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**Is the self a higher-order or fundamental function of the brain?
The “basis model of self-specificity” and its encoding by the
brain’s spontaneous activity**

Georg Northoff (1,2,3,4, 5)

(1) University of Ottawa Institute of Mental Health Research, Ottawa/Canada; (2) Centre for Cognition and Brain Disorders, Hangzhou Normal University, Hangzhou/China; (3) Centre for Brain and Consciousness, Taipei Medical University (TMU), Taipei/Taiwan; (4) College for Humanities and Medicine, Taipei Medical University (TMU), Taipei/Taiwan, (5) ITAB University of Chieti/Italy

Corresponding author

Dr. Georg Northoff, MD, PhD, PhD, FRCP

Research Director

Mind, Brain Imaging and Neuroethics

Canada Research Chair

EJLB-Michael Smith Chair for Neuroscience and Mental Health

Royal Ottawa Healthcare Group

University of Ottawa Institute of Mental Health Research

1145 Carling Avenue, Room 6467

Ottawa, ON K1Z 7K4

Tel.: (613) 722-6521 Ext. 6801

Fax: (613) 798-2982

Email: georg.northoff@theroyal.ca

Website: www.georgnorthoff.com

Abstract

What is the self? This is a question that has long been discussed in (western) philosophy where the self is traditionally conceived a higher-order function at the apex or pinnacle of all functions. This tradition has been transferred to recent neuroscience where the self is often considered to be a higher-order cognitive function reflected in memory and other high-level judgements. However other lines of research demonstrate a close and intimate relationship between self-specificity and more basic functions like perceptions, emotions and reward. This paper focuses on the relationship between self-specificity and other basic functions relating to emotions, reward, and perception. I propose the basis model that conceives self-specificity as a fundamental feature of the brain's spontaneous activity. This is supported by recent findings showing rest-self overlap in midline regions as well as findings demonstrating that the resting state can predict subsequent degrees of self-specificity. I conclude that such self-specificity in the brain's spontaneous activity may be central in linking the self to either internal or external stimuli. This may also provide the basis for coding the self as subject in relation to internal (i.e., self-consciousness) or external (i.e., phenomenal consciousness) mental events.

Introduction

General Background – Model of Self in Philosophy and Neuroscience

The self is a complex concept that originally stems from philosophy and is now heavily discussed in both neuroscience and philosophy. Historically, philosophers like Descartes and Kant characterized the self and the subjective effects it exerts as the highest or pinnacle of all functions that characterized the mind (as distinguished from the brain) [1, 2]. This has been somewhat transferred into our times. Though the self is no longer associated with a mind distinguished from the brain but rather with the highest function of the brain, it remains conceptualized as a higher-order cognitive function with meta-representation and a specific higher-order network or regions like the prefrontal cortex (see for instance [2-6]). The self, as discussed in these views, is conceived as not driving behaviour such as basic functions like emotions and reward or a lower-level processing stage like perception. However, recent findings seem to shed some doubt on this view.

The self has been operationalized in many experimental studies in terms of the degree of self-relatedness of stimuli (see below for exact definition) and/or how self-relatedness influences behavioural performance. Most interestingly, self-relatedness has been associated with functions as basic as perception (see [7-11]), action [12], reward [13], and emotion (see [14, 15]). Moreover, some studies have shown links in brain activity for self-relatedness and resting state, consistent with the assumption of the self-reflecting a basic aspect of brain function and connectivity, even when the brain is at rest (see [16-20]). Taken together, these findings shed some doubt on the characterization of self as higher-order cognitive function. We may thus need a novel model of self, one that is different from the original philosophical one, to accommodate these novel findings.

The main and most general aim of this paper is to show these recent findings and discuss what they imply with regard to the model of self. Put in a nutshell, I postulate that we need to reverse our model of self, instead of the self being a higher-order cognitive function of either brain or mind, the self may be the most fundamental function of the brain and its intrinsic or spontaneous activity.

Specific Background – Definition of self-related processing, self-specificity and self-expansion/association

Different terms or concepts are used to describe self; I shall briefly review them and indicate how I will use them in the following. There is the distinction between self as subject and self as object [21-24] which can be traced back to William James' distinction between "I" (self as subject) and "Me" (self as object) [25, 26]. The self as subject concerns the experiencing self, the subject that experiences itself and external objects, events or persons in the environment. Due to its focus on experience, the self as subject is closely related to consciousness entailing self-consciousness, the consciousness of oneself and/or external objects, events or persons.

This is different in the case of the self as object. The self as object concerns the attributes related to and characterizing the own self like particular contents as the own name (or autobiographical memories). The self is then no longer subjective but represented in particular contents; it is content-based which is often described as self-representation of contents (see [4, 6, 21, 22]). Depending on the content represented one can characterize the self as object as the physical or bodily self (own body is represented as content of the self), the inner bodily or vegetative (or interceptive) self [27, 28], the mental self (own thoughts or others mental states are represented as content of the self), the autobiographical (or extended) self (own autobiographical memories are represented as content of the self) and the social-cultural self (own social contacts with other person and culture is represented as content of self) [4-6, 21, 22, 29, 30].

Self-*referential* processing refers to a content that is already there and established while it is linked or referred to the self (see [23, 24, 31]). Due to such reliance on contents, self-referential processing seems to be closely associated with the self as object that is content- or representation-based. Since it concerns specific contents and their representation for the self, one may also speak of self-representation or self- processing (see [21, 22, 32, 33]). This has its experimental roots in the self-reference effect in behaviour (like reaction time and accuracy) that first has been observed in the domain of memory [22, 32, 33]; and recently also in perception [7-11] and action [12] (see below for details).

Taken in this way, self-referential processing may be a term indicating the process that leads to self-reference effect as its outcome. Finally, both self-reference effect and self-referential processing are conceived on the personal (rather than sub personal or even non-personal), psychological, and neural level, linked to explicit (rather than implicit) processing, and can at least in part be modulated by voluntary control and is therefore not completely automatic (which may be debated though; [8, 10] (see Figure 1).

Insert Figure 1 here

Another term often used is self-related processing. Many authors use the terms self-related and self-referential processing interchangeable with the meaning of the former supposedly signifying the definition of the latter. However, I distinguish both terms (see [23, 24, 31]). Self-related processing is supposed to describe the processing of a stimulus in relation to the self – the emphasis is here on the *relational* (rather than *representational*) character of such processing as well as on stimuli as distinguished from contents. This distinguishes self-related processing from self-referential processing that is rather about content (than stimuli) and representation (rather than relation). Moreover, I assume such self-related processing to operate on a sub personal if not non-personal and neural (rather than psychological) level as well as to be automatic and implicit rather than being voluntarily controlled and explicit (as self-referential processing).

A distinction which is more or less analogous to the one between self-related processing/self-specificity and self-referential processing/self-reference has recently been introduced by Sui and colleagues [7-11, 34, 35]. They speak of “self-prioritization” that describes the “clear prioritization in perceiving and processing self-related information” [7, 9]. Based on their lesion data with regard to face recognition [7, 9, 34], they distinguish between automatic and task-based self-prioritization: automatic self-prioritization operates beyond voluntary control and is implicit, while task-based self-prioritization is subject to voluntary control, and explicit (which they associate with different neural pathways) (see below for more discussion). What they describe as automatic self-prioritization may thus more or less correspond to what I designate as self-related processing and self-specificity while task-based self-prioritization finds its analogue in self-referential processing and self-reference.

Does automatic self-prioritization really correspond to self-related processing and self-specificity? Self-related processing presupposes that the assignment of self-specificity to external (and internal cognitive and vegetative)) stimuli is an active process rather than being an intrinsic feature of the stimuli (or contents) themselves. Even content like one’s own name, which appears to be intrinsically self-related, must undergo self-related processing in order for it to assign self-specificity. Self-specificity is not a feature intrinsic to the stimulus (or content) that comes with the stimulus but must be assigned by the brain and its particular ways of processing to the stimulus. This process of assignment of self-specificity to either internal or external stimuli, e.g., contents has also been described as self-association or self-expansion [7, 9] .

For instance, even when learned well to assign self-relatedness to our own name, we may nevertheless fail to do so when our mind is internally directed consumed by its own thoughts as related to the brain’s resting state activity. Self-relatedness may not come primarily with the stimulus itself but may be assigned to it by the way the brain and its resting state activity can (or cannot) process that very same stimulus (which is based on past experiences, e.g., learning and actual contextual, e.g., internal mental and external social circumstances). Such assignment of self-relatedness to (internal vegetative and cognitive as well as external social) stimuli is assumed occurring automatic and implicit rather than explicit and underlying

voluntary control (as in self-referential processing). I assume the resting state to be central for self-*related* processing in this sense which is manifest in the assignment of self-specificity to both internal and external stimuli accounting for what Sui describes as self-expansion (or self-association). This origin or basic roots of such self-related processing and self-expansion are the focus in the present paper.

General and Specific Aims –Neural relationship between self-specificity and other functions

The *general aim* of this paper consists in investigating the neural relationship between self and other functions and thus in what Sui [7-11] describe as self-association or self-expansion. I hypothesize that self-association or self-expansion is possible on the basis of a specific neural relationship between internally-based intrinsic or spontaneous activity and externally-based task-evoked or stimulus-based activity and hence on what has been called rest-stimulus interaction [36]. My main focus is on the neural rather than behavioural underpinnings of such self-association. Moreover, focusing mainly on self-association or self-expansion, I will neglect all other studies that focus on experience, reflection, recognition, evaluation, or introspection of self.

The *first specific aim* is to review some of the recent data on the relationship between self-specificity and non-cognitive functions like perception, emotion and reward. I demonstrate that self-specificity can indeed modulate the neural processing of non-cognitive functions and their external stimuli with this modulation centrally involving the cortical midline structures. This is the first part of the manuscript.

The *second specific aim* is to develop a model of self which can accommodate evidence on the self on low-level aspects of processing (as in perception) and its close relation to basic functions or drivers or behaviour like emotion and reward – this amounts to what I describe as basis model of self-specificity. The basic model postulates that self-specificity is a basic internally-based function of the brain prior to and independent of subsequent externally-triggered functions like perception, action, emotion, reward, and cognitive functions (like memory, attention, etc.). Self-specificity is conceived here as a basic and fundamental function of the brain's intrinsic or spontaneous activity. I postulate that self-specificity is manifest in particular spatiotemporal schemata and encoded in terms of past and (possible) future input-output relationships into the brain's intrinsic or spontaneous activity. This will be discussed and detailed in the third part of the manuscript.

I./ Empirical data: Does self-specificity modulate other functions?

As mentioned above the self-specificity effect was first established in memory with self-related items being better memorized than non-self-related ones (see [32, 33]). Such memory enhancement by the self is mediated by the medial prefrontal cortex (see [37]). This would still be well compatible with self-specificity being a higher-order cognitive function. There are however findings showing that self-specificity modulates even more basic functions like perception [8-11, 38], action [12], emotions [14, 15], and reward [13, 35]. That argues against self-specificity being a higher-order cognitive function. How is such association or expansion of self-specificity mediated neurally? I will briefly review these studies in the following with a specific focus on their underlying neural correlates.

Perception (and Action) and Self-specificity

Sui [7-11, 38] investigated how the processing of geometrical shapes like circle, triangle, and square can be modulated by associating them with a label signifying the self, a friend, or a stranger. Theoretically, the assumption is here that the geometrical shapes reflect external stimuli that by themselves remain neutral with regard to the distinction between self and non-self. While the label signifies the self or self-specificity and may interact or associate with the geometrical shapes and thereby impact their subsequent processing. The task is thus about self-association or self-expansion in the domain of perception.

In their experiments, Sui and colleagues typically let subjects form associations between the three geometrical shapes and three labels. Afterwards participants are presented pairs of shapes and labels (like circle-self, and so forth) that either matched or not matched (non-matching) with the learned associations. Reaction times were fastest and accuracy highest for those pairings where the self was involved with performance decreasing from self over friend to stranger. The data clearly demonstrate behavioural effect of the self-label on (self-) neutral perceptual stimuli like geometric shapes in both reaction time and accuracy.

Self-associations also appear to directly affect action. Frings and Wentura [12] paired four different movements (right, left, up, down) with four different labels (self, mother, stranger, and a neutral one). Subjects had to form (or learn) associations between movements and labels and afterwards had to perform the cue-based movements in conjunction with the brief presentation of a matching or non-matching label and subsequent judgment (whether they matched or not). Trials implicating the self (when compared to mother and stranger and neutral conditions) showed the fastest reaction times and were most accurate. Hence, as in the case of “perception-self links”, there are clear behavioural effects of self-specificity on action suggesting “action-self links” (as [12] say). Self-association effects can thus be observed behaviourally in both domains, perception and action.

How about the neural underpinnings of such self-association effects? Sui [8, 10, 11, 38] investigated the same paradigm in fMRI. They observed two main regions, the ventromedial prefrontal cortex (VMPFC) and left posterior superior temporal sulcus (LpSTS) to be implicated in the self-association effects. More specifically, activity changes in the VMPFC were mainly related to the label of self by itself (during both matching and matching

pairs) as distinguished from the other two, friend and stranger. In contrast, the same region was not implicated in the external stimuli themselves regardless whether they were labelled by self or not. VMPFC activity was thus label-specific or self-specific. This was different for the LpSTS. This region responded to both self-label itself and those stimuli (the geometrical shapes) that were labelled by the self (“Self-tags”). To underline the behavioral relevance of both regions, their activity changes correlated with the respective reaction times with higher activity changes predicting faster reaction times. Functional connectivity between VMPFC and LpSTS was also increased during specifically matching pairs that labelled shapes by the self. This also correlated with behavioural measures showing that increasing VMPFC-LpSTS functional connectivity predicts increased accuracy and reaction times (see Figure 2a).

Insert Figure 2a here

Based on their data the authors assume differential roles for VMPFC and LpSTS. The VMPFC may be implicated in internal self-representation which then is linked to the processing of external stimuli as in LpSTS that is implicated in attributing salience or attention to stimuli. By coupling VMPFC and LpSTS the internal self-representation can impact the external stimulus processing as in the self-labelled shapes. Considering their functional connectivity data, they assume that the VMPFC receives the visual input (from the external stimuli, the shapes) even earlier than visual associative areas (which though due to the sluggishness of the BOLD response in fMRI would need to be demonstrated in EEG). That in turn makes it possible for the VMPFC (and its self-specificity) to impact their subsequent processing in posterior regions like the LpSTS and to attribute higher degrees of salience or attention to them which psychologically can be described as self-association. Such self-association reflects the assignment of self-specificity to otherwise self-neutral stimuli (see above).

Emotions and Self-specificity

The previous study on perception and self-tested for the neural underpinning of linking self to perceptual stimuli thus accounting for self-association. Does self-processing relate to the neural basis of other basic driving processes, such as emotions and reward? Though not explicitly testing for such linkage of rewarding or emotional stimuli to the self, there are data indicating neural overlap between emotions and self as well as between reward and self.

Both positive and negative emotions have been shown to recruit the anterior cortical midline structures including the sub- and pregenual anterior cingulate cortex as well as ventro- and dorsomedial prefrontal cortex [39, 40]. Since the very same regions are also recruited in the various studies on self, one can suggest overlap and interaction between self and emotions. Consider the study of Phan [15] who let subjects view emotional pictures while being scanned using fMRI. Afterwards, subjects were asked to evaluate the degree of self-relatedness or personal relevance of the same pictures in order to correlate them with the fMRI signal. Signal changes in the VMPFC during emotional picture presentation predicted

the degree of personal relevance (or self-relatedness) subjects attributed to the same pictures post scanning.

Further support for direct neural interaction between self and emotion comes from a study by Moran and colleagues [41]. One early study by Moran [41] applied a two-by-two factorial design in which they presented words corresponding to personality characteristics varying emotional valence (positive or negative) and self-specificity (high and low) (which had to be judged by subjects as personally favourable or unfavourable). They showed an interaction between high degrees of self-specificity and (positive) emotional valence in specifically the pregenual and subgenual anterior cingulate cortex [41].

The central involvement of these regions was further supported by a study of ours [14]. To exclude task-related effects like the cognitive efforts related to judgments (and to focus on stimulus-related effects related to perception itself independent of subsequent judgment), we let subjects passively view emotional pictures in the scanner. Afterwards outside the scanner subjects had to judge the emotional arousal (i.e., excited/aroused or not) and valence (i.e., positive or negative) as well as the degree of self-specificity of the same pictures.

The results from the subjective ratings were then parametrically correlated with the neural activity changes during the perception of the same pictures. The correlation yielded a significant relationship between the neural activity in several subcortical/cortical regions and the pictures' degree of self-specificity. Subcortical regions included the tectum, colliculi, amygdala, ventral tegmental area (VTA), mediodorsal thalamus, and ventral striatum (VS), while cortical regions included the perigenual anterior cingulate cortex (PACC), the ventromedial prefrontal cortex (VMPFC), the dorsomedial prefrontal cortex (DMPFC), and the posterior cingulate cortex (PCC; see [14]). The higher the subjects' neural activity in these regions during the viewing of the emotional pictures, the higher the degree of self-specificity subjects assigned to the stimuli.

Is the parametric dependence of the neural activity in these midline regions really due to the stimuli's degree of self-specificity or, rather, to their affective-emotional components, that is, emotional arousal and valence? The regions whose neural activity was parametrically dependent on the degree of self-specificity also showed parametric dependence on the emotion dimensions like valence and intensity (arousal). However, the direction of their correlation was different in cortical and subcortical regions. Cortical regions like the PACC, VMPFC, and DMPFC showed opposite directions in their dependence on self-specificity and arousal/valence. Increased degrees of self-specificity of the stimuli were associated with increased degrees of neural activity in the cortical regions, whereas increased degrees of arousal/valence of the same stimuli led to lower degrees of neural activity in the same regions (see Figure 2b).

Insert Figure 2b here

These data contrasted with the activity patterns observed in the subcortical regions. Subcortical regions like the tectum, the periaqueductal gray, and amygdala did not show such opposite directionality of self-specificity and arousal/valence - both self-specificity and arousal/valence positively correlated with neural activity

Taken together, these findings demonstrate a close relationship between emotion and self-specificity in neural activity. Northoff and Panksepp [42] proposed a subcortical-cortical midline system as being central for self-representation. Panksepp [43-45] proposed that emotional feelings are associated with activation in subcortical regions. Since emotional feelings (rather than mere emotions) are intrinsically subjective, they, so Panksepp, must presuppose some kind of basic primitive self, a primarily affective rather than cognitive self which is closely related to the body and its homeostatic functions.

Reward and Self-specificity

Reward is considered a basic motivational function of the brain. If coupled to a particular reward (like money), certain stimuli are valued differently in that they are preferred over others that are not coupled to such reward even if the stimuli themselves and their respective contents (like a suitcase or bag) are identical. The neural correlates of reward can be found in subcortical regions like the ventral tegmental area (VTA) and the ventral striatum (VS) as well as in the ventromedial prefrontal cortex (VMPFC). Many recent studies have been conducted to show that the assignment of reward is highly dependent upon the social context: if for instance a particular person gets each time 30 \$ while another person typically gets once less (15 \$) but once receives double the sum (60\$), then activity in the VS and VMPFC is higher for the first compared with the second scenario (see[46]).

How about the relation between reward and self? Ersner-Hersfield, Wimmer, & Knutson [47] conducted an fMRI study in which subjects had to judge personality traits with regard to themselves and other people both in the present and the future (i.e., 10 years from now). After one week subjects came back and had to perform a behavioral temporal discounting task in which they had to make choices between immediate monetary rewards and delayed but larger monetary gain. The VMPFC showed greater activity for self-versus other trials as well as for self-present versus self-future trials. Most relevant here the contrast between self-present and self-future activity in the VMPFC predicted the degree of temporal discounting in the reward task (i.e., the ratio between immediate and delayed rewards chosen): the greater the VMPFC activity for the present self (when compared to the future self), the greater the tendency to choose immediate (rather than delayed) monetary rewards (see analogous results by Mitchell, Schirmer, Ames, & Gilbert, [48]).

These data suggest a close neural relationship between reward and self. The assumption of self-reward neural overlap is further supported by studies from our group. De Greck and colleagues [13] presented different pictures (alcohol, gambling, and food) which subjects had to evaluate either with regard to both their rewarding and self-related features. The focus was on the neural overlap of self-relatedness with reward (whereas the reverse focus, overlap of reward with self-relatedness was not tested). The reward system typically involved VS, VTA and VMPFC. Interestingly, stimuli evaluated as highly self-related by the subjects elicited high signal changes in the same regions while those assessed as low self-related did not show

any signal changes in these regions. These findings suggest neural overlap of self-relatedness with reward-related tasks in the reward system (see Figure 2c).

Insert Figure 2c here

Are self and reward identical? Is self-relatedness nothing but reward and apparent self-related activity changes in the VMPFC really due to the effects of reward (see also [49])? This has been argued by some authors such as D'Argembeau [21] who suggests in his "valuation hypothesis" that the VMPFC encodes personal value and assigns it to both internal and external stimuli [21], 5.

We have to be careful, however. Reward-self overlap in VMPFC does not entail reward-self-identity. Both may for instance dissociate from each other. Behaviourally, such dissociation has been demonstrated in a recent study by Sui and Humphreys [35] where an increase in the size of the stimuli did not affect the reward bias but did increase the self-bias effect. There is thus behavioural dissociation between self and reward while both, reward bias and self-bias, were found to correlate with each other. Neurally, deGreeck [50, 51] demonstrated that reward-related activity signals in the three reward regions they observed were normal in recovered alcoholic and gambling patients while their self-related activity was virtually absent, showing no distinction between high and low self-related stimuli in VS, VTA, and VMPFC.

Such dissociation of self-relatedness from reward in reward regions suggests that the same regions, VTA, VS, and VMPFC may be utilized in different ways by reward-related and self-related processing. This tentative conclusion requires further experimental support. In addition to any common regions for self and reward, there may also be different regions implicated. Enzi [52] took the same data set (as [13]) and re-analysed the results with regard to self-specific regions by conducting exclusive masking (with masking of reward-related regions during self-relatedness condition, e.g., high versus low self). This revealed the premotor cortex and the insula (see also [53]) as regions that were specifically related to the distinction between high and low self-related stimuli rather than to their rewarding features.

In sum, the data suggest regional overlap between self and reward in the regions of the reward system including VTA, VS, and VMPFC. Though their exact relationship remains to be clarified, there is nevertheless some evidence that self-relatedness seems to recruit core regions (like VTA, VS, and VMPFC) and processes (like valuation) of a basic motivational process like reward. There is at least some partial regional reward-self overlap but future work needs to explore whether such reward-self overlap translates and extends into self-expansion or self-association of rewarding stimuli. One would consequently expect the assignment of reward to otherwise non-rewarding stimuli to be strongly impacted and modulated by the degree of self-expansion or self-association (as described above for perception). Despite the current unclear relationship between self and reward, it is notable that self-related stimuli recruit subcortical regions like VTA and VS (as analogous to emotions where other subcortical regions like thalamus, amygdala and tectum were

recruited). The involvement of subcortical regions argues against the higher-order cognitive model of self: subcortical regions have been associated with lower-order functions like reward and emotions rather than higher-order cognitive function which are assumed to be relayed by cortical regions such as the prefrontal cortex.

II./ Basis Model of Self: Self-specificity and its encoding by the brain's spontaneous activity

How can we account for the above described findings of self-expansion or self-association in domains like perception, action, reward and emotions? Below I present a new, basis-account of how the self may be related to intrinsic activity in the brain, operating at both low and high-levels of representation.

“Rest-Self overlap” – Resting state and self-relatedness recruit cortical midline structures

The cortical midline regions are the core part of the so-called default-mode network (DMN) [54, 55]. Originally this network was defined in a metabolic way by high degrees of metabolism and oxygen extraction when compared to other regions [55]. Moreover, the DMN shows high degrees of intrinsic functional connectivity especially between the anterior and posterior cingulate cortex [54], high degrees of variability (within and across individuals) [56], high degrees of dynamic functional connectivity to other regions and neural networks in the brain [57], and a reciprocal relationship to other networks including the executive control network (CEN) in lateral prefrontal and parietal cortex (see [58, 59]).

Psychologically, the DMN has been associated with a variety of different functions such as spontaneous internal mentation [54, 60-63]; random thoughts [64], mind wandering [65-68], episodic memory recall [54], and social processing [69]. In addition to these functions, the processing of self-related or personally relevant stimuli or tasks has also been suggested yet another function of the resting state activity in DMN and especially in CMS as it is supported by what I describe as “rest-self overlap”.

D’Argembeau and colleagues [16] conducted an H20 positron emission tomography (PET) investigation involving four conditions: thinking/reflection about one’s own personality traits, thinking/reflection about another person’s personality traits, thinking/reflection on social issues, and a ‘pure rest’ condition where subjects could relax. This design allowed comparisons between self- and non-self-conditions as well as comparisons between self-conditions and the resting state.

As expected, the VMPFC showed significant increases in regional cerebral blood flow (rCBF) during the self-condition when compared to the conditions of reflecting on another person and on social issues. In addition, a comparison of all three task-related conditions (thinking about one's own personality traits, another person's personality traits, and social issues vs. the rest condition) yielded increased rCBF in the DMPFC and temporal cortex, while no differences were observed in the VMPFC. Conversely, the rest condition (when compared to the other three conditions) showed rCBF increases in a large medial fronto-parietal and posterior medial network with no differences in the VMPFC.

A direct comparison of the self and rest conditions indicated strong overlap in the VMPFC for both rest and self-specificity, with similar degrees of rCBF increases in each case. In contrast, thinking about another person and about social issues condition induced rCBF decreases in the same region. Post-scanning subjective measures demonstrated that self-referential thoughts were most abundant in the self-condition while being more diminished in the other three conditions. A correlation of the post-scanning measures of self-referential thinking with the rCBF changes demonstrated a positive relationship in the VMPFC. The higher the rCBF in the VMPFC, the higher the degree of self-referentiality in the thoughts subjects reported.

The strong neural overlap between resting state and regions recruited during self-specificity was further confirmed in a recent study by Whitfield-Gabriel and colleagues [20]. They conducted two experiments with different subject groups. Each group underwent (i) a self-reference task, explicit judgment of trait adjectives as self- or non-self-related, (ii) a control task with a valence judgment of trait adjectives as either positive or negative, and (iii) a pure resting state (of about 10 s). In both experiments there was recruitment of stronger neural activity in anterior and posterior midline regions (VMPFC, DMPFC, PACC, PCC, precuneus) during the self-task when compared to the valence task. Moreover, the rest condition was associated with stronger activity than the valence task in the midline regions, whereas this was not the case for the self-task when compared to rest. The level of neural activity in the midline regions did not differ between the self-task and the resting-state condition.

Whitfield-Gabriel et al. also conducted analyses that allowed them to directly investigate overlapping and dissociating regions between self and rest. Overlapping regions (i.e., conjunction analysis) between self and rest included the PACC, the VMPFC, and the PCC, while dissociating regions included the DMPFC (stronger during self) and the precuneus (stronger during rest). These findings were confirmed in the second experiment where the relevant regions, as yielded in the first experiment, showed the same pattern of neural activity during the three conditions, self, non-self, and rest. Finally, as in the earlier study by d'Argembeau et al. [16], they also found significant correlation between the degree of spontaneously experienced self-referential thoughts (as obtained by scales and verbal reports after each scan) and the degree of activity in VMPFC.

The overlap between rest and self is further support by a recent magneto-encephalographic (MEG) study by Lou et al. [70]. They investigated judgments of self-related words and focused on three main neural regions: the precuneus, the thalamus/pulvinar, and anterior midline cortices (including the VMPFC, DMPFC, and PACC). Using Granger causality analysis (which allows testing for the direction of functional connectivity), they observed that

the magnetic activities in the sites related to the three regions were bi-directionally connected to each other (i.e., showing high degrees of statistical covariance in their signal changes). Most interestingly, the increase in functional connectivity occurred 900 ms before stimulus onset and thus in the resting-state period preceding the stimulus. The pre-stimulus increase in functional connectivity was then further enhanced by the onset of the stimulus in the subsequent time period. Such functional connectivity was strongest in the gamma frequency range between 30 and 45 Hz before and after stimulus onset and it was strongest in the self-condition after stimulus onset. These results lend further support to there being a special relationship between self-specific activity and resting-state activity in subcortical and anterior cortical midline regions.

Based on these findings, we conducted a meta-analysis of imaging studies on self and resting state[18]. The regional activities during the processing of self-specific stimuli and those during the resting state overlapped especially in the PACC extending to the VMPFC, while no such regional overlap with the resting state was observed in the non-self-specific conditions. These results suggest neural overlap between self-specificity and resting-state activity in anterior midline regions like the PACC and the VMPFC. I therefore introduce the concept of “rest-self overlap” that describes the regional convergence between resting state activity and self-related activity in anterior and posterior cortical midline structures (see Figure 3a).

Insert Figure 3a here

In sum, these findings show that neural activity as induced by self-related stimuli recruits exactly those regions like the cortical midline structure that, as part of the DMN, also show high levels of resting state activity. There is thus regional overlap between resting state and self-related activity with respect to the CMS (as core of the DMN). Such regional and activity overlap amounts to what I describe as ‘rest-self overlap’ in specifically CMS.

“Rest-Self containment” – Resting state contains self-specific information

The observation of rest-self overlap raises a central question. The resting state activity in the CMS, as a core part of the DMN, has not only been associated with the processing of self-related stimuli but also with other functions (e.g., random thoughts, autobiographical memory, mind wandering; see below) . How is the processing of self-related stimuli related to these various functions? In their early study, Andreasen et al. [64] observed regional overlap between resting state and an autobiographical memory condition (when compared to a semantic control task) in the VMPFC and precuneus. To explain this finding, the authors suggested that resting state and autobiographical memory “both involve something personal and highly individual” (p.1583) – I would suggest self-related or self-specific.

The same may apply for internal thoughts that also show a certain degree of self-specificity [60-62] and may therefore show overlap with the resting state. An analogous argument may be applied to other functions showing overlap with the CMS/DMN resting state activity (e.g.,

mind wandering, random thoughts, inner mentation, and social processing). Self-related processing would then be the main process underlying these functions.

This hypothesis entails that the resting state itself may contain some self-specific information that is recruited during and assigned to the subsequent processing of internal contents as in mind wandering, episodic memory retrieval, social processing, and random thoughts as well as during processing of external stimuli (e.g., contents) in perception and in the processing of reward, and emotion. The self-specific information contained in the resting state may then provide the very fundament or basis for its assignment to the contents as processed in sensorimotor, cognitive, affective, and social functions, the so-called self-expansion or self-association (See above and below). The assumption of the resting state in CMS/DMN itself containing self-specific information goes beyond mere rest-self overlap leading us to what I describe as “rest-self containment” in the following.

How can we further detail the relationship between resting state and self-related activity? It is possible to suggest (at least) two models for the relationship between resting state activity and self-related activity both signifying what I describe as the “basis model”. The basis model holds that self-specificity is a basic and fundamental function of the brain as manifest in its spontaneous activity prior to and independent of any specific function (sensorimotor, affective, cognitive, social, vegetative) (see Figure 3b)

Insert Figure 3b here

In the first version of this model, spontaneous activity levels and self-related activity levels are independent of each other but overlap in their respective regions, the anterior (and posterior) midline cortices. The same regions are recruited though in different ways by either spontaneous activity or self-related activity. While regionally overlapping, their respective neural activity may remain independent of each other (even if their activities overlap in their respectively recruited regions). Regional dependence is here thus accompanied by activity independence. Due to the regional overlap I designate this model as “rest-self overlap.” The data would be compatible with such rest-self overlap since they show recruitment of the same regions during spontaneous activity and self-related activity (See above).

An alternative version is that not only are the same brain regions recruited by resting state activity and self-related activity but also the same neural activity reflects both resting states and the self. Rather than mere rest-self overlap this model assumes that spontaneous activity contains self-specificity, and this can be described as “rest-self containment”. One way to test for such rest-self containment is whether the resting state is modulated by the preceding self-related stimuli. Wang and colleagues [71] performed first a self-construal priming task (participants had to cancel personal pronouns like I, me etc., to evoke self-reference or they had to cancel pronouns related to other people; independent vs. interdependent priming) followed by a resting state analysis. They observed that the contrast between interdependent versus independent priming was followed by increased regional local synchronization in dorsomedial prefrontal cortex (and left middle frontal cortex) and decreased synchronization in the PCC and precuneus (and left superior temporal gyrus). Additionally, resting state

functional connectivity (rFC) between the VMPFC, DMPFC and PCC after the control priming correlated positively with the behavioural scores for independent (VMPFC-PCC rFC) and interdependent (VMPFC-DMPFC rFC) self construal as trait features of the self (as measured with the self-construal scale with scores for independent and interdependent self-construal): the larger VMPFC-PCC rFC, the higher the score for independent self-construal while larger VMPFC-DMPFC rFC indicated increased interdependent self-construal priming. These data suggest that the brain's spontaneous activity can indeed be modulated by preceding self-related stimuli and, moreover, predicts the form of self-construal, i.e. interdependent and independent.

Rather than using a block design as done by Wang et al. [71], we [19] presented emotional pictures and let subjects assess their degree of self-relatedness in a post scanning session. The analysis focused on the intertrial intervals (ITI) following each picture – we compared those ITI's following high-self related pictures with the ones preceded by low self-related pictures. This yielded significant activity changes in VMPFC, DMPFC, PCC, amygdala, and thalamus during the subsequent ITI. Importantly, the observed signal changes could not be traced back to emotional dimensions like valence, intensity or arousal, but were related to the degree of self-relatedness of the preceding stimuli.

Taken together, these studies suggest the malleability of the brain's spontaneous activity to self-related stimuli, consistent with self-specificity being encoded into the subsequent resting state. If this is indeed the case, one would also expect that resting state activity (e.g., even prior to a stimulus) should predict the degree of self-specificity of the subsequent stimulus (see [72, 73]). We thus need to test whether the resting state itself can predict the degree of self-specificity assigned to either internal (as in mind wandering or random thoughts) or external (like perception, reward, emotions, etc.) stimuli.

“Rest-Self containment” – Activity dependence between resting state and self-related activity

Does the resting state predict the assignment of self-specificity to internal or external stimuli? Recent studies on decision making by Nakao[74, 75] can contribute to this argument. They first compared all fMRI studies on decision making that relied on external criteria (e.g., the amount of money) with those where subjects had to base their decision on internal criteria (e.g., subjective preferences as in moral judgment or occupation choice). The data showed that externally-guided decision making involved the lateral frontal and parietal cortical regions while internally-guided decision making implicated the CMS and especially VMPFC, PACC and PCC/precuneus. Since the latter regions are linked to self processing, one would assume that internally-guided decision making implicates the self as manifest in subjective preference.

Does this imply that the resting state can account for subjective preference in internally-guided decision making? Nakao et al.[74, 75] recorded EEG data during rest and measured

the N200¹ during both internally and externally guided decision making (judgements of subjective preference and word frequency respectively). Although both conditions, e.g., internally- and externally-guided decisions showed similar amplitudes for the N200, only the N200 amplitude during the internally-guided condition was predicted by the power (in delta, theta and beta activity) in the resting state. In contrast, the N200 for the externally-guided condition did not correlate at all with resting state power. These data go beyond mere rest-self overlap and suggest that the resting state must contain some information about self-specificity in order to predict the N200 during internally-guided decisions. The results are compatible with my proposal for rest-self containment (as distinguished from mere rest-self overlap).

Evidence for the direct impact of resting state activity on self-specific processing was recently reported by our group in a combined EEG-MRS study [76]. These authors show that pre-stimulus power (-400-200ms) in specifically the alpha frequency range (8-12Hz) directly predicts whether subjects evaluated a subsequent picture as high- or low in self-specificity: the higher the alpha power -600 to -400ms prior to stimulus onset, the more likely subjects rated the respective stimulus (e.g., the emotional picture) as high self-related (rather than low self-related). Most interestingly, the degree of such pre-stimulus alpha power was related to the level or concentration of glutamate in perigenual anterior cingulate cortex (PACC) (as measured with MRS/magnetoencephalography): the higher the glutamate concentration in PACC, the higher the pre-stimulus alpha power (and the more likely subjects will rate the subsequent stimulus as high self-related). This suggests that the pre-stimulus resting state activity level as indexed by alpha power and Glutamate concentration impacted on the judged degree of self-specificity such that information about the latter must be somehow contained in the former (as for instance in its alpha power).

Further support for rest-self containment comes from the cellular level in subgenual anterior cingulate cortex (see in [17] and [24]). We have found that pre-stimulus local field power in the gamma range can predict whether subjects evaluated the subsequent stimulus as high- or low-self-related (higher pre-stimulus gamma power is associated with high-relatedness judgment). This further indicates that, even on the level of local field potentials, the pre-stimulus resting state already contains some information about self-specificity.

Finally, if the latter argument is correct, we would expect that highly self-specific stimuli like one's own name (or trait adjectives) do not induce any activity change in these regions. Data on this have recently been reported in an intracranial recording study by Lipsman et al.[17]: single neurons in the subgenual anterior cingulate cortex did not change their firing rates when the participant's own name was presented, when compared to the baseline spontaneous firing rates. Interestingly, this distinguished the subgenual cingulate cortical firing rates from the activity in a subcortical region, the nucleus subthalamicus, where the participant's own name induced significantly higher firing rates when compared to the baseline. I postulate that the null effect of own-name stimuli here occurs because spontaneous activity in the brain already contains some information about self-specificity and hence activity does not change when a highly self-specific stimulus is processed.

¹ A stimulus-evoked component associated with attention and stimulus saliency.

In sum, the cellular, regional, and electrophysiological data reported here suggest that the relationship between resting state and self-related activity extends beyond mere neural overlap with regard to both regions and activity as conceptualized in rest-self overlap. The data lend evidence to the assumption that the resting state activity itself contains some self-related information which accounts for the pre-stimulus prediction effects observed on regional, electrophysiological, and cellular levels of activity (as described above). Accordingly, the data speak in favour of activity dependence (rather than activity independence) between resting state and self-related activity which opts for rest-self containment (rather than mere rest-self overlap).

“Rest-Self **containment**” - Encoding of self-specificity in spatiotemporal schemata

How does the brain’s spontaneous activity contain or better encode information about self-specificity? The above described data suggest that self-related information is manifest in the resting state in terms of specific temporal and spatial activity patterns amounting to spatiotemporal schemata. Let us start with the spatial activity pattern first. The brain’s spontaneous activity pattern can be characterized by spatial features like different neural networks that include the DMN, the control executive network (CEN), the salience network, the sensorimotor network, the visual and auditory networks, and the ventral and dorsal attention network (see [80] for a recent review). Importantly, the different networks stand in a particular relationship to each other. For instance, the DMN and CEN stand in a negative relation meaning that they anti-correlate with each other thus showing reciprocal modulation: if one is strong the other is weak and vice versa (see [58, 59] for details).

How is this reciprocal modulation between DMN and CEN linked to self-specificity? Most interestingly, Sui_ [8, 10, 11; see also Figure 3 in Humphreys and Sui 2015, in press] show in their study on perception and self-association (see above) not only recruitment of VMPFC and LpSTS but also the bilateral DLPFC – part of the CEN. However, the DLPFC showed the opposite activity pattern: activity was strongest for stimuli associated with a stranger and weakest for stimuli associated to the self. The VMPFC showed the opposite pattern. This suggests that the reciprocal modulation with negative correlation between VMPFC and DLPFC that has been shown for emotion and cognition [58, 81, 82] applies also to self- and non-self-relatedness.

Based on these findings and on the observed anti-correlation between VMPFC/DMN and DLPFC/CEN in the resting state, I postulate that their reciprocal relationship may encode self-specificity in the brain’s spontaneous activity: the higher activity levels are in the VMPFC/DMN and the lower they are in DLPFC/CEN in the brain’s resting state, the higher the degree of self-specificity assigned to either internal or external stimuli (see Figure 3 in Humphrey and Sui 2015, in press, for some indirect support). While direct support for this assumption is currently lacking, there is some indirect support from major depressive disorder where one can observe abnormally high resting state hyperactivity in VMPFC/DMN and abnormally low resting state activity in DLPFC/CEN which results in abnormally high

self-relatedness to especially internal stimuli, e.g., increased self-focus (see [59] for details as well as [83] for some indirect support in this direction). Finally, disruption of this anti-correlation between VMPFC/DMN and DLPFC/CEN may lead to disruption of self-specificity altogether. That can for instance be observed in psychosis as induced by Psilocybin (a hallucinogenic drug) which serves as model for schizophrenia. The negative correlation between VMPFC/DMN and DLPFC/CEN is here disrupted and transformed into a positive correlation which in turn may lead to the breakdown of the resting state's self-specificity altogether and its assignment to either internal or external stimuli [84, 85]. How about the temporal domain? Spontaneous neural activity shows fluctuations in different frequencies ranging from the ultraslow (0.01 to 0.1Hz) (as measured with fMRI) over slow and fast (1-40Hz) to extremely fast (up to 180Hz) (as measured with EEG). Most importantly, these different frequencies are coupled with each other in the resting state amounting to cross-frequency coupling (see [80] for review).

EEG studies on self-related stimuli provide some support for the involvement of alpha (8-12Hz) (see [24, 76, 86] as described above) for review). fMRI studies, in contrast, lend support to the relevance of rather slow, e.g. infraslow as they are called, frequency fluctuations (0.001 to 0.1Hz) which are especially abundant and strong in CMS (Lee et al., 2014) in self-specificity. However, the exact relationship between infraslow and slow and fast frequency fluctuations including their respective temporal schemata encoding self-related activity remain to be explored. Therefore exact details about its underlying temporal schemata remain open at this point in time (See Figure 3c).

Insert Figure 3c here

In sum, I assume that the spatiotemporal features of the brain's spontaneous activity encode self-specific information. For instance spatial pattern as the relationship between different neural networks like DMN and CEN in the resting state may encode self-specific information. On the temporal side, one candidate is the alpha frequency band including its possible relationship to infraslow frequency fluctuations. One may consequently tentatively hypothesize that self-related information may be encoded into the brain's spontaneous activity in terms of spatiotemporal schemata whose exact structure or pattern needs to be detailed in the future though.

Conclusion

I here focused on the relationship between self-specificity and other functions in the brain. I have presented evidence indicating that there is significant regional overlap and modulation of perception, reward, and emotions by self-specificity, especially in the midline cortices. To account for these results I propose a basis model of self-specificity where self-specificity is conceived as a intrinsically linked to and encoded into the brain's spontaneous activity, e.g., its input-output relationships and spatiotemporal schemata. This is empirically supported by

various findings showing not only rest-self overlap but also predictions of self-specificity by resting state activity entailing what I describe as rest-self containment.

The degree of the spontaneous activity's self-specificity may in turn predispose the degree to which self-specificity can be assigned to external or internal stimuli, i.e., the degree of self-association that can be observed [8-11]. I postulate that the spontaneous activity's degree of self-specificity predicts the degree of the subsequently possible degree of self-expansion to internal or external stimuli which in turn may modulate subsequent behaviour. Moreover, though tentatively, I postulate that the spontaneous activity's degree of self-specificity and self-expansion may provide the basis for the self not only as an object in cognition but also as a subject in experience, e.g., consciousness. These are rather tentative if not speculative assumption at this point in time though.

The here suggested basis model of self-specificity provides a novel approach to the self that is no longer considered as higher-order features of cognitive function but a basis function of the brain's spontaneous activity. Based on the various suggested predictions, the basis model may be tested experimentally in the future. I postulate that the results will not only reveal the neural mechanisms of self-specificity but, at the same time, will provide novel insights into the spatiotemporal features of the brain's spontaneous activity in general including its predisposition of other mental features like consciousness [23, 24].

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Captions to Figures

Figure 1 Different concepts of self

The Figure demonstrates the different concepts and levels surrounding the concept of self. The middle describes the kind of processes like self-related or self-referential processing. These processes are further characterized on the left while their outcome or effects are described on the very right (self-specificity and self-reference). The self as object is associated with self-referential processing and self-reference. The exact origin of the self as subject remains unclear. Many authors in both philosophy and neuroscience consider the self as subject a higher-order meta-representational function (and liken it to a cognitive self as is at the top). In contrast, as it turns out, that the self as subject may rather need to be placed at the very bottom as based on self-related processing and self-specificity which though remains open at this point (though it is supported by the basis model as I introduce it in this paper).

Figure 1 Different concepts of self

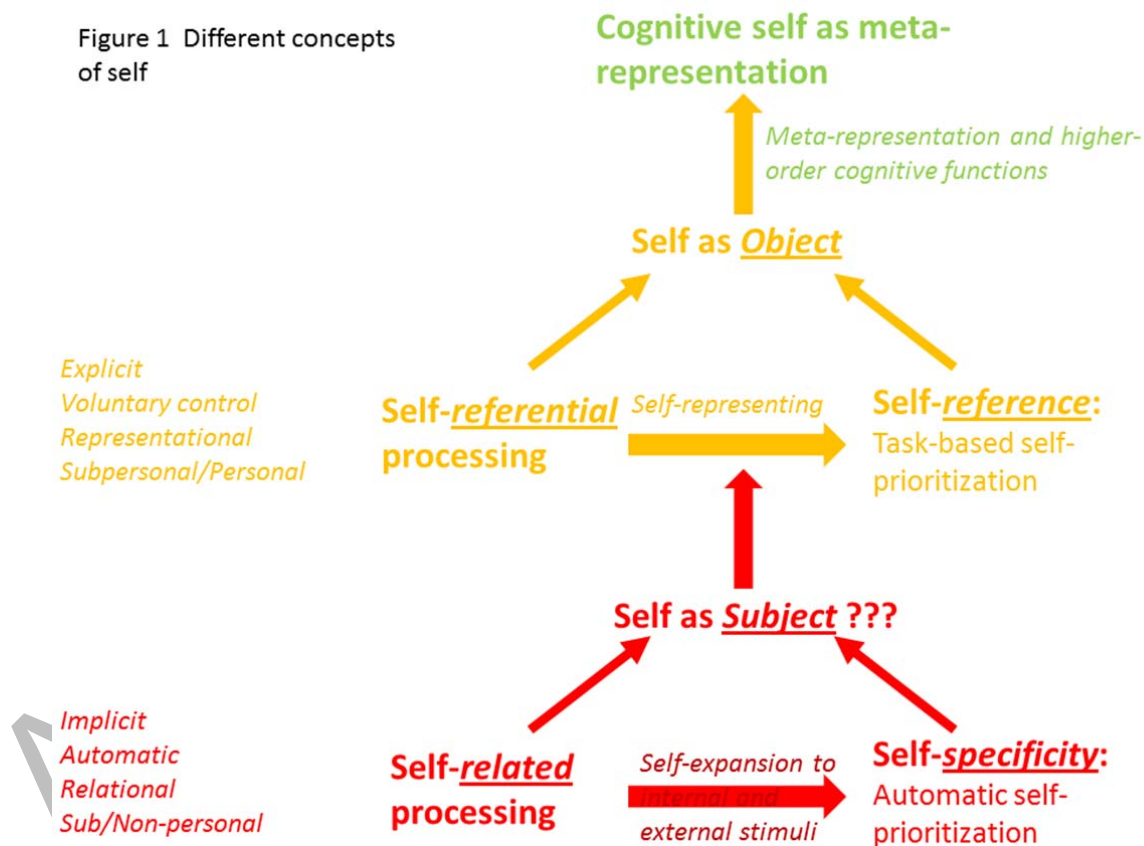


Figure 2 Self and different functions

Figure 2a

The figure is about the relation between self and perception and demonstrates how the internally generated self-related activity in the ventromedial prefrontal activity modulates subsequent externally based stimulus-induced activity as related to the left posterior superior temporal sulcus [8, 10, 11]. This can be understood as an expansion of internally-generated self-related activity in ventromedial prefrontal cortex to externally-induced stimulus-related activity in let posterior superior temporal sulcus.

Figure 2 Self and different functions
Figure 2a Self-expansion in perception

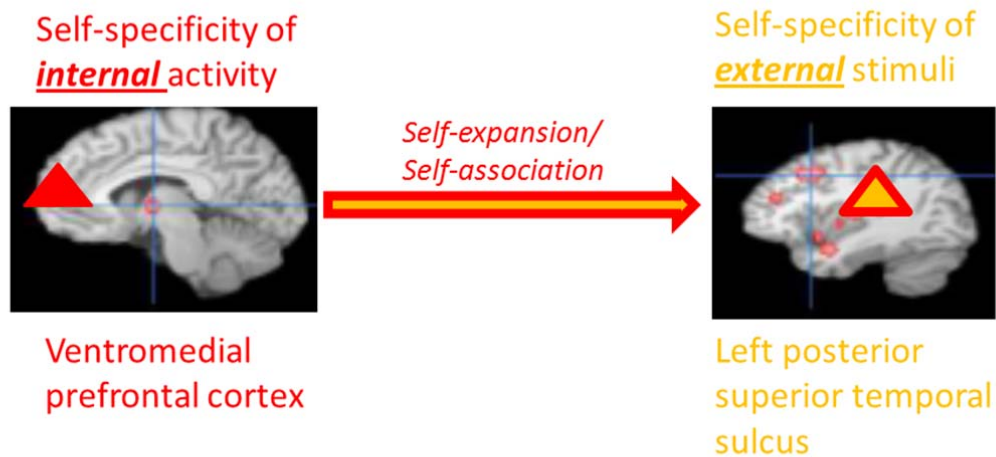


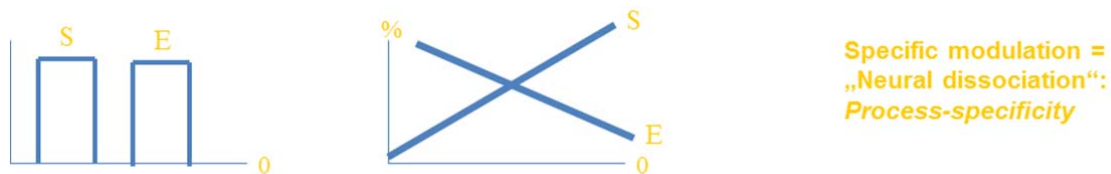
Figure 2b

The figure concerns the relation between self and emotions and shows the differential parametric relationships between self-relatedness and emotional arousal/valence (as subjectively assigned to the stimuli by the subjects) within the same regions.

DMPC = dorsomedial prefrontal cortex, VS/NACC = ventral striatum/nucleus accumbens, VLPFC = ventrolateral prefrontal cortex

Figure 2b Relationship between self-specificity and emotions in different regions

DMPFC and VS/NACC: Process-specificity for self-specificity as distinguished from emotional valence



Right VLPFC and amygdala and tectum: Process-nonspecificity for self-specificity and emotional valence

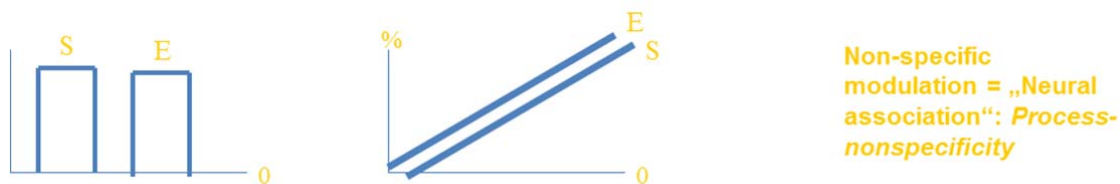
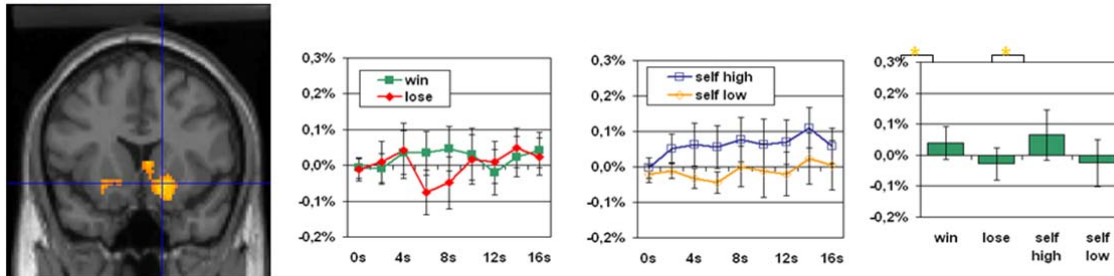


Figure 2c

The figure shows neural activity related to reward and self (high vs low self-relatedness) with regard to the same stimuli in the same regions as based on reward. This shows clear neuronal differentiation between low and high self-relatedness in the typical reward regions including both subcortical and cortical regions.

Figure 2c Overlap of self-related activity with reward-related activity in typical reward regions

Right Nucleus Accumbens



Left Nucleus Accumbens

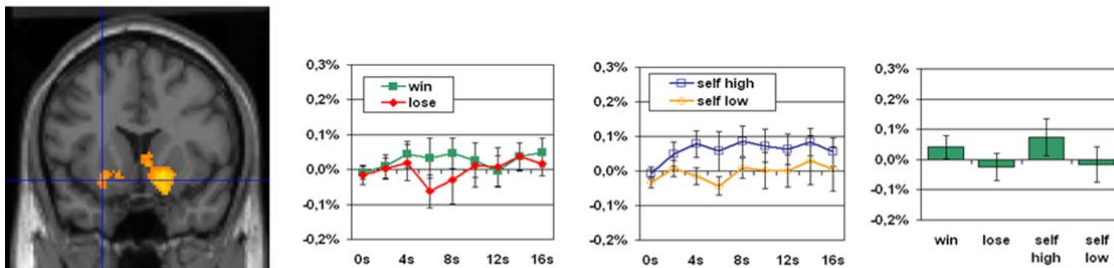
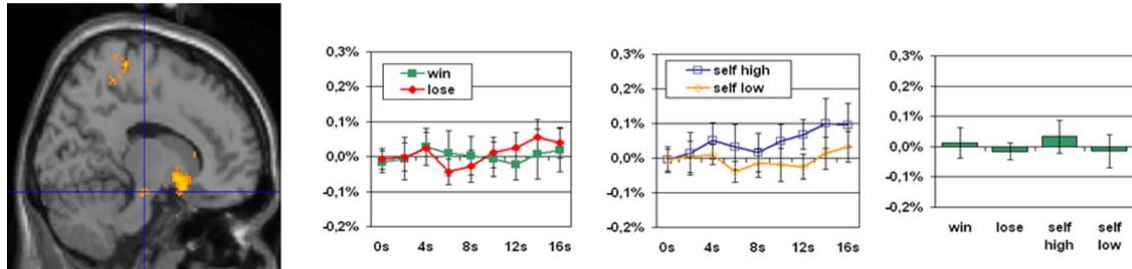


Figure 2c Overlap of self-related activity with reward-related activity in typical reward regions

Right Ventral Tegmental Area



Left ventromedial prefrontal cortex

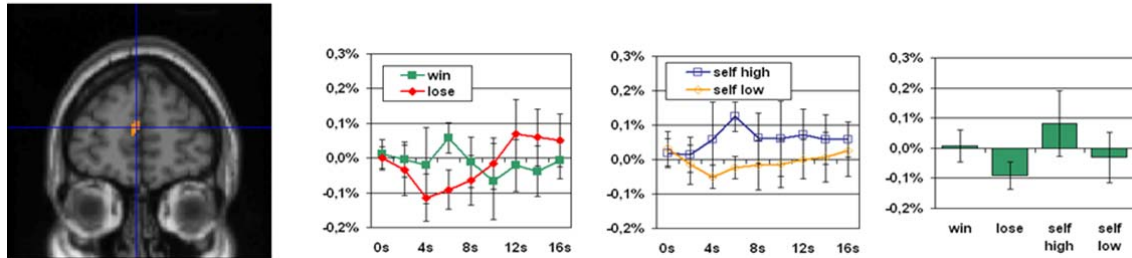


Figure 3 Basis model of self-specificity

Figure 3a

The figure shows a regional overlap of imaging results from spontaneous activity in default-mode network (DMN) and self-related activity.

Figure 3 Basis model of self-specificity

Figure 3a Neural overlap between resting state activity (DMN) and self-related activity

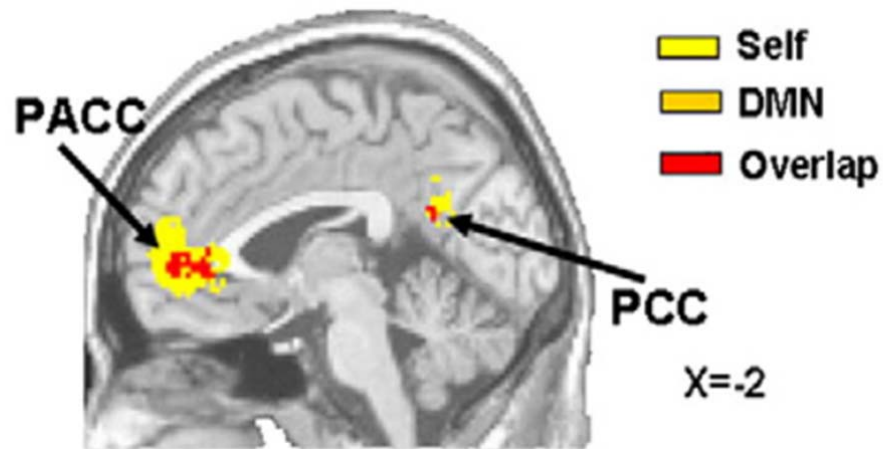


Figure 3b

The figure shows the basis model where self-specificity is considered a basis function of the brain's spontaneous activity (middle part). This in turn impacts all subsequent functions that are thus driven by the degree of the spontaneous activity's degree of self-specificity (upper part). Relationship between resting state and self-specificity can indicate either rest-self overlap (lower part left) (where there are two distinct kinds of neural activities in one and the same regions/networks) or rest-self-containment (lower part right) (where one and the same neural activity signifies both spontaneous activity and self-related activity).

Figure 3b Basis model of self-specificity

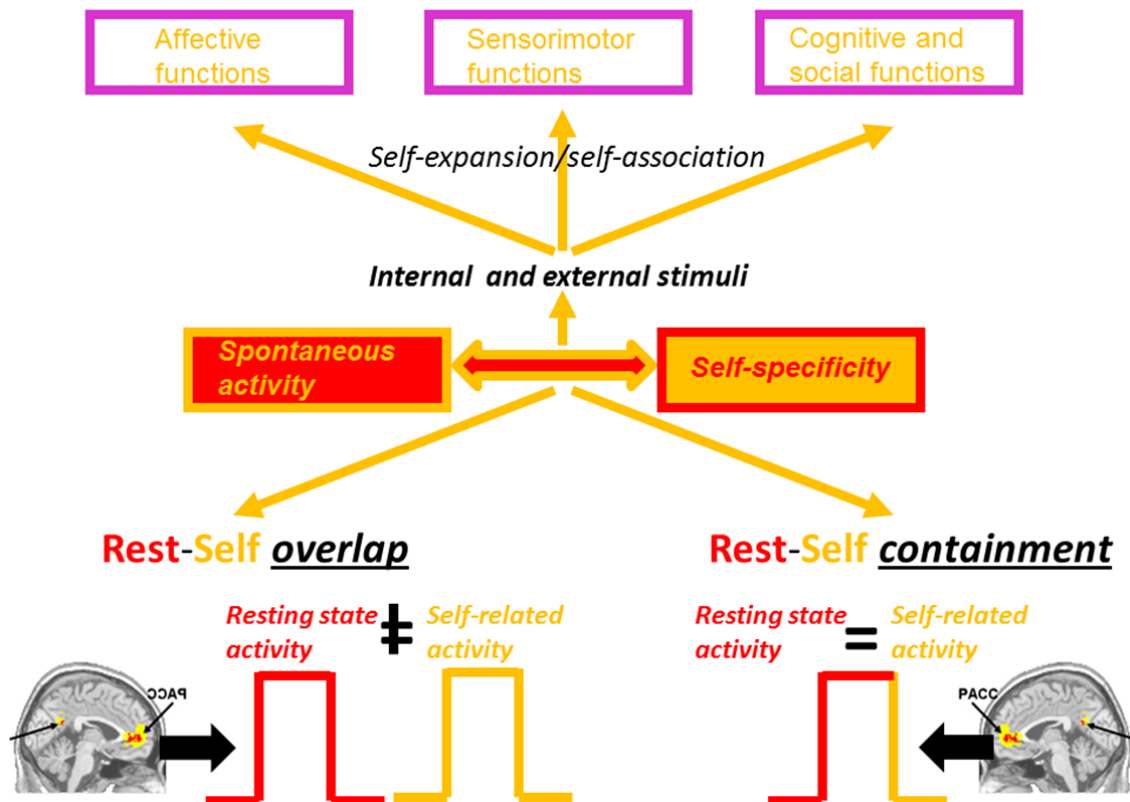
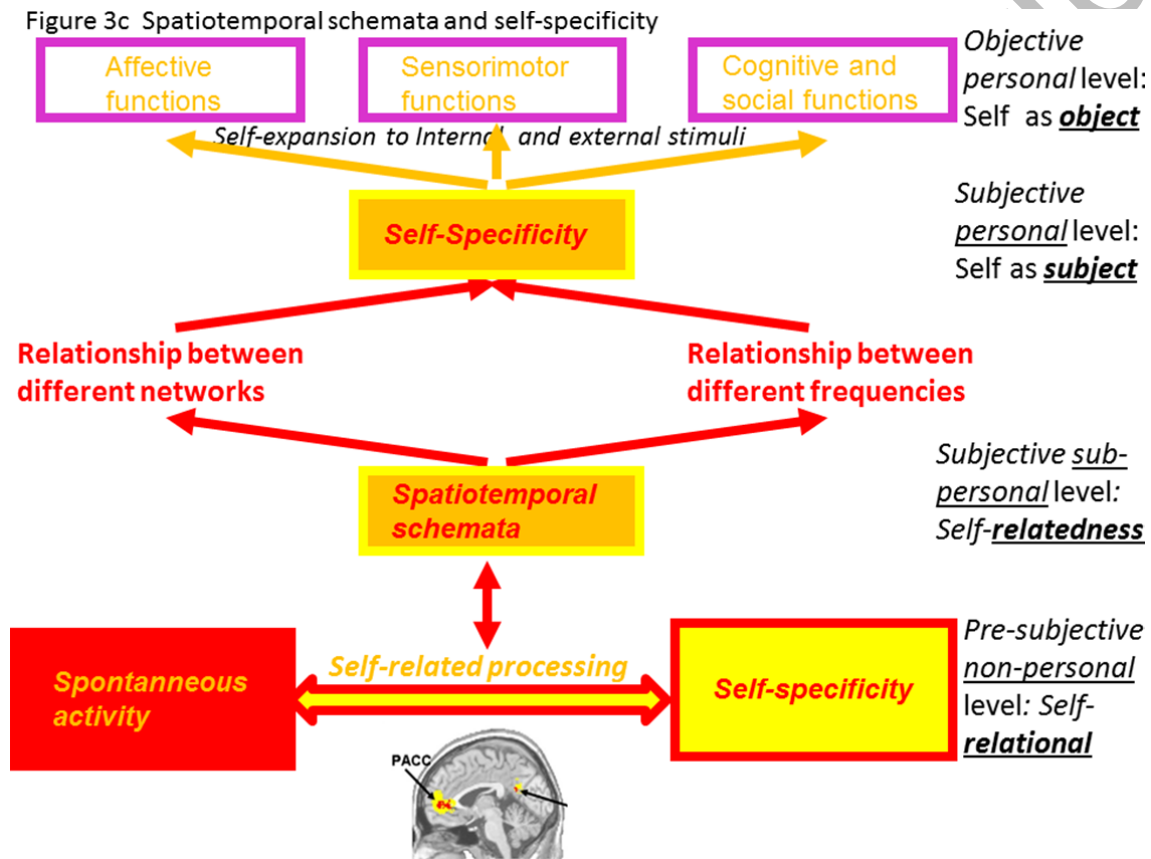


Figure 3c

The figure illustrates the step from the brain's spontaneous activity to self-specificity with intermediate steps consisting in input-output relationships and spatiotemporal schemata. Self-specificity, in turn, impacts and modulates the processing of all subsequent internal and external stimuli and the respective functions amounting what Sui (Jie Sui et al., 2013b; Jie Sui et al., 2012a; Jie Sui et al., 2013a; Jie Sui et al., 2013c) describe as self-expansion (or self-association).



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