuously knocking (positive connectivity) and the M-MPFC inviting in or rejecting the visitor with either an opening or closing of its doors. But further, Davey et al. (2016) appear to attribute the tripartite system of M-MPFC, PCC, and L-IPL to the agentic function, appearing perhaps to locate it as James’ “innermost centre within the circle” or “sanctuary

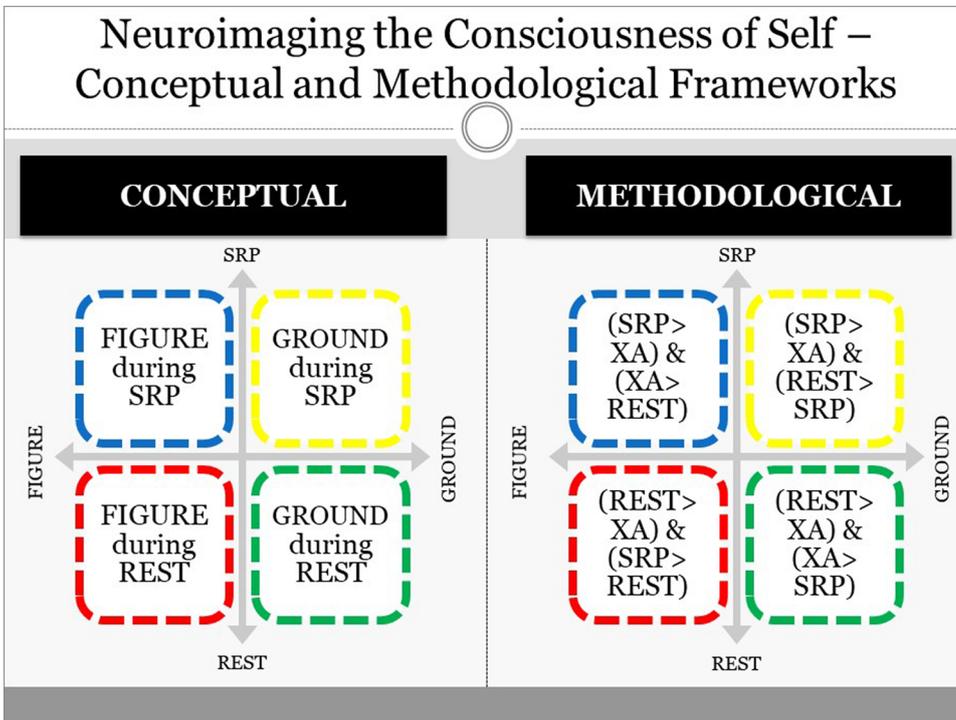


Fig. 22. Title: Figure-ground model of SRP and resting state – conceptual and methodological frameworks.

Caption: In the left panel, four conceptual definitions of SRP are extrapolated either as they occur during active SRP (TOP quadrants, blue and yellow, e.g., during top-down, controlled self-focused attention such as occurs during introspective or interoceptive tasks) in comparison with passive SRP (BOTTOM quadrants, red and green, e.g., during bottom-up, spontaneous self-focused attention such as occurs during resting state as in mind-wandering and body-wandering). SRP takes the position of “figure” only in the LEFT quadrants (blue, red), while taking a position in the “ground” in the RIGHT quadrants (yellow, green). Figure- and ground-SRP may align with conscious- and unconscious-processing, respectively. How these conceptual definitions are operationalized for subtraction and conjunction analyses is defined in the corresponding right panel where XA refers to a non-SRP external attention task. Please see text for further description.

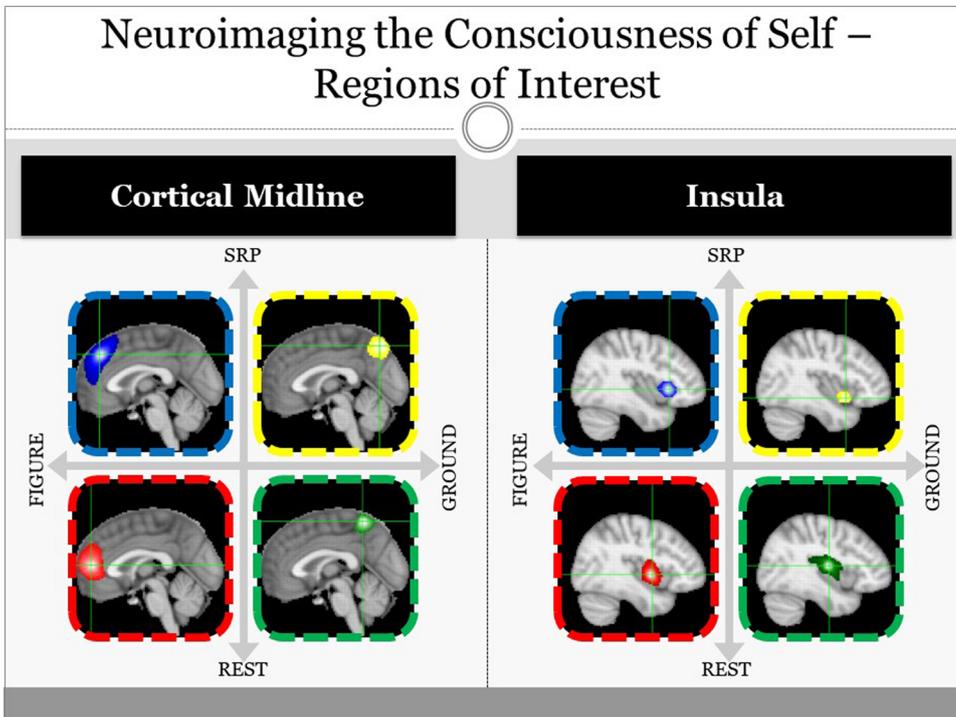


Fig. 23. Title: Figure-ground model of SRP and resting state – cortical midline and insula regions of interest.

Caption: As per the colour-coded conceptual and operational definitions described in the previous Fig. 22, at left for the anterior and posterior cortical midline structures (CMS) and at right for the insula are hypothesized brain ROIs possibly involved in various aspects of SRP, the CMS perhaps more so active in V-SRP and the insula perhaps more so active in NV-SRP. However, we emphasize that these ROIs are not understood to act alone but rather as part of distributed and complex neural networks. Please see text for further description.

within the citadel” of the consciousness of self. For example, in the authors’ own words: “this tripartite core-self system is responsible for engendering conscious self-awareness –providing a sense of oneself as a subjective agent in space and time.” (Davey et al., 2016, p. 396). In contrast to that, as we have stated earlier, we instead hereby attribute M-MPFC to a bottom-up rather than top-down active function within SRP, and so do not believe it quite represents the subjective sense of “agency” taking place in SRP that James’ original writings seem to imply. Instead, we hereby attribute the “active element” of consciousness that he intuitively to executive processes taking place in more dorsal aspects of the MPFC as opposed to the frontopolar cortex proper. That

said, moving beyond the metaphorical to the measurable, we find in Davey et al.’s conjunction methodology an appropriate means of operationally defining what may be thought of as the neurobiomarkers for SRP taking place during both task-focused SRP and during the resting state (Davey et al., 2017, 2016). We turn to the task of more fully explicating this methodology in the next section.

11. Conceptual and methodological framework for a figure-ground representation of SRP and resting state

As we see it, the conjunction methodology of Davey et al. (2016)

can be elaborated upon as the basis for an integrative conceptual and methodological framework for understanding SRP. This operational framework requires three tasks: SRP, rest, and non-SRP control (e.g., external attention [XA]); the distinction between internally-focused and externally-focused processing was also fundamental to Lieberman's (Lieberman, 2007a,b) early annual review of social cognitive neuroscience (see Fig. 22 for a conceptual and operational definition of the conjunction analyses advocated for herein). Modeling conjunction analyses, SRP during resting state is operationalized as responses that occur during both SRP and rest more so than XA, but also more so during SRP than resting state. This indeed was the previously mentioned conjunction modeled by Davey and colleagues and found to constitute in the M-PFC, PCC, and L-IPL/TPJ during a V-SRP task, leading the authors to suggest that these regions might be the brain basis of our capacity for conscious self-awareness and subjectively perceived agency within the spatiotemporal domain (Davey et al., 2016), p. 396). Nevertheless, in so far as these ROIs were identified during a V-SRP task, they likely at least partially reflect primarily the verbal-semantic dimension of self-experience, and less so the non-verbal-somatic aspect (NV-SRP, BSC). In other words, a more inclusive set of ROIs might have been found if their task had instead involved not only V-SRP but also NV-SRP as was compared in the study conducted by Araujo, Damasio and their colleagues (Araujo et al., 2015), for example, also inclusive of the insula or R-IPL/TPJ both of which feature prominently in the literature on interoceptive and exteroceptive BSC, respectively. Entirely consistent with this, Davey et al. actually reported that the R-IPL/TPJ was also found to activate during both V-SRP and resting state more so than XA in their experiment, but was not found to be more active during V-SRP than resting state.

We therefore recommend that a fourth condition be included, involving NV-SRP, as was conducted in Araujo and Damasio and colleagues' study (Araujo et al., 2015). An interesting result of doing so would be to allow investigation of whether, as compared to the resting state, ROIs more often found during active task-based NV-SRP or BSC might move into the background during V-SRP (introspection), while ROIs more often found during active task-based V-SRP might represent the background state during V-SRP, as depicted by the meta-analytic results shown in the previous Fig. 21. This would also allow the investigation of what ROIs are conjunctively involved in both V-SRP and NV-SRP as compared with the resting state, and facilitate answering a question relevant to the current framework, that is, whether and how different forms of (interoceptive vs. exteroceptive) NV-SRP and V-SRP might be integrated, facilitating or hindering SRP of each type. Here, the results of Ainley and colleagues (Ainley and Tsakiris, 2013) are particularly noteworthy, who had participants undergo a heartbeat detection task in a control condition, a visual SRP condition (consisting of a mirror image of the participant's face), and a narrative (V-SRP) condition (consisting of six self-referential words generated by participants). Interoceptive performance in the mirror and narrative conditions was significantly better than in the control condition, suggesting that enhanced perceptual and conceptual self-focus increases interoceptive BSC and positing a more integrated relationship may exist between somatic (NV-SRP) and semantic (V-SRP) representations regarding the self, perhaps in the form of a reciprocal relationship between implicit (bottom-up) and explicit (top-down) SRP. In any case, consistent with the current emphasis in the literature and the operational definitions outlined in Fig. 22, Fig. 23 illustrates the hypothesis that while M-MPFC might meet the contingency operationalized by Davey et al. during an introspective V-SRP task in contrast to the resting state (among other regions for example the V-PCC/PRC), the right middle insula might be hypothesized to meet the same contingency specifically in the context of an interoceptive NV-SRP task; both ROIs are illustrated in red in Fig. 23 in correspondence with the colour coding utilized in Fig. 22.

But we may also talk about the neural correlates of uniquely conscious SRP as those responses that are selectively more active during task-based SRP than external attention while *not* being more active

during rest than during XA but rather the opposite, that is, potential unique aspects of SRP that exhibit independence from the kinds of SRP taking place during resting state. As regards the cortical midline structures, based on the literature reviewed previously, we hypothesize that such responses may be more reliably found in the D-MPFC. Moreover, although the D-MPFC is thought here to be involved in top-down processes independent of self-referential stimulus modality, a similar representation might also be found within the so-called "cognitive" subregions of the DA-Ins, which were found to correlate most negatively with the DMN regions in RSFC analyses, indirectly suggestive of the relative lack of activity of DA-Ins during resting state. Both of these regions are illustrated blue in Fig. 23, corresponding to the colour coding used in Fig. 22. In summary, this framework is hypothesizing that *in the more dorsal-anterior subregions (D-MPFC, DA-Insula) may be the neurobiomarkers of self-focused attention as it uniquely occurs in the foreground of consciousness during performance of top-down SRP tasks rather than during resting state.* In comparison, *the middle subregions (M-MPFC, M-Insula) may be the markers of SRP when occurring in the foreground of consciousness due to bottom-up processing during resting state.*

Comparably, we may operationalize the endogenous background activity as those responses that are active during both SRP and resting state, but are unique to neither. Technically this definition is akin to the uniformity test statistics as defined by the neurosynth meta-analytic tools (Yarkoni et al., 2011). The psychological referent of such endogenous activity is not obvious although, as we have said, an interesting question to evaluate in future studies will be whether ROIs more often attributed to introspective V-SRP in the neuroimaging literature will be relegated to the background of consciousness during active interoceptive NV-SRP, and vice versa in the case of active introspection. Such an interpretation would seem to fit the results of Araujo and Damasio and colleagues who report activations and deactivations for V-SRP and NV-SRP relative to a passive external attention task (Araujo et al., 2015). In fact, if we consider the insula as possibly preferentially involved in NV-SRP as compared to V-SRP, this hypothesis would also fit findings reviewed herein for many of the insula subregions to correlate negatively with MPFC regions during resting state. Referring to this ground state and further elaborating the methodology of Davey and colleagues (Davey et al., 2017, 2016) we can therefore develop the conjunction as those ROIs that are more active during task-focused SRP than XA but even more active during resting state than task-focused SRP. Although there is less literature upon which to base hypotheses here, the MSPL may be one candidate ROI within the cortical midline at least in so far as it has been contrasted with control conditions in SRP experiments. Considered part of the dorsal attention network (DAN) as identified at rest (e.g., Yeo et al., 2011), the MSPL is *not* generally considered a ROI to V-SRP, was more active during the resting state ISI than during V-SRP in Davey et al. (2016), and was more active during NV-SRP in comparison with V-SRP in the study by Araujo et al. (2015). Moreover, particularly in its most anterior aspects, the A-MSPL exhibits a striking pattern of RSFC involving the whole of the MSPL but evidencing no direct connectivity with the PCC, PRC, MPFC, or insula. In fact, the RSFC exhibited by this seed in our analyses is highly reminiscent of the figure shown in Davey et al. (2016) for maps that were more active during resting state than V-SRP, depicting possible activation spreading down the cingulate sulcus toward the D-ACC rather than toward the PCC (e.g., as shown in our Figs. 8 and 9). In comparison, in its posterior aspects, the P-MSPL does correlate with the PCC and negatively with the M-Ins, but also appears to exclude any RSFC with the MPFC whatsoever as was reported herein (also shown in our Figs. 8 and 9). As for the V-PRC, it correlates positively with the MPFC as is well known, as well as negatively with the supplementary motor area suggestive of its function during resting state. In this case we are led to speculate that the P-MSPL through to the PRC might meet the conjunctive principle of being more active during SRP than an external attention control (XA) but nevertheless more active during resting state than SRP, depicted yellow in Fig. 23, whereas the A-MSPL could exhibit

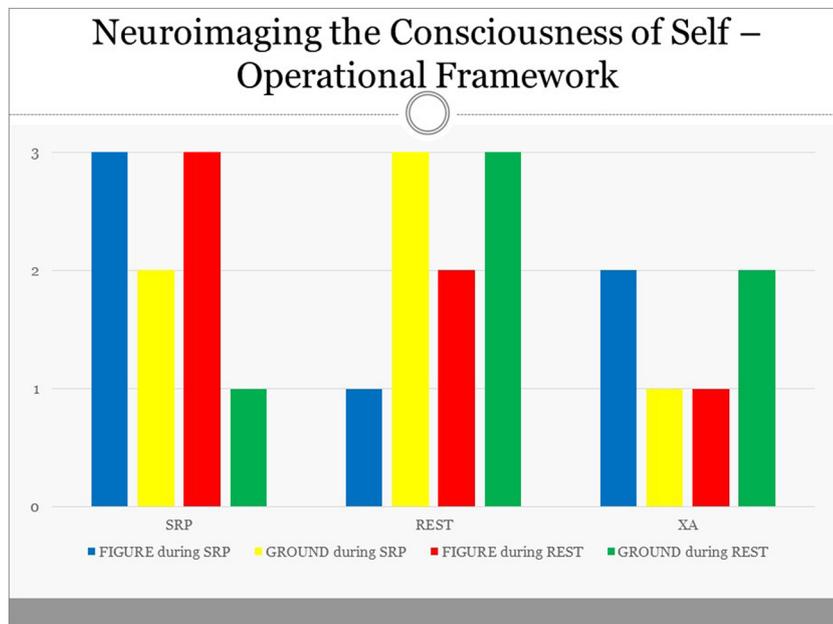


Fig. 24. Title: Idealized results of the figure-ground model in defining the relative contributions of ROIs to self-referential processing, resting state, and external attention.

Caption: As per the colour-coded conceptual and operational definitions described in the previous Fig. 22, the bar graphs depict the relative contributions hypothesized across distributed (i.e., multiple) ROIs during the tasks of self-referential processing (SRP), resting state (REST), and external attention (XA), thus exemplifying neural networks. For example, SRP is predicted to be mediated strongly by ROIs identified in the figure position during SRP (blue) and resting state (red), moderately by ROIs identified in the ground position during SRP (yellow), and weakly by ROIs identified in the ground position during rest (green). Note that distributed activity during SRP is predicted as a mirror image of that observed during REST.

the pattern of being more active during resting state than XA but nevertheless more active during XA than during SRP, depicted green in Fig. 23, in respect of the colour coding conventions used for the corresponding operational definitions given in Fig. 22. Similarly, referring to the insula, our review leads us to the hypothesis that a similar contingency might hold for the VA-Insula as being active during SRP than XA but more active yet still during resting state. The VA-Insula, thus also depicted yellow in Fig. 23, shows a less strong negative RSFC with the DMN when compared to the DA-Ins, whilst exhibiting a strong representation in the neurosynth automated termed-based meta-analysis of “resting state” specifically in the uniformity maps including in the nearby operculum. Comparably, the P-Insula, depicted green in Fig. 23, could complete the picture as an ROI most active during resting state in comparison with XA and SRP each in turn, implied by the neurosynth automated meta-analytic uniformity maps constructed herein and its general presentation within Craig’s (2009) model as in the “background” of consciousness, wherein bodily signals are thought to become conscious only when representations within the posterior insula are remapped to the anterior insula.

In summary, in this section we articulated some hypotheses based on the current literature review that would seem to fit specific operational criteria for defining different roles for brain ROIs in SRP versus resting state as exemplifying a figure-ground relationship. In any case, we consider explication of the detailed methodology itself to be more important than the specific predictions we made, that is, as a means of identifying whatever ROIs - if any - do in fact meet the stated contingencies. Along these lines, it is interesting to consider how these contingencies, taken collectively, in turn define the neural networks (that is, distributed correlated ROIs) thought to mediate SRP, resting state, and external attention in turn. For illustrative purposes, Fig. 24 depicts an idealized result whereby the four operational definitions given in Fig. 22 are plotted as bar graphs differing by an equal increment of one above a minimum response of one. Utilizing the same colour coding as in Figs. 22 and 23, Fig. 24 defines the task of SRP to be produced by strong inputs from the ROIs identified in the figure position during both SRP (blue) and resting state (red), together with a moderate input from the ROIs identified in the ground position during SRP (yellow). In comparison, the task of resting state is considered to be produced by strong inputs from the ROIs identified in the ground position during both SRP (yellow) and resting state (green), together with a moderate input from the ROIs identified in the figure position during resting state (red). Finally, this framework considers the task of external

attention to be produced by moderate inputs from the ROIs identified in the figure position during SRP (blue) and resting state (green). As such, this figure hypothesizes each task or psychological function to be mediated by different ROIs as neural networks, varying in magnitude of contribution. We hope that this integrative operational framework for conceptualizing the brain processes involved in SRP, resting state, and external attention can be put to empirical test in the future.

Perhaps the best measure of any neuroscience or biobehavioral theory or methodology, however, is the potential breadth with which it can be applied not only toward basic questions of the subject matter but also more pragmatically in clinical-translational sciences. In the next section we will therefore briefly consider how this approach could provide an account of various psychological and neurological disorders known to be associated with abnormal SRP. Unfortunately, however, due to the inadequacy of current literature, the framework can at present only be applied in its metaphorical rather than operational presentation.

12. Disorders of the self

We have suggested that, when tasks require it, V-SRP as taking place in introspective tasks, and NV-SRP as taking place in interoceptive tasks and tasks involving multisensory perception of outer body parts (e.g., limbs) or the body as a whole (i.e., BSC) can be voluntarily deployed in controlled manipulation of something akin to an attentional spotlight in a theatre of the consciousness of self. We have suggested that doing so entails bringing to the foreground (i.e., via top-down, controlled processes) information that will otherwise be processed continuously primarily in the background (i.e., via bottom-up, automatic processes). Doing so brings such contents into greater view, thereby defining a figure-ground relationship. Further, during the default resting state, both V-SRP and NV-SRP feature, with individual differences in the balance between these SRP streams representing a basis for dispositional psychological traits, akin to the bottom-up spotlight of V-SRP being somewhat brighter than the spotlights of NV-SRP or vice versa.

However, what has not yet been discussed is how abnormal influences of V-SRP and/or NV-SRP may also be the basis for neurological and/or psychological disorders. On the one hand, extreme influence of typically “off-task” valenced V-SRP and/or NV-SRP may distract attention away from the various non-SRP tasks that are also part of everyday life, creating functional impairment. Alternately, a lack of influence of either form of SRP on behaviour, for example brought about

brain injury or disease, should also eventuate in equally problematic psychosocial outcomes. In this section, we briefly apply the presently developed heuristics as a means of conceptualizing certain neurological and psychological disorders as each involving abnormalities in the V-SRP and/or NV-SRP systems we have described. The specific disorders addressed are by no means meant to be a comprehensive list; for example, it may be argued that multiple disorders not discussed herein, including dissociative disorders, obsessive compulsive disorder, Tourette's syndrome, and body dysmorphic disorder could be interpreted within the present framework. Moreover, space limits preclude a full consideration even of each of the disorders that are included. However, we believe that the understanding that may be facilitated by the transdiagnostic framework described herein at a symptom level may fit with conceptualizing certain mental health problems as abnormalities in the “perception and understanding of self” partly as described under (but in some way calling for an expansion of) the self-knowledge sub-domain of the current research domain criteria (<https://www.nlm.nih.gov/research/research-funded-by-nimh/rdoc/index.shtml>; e.g., (Clark, 2017; Sanislow et al., 2019)) We therefore briefly consider several examples of such “disorders of the self” below that, based on face validity, might be primarily categorized as disorders of V-SRP vs. NV-SRP. Indeed the theoretical distinction between V-SRP and NV-SRP is made most apparent in cases where certain disorders appear to affect the two forms of SRP differentially, for example, affecting one severely but leaving the other relatively spared. This stated, based on symptomatic analysis alone, it appears more likely that most of the disorders discussed below affect both V-SRP and NV-SRP to varying degrees. We briefly speculate how the current framework would conceptualize each of the disorders listed with a focus on the aforementioned ROIs for V-SRP and NV-SRP. Where possible, we have also tried to focus on how each disorder affects the kinds of introspective (V-SRP) and interoceptive (NV-SRP) tasks that have already been reviewed earlier, as well as resting state studies, in order to make transdiagnostic comparisons more feasible, although for many disorders no studies along these lines have yet been conducted.

Considering the number of neurological and psychological conditions that might reasonably be considered “disorders of the self”, identifying relevant transdiagnostic interventions will be an important endeavour for clinical research. Our hope is that a better neuroscientific and biobehavioral understanding of V-SRP and NV-SRP will facilitate treatment innovations, including the application of various brain-based technologies. In particular, a better understanding of the underlying neurocircuitry of V-SRP and NV-SRP could be applied in guiding NIBS and NFB protocols. Moreover, a clearer understanding of different forms of SRP might further validate and guide the future development of certain forms of experiential psychotherapy and mindfulness meditation practices. The notion that insights gained from the neuroscientific and biobehavioral study of SRP might be directly translated into clinical interventions such as in NIBS and NFB would seem to represent a relevant and novel direction for clinical research to treat various disorders of the self.

12.1. Anxiety and affective disorders

Although RSFC studies have been touted as a new way to identify both differences and similarities among the anxiety disorders (Peterson et al., 2014), the majority of the neuroimaging literature investigating anxiety disorders has rather tended to focus on visual threat perception, for example, response to angry facial expressions, or the neural correlates of the generation of the state of anxiety itself. However, on face validity alone, several anxiety disorders would appear to be associated with negative V-SRP. One such anxiety disorder is *Generalized Anxiety Disorder* (GAD), which is associated with chronic worrying that is often but not exclusively self-referential in nature (i.e., worries may concern the self or others). A key clinical symptom of GAD involves the inability to control one's worrying, that is, to stop worrying when it is not helpful

or when one does not want to worry. Accordingly, from the perspective of the current framework, GAD may be conceptualized as a disorder of negatively-valenced V-SRP occurring during the resting state. Consistent with this, Wang et al. (Wang et al., 2017) found greater activity in the M-MPFC and D-PCC/PRC in persons with GAD at rest which have been more strongly implicated in V-SRP, together with greater bilateral DLPFC activity, implicating cognitive control. Further seemingly consistent with a focus on negative V-SRP in GAD, the L-DLPFC was more strongly correlated with left pars opercularis, or Broca's area, possibly implicating the influence of internal speech production (e.g., worrying) on the FPCN during resting state. However, RSFC was also greater in GAD between the M-MPFC and the VA-Insula bilaterally, as well as with the right P-ACC, while the D-PCC/PRC was more strongly correlated with the A-SPL; collectively these findings implicate connectivity between ROIs implicated in valenced NV-SRP, perhaps representative of the state of anxiety itself at rest. In fact an influential psychological theory posits that the person with GAD utilizes worry as a verbal-cognitive coping strategy in order to avoid even more feared tendencies toward valenced NV-SRP occurring in the form of bodily hyperarousal (e.g., panic symptoms; (Borkovec, 1994).

Although there have been few neuroimaging studies explicitly of NV-SRP in GAD, Pang et al. (Pang et al., 2019) found that the amplitude of heart-evoked potentials recorded in EEG under right prefrontal cortex were predictive of anxiety symptom severity in GAD patients when their eyes were open (but not when their eyes were closed); importantly the authors discuss that the HEP is automatically higher during eyes closed than open conditions, therefore reflective of background endogenous activity at rest. The authors thus conclude that “higher HEP amplitudes during the eyes open state in patients with GAD may reflect excessive cortical processing of afferent cardiac signals when external visual information needs to be processed” (p. 6), seemingly reflecting a bottom-up intrusive NV-SRP that distracts from exteroceptive non-SRP. Moreover, RSFC in ROIs of interest to both V-SRP and NV-SRP has proven sensitive to psychological treatment outcomes in GAD. Interestingly, Fresco and colleagues (Fresco et al., 2017) showed that reduced connectivity between the M-MPFC and the left P-SPL and reduced connectivity between the insula ROIs and left A-TPJ and A-SPL was associated with greater improvement in worry following treatment, closely consistent with ROIs to both V-SRP and NV-SRP as discussed herein. Critically, the authors also showed that improved “decentering” following treatment, a psychological construct believed by the authors “to be a metacognitive capacity that leads to less self-referentially biased awareness of exteroceptive and interoceptive cues” (p. 9), and understood herein to reflect the allocentric operation of an “observing ego”, correlated with *increased* connectivity between the D-MPFC and the P-ACC, left anterior insula, and superior frontal gyrus; increased connectivity of the PCC with the P-ACC was also seen with increased decentering following treatment. These striking findings suggest decentering might be improved in emotion-regulation and mindfulness-based psychotherapies for GAD, encouraging the expression of an “observing self” as a means of reducing first-person egocentric negative V-SRP in the form of worrying.

Hyperactivation of V-SRP also seems to play a central role in the symptomatology of social anxiety disorder (SAD) which involves fear of one or more social situations leading to anxiety, distress and avoidance of social situations, substantially interfering with daily living. It is held that negative V-SRP is a core problem in SAD differentiating it significantly from other phobias (Yoon et al., 2019a). Most early neuroimaging studies of SAD focused on visual processing of external social threat stimuli as opposed to the task-related paradigms more often used to study SRP. However, early research showed that increased processing in cortical midline structures as ROIs in V-SRP were found in SAD related to perception of negative social stimuli as self-referring (Blair et al., 2008) and altered processing of social transgressions (Blair et al., 2010). Critically, SAD is also understood to be a disorder involved in taking the “observer” perspective (allocentric) rather than the first-

person self-perspective (egocentric), implicating D-MPFC processes rather than only M-MPFC processes as understood herein (Blair et al., 2011; Wells et al., 1998; Yoon et al., 2019a). Intriguingly, in comparison to GAD and other anxiety disorders, these findings might conceptualize SAD as more uniquely a disorder of the “observing self” than only a disorder of negatively-valenced V-SRP occurring in first-person perspective. For example, while in healthy subjects V-MPFC was activated in response to first-person viewpoints, patients with SAD showed the opposite pattern: activation of V-MPFC in response to second-person viewpoint (Blair et al., 2011). Observing unintentional awkward social situations by patients with SAD also not only leads to activations in V-MPFC but also in D-MPFC, while control patients rather showed activation in these regions more so in response to intentional transgressions (Blair et al., 2010). An increased activation of M-MPFC, extending to V-MPFC and D-MPFC, has thus been consistently reported in response to negative self-referential stimuli in patients with SAD, suggesting the whole of the M-MPFC may be involved (Blair et al., 2008, 2011; Boehme et al., 2014; Goldin and Gross, 2010). Similarly, SAD is thought to be associated with predominant hyperactivation of cortical midline structures in combination with altered functional connectivity with other brain networks such as the limbic and ventral attention networks (Yoon et al., 2019b), such that significantly increased activations for negative self-referential stimuli have also been reported in the amygdala, insula, PCC, V-ACC, fusiform and lingual gyri as well as middle frontal gyrus, superior temporal sulcus and inferior frontal gyrus (Blair et al., 2008); (Blair et al., 2010; Goldin and Gross, 2010; Heitmann et al., 2017). Moreover, while resting state fMRI studies in SAD are heterogeneous in methods and designs too numerous to detail here, more recently reported results include reduced RSFC in medial posterior structures specifically for the A-SPL (Liu et al., 2015) and PCC (Peterson et al., 2014). These findings may implicate reduced bottom-up influence of the posterior structures coupled to increased response in the aforementioned MPFC regions.

In comparison, referring to depression, we should rightly distinguish between the negative thoughts concerning self-worth, failure, and loss (V-SRP) and the somatic symptoms of sadness and anhedonia (NV-SRP) that are each symptomatic of this mood disorder. However, referring specifically to negative V-SRP, these so-called cognitive symptoms are considered highly characteristic of people with major depressive disorder (MDD; e.g., (Lou et al., 2019)), and may even reflect an endophenotype of complicated and treatment refractory patients (Mennin and Fresco, 2013). Interestingly, a meta-analysis of resting-state studies in medication-free depressed persons showed increased blood flow in right V-PCC and left insula, while decreases were found in right V-MPFC (Lv et al., 2018), emphasizing ventral cortical midline structures thought to underlie valenced V-SRP as described in the present review. Moreover, MDD is associated with abnormally increased activity in the DMN, while DLPPFC activity is generally reduced, which may disinhibit cortical midline structures leading to increased valenced V-SRP (e.g., (Nejad et al., 2013)(Hamilton et al., 2011)). Considering the bottom-up nature of negative V-SRP in MDD, other research (Shestyuk and Deldin, 2010) shows heightened P2 amplitudes in response to negative relative to positive self-referent items, which the authors conclude may reflect automatic attentional capture and orienting to negative information, even more rapidly identified in the P1 component in adolescents (Auerbach et al., 2015). Besides these rapid automatic responses, later stages involving elaborative processing of negative valence self-referential words have also been identified around 380 ms–1000 ms (Dainer-Best et al., 2017) including for the N400 and late positive potentials (Kiang et al., 2017) (Benau et al., 2019). In these cases, it remains a matter of debate as to whether conscious, top-down (Davey et al., 2017) (LeMoult and Gotlib, 2018) or automatic, bottom-up (Knyazev et al., 2016) mechanisms contribute more so to the negative V-SRP that is symptomatic of MDD (Shestyuk and Deldin, 2010). In any case, in the context of the slower and more passive V-SRP typically used in neuroimaging research, studies have found increased M-

MPFC and P-ACC in response to negative V-SRP that correlated with depressive symptoms (Yoshimura et al., 2010) together with lower response in the D-MPFC (Li et al., 2017). Therefore while increased response in V-MPFC has been found as a reliable neurobiomarker of MDD, decreased response may be found in D-MPFC, suggesting possible increases in valenced first-person “ownership” of negative self-referential thoughts coupled to a decreased capacity for decentering or engagement by an observing ego or the capacity for executive control.

12.2. Posttraumatic stress disorder and its dissociative subtype

No longer purely conceptualized as an anxiety disorder, posttraumatic stress disorder (PTSD) symptoms can nevertheless be differentiated, on the one hand, between a focus in negative cognitive and mood alterations including negative self-referential thoughts and negative self-conscious emotions of guilt and shame, thereby emphasizing valenced V-SRP, and on the other, between their focus on bodily symptoms of hyperarousal and physiological reactivity, thereby emphasizing NV-SRP, as has been reviewed by others (Fenster et al., 2018). Concerning direct evidence of abnormal V-SRP in PTSD, Frewen et al. (Frewen et al., 2017, 2011) showed that during a combined visual and verbal SRP task women with PTSD evidenced altered response either in ACC and amygdala (Frewen et al., 2011) or reduced activity in visual cortex (Frewen et al., 2017) during SRP, while Bluhm et al. (Bluhm et al., 2012) demonstrated less response in D-MPFC, V-MPFC, and V-PCC during V-SRP. This said, PTSD is also a disorder that clearly encompasses disturbances in NV-SRP, where participants frequently experience physiological manifestations of anxiety, for example, increased heart-rate and startle reactivity (e.g., reviewed by Pole et al., (Pole et al., 2006)). Concerning RSFC studies, it is therefore not surprising that researchers have focused not only on PCC-MPFC circuitry indicative of the DMN, whereby reduced posterior to anterior connectivity was the first finding (Bluhm et al., 2009) and has since been replicated (e.g., review by Peterson et al., (Peterson et al., 2014)), but also on brain systems thought to be involved in NV-SRP as discussed herein. For example, seed regions placed in the anterior and posterior insula have variably evidenced reduced RSFC with the pre- and post-central gyri together with increased RSFC with the periaqueductal gray (PAG; Harricharan, Nicholson, Thome, Densmore et al., 2019). Moreover, examining PAG regions directly, the same research group showed increased RSFC in PTSD with the D-ACC and SMA, suggesting NV-SRP indicative of anxiety-threat processing (Harricharan et al., 2016), where the PAG has been considered a core region to understanding the effects of traumatic events for hyperarousal and threat perception (e.g., (Terpou et al., 2019)).

As an important clinical development, a certain minority of persons with PTSD, estimated to be about 30 %, also report significant dissociative experiences associated with depersonalization (i.e., out-of-body experiences, emotional numbing), suggesting more severe disturbances in NV-SRP and BSC. Moreover, researchers have identified putative brain bases for these clinical differences, whereby MPFC has been found to be more active in persons with the so-called dissociative subtype of PTSD as compared to people with PTSD who do not endorse the dissociative experiences (e.g., (Lanius et al., 2011)). In fact, many of the aforementioned RSFC studies have compared brain maps more specific to PTSD patients with the dissociative subtype as compared to controls. Moreover, relating to the present framework, studies have shown differential abnormalities in response to the rubber-hand illusion reflective of exteroceptive BSC in persons with PTSD with vs. without the dissociative subtype (Rabellino et al., 2018), while other literature investigating persons with depersonalization disorder shows a lack of interoceptive awareness in this condition (Seth et al., 2011). The idea that persons with PTSD who exhibit the dissociative subtype might display a qualitatively different form of altered SRP and phenomenology than those with PTSD without the subtype is taken up in much detail in the text by Frewen and Lanius (2015), emphasizing differences

in V-SRP and NV-SRP between the two clinical phenotypes of PTSD.

12.3. Eating disorders

Eating disorders (EDs) involve abnormal eating habits such as a restriction of energy intake leading to a significantly low body weight (anorexia), or recurrent episodes of binge eating followed by recurrent inappropriate compensatory behaviors (bulimia). Anorexia also includes two subtypes: a restricting type (AN-r) in which individuals with AN-r purely restrict their food intake and increase activity, and a binge-eating/purging type (AN-bp) in which individuals with AN-bp usually restrict their food intake and regularly engage in binge eating and/or purging behaviors. However, the etiology of these abnormal eating habits is still an open question. On one side, the ego-syntonic nature of EDs (Marzola et al., 2015) - the fact that these disorders are often highly valued by those who suffer from them - and the importance of shape and weight experience in the personal experience of the patients, underline a possible link between anorexia, bulimia, and both V-SRP and NV-SRP (Amianto et al., 2016), in particular for the AN-bp type showing a higher emotional and somatosensory arousal for potentially punishing stimuli (Murao et al., 2017).

Functional connectivity impairments (Donnelly et al., 2018; Gaudio et al., 2018, 2017; Gaudio et al., 2016; Trevor et al., 2017), together with affective, proprioceptive (Zopf et al., 2016), interoceptive (Jenkinson et al., 2018), motor (Guardia et al., 2013) and tactile deficits (Gaudio et al., 2014) present in individuals with EDs are suggestive of alterations in NV-SRP. Specifically, the neuroimaging studies underline alterations in the corticolimbic and frontostriatal circuits and in the insula. Interestingly, these networks and areas are directly connected both to critical symptoms of these disorders and to disturbances of cognitive inflexibility, altered self-regulation and processing/integration of body signals (Donnelly et al., 2018; Gaudio et al., 2018, 2016). In particular, multisensory processing may be affected in EDs (Riva, 2018; Riva and Dakanalis, 2018; Riva and Gaudio, 2018b; Zopf et al., 2016) which may result in: “(1) an impairment in the ability of correctly linking internal (interoceptive) bodily signals to their potential pleasant (or aversive) consequences; and (2) an impairment in the ability of updating the body memory (allocentric, offline) with new contents from real-time perception-driven inputs (egocentric, online)” (Riva and Gaudio, 2018a) (p. 57). If the first impairment can explain the emotional problems experienced by the patients with EDs including emotional rigidity, lack of emotional clarity and difficulties in emotion regulation, the second can offer an explanation of the link between self-objectification and EDs. From the current conceptual perspective, whereas lay intuition might suggest a conceptualization emphasizing only a misperception in visual bodily self-recognition (e.g., size and shape), the cited literature rather also emphasizes abnormalities in the interoceptive signals.

Nevertheless, additional contribution from V-SRP are also likely in the form of a maladaptive narrative (thin-body ideal). From a cognitive-affective neuroscience view-point, an individual self-objectifies himself/herself when he/she uses an allocentric frame of reference (i.e., using an observer’s viewpoint) to remember events in which he/she evaluates himself/herself based upon bodily appearance (Riva et al., 2015). When these events are recorded in long-term autobiographical memory and directly connected to the ideal-self (i.e., being fat is ugly), they are used during the process of multisensory integration to recalibrate the bodily data arriving from real-time multiple sensory modalities (exteroception; i.e., touch and vision) and internal information (i.e., interoception and proprioception). For example, these processes can explain the mismatch between individuals’ objective bodily dimensions and sensorimotor representations of body size (horizontal passability judgments through an aperture) (Wignall et al., 2017). Commenting their results, Wignall and colleagues conclude: “[These results] indicate that the internalization of these sex-specific bodily ideals might not only affect how we think about our bodies, but also our

internal, sensorimotor representations of body size.” (p. 143). As noted by Liu and Medina (2018), inputs from different modalities and information from representations with different frames of reference are differentially weighted according to causal inference models. In particular, when inputs are coded in different reference frames (i.e., allocentric for the bodily data stored in autobiographical memory; egocentric for the real-time sensory data) they are translated by the retrosplenial cortex, with the support of place and grid cells (Byrne and Becker, 2008; Byrne et al., 2007). If this process is impaired, the individual will be unable to update the stored representation of the body with new real-time sensory data. Different factors common in EDs (Gaudio and Riva, 2013; Riva, 2014, 2016) – from stress, to functional connectivity alterations, to an altered monoamine neural modulation – may impair this translation process, blocking the updating of the existing memory of the body. In other words, ED patients may be locked to an allocentric disembodied negative memory of the body that is not updated even after a demanding diet and significant weight loss. Therefore, successful dieting attempts are not able to improve body dissatisfaction and subjects may either start more radical dieting attempts or, at the opposite end, engage in “disinhibited” eating behaviors. As described symptomatically, eating disorders therefore would appear to represent a disorder seemingly involving all three bottom-up “spotlights” as described by the current “theatre” metaphor: exteroceptive BSC in the form of allocentric perspective possibly partly mediated by right temporoparietal cortex, interoceptive NV-SRP in the sense of negative affect and distress (e.g., disgust, guilt, shame) experienced during eating and possible top-down inhibition of bottom-up bodily-felt experience in support of restricting food intake (e.g., hunger), possibly mediated by the insula, ACC, and V-MPFC, and finally a negatively-valenced verbal narrative concerning self-image coupled to reward circuitry further promoting body thinness as a motivational drive. Due to the multifaceted nature of the condition, eating disorders also appear to represent an excellent test case for further exploration of the current conceptual framework.

12.4. Psychotic disorders

The proposed figure-ground SRP model can also be applied to several clinical features of schizophrenia especially in emphasizing the cognitive alterations accompanying the disease (V-SRP). To begin with, the conceptual formulation of schizophrenia itself rests on this disorder being a disturbance of the self and its relationship with the world (Mishara et al., 2014). Two prominent schools of thought in this regard are the Apollonian notion of *ipseity* disturbance (i.e. disturbed intentional first person perspective of the world (Sass and Parnas, 2003) and the Dionysian notion of disturbances in the unintentional (automatic, bottom-up) emergence of the sense of self (Gallagher, 2007; Mishara, 2007); these two forms of SRP disturbance might differentially reflect the operation of top-down vs. bottom-up SRP as described in the current framework. In particular, *ipseity* disturbance refers to hyper-reflexivity (self being perceived as other, associated with allocentric perspective), diminished self-affection (i.e., reduced sense of self-presence and positive self-feelings) and reduced spatiotemporal structuring required for getting a ‘grip’ of experiential affairs (Sass and Parnas, 2003). Expanding on these notions, *passivity symptoms* can be considered to be the result of an anomaly in self-other distinction (loss of ego boundaries) (Fletcher and Frith, 2009). Given the failure to demarcate one’s self relative to others, the symptoms of delusional *grandiosity or guilt* can also be seen as instances where self can be construed as having undue influence on others (with opposing valences), while *paranoia* can be seen as instances where others unduly influence one’s self, therefore emphasizing that the distinctions between SRP and ORP described herein likely both apply to conceptualizing schizophrenic illness. In addition, the *lack of insight*, often seen as a defining feature of psychosis, can be seen from the perspective of the current conceptual framework as a deficit specifically of an “observing

self”, in turn linked to the lack of appropriate SRP of cognitive events as well as the verbal feedback from others. Finally, negative symptoms such as *anhedonia* can be seen as a deficit in positive-valenced emotional first-person SRP in the V-MPFC, as well as instances where a proprioceptive self-representation fails to emerge from the background stream of BSC, the product of NV-SRP as understood in the current framework.

Increased functional coupling between V-MPFC and PCC is associated with increased severity of the disturbances in subjective self-experience in schizophrenia (known as prodromal Basic Symptoms) (Ebisch et al., 2014). This increased coupling during passive resting state is also seen among non-symptomatic siblings who are at risk of psychosis (van Buuren et al., 2012). When V-SRP is required, this coupling reduces significantly among healthy controls but remains higher among siblings (van Buuren et al., 2012). In terms of the attentional spotlight metaphor explicated in the current review, the risk for developing schizophrenia can be formulated as a condition where regions involved in V-SRP tend to have an exaggerated influence over the ground state such as in the convergence zone of PCC/PRC, and the degree to which such exaggeration of V-SRP over the ground state occurs may relate to the altered self-experiences. Nevertheless, during explicit task-focused V-SRP, when compared to healthy controls, V-MPFC shows reduced activity (Holt et al., 2011; Pankow et al., 2016) while PCC has higher activity (Holt et al., 2011) in patients, illustrating an anterior-to-posterior shift in midline activity (Holt et al., 2011). Nevertheless, the PCC region with higher activity shows reduced connectivity with D-ACC (overlapping with M-MPFC and D-MPFC) (Holt et al., 2011). If we consider the notion that the ground state may be particularly mediated by posterior nodes of the DMN particularly the PCC, and M-MPFC connectivity, while the conscious figure-ground relationship in SRP may be contingent on the activity of the anterior MPFC nodes, in this context, the observed PCC-MPFC dysconnectivity in schizophrenia, in combination with increased PCC but reduced V-MPFC activity during SRP, may relate to an aberrant self-experience characterized by the ipseity disturbances that form the seeds for distorted reality (Sass and Parnas, 2003). Indeed, among patients, the degree of reduced V-MPFC activity during V-SRP related to the degree of aberrant salience attribution (speed with which irrelevant cues are attended to) (Pankow et al., 2016).

However, the impact of alterations in NV-SRP in schizophrenia, and their interaction with V-SRP, should not be neglected. How might this imbalance in the influence of the various domains of SRP over the ground state relate to psychosis? Expanding on Synofzik’s Multifactorial Weighting Model of sense of agency (Synofzik et al., 2008), Robinson et al. (Robinson et al., 2016) posit that under normal conditions, reliable (and precise) information emanates from interoceptive domains (indexed by activity in the NV-SRP regions), leading to a greater weight being ascribed to those cues, instead of the higher level domains such as intentions, social or contextual cues (mediated by the executive system), in determining the agent (i.e., the figure from ground). In fact, the self/other-agency judgment seems dependent upon the dynamic switching between the SRP-related DMN regions and the cognitive networks such as the central executive system (Spaniel et al., 2016). In schizophrenia, there is also a relative reduction in interoceptive accuracy (Ardizzi et al., 2016), which may mean that external cues as well as higher order goals are given greater or equal weights to interoceptive cues (NV-SRP) (Robinson et al., 2016). This aberrant weighting may culminate in a periodic failure in agentic inferences, for example, a sense of being controlled by outside alien influences, especially when the cues necessary for this judgement are unreliable, leading to misattributions. For instance, behavioral studies also show how schizophrenia patients tend to misidentify their own voices (Allen et al., 2004) and poorly discriminate self-generated tactile sensations from those generated by others (Blakemore et al., 2000). We therefore posit that the abnormally increased connectivity between the PCC and the V-SRP region of V-MPFC may also potentiate the misattribution of agency,

resulting in positive symptoms of psychosis, partly also underpinned by reductions in NV-SRP and perceived BSC. In support of this notion, Ćurčić-Blake et al. (Ćurčić-Blake et al., 2015) used dynamic causal modelling and observed that the increased connectivity from the PCC to V-MPFC during judgment of traits related to self was associated with poorer insight among patients with schizophrenia.

Additional insights into the nature of SRP disturbances in schizophrenia come from an analysis of delusions (Breier and Berg, 1999). Although different types of delusions have been defined, delusions of reference are common positive symptoms in schizophrenia (Fletcher and Frith, 2009) and are thought to result from misattributions of relevance of self to neutral events. That is, delusions of reference may reflect heightened attributions of salience to mundane or impersonal events or stimuli that lead the individual to consider them as personally significant or directed at the observer. Indeed, Menon et al (Menon et al., 2011) identified differences in brain activation between healthy individuals and schizophrenic patients with referential delusions and found that when reading sentences that were not directed toward anyone in particular (e.g., “She likes to drink coffee”) self-attributions were associated with response in M-MPFC, D-MPFC and anterior insula bilaterally across patients and non-patients alike, although a follow-up study by Girard, Lakatos, and Menon (2017) found that whereas M-MPFC and D-MPFC response was correlated with positive affect during the task in healthy controls, such responses were instead correlated with negative affect in patients. Girard et al. (Girard et al., 2017) also investigated the emotional modulation of brain activation during SRP in schizophrenic patients with and without delusions of reference and confirmed that cortical midline structures play key roles in SRP in this patient group as involving attributions of self-relevance to ambiguous stimuli (Lariviere et al., 2017; Menon et al., 2011; van der Meer et al., 2010). More specifically, schizophrenic patients without delusions of reference showed decreased activation in PCC, PRC, and ventral striatum, emphasizing posterior regions, whereas schizophrenic patients with delusions of reference showed an increase in activation in MPFC, emphasizing anterior regions; moreover, self-attributions were also correlated with response in the ventral attention network comprising D-ACC, bilateral anterior insula, as well as sensorimotor regions. Overall, these results seem to confirm an abnormal attribution of personal salience to stimuli in schizophrenia, which may indicate an irregular representation of irrelevant stimuli as self-referent, or an abnormality of the gating function of PCC-PRC background representations into V-MPFC and M-MPFC foreground awareness.

12.5. Psychedelic-induced altered states of consciousness

Alterations in SRP induced by psychedelic drugs (e.g., 4-phosphoroxo-*N,N*-dimethyl tryptamine [psilocybin], *N,N*-Dimethyltryptamine [DMT], 3,4,5-Trimethoxybenzeneethanamine [mescaline]), lysergic acid diethylamide [LSD], methylene dioxymethamphetamine [MDMA]) should strictly speaking *not* be considered a disorder of the self per se in so far as the psychological effects, while potentially mimicking certain aspects of psychosis in the short term (e.g., (Carhart-Harris et al., 2016b)) are not normally associated with long term functional impairment (e.g., (Krebs and Johansen, 2013)). In fact, contrasting with their legal status at least within North America, many participants with lived experience with these substances provide testimony to their potential psychological benefits for promoting empathy and self-insight (e.g., (Carhart-Harris and Nutt, 2013)). Moreover, experiences occasioned by psychedelic substances have been associated with beneficial long term psychological outcomes including increased trait openness to experience (MacLean et al., 2011) and trait mindfulness (Soler et al., 2016). Ingestion of these substances sometimes also occasion highly valued altered states of consciousness including “mystical” experiences that, for the majority of research participants in one study, were considered one of the top five “most personally meaningful” and “most spiritually significant” experiences of

their lives (Griffiths et al., 2008, 2006) and in a more recent online survey often included divine encounters (Griffiths et al., 2019). Accordingly, a resurgence of clinical interest has also occurred into the therapeutic potential of this class of substances in mental health treatment, particularly as a catalyst for psychotherapy, including in order to address existential angst, anxiety, and depression in persons facing terminal illness and in those experiencing chronic posttraumatic stress (Mithoefer et al., 2016).

Besides these possible therapeutic applications, neuroimaging studies have investigated the effects of psychedelic drugs primarily on resting-state. Among the most strong, reliable and basic outcomes of this research includes that these substances tend to engender a marked reduction of neural activity in the V-MPFC, PCC and PRC, particularly as measured by slow frequency oscillations up to ~20 Hz (Carhart-Harris and Nutt, 2013; Komater et al., 2013; Muthukumaraswamy et al., 2013; Palhano-Fontes et al., 2015; Riba et al., 2004, 2002). It is however worth pointing out that by contrast to V-MPFC, both M-MPFC and particularly D-MPFC activity seems to be preserved in the psychedelic state, as possibly with the function of an “observing ego”. Further, the effects of psychedelic substances on slow frequency oscillations, particularly within midline-posterior cortex, appear to partially mediate their consciousness-altering properties, where positive correlations have been reported between variability of alpha (8–11 Hz), theta (4–7 Hz), and delta (1–4 Hz) amplitude as well as BOLD-fMRI reduction achieved in PCC on the one hand, and individual differences in the intensity of the alterations in consciousness experienced across participants, on the other (e.g., (Carhart-Harris et al., 2016a, b; Komater et al., 2015; Muthukumaraswamy et al., 2013)). This intensity can vary from euphoric to intensely distressing, the latter often associated with the experience of “ego dissolution”, or the fear of the permanent loss of identity or rationality, a function primarily attributed to V-SRP as described herein. However, together with the signal decreases seen in the PCC, nevertheless global functional connectivity may in fact be increased in the same and other ROIs, effects that are also correlated with the experience of ego dissolution (Tagliazucchi et al., 2016).

Beyond a disruption of the normal ego function of V-SRP, it is also worth pointing out that disturbances in NV-SRP may also be engendered, where the third most highly endorsed psychedelic effect of those surveyed in the first neuroimaging studies of psilocybin was, after altered visuospatial perceptions, that the subject “felt unusual bodily sensations” ((Carhart-Harris et al., 2012) (Muthukumaraswamy et al., 2013)). From the perspective of the current framework, we speculate that a relative loss of amplitude and functional connectivity between the V-MPFC and PCC may partly engender the relative loss of V-SRP characterizing the psychedelic state of ego dissolution, which may also be accompanied by alterations in NV-SRP in some participants. However, there may be a relative preservation or even enhancement of observing ego functions within this qualitatively altered state of consciousness to the extent that insight is preserved, in turn associated with increased cognitive flexibility and an openness to qualitatively new kinds of experience.

12.6. Dementias

In Alzheimer’s Disease (AD), extensive data has been gathered on the impact of the dementia process on V-SRP. For example, Simm et al. demonstrated that a valenced reduction in the narrative sense of self was present in mild AD in both personal and social domains related to shortfalls in new learning ability and speed of information processing, contributing to “a reduced ability of people with early AD to understand their mental world and interpret thoughts, feelings, and beliefs about themselves” (Simm et al., 2017). Alternatively, another mechanism that has been proposed to explain the distortion in SRP in AD is the difficulty of these patients to precisely experience reliving previous events due to deficits in episodic autobiographical memory which may be at the root of AD patients’ loss of self-awareness and self-concept (Kalenzaga and

Clarys, 2013). By contrast, a relative preservation of NV-SRP relative to V-SRP may be characteristic of AD. For example, in a study investigating four markers of ‘self’ (self-knowledge, mirror self-recognition, the bodily distinction between self and others, and self-reported age), Nizzi and colleagues found that despite the early deterioration of self-knowledge and episodic memory, that is, V-SRP, AD patients at advanced stages of the disease seemed to maintain the capacity for NV-SRP and BSC rooted into mirror self-recognition and the bodily self/other distinction (Nizzi et al., 2016). Indeed this persistence of BSC even in advanced stages of AD seems to have wide support in the literature (Skaalvik et al., 2016; Tappen et al., 1999; van Gennip et al., 2016). Supporting this conclusion somewhat, Fargeau et al. found further that not all aspects of the self are affected equally in AD, with the “social self” being most affected (a finding also supported by (Hedman et al., 2013) while the “spiritual self” was relatively spared (Fargeau et al., 2010); see also (Owolabi, 2011)). Moreover, in functional MRI studies, it was demonstrated that patients with AD who had demonstrated significantly poorer self-discrepancy scores (impaired verbal self-awareness or anosognosia) had decreased activation of MPFC (Fujimoto et al., 2017; Zamboni et al., 2013) and anterior (Zamboni et al., 2013) and medial temporal cortices (specifically in the right hippocampus) (Arroyo-Anllo et al., 2015; Tondelli et al., 2018).

Widening the scope to other types of dementia, it has been suggested that when comparing AD to other types of neurodegenerative diseases in terms of loss of personal identity and sense of ‘self’, structural equation models revealed that injury to the ‘moral faculty’ - as perhaps directly related to V-SRP as discussed herein - plays the primary role in identity discontinuity (Strohming and Nichols, 2015), whereas other cognitive deficits, including amnesia, have no measurable impact on identity persistence. Accordingly, Behavioral Variant Frontotemporal Dementia (FTD) has the greatest effect on perceived identity, whereas Amyotrophic Lateral Sclerosis has the least (Strohming and Nichols, 2015). Thereby, if one takes into account the prototypical neural networks involved in neurodegenerative diseases as revealed by meta-analyses, bvFTD seems to be one of the diseases specifically impacting the neural circuits realizing V-SRP. Meta-analyses across studies on atrophy and glucose hypometabolism have indeed identified the frontomedian cortex (M-MPFC) as the most central or core hub in this disease besides the lateral prefrontal cortex, anterior insula, thalamus and basal ganglia, in contrast to other neurodegenerative diseases (Schroeter, 2012; Schroeter et al., 2015, 2014; Schroeter and Neumann, 2011; Schroeter et al., 2008). Atrophy and glucose hypometabolism in these regions are related to changes in personality and behavior, in particular disinhibition, apathy and changes in eating behaviors (Rosen et al., 2005; Schroeter et al., 2011). The impairment of M-MPFC in particular might further lead to a loss of self-awareness and self-knowledge in bvFTD making it a paradigmatic clinical syndrome affecting the “self” (Irish et al., 2012; Miller et al., 2001; Wong et al., 2018). Interestingly, Arroyo-Anllo et al. (Arroyo-Anllo et al., 2017) demonstrated that, although both bvFTD and AD deteriorate self-consciousness, bvFTD showed generally a greater impairment, in particular in anosognosia, introspection and moral judgments, whereas AD although also exhibiting anosognosia was associated more specifically with respective deficits in prospective memory. Moreover, a critical study by Wong et al. further showed the bvFTD and AD were differentiated by gray matter atrophy encompassing more so the anterior CMS inclusive of all of the V-MPFC, M-MPFC and D-MPFC in bvFTD and the posterior CMS in AD (including the PCC-PRC, extending to the P-SPL). Moreover, results comparing the groups in a self-referential encoding task showed an absence of the self-reference effect in memory for both patient groups, but poorer memory was mediated by the extent of loss primarily in D-MPFC and M-MPFC in both groups, although with volume loss in V-MPFC in the bvFTD patients and PCC in the AD patients also contributing to memory performance (Wong et al., 2018). Taken together, in comparison to AD wherein a loss of the narrative aspects of V-SRP as in autobiographical memory appears to

represent the dominant clinical features, perhaps associated primarily with the function of the PCC-PRC, in respect of the conceptual framework advanced here, the lack of insight (anosognosia) leading to overt personality-behavioural disorders especially in bvFTD patients may be more suggestive of a disturbance of the “observing self” circuitry, specifically, D-MPFC and related structures involved in the bottom-up gating of background SRP into foreground awareness (M-MPFC).

12.7. Asomatognosia and somatoparaphrenia, and anosognosia

In comparison to the emphasis of dementia in affecting V-SRP, asomatognosia is broadly defined as the inability to recognize an affected limb as one’s own, and most frequently occurs following right parietal damage (e.g., (Keenan et al., 2005; Meador et al., 2000)) and hence emphasizes a disorder of NV-SRP. Indeed as a consequence of different neurological impairments, part of the body can be entirely or partly ignored, refuted, disclaimed, or misperceived. Patients can experience the existence of non-present body parts or, on the contrary, the disappearance of existing body parts. They can also refute their bodily disabilities and, eventually, the ownership of their own body parts. The form and intensity of the asomatognosic responses differ substantially among patients. In fact, in some cases patients appear simply unaware of or bemused as to the ownership of their limb, but they may often correct the error if the actual identity of the arm is remarked on to them or they identify the connection between the arm and the shoulder. However, in other cases of asomatognosia, the misidentification of the limb may be accompanied by significant confabulatory elaboration and elaborate delusions (i.e., somatoparaphrenia; (Vallar and Ronchi, 2009)). Thus, patients affected by somatoparaphrenia obstinately refute the ownership of their limb despite convincing contradictory evidence and produce elaborate confabulations as to how the arm got there or who it ‘really’ belongs to, to the extent of giving it a name, or treating it as a distinct person with a separate identity (Feinberg and Keenan, 2005)(Feinberg et al., 2010; Meador et al., 2000)). The careful analysis of these conditions has proven to be essential for understanding how our brain constructs the experience of having and being a body, that is, NV-SRP and BSC (e.g., (Dieguez and Annoni, 2013; Dieguez and Blanke, 2011; Legrand, 2007)).

Given the tight link of these conditions with anosognosia for hemiplegia (AHP), investigations of the underlying anatomy have yielded varying results (e.g., (Baier and Karnath, 2008)(Dieguez and Annoni, 2013; Feinberg et al., 2010)). Some studies emphasized the importance of right parietal areas, such as the somatosensory cortices, the inferior parietal lobe and the supramarginal gyrus for sustaining a coherent sense of bodily self-localization and identity (e.g., (Daprati et al., 2010; Felician et al., 2004)). Baier and Karnath (Baier and Karnath, 2008) also found an association between right posterior insula damage and a disturbed sensation of limb ownership, fitting also the link between SMG and insula activity at rest in the healthy brain that was reviewed herein. Moreover, prior studies of somatoparaphrenia indicated a key role for TPJ lesions to the origin of the condition, in addition to cases with extensive fronto-temporo-parietal lesions (e.g., (Aglioti et al., 1996; Feinberg and Keenan, 2005; Moro et al., 2004)). More recent studies have reported that parietal involvement is a necessary but possibly insufficient condition for the occurrence of asomatognosia, and that while MPFC damage may play a role in the development of asomatognosia in general, orbitofrontal lesions also seem to be critical in the development of somatoparaphrenia versus simple asomatognosia (Feinberg et al., 2010). Additionally, somatoparaphrenia has also been linked to the de-afferentation of somatosensory and visual information in the right hemisphere with respect to the left-hemispheric “narrator” (i.e., V-SRP). The narrator, whose role is understood as to make sense of conflicting or missing sensory information, may also lack a sense of familiarity for his/her own left limbs following damage to the hippocampal-amygdaloid complex or the fibre bundles projected to this area. This additional damage may increase the sense of

non-belonging for the paralyzed limbs (Gandola et al., 2012). In light of the prior discussion and conceptual framework, we speculate that the absent or abnormal involvement of the right IPL/TPJ into the DMN as a consequence of lesion would be the necessary factor underlying asomatognosia, whereas intact left hemisphere parietal and MPFC regions might be the fault of the somatoparaphrenia, where D-MPFC might be an underlying factor for the lack of insight, that is, anosognosia. However, comparably little is as yet known regarding the role for interoceptive (as opposed to exteroceptive) NV-SRP in these disorders, which might be a relevant focus for future study. Should the interoceptive systems remain intact, this would be good reason to continue to differentiate between such systems (Park and Blanke, 2019a).

As a somewhat conceptually related condition but one more related to the motor domain, the term anosognosia originally referred to a specific unawareness of paralysis following stroke (Langer and Levine, 2014) and may also be understood as a disorder of NV-SRP in that case. Subsequently, however, the term has been used to refer to unawareness of other clinical conditions, such as blindness, memory and speech problems (Ansell and Bucks, 2006; Goldenberg et al., 1995). Anosognosia is generally more frequent after right than after left hemisphere lesions; however, this difference might be due to the exclusion of aphasic patients in most studies. Referring specifically to motor unawareness, several forms have been identified ranging from partial to complete anosognosia. In fact, some individuals may verbally deny problems but show behaviors consistent with paralysis (e.g., executing a bi-manual task using a unimanual strategy) whereas others verbally accept their paralysis but behave in an inconsistent manner (e.g., attempting to walk). Accordingly, explicit (verbal) and implicit (behavioral) awareness seem to be dissociable (Jehkonen et al., 2006), seemingly consistent with the distinction between V-SRP and NV-SRP as discussed herein. Moreover, unawareness can also vary from complete failure to recognize paralysis (severe anosognosia), to a partial unawareness in which an individual does not recognise or acknowledge the consequences of paralysis (Orfei et al., 2007).

As a frequent cause of anosognosia and asomatognosia, an analysis of the impact of stroke sheds further light on the role of NV-SRP, where stroke’s most intuitive impact on the experience of “self” would appear to lie in the domain of BSC rather than V-SRP. Deficits in body-ownership and agency such as seen in tasks involving the ability to distinguish between the left and right sides of the body, and also in higher order somatosensory function (such as finger gnosis, subjective sense of body ownership; i.e. acknowledging body parts as “parts of the ‘self’” etc.) following stroke have been well documented, with one deficit often being predictive of the other (Borah et al., 2016; Llorens et al., 2017; van Stralen et al., 2018, 2013). It has been suggested that pathological brain lesions such as strokes result in a sudden increase in the plasticity of the otherwise static body schema (Llorens et al., 2017), resulting in increased distortions of BSC. Concerning laterality, it is worth emphasizing that these distortions in body schema (specifically in body-ownership and agency - the sense that the ‘self’ can move and control the body) actually appear to be mainly present when brain lesions occur in the left hemisphere (Jenkinson et al., 2013; Nishio and Mori, 2012) particularly involving the premotor cortex (Llorens et al., 2017; Zeller et al., 2011) mainly areas 1 and 2 (Martuzzi et al., 2015). However, the right insular cortex has also been implicated in these processes (van Stralen et al., 2018). In going deeper into possible mechanisms for these observations, Martinaud et al. also localized this distortion to the right TPJ and a large area of the supramarginal gyrus, and to a lesser degree the middle frontal gyrus, suggesting that “our sense of ownership includes dissociable mechanisms of multisensory integration” (Martinaud et al., 2017). Interestingly though, it has been documented that in five cases of right-hemispheric stroke, although the subjects maintained an intact sense of body-ownership when viewing their body part in a mirror, they nonetheless attributed part of their body to someone else when viewing it directly, leading the investigators to suggest that a neural network involving the perisylvian areas of the

right hemisphere may be necessary for the integration of multiple representations of one's body and for a higher order re-representation of various bodily signals (both subjectively felt and objectively seen) into a first-person sense of body ownership (Fotopoulou et al., 2011; Jenkinson et al., 2013). Finally, Burin et al. postulated that a possible explanation for this weakened sense of body-ownership might be the disruption of the integration of contralateral afferent and efferent motor signals following stroke (Burin et al., 2015).

Whereas these studies focused on the role of the cortical layer alone, Moro and colleagues went a step further to map out the role of subcortical structures in the sense of NV-SRP and found that while bodily awareness is processed by areas widely distributed across the brain, intact subcortical structures and white matter tracts may be necessary to support basic feelings of owning (parts of) the body, as well as controlling it (Moro et al., 2016). Moreover, a study from Marcel et al (Marcel et al., 2004) also evidenced that anosognosia cannot be considered as a single defective neurological mechanism. Despite the co-occurrence of other deficits and the different possible mechanisms that have been posited (see (Heilman, 2014; Prigatano, 2009)), it was shown that the most frequently damaged areas associated with anosognosia are fronto-parietal areas or lesions extending to other lobes, but involving also fronto-parietal or subcortical (e.g., basal ganglia and internal capsule) structures, suggesting the crucial role of frontal and subcortical damage in the development of anosognosia (Pia et al., 2004). In fact, awareness of motor functioning is a multifaceted process that requires integration of sensory, motor, and emotional information involving several brain circuits. Moreover, several studies have identified the insula, and principally its posterior part, as another key structure commonly damaged in patients showing the false belief about the functioning of their own limbs, suggesting its role for self-awareness of limb actions (e.g., (Berti et al., 2005; Farrer et al., 2003; Karnath et al., 2005; Spinazzola et al., 2008)).

In contrast to the devastating effects stroke can have for NV-SRP, V-SRP can often be preserved. Owolabi et al. in a series of studies on health-related quality of life after stroke found that stroke had a far greater impact on the 'physical spheres' of quality of life than on the 'spiritual spheres' (Owolabi, 2008, 2011; Owolabi and Ogunniyi, 2009) using a measure of health-related quality of life based on the "Seed of Life Model" (Owolabi, 2008, 2010). Domains in the spiritual spheres that were assessed comprised of items assessing verbal self-referential concepts such as self-determination, self-esteem, personal growth and autonomy, among other parameters, and these were found to be relatively stroke-resilient across diverse cultural settings (Owolabi, 2011). This resilience of adaptive V-SRP despite impacts on NV-SRP is probably due to its documented pivotal role in the re-establishment of a continuity of self-experience following the stroke along the path to recovery, self-rediscovery, and self-rejuvenation after stroke (Clarke, 2009; Clarke and Black, 2005; Giaquinto et al., 2007; Kalra, 2007; Owolabi and Ogunniyi, 2009). As such, the condition often provides an impressive dissociation between impaired NV-SRP and intact V-SRP. Considering this literature in light of the current review, these conditions would seem to be involved not only in abnormal NV-SRP but more broadly and fundamentally in the sense of agency that may be the product of the integration of V-SRP with NV-SRP, consistent with the pattern of damage as also involving ROIs within the insula, frontoparietal networks as well as left motor cortex and subcortical structures. The preservation of V-SRP and sense of agency despite deficits in NV-SRP may be regarded as a positive prognostic indicator.

12.8. Parkinson's disease and corticobasal syndrome

Many of the non-motor symptoms of Parkinson's disease – from autonomic and somatosensory dysfunctions to cognitive and behavioural disturbances – have been connected to dysfunctions of corticostriatal circuits, in particular the insular cortex (Christopher et al., 2014; Criaud et al., 2016). Specifically, the tremor dominant (TD)

subtype of the syndrome showed a reduced interoceptive accuracy and sensibility (Santangelo et al., 2018) connecting it to the concept of impaired NV-SRP. More, between 20 % and 40 % of individuals with Parkinson's Disease experience vivid hallucinations which, in some cases, may consist in 'presence hallucinations' (Fenelon et al., 2011), that is, sensations of someone invading one's personal space (Llorca et al., 2016). As noted by Llorca et al. (2016), Jaspers described this phenomenon in General Psychopathology (Allgemeine Psychopathologie) in 1913 (see (Park, 2019)), under the name of "leibhatige Bewusstheit", which has been translated as "sense of presence", or "idea of presence". In these hallucinations, patients have the awareness that someone is close by, someone that they can in no way perceive with the external senses, yet whose actual presence is clearly experienced. These hallucinations are associated to progressive atrophy involving the hippocampal limbic, paralimbic and neocortical areas (Ibarretxe-Bilbao et al., 2011). For example, one study identified abnormal frontal cortex and reduced grey matter in left sided insula, frontal opercular, and orbital frontal cortex as a possible source of these hallucinations (Gama et al., 2014), emphasizing ROIs to both NV-SRP and V-SRP as discussed in the current review.

Two other remarkable clinical features with an impact on NV-SRP appear mainly in corticobasal syndrome, an atypical Parkinsonian syndrome (Armstrong et al., 2013). Whereas the alien limb phenomenon is associated with a feeling of non-belonging and disowning toward one's own limb, the anarchic limb phenomenon is characterized by involuntary but goal-directed movements affecting either the experience of self-ownership or self-agency (Brion, 1972; Della Sala et al., 1991). Anatomically, the alien limb has been related to the postcentral gyrus and somatosensory cortex, whereas the anarchic limb has been related to the supplementary motor area and MPFC (Hassan and Josephs, 2016; Marchetti and Della Sala, 1998), structures also affected in corticobasal syndrome and its histopathological counterpart – corticobasal degeneration – according to systematic and quantitative meta-analyses on structural imaging data (Albrecht et al., 2017). Adding to this literature, a structural MRI study in patients with corticobasal syndrome revealed frontoparietal atrophy including the supplementary motor area and cingulate cortex contralateral to the side of the affected alien or anarchic limb, and hints for frontotemporal atrophy including the pre- and postcentral gyrus in alien limb syndrome (Albrecht et al., 2019). Remarkably, machine learning in structural imaging data was able to predict not only the disease but also the peculiar alien / anarchic limb syndrome in the patient group.

12.9. Suicidal ideation

No review of the neuroscientific and biobehavioral literature regarding the consciousness of "the self" could be complete without at least brief mention of the self-feelings associated with the desire to end it. Psychological research describes different forms of SRP associated with motivations for suicide attempts (May and Klonsky, 2013) including the wish to escape negatively-valenced SRP described as aversive self-awareness (e.g., (Baumeister, 1990)), in turn potentially associated with shame, hopelessness, and other markedly negative self-feelings. According to epidemiological research, nearly one in every ten of us will experience suicidal ideation at some point in our lifetime, with nearly one in three of such persons making an attempt at ending their life (e.g., (Nock et al., 2008a, b)).

Nevertheless, acute suicidal ideation remains rare and so is difficult to study neurobiologically as a state (Karam et al., 2012), particularly in so far as its self-reported presence compels the ethical obligation to intervene (Klonsky et al., 2016). Accordingly, neuroimaging studies tend to compare response during resting state or other psychological tasks not directly related to the experience of suicidal ideation, making interpretations less straightforward. Moreover, most studies focus on persons who have been diagnosed with various mental disorders such as affective disorders, PTSD, and substance use disorders, comparing

subgroups who do vs. do not experience suicidal ideation with at least some regularity. Doing so makes sense because the presence of these disorders increases the risk of suicidal behaviour only in so far as the disorders are associated with increased risk for suicidal ideation; in other words, after accounting for that relation, it can be shown that mental disorders do *not* strongly confer increased risk of suicide (Nock et al., 2010). Nevertheless, conclusions coming from these studies may tend to reflect the interaction of suicidal ideation as it is expressed within the condition of various heterogeneous mental health problems, making conclusions across disorders difficult.

Interestingly, attempting some trandiagnostic observations that might generalize across mood disorders, psychosis, and borderline personality disorder, Bani-Fatemi et al.'s (2018) systematic review highlighted roles for reduced response within the ACC, insula, and supramarginal gyrus in conferring suicidal risk, ROIs considered more so to reflect NV-SRP in the current review (Bani-Fatemi et al., 2018). This could be interpreted as a greater involvement of negative V-SRP relative to NV-SRP in the context of suicidal ideation, where "ideation" itself would seem to be a term that emphasizes verbal thought as compared with non-verbal feeling. Further, this could be congruent with findings that increases in coherence within the salience network (D-ACC, insula) were associated with decreases in suicidal ideation in adolescents across time (Schwartz et al., 2019). Bani-Fatemi et al. also emphasize roles for the DLPFC and orbitofrontal cortex involved in executive control and inhibition, as well as reward processing. Moreover, the authors found altered RSFC in the PCC, PRC, MPFC, and temporoparietal areas to be associated with suicide risk, all ROIs considered herein to primarily underlie V-SRP (Bani-Fatemi et al., 2018). Most directly overlapping some of the ROIs discussed herein, Chase et al. (2017) also compared the differential connectivity of the D-PCC vs. V-PCC in persons with vs. without suicidal ideation and, replicating Bzdok et al.'s (Bzdok et al., 2015) results, the authors found that the D-PCC correlated more strongly with the D-ACC and D-MPFC whereas the V-PCC correlated more strongly with the PFC and M-MPFC across both groups. However, the authors further found that the ratio of low to high frequency BOLD power was lower in both the V-PCC and D-ACC (but not D-PCC) in persons experiencing suicidal ideation, while the RSFC between the V-PCC and D-ACC was higher in persons experiencing suicidal ideation, but the RSFC between the D-PCC and D-ACC RSFC was lower. This study is especially noteworthy for relating the within ROI activity to its RSFC with other ROIs, which is rarely investigated in the literature. Another measure less often described in the literature is the regional homogeneity, consistent with the amount of within-ROI RSFC exhibited by a brain region as compared to the long-range (across ROI) RSFC that is typically described; Cao et al. (2015) showed that the regional homogeneity was increased in VMPFC, PCC-PRC, and right IPL, while decreases were observed in bilateral frontal, hippocampal, and cerebellar regions, even among persons not otherwise meeting diagnostic criteria for any mental disorder.

In summary, neuroimaging studies of suicidal ideation are at a nascent stage but suggest a strong overlap with ROIs that have been found in investigations of valenced introspection (V-SRP) and interoception (NV-SRP) as described in the present review. Suicidal ideation represents a case of valenced SRP whereby self-awareness is experienced as unbearably distressing and aversive; at the acute moment of suicidal ideation, the subject considers it in preference that he was no longer self-aware. A greater understanding of the condition from an affective neuroscientific point of view might lead to preventative strategies to decrease risk of mortality, and increase positive SRP and perceived quality of life in those at risk for suicide.

13. Limitations and conclusion

This essay overviewed neuroimaging research that has investigated SRP, together with a lexical-thematic analysis of words indicative of "self-feelings", and several informal automated meta-analyses and seed-

based RSFC analyses were conducted via neurosynth.org to replicate original findings previously reported in the literature in support some of the arguments made. We considered various "self-feelings" and their basis in what we regard to be two distinctive kinds of SRP, that is, SRP as it occurs verbally (V-SRP) and nonverbally (NV-SRP). We discussed the active expression of V-SRP and NV-SRP in top-down structured tasks, namely *introspective* and *interoceptive* tasks, as well as its bottom-up expression in the resting state. We also considered how top-down attention directed toward V-SRP and NV-SRP as it occurs during resting state could be understood to reflect the operation of an "observing self" and how central executive, cognitive control processes could also be expressed during SRP. These considerations brought us to recommend a conceptual and methodological framework for understanding SRP based on figure-ground relationships, referencing the attentional spotlight and theatre of consciousness metaphors. We also made some observations and predictions about what may be some of the neural correlates of SRP. Finally, we briefly applied the conceptual framework we developed toward understanding certain psychological and neurological disorders.

Limitations of the present review, however, are numerous, and it is important that they do not go overlooked. For one, we did not conduct a systematic review, and so what is written must be considered to represent the theoretical impressions of the authors. Additionally, our review was limited to neuroimaging (primarily fMRI and EEG) studies as well as the few NIBS studies that have so far been conducted in this area of research, and so is limited to the neural systems perspective. In other words, it does not directly address other levels or units of analysis for example the unique effects of certain neurotransmitter and neurohormonal systems or genetics. Further, we primarily address cortical representations and lack a correspondingly careful consideration of the subcortical systems as they may relate to SRP. We neither attended to the impact of the demographic distributions of research participants, for example, comparing results between the sexes or by age, which are likely to be highly relevant for example in considering that the prevalence of certain self-related disorders such as affective disorders is not uniform across such demographics.

Whilst acknowledging these limitations, we hope that we have been able to provide some modest contribution to the neuroscientific and biobehavioral literature seeking to understand the consciousness of self and specifically the nature of self-feelings, following some of the original psychological principles established for this subject area by William James (James, 1890). We are especially hopeful that a yet better understanding of such principles sometime in the near future will ultimately yield better treatments for various disorders of the self.

Declaration of Competing Interest

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.neubiorev.2020.01.023>.

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