

The trans-species concept of self and the subcortical–cortical midline system

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The nature of the self has been one of the central problems in philosophy and most recently in neuroscience. Here, we suggest that animals and humans share a ‘core self’ represented in homologous underlying neural networks. We argue that the core self might be constituted by an integrative neuronal mechanism that enables self-related processing (SRP). Because mammalian organisms are capable of relating bodily states, intrinsic brain states (e.g. basic attentional, emotional and motivational systems) and environmental stimuli to various life-supporting goal-orientations, SRP appears to be a core ability preserved across numerous species. Recent data suggest that SRP is operating via a central integrative neural system made up of subcortical–cortical midline structures (SCMSs), that are homologous across mammalian species.

Self in animals and the subcortical–cortical midline system

The topic of self – what it is and among whom it is endowed – has been a conceptual dilemma since the early Greeks. Formerly considered unique to humans, the self – much like culture, abstract reasoning, language and altruism – appears to exist in some other species. Neuroscience can now pursue what ethology has surmised [1], which is the idea that all mammals share foundational brain substrates for a core self that allows them to be active creatures in the world as opposed to simply passive recipients of information.

Recognition of homologous mammalian neural substrates that give rise to similar core-self-related, primary-process emotions and motivations as well as certain cognitive abilities reduces difficulties that have plagued definitions of self across species, without denying or contradicting discussions in humanistic disciplines that postulate diverse idiographic selves [2,3]. The data now dictate that the onus in future research should shift from the assumption of human uniqueness to one of sameness in terms of the self because on basic emotional, cognitive and neural levels there exists a significant degree of homology and similarity across mammalian species [4]. This assertion is based on emerging evidence that the core self, which relates an organism’s interoceptive stimuli to its goal orientations (and the world’s exteroceptive stimuli), appears to be a basic neural function shared across species.

Subcortical bodily representations and drives, which are affective and emotional [4,5], network with cognitive structures in medial frontal regions [6]. This system provides the basis for the postulated self-related processing (SRP) as the way intrinsic emotional brain states and intero- and extero-ceptive stimuli coordinate the needs and desires of each mammalian organism with its particular and unique goal orientations [7]. We propose that this occurs through the existence of a specific neural network that is homologous across species and allows organisms to integrate diverse bodily and brain states with environmental stimuli (Box 1). Specifically, our hypothesis postulates a coherently operating subcortical–cortical midline structures (SCMSs), where several neural systems are concentrated and control basic emotions and the body’s internal milieu, for example, interoceptive processing (Figure 1). These networks provide a primal form of self-representation across mammalian species [4–7]. The existence of such a preserved system suggests translational research strategies for clarifying both cognitive and affective function in humans, including psychiatric disorders such as depression.

Trans-species concept of SRP: a notion of the core self

SRP describes the coordination of various basic emotional processes and bodily interoceptive stimuli (e.g. emotional, motivational, homeostatic, bodily need states) with exteroceptive stimuli (e.g. sensory stimuli) in relation to the organism’s goal-directed activities [7–10]. This relation is strongly and affectively coloured because it allows external events to be linked to the organism’s basic (unconditional) values – felt emotional and motivational urges [5]. For example, neuroimaging studies in humans have demonstrated that precisely those words and pictures that are considered to be highly related to the respective individual’s self are considered to be more emotional than those that showed rather low degrees of self-relatedness [6,7]. The affective ‘colouring’ of the world might yield phenomenal experience of survival-relevant objects and events experienced as ‘mine’ or as ‘belonging to me’ (i.e. my picture rather than your picture, reflecting what has been called ‘belongingness’ or ‘mineness’) [11]. This implies that phenomenological experience of the core self is primary in affective processing rather than secondary.

We envision that core self emerged early in evolution, permitting animals to flexibly use rough-and-ready intrinsic

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Box 1. Functional brain organization and self-related processing

Subcortical midline networks regulate core attentional, homeostatic, emotional and motivational functions of the body (Figure 1). Although both the microscopic neurochemical details and the macroscopic psychological functions are well known, subcortical regulatory functions and mechanisms that mediate between these levels remain somewhat unclear. This gulf between behavioural and cognitive neuroscience has been partly bridged by affective neuroscience through clarification of animal emotions by focussing on the intrinsic instinctual tendencies of animals, readily evoked with localized electrical and chemical brain stimulation. Many basic emotional systems have been identified, and it is clear that various basic affective states are intimately linked to these instinctual arousals [5]. Such brain activations routinely yield a variety of 'rewarding' and 'punishing' effects that can be parsed neuropsychologically.

These self-centred affective states could be conceptualized in two general ways: they might reflect 'read-outs' by higher cognitive mechanisms, yielding propositional attitudes by interacting with neocortical functions. Alternatively, affects might reflect intrinsic properties of the medially situated subcortical emotional networks. The latter position has more empirical support because of three robust lines of evidence: (i) Neocortical brain stimulation, with the exception of orbitofrontal and medial frontal cortex, does not evoke strong affective feelings compared with those obtained via subcortical brain stimulation. (ii) Damage to subcortical substrates, especially where emotional systems converge in the PAG, within medial and intralaminar nuclei of the thalamus (along the trajectory of the mesolimbic dopamine seeking systems) can dramatically compromise consciousness and organismic competence (i.e. ability to take care of one's own needs). Damage to higher cortical regions does not influence an organism in this manner [20]. (iii) Neodecortication in infancy leaves essentially all the instinctual urges of animals intact [5], and children born with such brain damage appear to retain phenomenal consciousness both in sensory perceptual and emotional-affective realms [17,46]. We suggest that a coherent form of self-representation arises directly from a complex integrative network made up from attentional, emotional and motivational abilities that are formed in the subcortical-cortical medial brain regions (Figure 1). These regions process the complexities of the internal world and relate them progressively to the external world, first within medial frontal regions and subsequently in dorsolateral prefrontal cortex and associated working-memory function. Our claim here is that SRP, as the linkage between intrinsic brain systems and the extrinsic world, allows brain subcortical-cortical networks to organize a psychologically, emotionally significant and meaningful world within the rest of the brain.

living skills (e.g. primary-process emotional urges) to begin fending for themselves in the quest for reproduction and survival. In this view several higher order neocortical cognitive functions of the brain are epigenetically created by experiences, without preordained evolutionary modularization of higher brain functions [12], including the widespread mirror-neuron systems of the neocortex. Because of space limitations, we only note one striking prototypic example: visual functions of the neocortex are not genetically preordained but epigenetically molded by genetically ordained subcortical visual inputs [13]. This might reflect a general principle for most neocortical functions, including language acquisition.

Although the infrastructure of the subcortical attentional, emotional and motivational systems is complex [5] (Figure 1), the lower aspects of the core self are involved with urges such as breathing, defecation and micturition; hunger-, thirst-, thermoregulatory- and hormonally driven

mandates; sleep-waking and attentional rhythms [14], and the dictates of at least seven key emotional networks [15]. We suggest these diverse functions can only function coherently through a shared underlying neuronal matrix of organismic coherence. We postulate a viscerosomatic neuronal groundwork for these various, initially objectless, body-brain states, promoting SRP in higher medial frontal structures and leading to environmental-ecological-cultural mouldings of diverse epigenetic selves and mirror-neuron systems in higher brain regions.

Conceptualized in this way, SRP supports the following processes: (i) development of sensorimotor coordination by relating both sensory and motor functions to actual goal orientations; (ii) processes of relating different kinds of stimuli to each other such as intero- and exteroceptive stimuli; (iii) intero-exteroceptive linking in relation to actual goal orientation and (iv) a strong affective colouring of such stimulus linkage, thereby enabling phenomenal experience of one's initially objectless internal states in relation to the world. In this process emotional arousals correspond to the organism's main urges that are developmentally related to objects and events in the world via learning and numerous other cognitive processes. Higher cognitive functions and the respective cortical mechanisms do then serve to cognitively differentiate the organism's main urges and its respective objects and events from the world. However, across mammalian species, one can easily observe the role of environmentally mediated effects in brain growth and development.

SRP and the SCMS

Human-brain imaging indicates that SRP is elaborated largely in the SCMS and other limbic cortices, such as the insula [6,7]. Convergent evidence indicates that subcortical and anterior cortical parts of the SCMS help process the four features of SRP described above. The periaqueductal grey (PAG) and its adjacent tectal maps [in the following subsumed under PAG and tectum (TEC)] show the highest convergence of sensory and motor processes with emotional networks within both animal and human brains [16–18], which make them best suited for relating bodily and environmental stimuli. A basic process to consider is reward seeking – the valuing of stimuli according to their significance to the organism – which has been neuroanatomically linked to widespread dopaminergic and opioid rich structures, such as the ventral tegmental area (VTA) and projection into ventral striatum (VS) and nucleus accumbens (NACC) in a pattern that is stable across species [5,8]. Interestingly, a recent study demonstrated that self-relatedness also induces neural activity in the same regions that are recruited by various rewards. This indicates that both reward processes and self-relatedness might share a similar evaluative process [19]. Subcortical reward-seeking regions converge with other subcortical structures (Figure 1), such as the hypothalamus, amygdala and dorsomedial thalamus (DMT), as well as medial prefrontal cortices (mPFC) in both animals and humans [5,7,17].

Abundant evidence from non-human species highlights the importance of subcortical networks for mediating affective quality and intensity for various rewards and punishments. Various types of reward and punishment

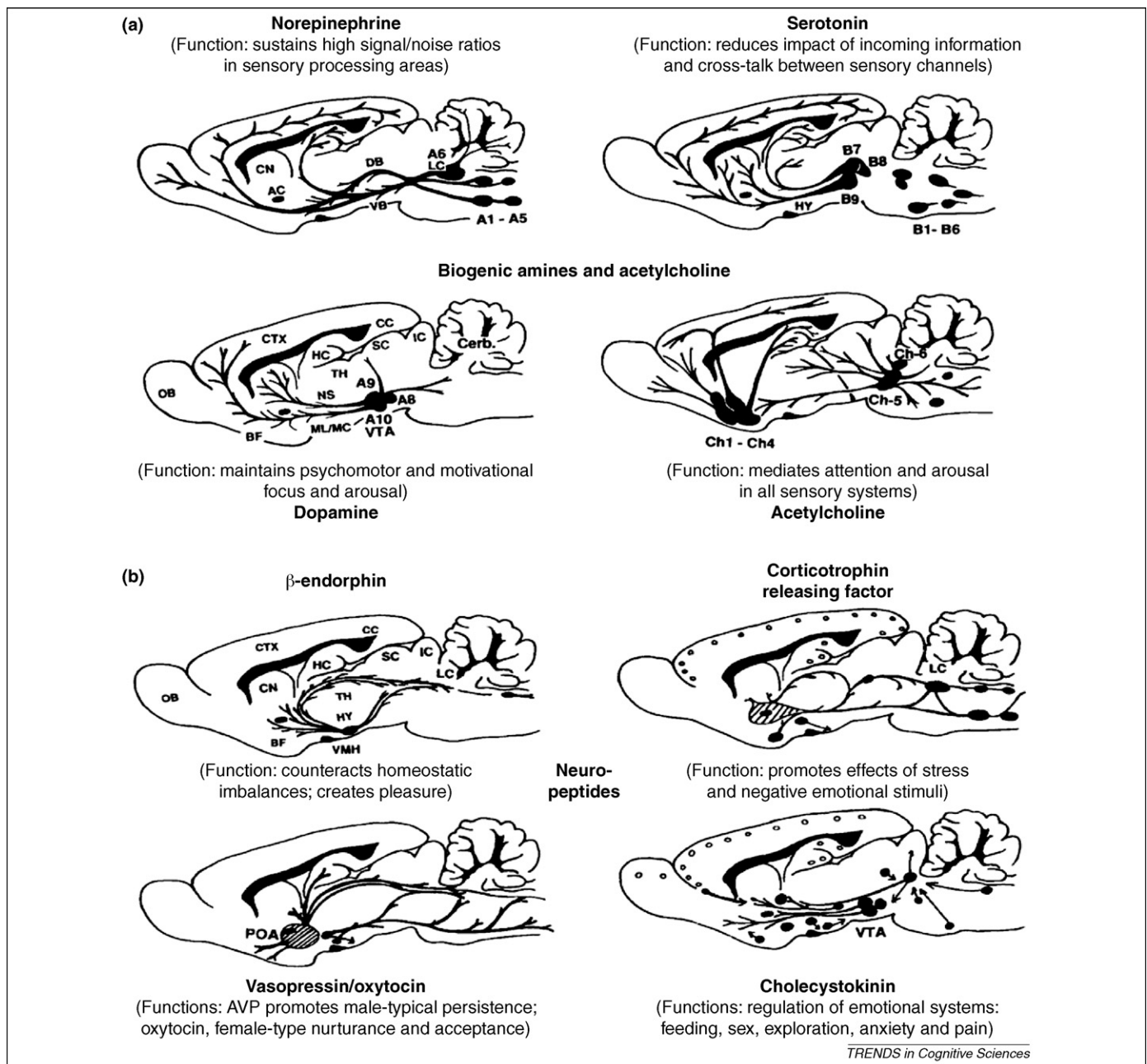


Figure 1. Parasagittal depictions of the dispersion of biogenic amine and acetylcholine systems (a) and several major neuropeptide systems (b) in the rat brain. These types of extensive, highly interactive networks that control global states by widespread medial brain effect characterize SCMS circuitry. It is not yet possible to specify precisely which are of primary and which are of secondary importance in the elaboration of a core self. There are reasons to believe that core glutamatergic and GABAergic systems here (not depicted) could serve a foundational role. These plates are meant only to convey the richness of SCMS territory that allows for integration of basic (genetically ingrained) attentional, emotional and motivational processes. Abbreviations: AC, anterior commissure; B, basal forebrain; CC, corpus callosum; CN, caudate nucleus; CTX, neocortex; DB, dorsal noradrenergic bundle; HC, hippocampus; HY, hypothalamus; IC, inferior colliculus; LC, locus coeruleus; ML/MC, mesolimbic and mesocortical dopamine pathways; NS, nigrostriatal pathway; OB, olfactory bulb; POA, preoptic area; SC, superior colliculus; TH, thalamus; VB, ventral noradrenergic bundle; VMH, ventromedial hypothalamus; VTA, ventral tegmental area. 'A' designations indicate major norepinephrine and dopamine cell groups; 'B' designations indicate major serotonin/raphe cell groups and 'Ch' designations indicate major cholinergic cell groups. In (b) small circles in the neocortex indicate the presence of local interneurons for CRF and cholecystokinin systems. Reproduced, with permission, from Ref. [5].

can be evoked with electrical and chemical subcortical brain stimulations (Box 1 and Box 2). Lesions there dramatically impair consciousness [20], especially with global PAG damage [21]. Lateral hypothalamic lesions impair goal directed activities, highlighting the importance of this narrow corridor that innervates medial frontal structures [22] (Figure 1).

Many human-brain-imaging studies have implicated medial forebrain structures in SRP (see [7] for a review).

Recent work has revealed robust correlations between affective valence and self-relatedness in medial subcortical regions, including PAG/TEC, DMT, hypothalamus and amygdala under passive viewing conditions. These effects are not seen in subjects making evaluative judgments in the scanner [23]. Feelings of self-relatedness to erotic pictures also correspond to neural activity in the hypothalamus, anterior cingulate cortex (ACC) and mPFC [24], and such patterns also are evident during other reward

Box 2. Self-relatedness and the default-mode network

The default-mode network was originally introduced to describe brain regions in both humans and chimpanzees who showed high neuronal activity and spontaneous fluctuations when no immediate task was present [25,26,40–42]. Based on previous studies [43,47], we assume that processing of high degrees of self-relatedness corresponds to high-resting-state neuronal activity. The resting state is characterized by a predominance of interoceptive and affective processing with exteroceptive input remaining almost absent so that only the former, but not the latter, is related to current goal-orientation in self-related processing during the resting state. Because it originates in the body and medial subcortical aspects of the brain, interoceptive input shows a high degree of self-relatedness, thus inducing high levels of baseline neuronal activity. Exteroceptive stimuli, by contrast, might vary in their degree of self-relatedness ranging from higher to lower degrees, as modulated by different levels of resting state arousal.

Results from imaging studies during emotional self-relatedness exhibit this pattern with varying degrees of deactivation or negative blood-oxygen-level-dependent (BOLD) responses in both subcortical midline regions (such as the ventral striatum) and cortical midline regions (such as the ventromedial prefrontal cortex) [19,24] (Figure 1). Even though subcortical midline regions, including the ventral striatum, show activation during tasks that involve reward, they seem also to be modulated by different degrees of deactivation, for example, negative BOLD responses, during conditions of self-relatedness with no external rewards [19]. The observed predominance of deactivation in subcortical and cortical midline regions in modulating different degrees of exteroceptive-based self-relatedness is highly compatible with our assumption of differential effects of self-related processing in resting and activation states.

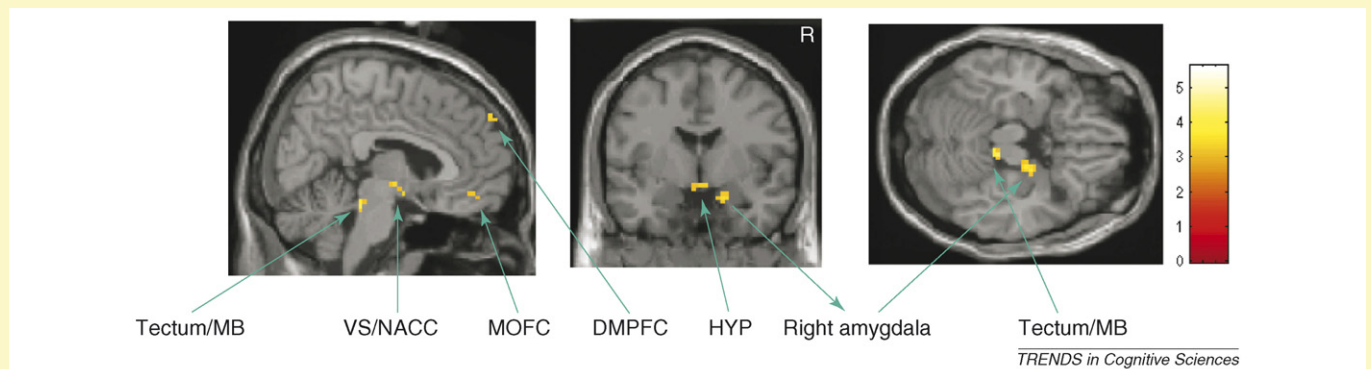


Figure 1. Recruitment of subcortical and cortical midline regions in human subjects. Shown are results from a study in which perception of high self-related stimuli was compared with perception of low self-related stimuli. The figure shows the signal intensities when one categorically compares perception of pictures rated as high self-related with those rated as low self-related. The sagittal view depicts the right hemisphere; the threshold of significance is set to $p < 0.001$ (uncorr), $k > 10$. Abbreviations: DMPFC, dorsomedial prefrontal cortex; DMT, dorsomedial thalamus; HYP, hypothalamus; MB, midbrain; MOFC, medial orbitofrontal cortex; R, right; VS/NACC, ventral striatum/nucleus accumbens.

tasks [19]. Together, these findings highlight SRP modulation of neural activity throughout SCMS.

Empirical implications

The fact that a core self exists and is integrated through subcortical mechanisms leads to the conclusion that similar psychological SRP exists throughout the mammalian class. In fact much of what we know about transdiagonal cephalic attentional, emotional and motivational systems (Box 1) has come via animal research [14,15], as well as functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) studies [25,26]. The implication is, therefore, that the self is generally preserved through species rather than being unique to humans. In the cases in which there is a phylogenetic break in terms of SRP, such as mirror-recognition, one can readily see the role of non-subcortical structures [27,28]. But even here it is noted that humans are not unique in their ability: chimpanzees and orang-utans have mirror-recognition capabilities, demonstrating that, in terms of SRP, one need not have a substantially overdeveloped front-parietal region to have an extended self. We can, therefore, apply these findings to the core self and subcortical structures – a subcortical homologue might be enough to sustain the core self. In other words aspects of the self appear even without an expansive cortical network. Reworking designs to test for higher order abilities should be done with the assumption of similarity in selves

rather than differences, and when appropriately adjusted for sensory modality, the results should reveal significant SRP in non-human animals [29].

For example, testing could be extended to evaluation of self-relatedness with favoured rewards [19], especially in systems in which underlying neurochemistries such as dopamine and opioids are well characterized [8,30,31]. When combined with finer grained electrophysiology and neurochemistry approaches, investigators could further illuminate trans-species mechanistic models of the self. Ultimately, one can easily argue the benefits of a core self, and, therefore, one would assume that a core self might be an essential feature of animals with a certain kind of subcortical networking.

Conceptual implications

Our conception of a trans-species core self – a sensorimotor, valiative, intero-exteroceptive and subjective-affective experience integrator – provides a basic SRP tool for organisms to reach out to other organisms and objects. This provides a basic scaffolding for engendering epigenetic emergence of higher social functions such as empathy, theory of mind and the developmental programming of mirror neurons in the cortex (for a more in-depth analysis, see [29]). Indeed, there is strong evidence that both empathy and self-relatedness recruit SCMS in humans [32,33]. Both empathy and SRP can be regarded as different aspects of a similar process, the process of selectively

relating and adapting to other organisms and the environment while at the same time maintaining organismic integrity and distinctiveness. Because rapid development of adaptive relatedness to the social environment is evolutionarily crucial, one also might characterize the core self as the 'relational self'. We assume that such a relational self is shared across species, consisting of strong affective colouring and manifested in the phenomenal experience of mineness and belongingness.

The core self as a relational self must be distinguished from more idiographic forms of self – the 'narrative,' 'autobiographical,' 'self-aware,' 'self-conscious' and 'extended' selves, etc. – that are more cognitive, explicit, reflective and representational [7,34–36]. Going beyond mere phenomenal experience of belongingness and mineness, these higher forms might allow certain organisms to reflect upon their own selves and their relatedness to the rest of the world. We assume these higher forms of self to be more species specific, arising rather late developmentally and requiring higher cognitive brain regions such as lateral prefrontal and parietal association areas. These networks probably are influenced by SCMS networks that allow for adaptations for unique environments. Specifically, these interacting levels form the basis for complex social interactions between and within individuals and, as such, might represent uniqueness in certain primates.

We consider the SCMS to be an anatomical–functional unit for several reasons. First, subcortical and cortical

midline regions are closely linked to each other anatomically with fewer connections to other regions [22,37]. Functionally, subcortical and cortical midline regions are coactivated during both emotional and self-related processing [5–7,31], whereas more lateral regions show converse patterns of neural activity [38,39]. Both subcortical and cortical midline regions show high neural activity in the resting state and are therefore considered part of the default-mode network. This activity has been demonstrated to be present in both humans [40–42] and non-human primates [25,26] (Box 2). It is, thus, reasonable to postulate that subcortical and cortical midline regions share an earlier common ancestor when compared to lateral cortical regions because these lateral regions are both functionally and anatomically unique in certain primates and appear to be more phylogenetically scaled [43].

There is, consequently, strong homology in subcortical midline regions, such as the PAG, that are remarkably similar in terms of anatomy, histology and connectivity in all animals that have been studied closely [14]. Finally, mental disorders such as depression show specific changes in the subcortical–cortical midline system rather than in other regions (see Box 3 for discussion).

Conclusion

The self, long considered uniquely human and dependent on the most encephalized brain regions, might be phylogenetically older in brain evolution than previously considered. The core self is apparently shared between humans and other mammals and consistently scientists have discovered more similarities than differences in terms of SRP between humans and other animals. We believe the mechanisms of SRP to be the crucial mechanism in adapting to unique ecological and cultural contexts. Certain aspects of higher order domains of the self could be unique to primates and even humans. Although these evolved increases in self-awareness might expand cognitive outcomes, they might be relatively minor in terms of understanding the core nature of selfhood among mammalian species upon which these expansions are built. Future research might be better suited with the null hypothesis being one of sameness of the core self across mammalian species. The uniqueness of idiographic selves across individuals and species might reflect secondary processes that are built upon SCMS networks that give rise to most aspects of the core self [44,45]. It is hoped that future studies will examine the self in these terms, both behaviourally and neurologically.

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Box 3. Self concepts and translational models in neuropsychiatric disorders

Many neuropsychiatric disorders are accompanied by changes in how the brain envisions itself. For instance, patients with depression show increased self-focusing, often with profound withdrawal from the environment and others, leading to persistent negative ruminations, anhedonia and even suicidality [48]. An abnormal balance between internal self-perception and perception of the external world has been related to abnormal SRP [48]. The exact psychological cause for this shift in psychic equilibrium remains unclear, though imbalances in several emotional paths seem likely. Animal models as well as human experiences highlight a prominent role for social loss that can lead to chronic psychic pain and despair. This is due, in part, to reduced opioid activity in the brain; correspondingly, therapy with opioids can rapidly reduce psychic pain [5]. Also, the urge to engage with the environment (which is characterized as a persistent disposition to interact with and relate to the environment) arises from elevated dopamine and SCMS activity [8,49]. Changes in seeking urges, mediated by VTA, VS/NACC, medial orbitofrontal cortex (MOFC), ACC and mPFC, also leads to altered reactions after social defeat in susceptible animals who demonstrate abnormally high neural activity in the VTA [50], which is inconsistent with a simple dopamine reward hypothesis but consistent with a dopamine-seeking hypothesis because such animals should exhibit heightened seeking of safety [9]. This would be in line with findings in depressed humans showing abnormalities in the above mentioned regions, including dysregulation in the ACC and mPFC with abnormal connectivity to subcortical regions including the VS/NAC, hypothalamus and amygdala [51]. Other psychiatric disorders can be analyzed in this way. For instance, anatomical or functional disconnections between lower affective and higher cognitive SRP activities might be evident in posttraumatic stress disorders (PTSD). This might explain why euthymic people show positive correlations between their levels of emotional awareness and arousal within ACC/mPFC regions, whereas PTSD patients exhibit negative correlations in the same brain regions [52].

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