The trans-species core SELF: The emergence of active cultural and neuro-ecological agents through self-related processing within subcortical-cortical midline networks ☆

Jaak Panksepp [a,*], Georg Northoff [b,1]

[a] Baily Endowed Chair of Animal Well-Being Science, Department of VCAPP, College of Veterinary Medicine, Washington State University, P.O. Box 646520, Pullman, WA 99164-6520, USA
[b] Department of Psychiatry, University of Magdeburg, Germany

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ABSTRACT

The nature of "the self" has been one of the central problems in philosophy and more recently in neuroscience. This raises various questions: (i) Can we attribute a self to animals? (ii) Do animals and humans share certain aspects of their core selves, yielding a trans-species concept of self? (iii) What are the neural processes that underlie a possible trans-species concept of self? (iv) What are the developmental aspects and do they result in various levels of self-representation? Drawing on recent literature from both human and animal research, we suggest a trans-species concept of self that is based upon what has been called a "core-self" which can be described by self-related processing (SRP) as a specific mode of interaction between organism and environment. When we refer to specific neural networks, we will here refer to the underlying system as the "core-SELF." The core-SELF provides primordial neural coordinates that represent organisms as living creatures—at the lowest level this elaborates interoceptive states along with raw emotional feelings (i.e., the intentions in action of a primordial core-SELF) while higher medial cortical levels facilitate affective-cognitive integration (yielding a fully-developed nomothetic core-self). Developmentally, SRP allows stimuli from the environment to be related and linked to organismic needs, signaled and processed within core-self structures within subcorical-cortical midline structures (SCMS) that provide the foundation for epigenetic emergence of ecologically framed, higher idiographic forms of selfhood across different individuals within a species. These functions ultimately operate as a coordinated network. We postulate that core SRP operates automatically, is deeply affective, and is developmentally and epigenetically connected to sensory-motor and higher cognitive abilities. This core-self is mediated by SCMS, embedded in visceral and instinctual representations of the body that are well integrated with basic attentional, emotional and motivational functions that are apparently shared between humans, non-human mammals, and perhaps in a proto-SELF form, other vertebrates. Such a trans-species concept of organismic coherence is thoroughly biological and affective at the lowest levels of a complex neural network, and culturally and ecologically molded at higher levels of neural processing. It allows organisms to selectively adapt to and integrate with physical and social environments. Such a

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psychobiologically universal, but environmentally diversified, concept may promote novel trans-species studies of the core-self across mammalian species.

1. Introduction

Consciousness, as one of the most crucial features of human existence, is increasingly becoming a topic of neuroscientific inquiry. This forces us to reconsider what it means for humans to possess a "self." Likewise, evolutionary perspectives coax us to entertain such issues in other organisms, for they too may possess such attributes of mentality. If we have core selves, perhaps they do also. This is rather likely since such a basic level of self may allow organisms to become spontaneously *active* organisms, able to relate intimately to the environment soon after birth. We envision the core-self to allow organisms to be active agents, as opposed to simply passive information-processing machines, as classical behaviorism and modern information-processing approaches have envisioned.

In our estimation, the most basic form of self is, at its core, relational in the sense that it constitutionally allows the selective and adaptive relation of the organisms to their environments. In this view, such a relational self, which we here call the proto-SELF (the most ancient form of coherent body representation), that provides a foundational infrastructure for the emergence of a core-SELF from which raw subjective experience and core phenomenal consciousness emerge, namely primary-process consciousness—the ability to perceive the world and to experience various raw affective states (Merker, 2007; Panksepp, 1998a, 2005a, 2005b)—upon which all other forms of consciousness may have been built in brain–mind evolution. We capitalize SELF (which can be envisioned as a Simple Ego-type Life Form, following Panksepp, 1998b) to highlight that we are referring to concrete evidence-based genetically ingrained neural networks which provide an infrastructure for the construction of higher selves. In other words the nomothetic SELF, a poorly understood genetically provided complex network infrastructure, similar across all mammalian species, is a necessary substrate upon which higher idiographic selves are epigenetically constructed. The use of capitalization has many functions, but the primary one is to highlight that we are specifying an actual brain process as opposed to a conceptual entity (Panksepp, 1998a). We will continue to use "core-self" in lower case where there is major divergence of the core-SELF into epigenetically created diversities, starting, perhaps, within medial frontal cortical regions.

Overall, our perspective is quite similar to that advocated by Merker (2007) but we focus more heavily on the affective-emotional aspects of core consciousness, while Merker focused more on primal perceptual aspects. Although our views overlap, they have emerged independently and from distinct intellectual traditions, except for the shared recognition that there was a period of neuroscience in the middle of the 20th century, demonstrating how important medial brain-stem functions were for consciousness as well as all the basic homeostatic regulations and emotional urges of animals (Denton, 2006; Merker, 2007; Panksepp, 1998a). Thus, the aim of this paper is to discuss the possible existence of an affective, nomothetic core-SELF in all mammals that may be the foundation for the diversity of higher selves—the many idiographic forms of selfhood that can emerge during development.

Probably the clearest data for the neural nature of experiential processes in animals is available from the study of basic emotional processes, where one can identify brain systems for specific emotions using localized electrical stimulation of the brain (ESB). Such artificially evoked instinctual arousals yield not only distinct emotional displays but also clear indications that animals like or dislike such brain states. These effects are obtained in homologous brain regions in all mammals studied (Panksepp, 1998a, 2005a, 2005b). This suggests that affect is a neurodynamic property of subcortical instinctual emotional arousal, concentrated in midline circuits. The fact that humans, who can provide verbal self-reports, have comparable affective feelings during such evoked states, with full felt ownership of such experiences, validates the cross-species nature of such primal emotional processes (Heath, 1996; Panksepp, 1985), although much more work needs to be done. Regrettably few are pursuing such work.

The fact that all basic emotional operating systems converge on primitive brain regions such as the periaqueductal gray (PAG), suggests how the affective foundation for a core-SELF may be constructed within the most ancient medial strata of all mammalian nervous systems (Panksepp, 1998a, 1998b). The massive interconnectivities of these medial brainstem regions to higher medial regions of frontal cortex (Holstege & Saper, 2005), brain areas implicated in self-related processing in human brain imaging work (Northoff et al., 2006), provide an integrated vision of how nomothetic core-SELF processes are constructed within the mammalian brain (Northoff & Panksepp, 2008). Further, the widespread influences of these medial cortical regions on the rest of the brain, suggest how various idiographic self processes, more widely represented throughout the rest of the neocortex, emerge in the epigenetic developmental maturation of higher regions of adult human brains and minds.

Epigenesis is the concept that covers all those lasting changes in gene expression profiles that are controlled by environmental inputs (e.g., via methylation of chromatin surrounding genes that control gene expression levels, as well as other distinct chemical processes such as "sexual imprinting" of genes) rather than the expression of the intrinsic information in gene nucleotide sequences. The key to higher human psychic development, including the emergence of various idiographic selves, may reside in the manner in which certain foundational evolutionarily provided tools for living (e.g., proto-SELF and core-SELF networks), along with epigenetic programming of higher brain regions by real-world experiences, engender

developmental landscapes that permit society, culture and the world in general, to mold *higher* brain organization, including our language abilities, much more so than the information encoded in genes.

It is much easier to study experiential states of animals rigorously in affective (internal valuative domains) than in cognitive domains (i.e., mind functions derived from exteroceptive information processing), but it is increasingly accepted that the very complex behavioral strategies exhibited by many vertebrate species provide evidence that they also have cognitive experiences (e.g., Clayton, Bussey, & Dickinson, 2003; Foote & Crystal, 2007; Smith, Shields, & Washburn, 2003). Of course, because of our capacity to talk about what is happening inside our minds, detailed cognitive-experiential states are much easier to study in humans. The mechanisms of affective states need to be worked out first in animal models (Panksepp, 2005a, 2005b) before incisive causal experiments (e.g., neuropharmacological) can be done in humans (Panksepp & Harro, 2004).

At present, the weight of functional neuroscience evidence, rather than just the weight of argumentation, supports the existence of various subjective experiences in animals, most especially affective/emotional feelings (Panksepp, 1998a, 2005a, 2005b). This opens up the possibility of using both human and animal data to illuminate the difficult concept of what it means to have a SELF, which some, including the present authors, believe is essential for any coherent understanding of consciousness and behavioral coherence. This kind of neuro-integrative thinking goes back to the work of the late Paul MacLean (1990), who envisioned rich emotional experiences to be part of the birthright of sub-neocortical limbic circuits, and we dedicated this paper to his memory and his seminal contributions that continue, regrettably, to be actively marginalized in the current era where ruthless reductionism prevails among those who pursue the most causally-informative neuro-empirical inquiries (Panksepp, 2002a).

Before detailing the current view, we would briefly acknowledge a massive literature on the self especially in psychiatric, psychoanalytic and related psychotherapeutic work which often covers the same territory from a much more complex conceptual, and often non-neuroscience perspective. Only a few of these pioneers can be noted, but we would acknowledge that there is an abundance of pre-neuroscientific ideas in this field which, for lack of space, we will not attempt to integrate into the present coverage: e.g., Brown (2005), Gedo and Goldberg (1973), Kohut (1977) and Krueger (2002) as well as, most dramatically, Schore (1994) who offered a wide-ranging neuropsychological synthesis of the developmental emergence of the self, where the focus was on the emergence of the higher forms of selfhood. To some extent this essay will be recursive, like consciousness and self-development themselves, to allow major themes to be emphasized and elaborated in slightly different contextualizations and to smoothly bring in a substantial sub-set of the abundant literature in this area.

2. Consciousness and the variety of selves

The psychological literature on the self and self consciousness is so vast that we will not attempt any summary, expect to highlight that many types have been postulated (e.g., Bukobza, 2007), but only a few have been connected to rigorous neuroscientific approaches. We restrict our discussion largely to lines of thought that have sought to clarify the underlying brain mechanisms of consciousness. In general, two or three alternative strategies have recently been applied to the neuroscientific investigation of self and consciousness. One view is that consciousness emerges from the complexities of neurodynamics, for instance gamma waves and other mechanisms of synchronization in higher cortical regions, or perhaps wherever those neurodynamics may arise in the brain (e.g., Edelman, 2006; Uhlhaas & Singer, 2006). Another emerging view privileges the perspective that an ancient central process required for experience is some kind of a "core-self" that helps generate a "core consciousness" which anchors the neural roots of experience within basic neurosymbolic evaluative (affective) representations of organisms (Damasio, 1999; Panksepp, 1998a, 1998b, 2007a, 2007b). Also, the human brain-imaging tradition, analyzing how human brains respond to self-related information, is yielding a view of how certain higher medial regions of the brain are selectively recruited when one views the world through a self-referential lens (Northoff, Bermpohl, Schoeneich, & Boeker, 2007; Northoff et al., 2006). In this paper we will discuss how these views could be integrated into a cross-species conception of a core-SELF.

Our aim here is also not to contrast the enormous number of philosophical approaches that have been taken to the concept of the self (Gallagher & Shear, 1999), but rather to envision how conceptions of a core-SELF process, potentially homologous in all mammals (Northoff & Panksepp, 2008), may relate to the epigenetic emergence of more complex self-related processing (SRP) in the brain. We will consider how a cross-species relational core-SELF concept (e.g., Panksepp, 1998a, 1998b) may be integrated with self-related information-processing mechanisms imaged in the human brain (Northoff et al., 2006), and how the former approach may provide a critical foundation for the latter.

We consider the originally philosophical concept of the self to be a very basic, objective mechanism for generating organismic coherence that first and foremost makes consciousness and other higher-order functions possible. The crucial criterion for such basic SELF is the ability of the organism to selectively and adaptively relate to its environment, which is why we, at times, call it a "relational self." An organism's capacity to experience such relations through complex neural networks clearly excludes plants from having any core-SELF. We distinguish our vision from concepts that 'locate' the diverse manifestations of experienced selves at the very pinnacle of consciousness thereby representing its highest cognitive manifestations. However, we have no wish to deny common views in the humanities, social sciences and culture studies—that unique, idiographic, subjective self-concepts ultimately elaborate through the highest regions of the human mind (Djikic & Langer, 2007). We simply suggest that during development, the biologically provided objective (nomothetic) self provides a solid platform for the emergence of diverse environmentally constructed subjective (idiographic) selves.

Once the SELF is considered a very basic brain/mind function rather than being just the highest form of human consciousness, it becomes only natural to consider the existence of objective, nomothetic SELF processes in species other than humans,

to consider how such processes may subserve the very genesis of consciousness, and thus to develop a neurobiologically-based trans-species model of a core-SELF. We consequently conceptualize the core-SELF as a coherent affectively anchored brain function and assume evolutionary continuity and progression from ancestral animals to humans (Panksepp, 2007a). To re-emphasize: when we discuss the core affective processes, concentrated in medial mesencephalic and diencephalic deep-subcortical regions, apparently shared homologously by all mammals (Northoff & Panksepp, 2008; Panksepp, 2005a, 2005b), we will capitalize the core-SELF (as in Panksepp, 1998a, 1998b), to highlight we are speaking of a universal mammalian brain process; we will use lower case when we discuss the higher medial cortical cognitive "core-self" processes that may have more variability among mammalian species, but which may often still be sufficiently similar (i.e., underlying emotional personality structures) to allow cross-species generalizations. We will not here discuss the emergence of idiographic cognitive selves, which we assume arise epigenetically from core-SELF processes programming higher associative, more strictly cognitive, regions of the brain such as lateral frontal and parietal cortices that mediate higher mental and body-image self-processes, that are intimately linked to the foundational neural "soil" of medial brain stem (Panksepp, 1998a, 1998b) and medial frontal core-self functions (Lou et al., 2004; Northoff et al., 2006).

Indeed, a proto-SELF, as a coherent neurosymbolic bodily representation, may already be present in a primordial form in early vertebrates, providing an evolutionary substrate for the emergence of an affective core-SELF concentrated within ancient emotion-regulating regions of the brain such as the PAG and medial diencephalons. These basic processes are experientially elaborated in humans and other well-cerebrated animals, to allow integration of their higher cognitive abilities in self-referential ways with ecologically-relevant information processing (Northoff & Bermpohl, 2004; Northoff et al., 2006). In sum, we envision this whole core-SELF continuum to constitute the "objective self"—the nomothetic SELF—which is a necessary foundation for varieties of more idiographic subjective selves. We here consider higher, idiographic self-related information processing to mediate between organismic givens and their physical body-image, cognitive, cultural and other environmental contexts, yielding a diversity of selves, emphasized by philosophical, humanistic and cultural studies. We will hardly discuss these elaborations, but accept them as givens of human complexities, as highlighted in the psychoanalytic and psychiatric literature noted earlier (end of Section 1).

We suppose the proto-SELF to be relational at its core thus constituting a selective and adaptive relation between the organisms' body and its respective environment (Fig. 1). The proto-SELF may thus be characterized as a relational self; this implicit relational self may by itself not be accessible to phenomenal consciousness and subjective awareness yet and may therefore be characterized as pre-phenomenal and pre-conscious. However, this archaic relational proto-SELF, as pre-phenomenal and pre-conscious, provides the basis and foundation for phenomenal consciousness and subjective experience to be possible which, as we assume, occurs once the proto-relational SELF comes to be linked to affective processing and thus to emotions. In this sense the proto-SELF may be said to be constitutive and necessary for the core-SELF to emerge as an affective functional entity with a raw form of phenomenal consciousness and subjective experience, what we would call "affective consciousness" (Panksepp, 2000a, 2005a, 2005b, 2007c). What is subjectively experienced here is the relation of one's body to the incentives in the environment as well as internally generated emotional arousals—the core-SELF thus enables the organism to access this relation in terms of subjective experience, e.g., a primitive form of phenomenal consciousness, which at this level is essentially affective.

Despite their close linkage in the core-SELF; affectivity and perceptual phenomenality must be considered distinct aspects of subjective experience; perceptual phenomenality may describe the form, e.g., format or code of experience (which, purely logically, is related to the structure of the physical world—i.e., cognitions are largely comprised of neural "information processing" of external events), whereas affectivity characterizes its internally generated value content (which, for instance, is engendered by activation of evolved within-brain value structures that are initially precognitive (pre-propositional—attitudes with no object-relations). The core-SELF being affective and phenomenal in turn provides the basis for higher forms of self like the reflective-self closely associated with access consciousness and the handling of cognitive contents. Finally,
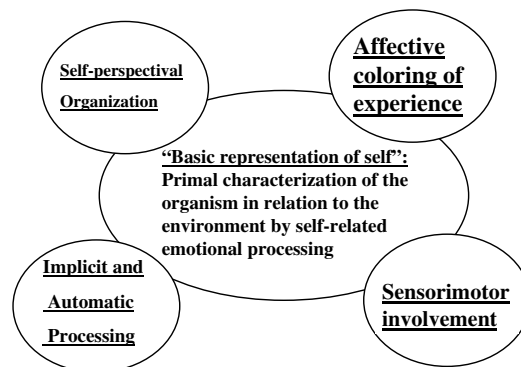

Fig. 1. A schematic summary of the different characteristic features of the self that may be shared between humans and animals. This amounts to a trans-species representation of basic sense of self.

it should be noted that the reflective self is envisioned to top-down modulate the core-SELF so that there is bilateral modulation between lower and higher aspects of selfhood. We assume that most animals and humans share the first two levels of the self, the proto- and the core-SELF, while the reflective or cognitive self (Fig. 2), which permits *awareness* as opposed to *raw experience* of phenomenal-affective contents, may be reserved for the more encephalized animals including, at the very least, cetaceans, elephants, higher primates and humans. What is shared is thus the very basic ability to relate selectively and adaptively to the environment and the subjective experience of this relation in phenomenal consciousness which may be evolutionary advantageous for survival. The affects—whether bodily states (homeostatic affects), emotional arousals or moods—are all within-brain barometers that signal survival utility. Since evolution seems more adept at solving discrete survival problems rather than providing general ones (cortical elaboration of primary-process feelings into thoughts), we think the original adaptations were very specific feelings, and only later did the more general feelings and moods (e.g., generalized positive and negative affects) arise, potentially through cognitive conceptualizations.

The nomothetic proto- and core-SELVES may be assumed to be constituted empirically by what we would call spontaneous affective (instinctual) self-related processing (SRP) while the higher idiographic cognitive-reflective selves permit awareness of oneself as an entity in the world and hence more deliberative decisions about what one wants and needs. At its core, SRP describes the integration of interoceptive and exteroceptive stimuli from body and environment in relation to the intrinsic organismic functions—the basic emotional and motivational systems of the brain that generate a purely affective form of consciousness (Panksepp, 2007b)—and hence elaboration of animals' various spontaneous goal-orientated survival activities (see below and Alcaro, Huber, & Panksepp, 2007; Northoff et al., 2006 & Panksepp, 1998a for details). As such, the higher reaches of self-related processing, in medial frontal cortical regions, may be crucial in constituting what might be the first glimmers of the high cognitive self—i.e., not only having the feeling tone of being a living creature that most higher animals and humans may share but being aware of being a certain type of creature within a specific environment which may be specific for higher-order (i.e., well-encephalized) animals including humans.

If coupled with higher-order cognitive functions in neo-cortically well-endowed animals, especially humans, SRP may also go beyond mere self-relating (see below for further explanation) by providing the basis for higher forms of self-awareness, self-consciousness, self-image, self-enhancement, self-regulation and self-cognition and the great variety of coalesced idiographic selves that constitute a fully-developed personality. However, the diversity of basic emotional influences that operate through the core-SELF level of organization may also, under certain developmental conditions, engender dissociative disorders such as multiple independent personalities in the higher order idiographic self structures. While the foundational core-SELF, characterized by raw affective feelings that mediate one's own bodily needs and emotional urges, as well as primary-process perceptual relatedness to social and physical environments provides the very basis for the organism's orientation within and adaptation to the world. The more cognitive higher-order forms of self may allow for more refined, selective and manipulative relations to the environment, often conceptualized as free-will, along with one's emerging derivative interests and desires. We assume that the lower-order more basic form of an affective core-SELF that generates raw emotional and motivational feelings (Panksepp, 2007b) is shared homologously across different species whereas the higher-order cognitive forms of emergent-selves may be more diverse across species as well as individuals within a species, depending more on differences in how cortical architectures have been epigenetically molded into diverse types of selves (personalities) by the way emotional affects have operated during development.

Neurobiologically, we suggest that such evolutionarily provided coherent affective-cognitive integration with these core-SELF/cognitive-self processes permits the emergence of coherently operating neural networks across different species that

Levels of processing and corresponding brain regions
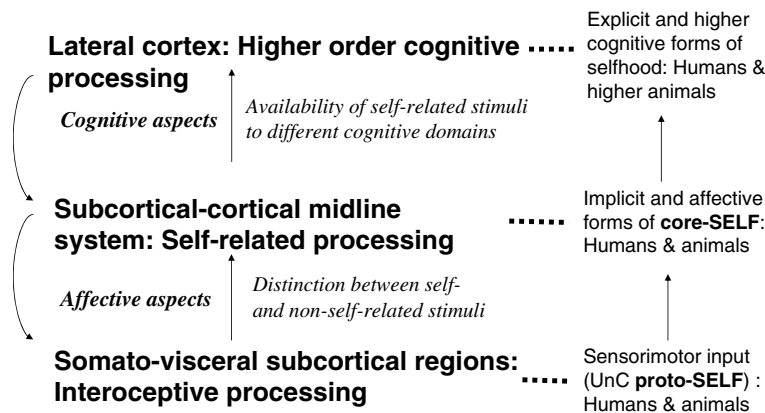

Fig. 2. A summary of the different levels of processing of the self in association with possible neural and psychological substrates in relation to different concepts of self given by different authors. Also highlighted is the level of organization that may be shared between animals and humans (proto-SELF is deeply unconscious (UnC).

integrates incoming stimuli from the environment with internal needs, drives and basic affects (Alcaro et al., 2007; Northoff & Bermpohl, 2004; Panksepp, 1998a, 1998b). We summarize evidence that a coherently operating subcortical-cortical mid-line system (SCMS) is the critical central neural processing network that mediates SRP across different species. At its lowest levels, it is largely instinctual, affective, but deeply embedded within life-supportive environments. At its higher levels it becomes immersed and molded by individual learning and cognitive functions as well as ecological and cultural issues. In so doing, we begin to articulate a common *psychobiological* basis for constituting diverse emergent expressions of self across species—a trans-species, neurobiologically based, multi-layered concept of an objective self. Again, we would re-emphasize that this multi-tiered process is more homologous at its lower levels (e.g., PAG and medial diencephalon) and ecologically and experientially diversified in its higher medial frontal regions that are richly connected to the rest of the higher cerebral apparatus. Of course, more detailed cross-species investigations are necessary since the abundant homology of structures within subcortical regions implies but does not necessitate homology of function across animals and humans. However, until demonstrated otherwise, there is no special reason to believe that influence of species-diverse higher brain regions, some of which control subcortical functions, would have yielded qualitative differences in the core structures, only the degrees and types of regulation higher regions can impose on lower regions.

We are advancing this idea, in a neuroscience context, so as to promote further empirical evaluation of this difficult, but probably essential, integrative concept. It basically reflects a new ontology, at least in modern experimental neuroscience, where behavioral coherence is envisioned from the inside out, yielding intrinsically *active* animals that manifest and confirm an integrated evolutionary-organismic-environmental—an embodied and ecologically situated—perspective. In this view, *passive* information processing and associative metaphors of animal minds are not enough. One has to envision internal-intrinsic neural *states* as large-scale network dynamics arising from emotional operating systems (Panksepp, 1998a, 2005a, 2005b) that allow organisms to be coherent *active* entities with self-referential brain dynamics that thrive within specific environmental contexts. We believe this requires the reconceptualization of the older visions of "the self" in new neuro-materialistic and neuro-dynamic ways (see a recent interview of the first author by Gallagher, 2008).

Although this concept remains to be fleshed out by abundant research, the empirical work has begun, with many implications for understanding psychiatric disorders (Northoff, 2007; Panksepp, 2004, 2006). We assume that such processes, e.g., SRP of information, provide the essential grounding and basis via which organisms develop into more mature, sophisticated beings. However, the present integration is not simply speculative (for abundant philosophical models, see Gallagher & Shear, 1999), but a viewpoint that arises from a rapidly increasing body of experimental findings, only some of which can be shared here (for more extensive coverage, see Northoff et al., 2006; Panksepp, 1998a, 2005a).

3. Definition of self-related processing (SRP)

In keeping with, but in substantial contrast to the recent analysis by Bekoff and Sherman (2004), we emphasize that SRP is not just limited to cognition but is a fundamental process allowing the organism to experience a variety of affective states and to strongly relate externally derived sensory stimuli and cognitive perspectives to basic organismic needs and affective feelings according to their relevance for survival, as indexed by various positive and negative affects. The term "relevance" is assumed to reflect intrinsic biological values that are coded as affective feelings (Panksepp, 2005a, 2005b) that help create relational values within the brain–mind that are related to organisms' growing knowledge of their environments. We believe much of the filtering of external stimuli for further integration is based upon their relationships to the emotional and other affective states of the organism. Thus, the phrase 'self-related' refers to the processes of coherently associating intero- and exteroceptive stimuli within an organism by means of which the organism becomes integrated with its environment. These potentialities are actualized within specific sensory, motor, attentional, emotional, motivational, morphological and psychoethological conformation of each species, but they are anchored in genetically provided and hence ancient, subcortical neurosymbolic representations of organisms as coherent creatures, laid out, we believe, in ancient viscero-somatic coordinates, where intrinsic affective-instinctual processes provide a center of gravity for organismic actions (Panksepp, 1998b, 2000a, 2000b, 2000c, 2002b, 2007a).

This coherent brain function has to be ancient and should not require a great deal of cortical encephalization. In this view, it is noteworthy that total neo-decortication of all young mammals appears not to compromise the autonomic and sensory-motor manifestations of organismic coherence, nor their ability to experience the world affectively and thus to have a basic sense of self (Kolb & Tees, 2000; Merker, 2007; Panksepp, 2005a, 2005b; Panksepp, Normansell, Cox, & Siviy, 1994; Shewmon, Holmse, & Byrne, 1999). We postulate that this ancient brain function allows SRP to occur in homologous ways across all mammalian species and perhaps other vertebrates. Most importantly, we assume that the primordial coherence of this kind of core-SELF allows for epigenetic processing of external sensory-perceptual and cultural information within the extended, more cognitively oriented self in a self-referential manner that, in turn, enables organisms to selectively adapt to their respective environmental contexts in "self-projective" ways (Buckner & Caroll, 2007).

Conceptualized in this way, higher SRP can be characterized by intrinsic integration of the following four features: (i) relation and colonization, (ii) appropriateness and belongingness, (iii) increasingly subtle affectivity and emotions, and (iv) the phenomenal dimension of *mineness* in experience as organisms relate to their environment. To elaborate on these themes: (i) external stimuli may be related to and colonized by the organism through sensory and especially motor function. (ii) Appropriateness and belongingness implicate the process of valuing, i.e., whether the stimulus is relevant for the organism in

biological terms, as for survival or reproduction, within its actual goal-orientation. (iii) Affectivity and emotions signal the linkage between evolutionarily ingrained values and those that are assigned epigenetically to the actual stimuli by SRP (see below for details). (iv) Finally, phenomenality and mineness signal the relational and affective character of SRP and thus the emergence of self-perspectival organization that shall be explained in further detail in the next section. (v) There must be a specifiable neural substrate, such as the SCMS, for such functions. Only if all five criteria are met may one speak of a "core-SELF". Though many organisms meet all five criteria, plants, for instance, do not. Even if we do not know whether plants may have phenomenal experience of "mineness," they at least lack the first, third and fifth criteria, sensorimotor and affective involvement arising from complex neural networks. Therefore, we would not speak of a self in the case of plants, since they lack what we call self-perspectival organization.

4. SRP and self-perspectival organization

Once there exists a primordial neural representation of the body that can generate raw affective experiences (Panksepp, 1998a, 1998b), the guiding developmental concept, elaborated by higher medial frontal brain regions, becomes what we call higher Self-Related Processing. Higher SRP is the process that transforms stimuli from simple signals to a meaningful (i.e., valuative) part of the organism's functioning. Stimuli are "colonized" by an organism's intrinsic neural organization, through their appropriation and self-related belongingness (reflecting evolutionary adaptations, signaled largely by intrinsic affects), which in turn generates complex, meaningful, cognitive experiences during development. By such a relationship, sensory stimuli become linked to intrinsic affective values, yielding the addition of the evaluative 'for me' by means of which that particular stimulus becomes "mine" resulting in "mineness" (Lambie & Marcel, 2002; Metzinger, 2003). By becoming "mine", stimuli make "something informational or neurophysiological into something phenomenological" (Lambie & Marcel, 2002).

Conceptualized in this way, SRP intrinsically integrates affectivity, appropriateness and belongingness, and the phenomenal dimension of mineness into the ownership of experience. By being deeply affective and motivational, the ancient universal core-SELF, allows the external world to be related to the organism and consequently to be imbued with vast diversities and varieties of "meanings." By means of SRP the large variety of universal affective experiences (sensory affects, bodily-homeostatic affects, and emotional affects), the genetically provided tools of the core-SELF (as outlined in Panksepp, 1998b), are transformed into organisms' more cognitive phenomenal experiences and, in the most well-cerebrated species, into awareness of themselves and their environments with specific spatial, temporal and conceptual organization of their ecological surrounds (see van Gulick, 2004).

There are a variety of basic affects, including various sensory feelings (from pleasant sweetness to disgust) and bodily imbalances (hunger, thirst, etc.). The types of experiences that have been most studied in animals are the basic emotions, where a *dual-aspect monism* strategy (e.g., that raw emotional experiences arise from the same brain networks that generate complex instinctual behaviors; see Panksepp, 2005a, 2005b), allows us to envision at least seven basic emotional feelings in all mammals: the appetitive desire characterized by activation of (i) the SEEKING system, (ii) a state of irritable anger when the RAGE system is aroused, (iii) feelings of scared-trembling trepidation when the FEAR system is activated, (iv) strong erotic feelings when somewhat distinct male and female LUST systems are activated, (v) nurturing, caring feelings when maternal CARE systems are engaged, (vi) a form of psychic pain when arousal of the separation-distress PANIC system is triggered and (vii) social joy and laughing playful feelings when PLAY networks are engaged (Panksepp, 1998a, 2005a). Many of these feelings are initially "objectless" with object-relations being learned through real-world interactions. As learning and higher cognitive systems come into play, these primary-process affects can serve as fundamental substrates for many secondary- (i.e., memory) and tertiary-process (i.e., thought related) feelings, the last of which is next to impossible to study in animals since the behavioral indicators become so subtle as to be endlessly controversial. However, the massive colonization of these feelings within complex human cognitive structures, guided by cultural and other environmental events, have enormous implications for the varieties of subjective selves that can emerge in the human mind.

The ability to organize such external "stimulus colonizations" of higher cognitive regions of the brain into extended selves by the very existence of a basic core-SELF, which is almost completely affective and relational, is a neuroscience project that has barely begun. However, the particularities of such epigenetic progressions are surely differentiated not only according to each species' morphology, physiology and ecological/cultural embeddedness, but also between individuals in a species depending on their affective temperamental differences. These higher idiographic varieties of subjective selves, so diverse across human beings and in different cultures, by being linked to the objective SELF-processes we focus on here, may sustain many of the attributes of the nomothetic core-SELF. In any event, through SRP a phenomenal sense of "mineness" emerges, and each organism's structure of phenomenal experience takes on a character that is philosophically described as self-perspectival organization (van Gulick, 2004).[2]

Self-perspectival organization describes experiences reflecting a certain point of view from which one experiences one's self, one's body and one's environment singly and in relation to others. According to Zahavi (2003, p. 72), self-perspectival organization and "mineness" arise from a primitive form of selfhood, what Damasio (1999) and Panksepp (1998a, 1998b) first described as core-self and the SELF, respectively, within the neuroscience literature. Drawing on the phenomenological

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[2] A rather broad meaning of the term phenomenal is assumed here to include various features like qualia, intentionality, unity and homogeneity, transparency, etc. which, due to reasons of space, cannot be discussed in further detail here.

tradition (Zahavi, 2003), we assume that at this basic lower-order level, self-perspectival organization and "mineness" constitute a conjoint phenomenal experience of both the environment and oneself. One may consequently speak of co-occurrence within primal phenomenal consciousness, as distinguished from reflective consciousness, and pre-reflective self-instantiation, as distinguished from reflective self-awareness.

Two features need to be emphasized here. First, the level described is what the phenomenologists call pre-reflective, pre-cognitive and pre-linguistic which must be distinguished from a reflective, cognitive and linguistic level—this distinction might correspond (more or less, requiring more in-depth discussion than can be pursued here) with the one advanced by Ned Block between phenomenal and access consciousness. Second, most importantly, at this pre-reflective, pre-cognitive and pre-linguistic level, phenomenal consciousness and pre-reflective self-instantiation probably go hand in hand, being inseparably linked to each other. This implies that the occurrence of some kind of basic SELF in the sense described here is linked to the occurrence of foundational phenomenal consciousness, which may be deeply affective (Northoff et al., 2007; Panksepp, 2005a, 2005b).

Following and extending this distinction, we conceptualize three different levels of the self, with the first two being nomothetic and the last a diverse group of idiographic processes. First, the foundational relational self—the proto-SELF, which is characterized as pre-phenomenal and pre-consciousness since as such it is not yet accessible to subjective experience at this level. Second, the affective core-SELF, that can be described as pre-linguistic, pre-conceptual and pre-reflective but characterized by phenomenal consciousness, and with primitive learning (e.g., classical conditioning), being able to develop object-relationships with the world. Finally, the third, the reflectively aware or cognitive selves that allow organisms to reflect upon the relationships within and to the environment, all of which requires access or reflective consciousness (which for the sake of simplicity we do not distinguish here).

The relational proto-SELF may be characterized by some kind of "sense of relatedness" between organism and environment—as a primordial attachment of the organism to and integration within its respective environment. We assume that this "sense of relatedness" describing the co-occurrence between proto-SELF and core-SELF, the latter of which adds affectivity and a basic form of affective consciousness which, based on available evidence (Panksepp, 1998a; Panksepp, 2005a, 2005b), is shared across species. However, this may no longer be true for higher forms of consciousness and self. At higher more cognitive levels, both self and consciousness may dissociate from each other; for instance, higher-order cognitions may allow introspection of one's self, thereby allowing an organism to distinguish and demarcate itself clearly from the environment. This demarcation may be experienced as a "sense of distinction" between self and environment. Due to different cognitive equipment, this "sense of distinction" and thus higher-order more cognitive forms of self (like "extended self", "narrative self", "dialogical self", "autobiographical self", etc.; see Bekoff & Sherman, 2004; Damasio, 1999; Northoff et al., 2006) may no longer be shared across species.

Of course, these levels of self always continue to interact with each other, and are almost impossible to distinguish in well-integrated adult experience. The basic sense of SELF may be considered the foundation upon which higher-order forms of self may be implemented; the former may thus be considered the "core" around which, similar to an onion, different evolutionary and epigenetic layers are constituted. There may consequently be two-way "circular" interaction among the various layers of the self. The core-SELF may drive and determine the higher-forms of self; if the interaction is deficient, the latter may be rather fragile and volatile as is the case in psychiatric problems like Borderline Personality Disorder, where patients no longer experience some stable "sense of relatedness" to a "core-SELF." However, the reverse direction may also be possible, i.e., the higher-order cognitive forms of self modulating the basic core-SELF by, for instance, overriding the "sense of relatedness," and the associated emotions, with a stronger "sense of distinction" and the respective cognitions.

To re-iterate, there is one critical empirical question for this whole agenda: Are the neural substrates and mechanisms involved in such self-related processing, and thus the core-SELF, common among species? We here assume a SCMS, running from midbrain, with greatest concentrations in the periaqueductal gray, which is a basic-emotion "epicenter," is well connected to higher midline cortical regions. This constitutes a core set of interrelated structures involved in creation of a basic sense of SELF—the "sense of relatedness" across different species. The lowest aspects of this network are substantially genetically provided (with their evolved raw affects being "the ancestral voices of the genes"), and they appear sufficient to sustain raw perceptual and affective levels of phenomenal consciousness co-occurring, as soon as organisms perceived the outside world, with a sense of relatedness (Merker, 2007; Panksepp, 1998a; Shewmon et al., 1999). The higher aspects of the SCMS system allow the rest of the thalamic neocortical axis—the self-related theater of the cognitive brain (Baars, Ramsoy, & Laureys, 2003), to become molded to fit cultural and ecological environments. We must re-emphasize that it has been much easier to clarify the lower substrates scientifically through animal brain research, where very similar basic emotional processes are elaborated across all mammalian species that have been studied (Panksepp, 1985, 1998a, 1998b), explaining partly why it has been neglected in cognitive and consciousness studies, and to empirically study the higher substrates through human neuropsychological and brain imaging approaches (Northoff et al., 2006). The conjunction of findings has fostered the present integration of perspectives to yield a more complete picture of the core-SELF.

5. SRP and the subcortical-cortical midline system (SCMS)

Recent imaging studies in humans show various cortical regions, predominantly the so-called cortical midline structures (CMS), to be involved in SRP (see Northoff & Bermpohl, 2004; Northoff et al., 2006; Uddin, Iacoboni, Lange, & Keenan, 2007)

that are integrated with subcortical SELF processes to yield an integrated subcortical-cortical midline system (SCMS). Although some authors, like Gillihan and Farah (2005), do not see supporting evidence yet for localizing the self in particular brain regions, that may be because the concept covers so much territory and needs to be parsed at minimum into nomothetic and idiographic variants. In our estimation, as supported by a mass of empirical evidence (Northoff et al., 2006), there are specific brain regions most critically important for constituting the higher reaches of a core-nomothetic self-referential network. The question arises whether the very same higher medial frontal brain regions are present and also implicated in self-relatedness in animals. The stream of evidence runs thinner here than with respect to the deeper, subcortical midline SELF systems (Holstege & Saper, 2005; Panksepp, 1998a, 1998b). Thus, even if the higher midline regions are structurally homologous across species, this does not yet confirm that there is functional homology, e.g., that they mediate SRP in animals as well as humans. How, then, does one develop translational models of SRP across species?

Trans-species investigations could employ various strategies to establish trans-species models of the self. One might investigate the same brain regions in human and animal resting states with the same imaging methodology as fMRI or PET and then directly compare regional neural activity and its intrinsic connectivity. Indeed, some recent work of this type has revealed that the above mentioned cortical midline structures do show a similar pattern of neural activity and connectivity (see below for details as well as Vincent et al., 2007; Rilling et al., 2007). Such trans-species anatomical models might be extended by employing the same task, with the same behavioral parameters, in both animals and humans during imaging. One such example is Gallup's self-face recognition—i.e. mirror test in monkeys (Gallup & Hamilton, 1998) and other animals (Plotnik, de Waal, & Reiss, 2006; Reiss & Marino, 2001)—which has already been applied in human imaging (Keenan, Wheeler, Gallup, & Pascual-Leone, 2000). Or one could stimulate pets (dogs, cats) and humans with the same empathy task (Vitulli, 2006) during imaging thus establishing what might be called a trans-species anatomical-functional model of the self. Finally, even the relationship between self-relatedness and consciousness may be studied across species. A recent study by Northoff et al. (2008) distinguished between subjective experience of emotions and self-relatedness and found both dissociation and overlap in their respective neural correlates, e.g., in different subcortical and cortical midline regions. Such investigation could also be done in animals though in a slightly modified way with for instance food preference stimuli and stimuli inducing anger. These various strategies might allow one to investigate not only structural but also functional homologies across species.

These higher regions of the brain provide abundant regulatory control over subcortical brain regions (Liotti & Panksepp, 2004), permitting robust top-down modulation of instinctual urges. However, as already noted, from a fully integrated system perspective, there should also be abundant bottom-up modulation. Indeed, there is likely to be, for damage to the lower substrates of this midline system impairs consciousness more than damage to higher brain regions (see Merker, 2007; Panksepp, 1998b; Watt & Pincus, 2004) and stimulation of the subcortical regions in humans and other animals powerfully controls cognitive processing (Heath, 1996). We envision the bottom-up control to prevail, rather massively, during early development, when organismic behaviors are controlled more by instinctual urges reflecting powerful (unconditional) emotional and motivational states, and the top-down to prevail in mature animals, especially in every-day decision making when affective states are more diverse and cognitively modulated. Higher brain maturation often leads to a denial of the more primitive forms of affective mentation, and in part this is explained probably by cultural demand characteristics (i.e., the value of rationality), but there is also a neurophysiological reason. There is a reciprocal relationship between the higher SCMS networks and the more laterally situated cognitive working-memory and conceptualization networks (Goel & Dolan, 2003; Northoff et al., 2004).

The lowest regions of this distributed SCMS network include the Periaqueductal gray (PAG), the superior colliculi (SC), and the adjacent mesencephalic locomotor region (MLR) as well as preoptic areas, the hypothalamus, and dorsomedial thalamus (DMT) (Holstege, Bandler, & Saper, 1996; Panksepp, 1998a, 1998b). For example, the colliculi and the PAG are among the most richly connected areas of the brain (Strehler, 1991); both receive afferents from several exteroceptive sensory regions (occipital, auditory, somatosensory, gustatory, and olfactory cortex) and, at the same time, afferents from other interoceptive subcortical regions (Holstege et al., 1996; for an overview of this area, see Watt, 2000). In addition, the PAG and the colliculi are connected with the cortical midline structures (CMS) (Dujardin & Jürgens, 2005; Holstege & Saper, 2005). Since the same is true for the other subcortical midline regions mentioned, it is important to conceptualize the self-integrative lower brain systems to have intimate relationships with the higher CMS structures, which is anatomically the case (see Strehler, 1991, for overview); thus yielding a highly integrated SCMS in normal organisms and providing a complex infrastructure for self-referential processing of external information. Functionally, higher cortical regions might represent the functions that are primarily represented subcortically in a more detailed, specific and refined way. This, for example, is realized in the case of sensory and motor functions. Though both complex sensory and motor functions are already represented in subcortical regions like the PAG, basal ganglia, mesencephalic locomotor system (as evidenced by the fact that the less-encephalized mammals like rats that have been decorticated soon after birth, are basically indistinguishable motorically from neurologically intact animals, even playing quite normally: Panksepp et al., 1994), those primitive sensory-motor functions are again represented in cortical regions, e.g., somatosensory and motor cortices. This may allow behavioral functions to be elaborated in more detail, with specific types of flexibility, especially with much greater regulation of and inhibition over instinctual outputs, than it is possible on the subcortical level.

Such an analysis is consistent with various lines of research showing that core-self-related functioning involves both cortical and subcortical regions (Northoff et al., 2007; Panksepp, 1998a; Phan et al., 2004). Many imaging studies in humans have focused on cortical regions, in part because of the involvement of strong cognitive components such as evaluative judgments in the respective tasks (see Northoff et al., 2006). A recent human imaging study on SRP pursuing a less cognitive approach (i.e., without an evaluative judgment in the task) observed involvement of various subcortical regions like the

hypothalamus, the DMT, the PAG, and the superior colliculi in addition to the higher cortical midline structures during evaluative SRP (Heinzel et al., 2005; Northoff et al., 2007). Interestingly, these subcortical regions are enriched in the pre-eminent anatomies of basic emotional systems in all mammals (MacLean, 1990; Panksepp, 1998a). This provides empirical support for the trans-species involvement of a SCMS in SRP in humans as well as other vertebrates. In further support, Mobbs et al. (2007) recently imaged the cascade of brain arousal in these regions from the higher cognitive structures when threat was far away to the most basic animal instinctual emotional integrative systems when it was nearby using a predatory imminence task during human brain imaging.

The assumption of the SCMS as common across species implies that it should be independent of particular sensory modalities and other domains. This has indeed been demonstrated in a recent meta-analysis that compared all imaging studies on SRP conducted in different sensory modalities (e.g., auditory, visual, olfactory) and different domains such as verbal/vocal, emotional, social, facial, spatial and memory (Northoff et al., 2006). These results support the idea of SRP domain-independence, reflecting a common process whose coordinated functioning comprises the basic sense of self. Since the SCMS is ubiquitous in all mammals, we propose a coherent cross species self-referential network for core consciousness that has more evolutionary homologies (universality) among the lower neural substrates and more diversity in the upper ones.

6. SRP and sensorimotor functions

Given these structures, how then does such an integrated SCMS account for a "primitive form of selfhood" creating the experience of a "sense of relatedness"? Since the lower reaches of this network are involved in integrative processing of interoceptive bodily functions and the convergence of basic emotional systems, the subcortical midline regions have been associated with what has been called "bodily-self" or "proto-self" (Craig, 2002, 2003; Damasio, 1999; Denton, 2006; Panksepp, 2003, 2005a, 2005b; Parvizi & Damasio, 2001; Strehler, 1991). We assume that interoceptive stimuli and various basic emotional systems are interactive with each other as well as to basic motor action schema so that the relation between the distinct stimuli from various core value systems and motor modalities is coded into an integrated form of neural activity. What is coded is thus not each process by itself, in an absolute way and independent from other stimuli, but rather their dynamic interactions.

Neuroanatomically, this presupposes strong convergence of anatomical connections in the subcortical midline regions (see above) from the different interoceptive, emotional and motor modalities (see Panksepp, 1999; Strehler, 1991). Neurophysiologically this may be achieved by synchronization or shared oscillation of neural activity (Panksepp, 1999). Even if, due to distinct sensory-motor equipment, the respective interoceptive and motor stimuli may differ between different animals, they may nevertheless share the mechanisms of how these stimuli are integrated and related to each other. In other terms, despite differences in sensory and motor contents, the mode of their processing, i.e., constituting relations among them by anatomical convergence and neurophysiological synchronization, may be shared across species. Anatomical interoceptive and motor convergence has indeed been shown in subcortical midline regions in both animals and humans (Holstege & Saper, 2005). However, neurophysiological relations and synchronizations in these brain networks during self-relatedness remain to be evaluated in both animals and humans.

This might be realized by a task that involves coordination between interoceptive and motor function with regard to a specific goal-orientation that might be employed in both animals and humans. Since mirror self-recognition is a common task, albeit one that is controversial when used across species with different sensory and cognitive strengths (Mitchell, 2002; Schilhab, 2004), perhaps variants of this approach, using sensory feedback and ecological conditions relevant to a species (e.g., touch or odor in rats, who do not have high visual acuity would be appropriate). For instance, one could put sticky pieces of tape on a rat, or perhaps a novel odor in an accessible bodily location, and evaluate brain changes as the animal exhibits intensified exploration of these regions. Would not this indicate some type of primal self-recognition in rats? What might be especially interesting is to put a dab of predatory odor on a rat that can provoke unconditional fear.

One potential problem with such strategies is that there may be a meaningful distinction in the brain between the processing of physical and mental selves (Gillihan & Farah, 2005), with the physical representations of one's own bodily actions being processed in frontopartietal mirror-neuron areas (Uddin et al., 2007), with access to a mental self within the CMS regions of animal brains being more difficult to access than the mere use of more cognitive bodily-self-recognition tasks. However, by making bodily recognition heavily emotional, as might be achieved by applying predatory odors to the body surface, such problems might be overcome. Further, we would entertain the possibility that most of the neocortical body-recognition functions, most evident in mirror-neurons, are not innate but developmentally acquired (Biven & Panksepp, 2007), while a more primal and diffuse, autonomically-affectively based body schema exists within the deep subcortical midline structures of the mammalian brain where basic emotional systems are concentrated (Panksepp, 1998b, 2002b). We would suggest that it is this comparatively primitive form of body representation, deep in the brain, not easily accessed by current human brain imaging technologies, that the higher CMS structures link to the external world.

On the basis of anatomical convergence of primitive autonomic-emotional bodily representations, and the attending global neurophysiological synchronizations within the SCMS, an archaic scheme of the entire body may be constituted in brain regions as low as the medial brainstem (autonomic regions of the mesencephalon and diencephalon)—the neural instantiation of a "virtual body" presumably laid out in coherent viscero-somatic motor coordinates, as indicated by the ability of localized brain stimulation in these regions to activate coherent emotional action patterns with all the bodily and affective

accompaniments of normal emotions (Panksepp, 1998a). It has been envisioned that these neural systems are the fundamental sources of distinct emotions and various other raw affective experiences (e.g., hunger, thirst, etc.) which in turn reflect specific organism-environment relationships and thus the relational nature of the basic sense of self (Denton, 2006; Panksepp, 2005a, 2005b). Since such a bodily representation is linked closely to brain instinctual emotional and basic internal sensorimotor functions, which in turn are linked to exteroceptive SRP within cortical midline structures, we prefer to speak of basic "sensorimotor/emotional-affective forms of *selfhood*" which may be homologous in humans and other mammals.

At this point we will temporarily speak of 'selfhood' rather than 'self' in order to highlight that we wish to avoid any allusion to some fixed, *content-oriented* entity which historically has often been associated with the term self (see also above). The core-SELF is initially largely object-less, as far as the exteroceptive perceptual system is concerned. Moreover, 'forms of selfhood' are referred to so as to indicate that selfhood can appear on different levels of organization (e.g., sensorimotor, affective, cognitive) and perhaps even within one level of organization in different gestalts. For instance, the core-SELF, especially concentrated in the emotional circuits converging on the PAG, can presumably take on different global field dynamics depending on which emotional system prevails (Panksepp, 1998b), albeit there are no technologies available that can yet measure such states (not unlike the problem in measuring gravity waves directly). Finally, the distinction between selfhood and self further underscores the idea of self as continuous and process-based in character, leading to a process-oriented definition of selfhood as opposed to the concept of self that has often been assumed to be fixed and discrete. Such a process-oriented definition of selfhood may also shed new light on abnormal changes in subjective experience of the self in psychiatric disorders like schizophrenia and problems like multiple personality or dissociative identity disorders (Kircher & David, 2003). We will now just revert back to this process linked usage of "the self".

Why do we need the concept of a SCMS originating core-SELF? What does it add? (i) It clearly envisions the organism as an *active* organism (Panksepp, 2000a)—one that is able to actively represent its needs in the world, based on learning, for instance where the dopamine based SEEKING system sets up an urge to explore the world, establishing a knowledge base, and facilitating foraging for resources (Alcaro et al., 2007; Ikemoto & Panksepp, 1999; Panksepp, 1982). (ii) We assume that by means of SRP the SEEKING system, and other basic emotional systems (Panksepp, 1998a) may be specifically and selectively related and adapted to the respective environment. For instance, it is by means of SRP that the SEEKING system becomes relational and consequently tuned to and eventually guided by environmental contexts through emotional learning. (iii) Thus, the core-SELF is a process through which consciousness first emerged (Panksepp, 1998a, 2000b) and we gain knowledge about ourselves and our environments. It is this emerging coordination and knowledge of internality and externality, a mind-body-world connection, from the periconscious substrates of the lower "core-SELF " to the higher "extended-selves" (which may lead to higher representations of selfhood, partly through the epigenetic programming of mirror-neurons in various regions of the neocortex (Uddin et al., 2007)) enabling "higher" (i.e., the well-cerebrated) animals to gradually become intentional and cognitively empathic agents in the world (for extensive discussion of this issue, see Watt, 2007 and accompanying commentaries).

With the resulting intentionality, foresight, and ability to make useful decisions (e.g., generate empathic responses), animals come to actively represent their needs in the world on the basis of the above-described world relatedness as established by self-related processing. The self-relatedness provides the organism a basic form of attachment to others and the environment on the basis of which the organism, by using its cognitive capacities, can identify itself with others, events, or objects in its environment. Due to different cognitive dispositions in different species, the ability to self-identify may differ among species whereas they may share the more basic sense of relatedness to their respective environments and circumstances. For instance, in the evolution of cooperation, the ability of animals to simply coordinate their behaviors with others (e.g., "generalized reciprocity") may precede the capacity to restrict reciprocity to specific others (Rutte & Taborsky, 2007).

From this perspective, what unifies and categorizes stimuli is no longer their primary sensory origins but the strength of their relation to the self (e.g., *ipseity* as discussed by Kircher & David, 2003) and to environmental contexts. The more a given stimulus is associated with the organism's sense of belongingness, the more strongly it is related to the self and, at the same time, to the self-referential aspects of environments (i.e., those aspects of the world that have affective-survival implications). Therefore, the strength of the self-stimulus relation emerges gradually, through learning, and is assumed to be determined not in absolute terms but only relatively since it depends on the contextual issues (e.g., autobiographical and exteroceptive and spatial factors) and the accompanying cultural and social environments.

In sum, the process of relating external stimuli to the self can't be considered an isolated cognitive process but rather a relational, contextualized and affectively embedded process that depends on the respective environmental and ecological contexts (Clark & Nothwehr, 1999; Northoff, 2004). The emergence of self-related information processing, therefore, is at heart affective and relational—involving stimuli from the external environment and relating them, often idiographically, to individual organismic needs and desires. In other terms, core-SELF constituted SRP becomes ecological and social and thereby may eventually also be understood within the broader functions of social-emotional communication (Izdebski, 2008; Zinken, Knoll, & Panksepp, 2008).

7. SRP controls actions

To be useful (adaptive not only in proximal mechanistic but also in terms of ultimate distal evolutionary perspectives), SRP has to (and had to) better relate organisms to their environments. Since the organism can connect to its environment

via both sensory and motor function, one would expect SRP to concern not only sensory but also motor integration. The self is expressed in motor function in terms of agency and ownership—two functions associated with the motor domains that are essential for an organism to relate to and to appropriate its environment. In this way organisms become intentional, active agents in their environments (Blakemore & Frith, 2003), where information is actively harvested from the environment.

Agency describes the sense or feeling of being causally involved in actions, engendering a "sense of effort" which may correspond to anticipatory mechanisms with pre-movement motor commands that characterize experience-expectant mechanisms. The feeling of agency, presumably arising from an integrated network of self-related processing, engages conscious use of an individual's body as an instrument in the surrounding environment—yielding a "stimulus appropriation," a sense of ownership for what happens, as organisms behave in the world. With similar intent, Jeannerod (2003) speaks of a "who system" that enables a subject to attribute an action to its proper owner. While ownership describes the attribution of action to a particular person, the "mineness" of action and movements, agency refers to the feeling of being the cause of an action—this action is "mine" (i.e., ownership), and "I caused the action" (i.e., agency), Both may need to be distinguished as distinct from the self-relatedness of action. Gallagher, Zhang, Morrow, & Forget (2004) associates ownership with the phenomenal level, there is phenomenal experience of "mineness," whereas he 'locates' agency on the reflective level as the result of higher-order cognitive involvement.

However, similar to agency, ownership, may also depend on sensory feedback mechanisms allowing the self-referential consequences of each movement or action to be perceived by each individual (Gallagher, 2000; Gallagher & Frith, 2003). Both ownership and agency may thus be considered as distinct forms of sensorimotor integration by means of which self-relatedness as the relation between sensory and motor stimuli is constituted. We will now consider how many other brain functions, especially action related ones, get into medial cortical SRP; these examples also help highlight how the varieties of extended selves, more idiographic in their structure, may be constructed by specific life experiences.

There is threefold support for the involvement of motor regions in SRP. First, studies of agency demonstrated involvement of motor regions. Farrer and Frith (2002) conducted PET studies investigating agency where subjects had to draw a circle and mentally attribute the action seen on the screen to themselves. In the control condition, subjects were also told to draw a circle but were shown that the experimenter drove the action on the screen. Being aware of causing the action was associated with activation in bilateral anterior insula, SMA (supplementary motor area), lateral premotor cortex, and primary sensorimotor cortex that are all closely connected with the SCMS described above. In contrast, attributing action to another person promoted activity in the right inferior parietal cortex. In a second set of experiments, Ehrsson, Spence, and Passingham (2004) investigated ownership in the process of self-relatedness of movements in *brain* imaging. In one experiment, the feeling of ownership increased activation in bilateral premotor cortex. Additionally, the magnitude of activation in premotor cortex significantly correlated to the degree of ownership measured with a visual analog scale. Other regions activated in studies of ownership include the ACC (anterior cingulate cortex), motor cortex, cerebellum, and the posterior parietal cortex; see Jeannerod (2003) for a summary of their many studies of motor ownership, as well as Blakemore, Wolpert, and Frith (2000), and Blakemore (2003) for various studies of sensory ownership. Finally, a third set of studies of SRP in other domains showed that the motor domain also demonstrated regions involved in motor processing like the MLR, the caudate and the lateral premotor cortex (see Heinzel et al., 2005; Northoff et al., 2007). Though all these regions are not by themselves part of the subcortical-cortical midline network, they are closely connected with midline regions and therefore assumed to be directly modulated by SRP (Öngür & Price, 2000).

Although the lower aspects of the autonomic motor apparatus (e.g., micturition, defecation, etc. have been well described in animal and human models (Holstege & Saper, 2005), the higher aspects of agency remain to be imaged in animal models. As noted earlier, the animal models are much more effective in characterizing the lower emotional-affective-instinctual aspects of brain functional systems that are similar in all mammals—the "intentions in action" and simple forms of emotional learning (e.g., classical and instrumental conditioning) that characterize the basic emotional systems (Panksepp, 2003). In this context, we should also note that complete damage of the lowest midbrain integrator for emotionality, namely the PAG, compromises all world-directed action tendencies in animals (see Bailey & Davis, 1943; Panksepp, 1998b). Such animals lose all intentionality, and seem to be barely conscious (Bailey & Davis, 1942); this highlights how severely compromised are both agency and ownership of experience when the most fundamental emotional-affective SELF-generating functions of the brain are destroyed.

In contrast, human studies are more effective in dealing with cognitive as well as cognition–emotion interaction functions of the brain. However, there are various studies indicating that humans and other animals can use their higher brain systems for generating cortical neuronal responses that can be used as surrogates for instrumental responses (Kübler & Kotchoubey, 2007), and the population vectors of neural systems that control specific kinds of movements are beginning to be characterized (Chapin, 2004; Sanger, 2003). These could be used as surrogates for measurements of cognitive "agency" in animal brains. Also, the discovery of mirror-neurons in animals (Gallese & Freedberg, 2007; Iacoboni & Mazziotta, 2007), provides a potential gateway into certain agency processes of higher regions in animal brain. These models remain to be used to try to map out higher core-SELF processes in animals.

8. SRP and emotions

SRP is not just a process of ownership identification. Each stimulus is either implicitly (e.g., affectively and autonomically) or explicitly (e.g., cognitively) evaluated according to its possible value for the organism. Value is expressed in action as well

as affect (Panksepp, 1998a, 1998b, 2005a, 2005b). When objects and events are viewed *through the 'eyes' of the organism,* stimuli are presumably no longer simply objective aspects of the world but, as in most humans, they become subjective and thereby affectively colored with various positive or negative associations. For example, the Implicit Association Task (IAT) used in humans, and based upon reaction time measures, assesses the degree of association between the self and positive versus negative concepts. Greenwald and Farnham (2000) observed that participants were much faster to respond when self-related items (e.g., their birth month) were paired with pleasant words than when self-related items were paired with unpleasant words. Hermans (1999) introduced a so-called valuation theory, a phenomenological theory of the self, where the self is conceived of as an organized process of valuation. This has also been a prominent theme in psychoanalysis (Green, 1999) and in neuroscience (Panksepp, 1998a, 2005a).

A valuation is considered any unit of meaning as having positive (pleasant) or negative (unpleasant) value by the individual—and these affects come in varieties that remain to be neuroscientifically tabulated (semantic tabulations are a pale shadow of the real things). Each valuation has an affective connotation, a feeling, which results in what James (1892) described as "self-feeling" or as "self-qualia" (Kircher & David, 2003). The process of valuation then is closely tied to what we describe as SRP. Subsequently, SRP may be understood more broadly as the cognitive categorization of stimuli as self-related through their association with specific affective or emotional qualities. Although experimental psychology commonly only accepts two primordial affects, negative and positive (e.g., Barrett, 2006), in fact the evidence suggests that the brain is genetically provided with the capacity to experience many distinct affects, and an epistemology has been outlined for how we can causally link certain ones (e.g., emotional affects) to neuroscientific understanding (Panksepp, 2005b, 2007a, 2007b, 2007c, 2007d, 2007e). We conceive these to be the basic tools of the core-SELF, which allowed at least one major form of mentality—experienced affective states of the nervous system—to emerge in brain evolution. It remains possible that this was the primordial neural scaffolding for all forms of consciousness, especially since damage to the primary convergence zone of emotional systems in the core-SELF, the PAG, has devastating effects on consciousness (Bailey & Davis, 1942, 1943).

The close psychological linkage between self and emotions makes it rather difficult to dissociate both SRP and emotional processing in neural terms. Several studies investigating emotions observed activation in anterior CMS including the vmPFC (e.g., ventromedial prefrontal cortex), the ACC, and the dmPFC (e.g., dorsomedial prefrontal cortex; see Phan, Wager, Taylor, & Liberzon, 2002, for an overview). Does this involvement of anterior CMS during emotions indicate self-related processing? Phan et al. (Phan et al., 2002, 2004) investigated the degrees of self-relatedness during emotional processing. Subjects had to appraise the extent of personal association of emotionally salient pictures during fMRI. The fMRI results were correlated with subjective ratings (conducted after imaging) appraising the degree of self-relatedness of the picture content in a visual analogue scale. Regions associated with self-relatedness were located in the CMS including vmPFC, pACC (e.g., perigenual anterior cingulate cortex) and dmPFC, the latter two appearing only with increasing degrees of self-relatedness (other regions activated in relation to self-relatedness concerned the insula and the N. accumbens): The more self-related the picture content was appraised, the more activation was observed in these regions.

Other studies directly compared ratings of self-relatedness and emotional intensity/valence and observed neural activity in the dmPFC to be directly linked to SRP (Macrae, Moran, Heatherton, Banfield, & Kelley, 2004; Moran, Macrae, Heatherton, Wyland, & Kelley, 2006; see also Heinzel et al., 2005; Northoff et al., 2007). Subcortically, the Nucleus Accumbens was also found to be parametrically modulated by the degree of self-relatedness (Northoff et al., 2007) which suggests that self-related processing, as suggested by studies of reward, somehow involves the anticipation of events and associated feelings of aliveness and eager anticipation rather than mere consummatory pleasure (Alcaro et al., 2007; Ikemoto & Panksepp, 1999; Panksepp, 1998a). Interestingly, the right amygdala, generally deemed to be *the* key integrator of negative emotions (in fact, many other brain regions are as important), has also been implicated in SRP (see Murphy, Nimmo-Smith, & Lawrence, 2003; Northoff et al., 2007; Phan et al., 2002, 2004). The apparent participation of these subcortical regions in self-relatedness is thus strongly indicative of the involvement of valuation and affective processes in self-related processing. We tentatively consider the amygdala and the N. accumbens as major convergence zones for self-related and emotional processing where the self-related relationships between core affects and valuation of external stimuli are solidified.

However, there are such a large number of basic affective processes that what applies to primal *emotional* affects (e.g., anger, fear, etc.), does not as clearly apply to *homeostatic* (e.g., hunger, thirst, etc.) and *sensory* affects (e.g., tastes, touches and other stimuli on the body surface). For instance, it is clear that the insula has a primal affective mapping system that appears to integrate various bodily-homeostatic conditions to sensory environments (Craig, 2002, 2003). Thus, these more laterally situated limbic regions of the old cortex, long implicated in affective issues (MacLean, 1990), should be envisioned as places in the brain where meta-representations of *sensory affects,* different from the basic *emotional affects* are organized. Providing the integration between intero- and exteroceptive stimuli, these regions may be crucial in intrinsically linking the organism to the environment in implicit and automatic ways and it is here where the basic sense of self, the trans-species core-SELF, may become reconstituted in an embedded and contextualized way.

9. SRP is implicit and automatic

We assume that self-related information processing does not typically occur on an explicit and consciously *aware* level—in a cognitively explicit way—even though it may be rich in affective consciousness (Panksepp, 2000a, 2007c). Instead, we assume it to be either cognitively preconscious or unconscious and thus implicit, but accompanied by experienced shifts

in affective feeling states that are pre-propositional and hence hard to put into words. Koole, Dijksterhuis, and Knippenberg (2001) demonstrated that the so-called "name letter effect" or initial preference, people preferring letters that are contained in their own names especially at the beginning of their first name, occurs without conscious awareness. People judged words and letters associated with their own name as more beautiful than non-associated ones while not reporting to have any thoughts about this. Another test tapping implicit self-esteem is the IAT as described above. Therefore, Lieberman, Jarcho, and Satpute (2004; see also Satpute & Lieberman, 2006) speaks of an X-system—an intuition-based implicit and automatic self-knowledge that is largely responsible for the social, intuition-based, context-dependent, affective and automatic processes that guide our habits and impulses in daily life. The X-system is contrasted with a C-system, an evidence-based self-knowledge that involves cognitive and controlled, i.e., non-automatic and conscious, processes of reflection that guide our cognitions when conflicts arise. Broadly speaking, the X-system may imply an implicit nomothetic self and thus what we called SRP whereas the C-system may rather refer to an explicit or cognitive self that is more variable across individuals and hence idiographic (see below). Interestingly, Lieberman et al. (2004) investigated the neural correlates of these two systems of self-knowledge. They observed activation in the vmPFC, the N. accumbens, and the amygdala during intuition-based self-knowledge whereas evidence-based self-knowledge induced activation in lateral prefrontal cortex, hippocampus and posterior parietal cortex.

Automatic processing can be defined in terms of various characteristics like lack of conscious awareness, effortlessness, lack of intentionality, and an inability to control the process (see Anderson, Reznik, & Glassman, 2005; Koole et al., 2001). For example, SRP cannot be activated and deactivated at will. An individual may be able to influence and modulate the degree of self-relatedness a stimulus is attributed but we remain unable to escape the process of SRP as such altogether. The term 'automatic processing' thus implies at least partial if not complete independence of SRP from cognitively conscious modulation as would be achieved through directed attention and explicit evaluation. Correspondingly, the concept of an automatic self (Koole et al., 2001) has been suggested and characterized by operating automatically at an implicit, cognitively non-reflective level, yielding automaticity in self-evaluation without deliberative thought, often in situations with decreased cognitive control, and commonly associated with positive emotions.

Automatic and implicit processing of the self may be relevant in both linguistic and non-linguistic species. Automatic and implicit SRP may account for a basic relation between organism and environment, the "sense of relatedness," which in turn may enable the organism to communicate non-verbally, independently of any linguistic abilities. Much of this could happen with emotional sounds. Conceptually, William James's assumption of rapid emotional processing occurring before conscious awareness and Damasio's concept of background feelings may reflect some automatic processing in non-linguistic species which provides the basis for subjective experience and primary, e.g., affective consciousness to occur. Empirically there is indeed some evidence for such assumption. For instance, even rats make positive affective sounds that fulfill many of the characteristics of social laughter (Panksepp, 2007c; Panksepp & Burgdorf, 2003); the circuitry of this response lies along the SCMS, especially the mesolimbic dopamine system, and hence mediates affectively rewarding feelings (Burgdorf, Wood, Kroes, Moskal, & Panksepp, 2007).

A more complex example of such non-verbal communication is empathy, whereby an organism can relate to another one emotionally, which is present in both animals and humans. It is increasingly realized that animals do exhibit empathic behavioral processes, from mice (Langford et al., 2006) to primates (Preston & de Waal, 2002) and that such abilities are dependent very much on social emotional systems (Watt, 2007), which may constitute the very foundation of higher forms of communication (Panksepp, 2008a, 2008b; Shanahan, 2007). Accordingly, the automatic and implicit processing of self-relatedness may provide us with a basic non-verbal means of communication with others which as such remains independent of the presence or absence of linguistic abilities, but which may have been a key communicative substrate upon which linguistic abilities were built.

Taken together, these results suggest that the linkage between self and affects occurs implicitly and therefore the underlying process remains pre- or unconscious. SRP may consequently be characterized as affectively felt but automatic and must therefore be distinguished from self-conscious awareness that is cognitive and explicit. How are the "implicit and affective forms of selfhood" (we assume these are the nomothetic aspects of the self) and the various "explicit and cognitive forms of selfhood" (the idiographic aspects) related to each other in neurobiological terms? Some studies reported activation (and increased functional connectivity) in anterior and posterior CMS during self-related tasks with low cognitive load (Greicius, Krasnow, Reiss, & Menon, 2003; Kjaer, Nowak, & Lou, 2002; Lou et al., 2004; Wicker et al., 2003). Conversely, deactivation (and low functional connectivity) in CMS has been observed in tasks with high cognitive load and low degrees of self-relatedness (Greicius et al., 2003; Gusnard, Akbudak, Shulman, & Raichle, 2001; Gusnard & Raichle, 2001; Kelley et al., 2002; Raichle et al., 2001; Simpson, Drevets, Snyder, Gusnard, & Raichle, 2001; Vogeley et al., 2004; Wicker et al., 2003).

These findings suggest reciprocal modulation between self-related and higher-order cognitive processing: activation in CMS corresponds to SRP predominating, with higher-order processing remaining in the background. In contrast, deactivation in CMS reflects increased higher-order processing while SRP shifts into the background. The assumption of reciprocal modulation between self-related- and higher-order deliberate cognitive processing is affirmed by recent observations of reciprocal modulation between medial and lateral prefrontal cortex during emotional–cognitive interactions (Goel & Dolan, 2003; Northoff & Bermpohl, 2004; Northoff et al., 2004). Comparable reciprocal modulation between medial and lateral prefrontal cortex remains to be demonstrated for the interaction between self-related- and higher-order information processing.

In addition to the reciprocal modulation between medial and lateral prefrontal cortical regions, we assume convergence in the interaction between subcortical and cortical midline regions. Subcortical regions may determine the basic

self-relatedness of the organism by coding the relation between different stimuli: interoceptive, exteroceptive, motor and emotional. This relation is expressed in affective and valuative terms. The resulting "sense of relatedness" may then be further elaborated in cortical midline regions in cognitive and temporal terms. Higher-order cognitive abilities like attention, impulse control, working-memory, executive functions, etc., may allow a representation of the "sense of relatedness" on a cognitive or high mental level independent of any actual stimulus. This allows an organism to distinguish one's "sense of relatedness" from others' "sense of relatedness" and thus from the environment, resulting in what we above called a "sense of distinction." Depending on the cognitive equipment and the prefrontal cortical development, different species may or may not share the ability to explicitly distinguish themselves to varying degrees from others and from their environment. However, the data stream runs thin on such a conjecture. In fact, even laboratory rats and mice are quite adept at distinguishing individual others via their olfactory signatures, a test that has been effectively used as a measure of social memory (Dantzer, 1998).

Beside such cognitive elaborations, cortical midline regions may also regulate the subcortically established "sense of relatedness" temporally. Recent studies in humans indicate that the cortical midline structures are involved in both anticipating future events and recollecting past events (see Schacter & Addis, 2007; Szpunar & McDermott, 2008; Buckner & Caroll, 2007; Addis, Wong, & Schacter, 2007). Furthermore, a recent human imaging study demonstrated that self-relatedness induced delayed signal changes more in cortical midline structures than subcortical ones (Northoff et al., 2008). What, however, is needed is further confirmation of these findings not only in humans but also in animals. Taken together, this leads to the rather speculative assumption that cortical midline structures may be crucially involved in temporally extending the subcortically processed here-and-now immediacy of self-relatedness. By delaying or anticipating neural activity and dissociating it from the presence of the actual stimulus, cortical midline structures may put the already established self-relatedness into a wider temporal context when compared to subcortical regions where it seems to be tied to the actual presence of internal or external stimuli and state-control functions (e.g., basic homeostatic and emotional states).

The main difference between different species might then lie not so much in the presence or absence of a basic sense of self-relatedness but rather in the width of the temporal span (e.g., from the disappearance of a stimulus) across which the stimulus' degree of self-relatedness can be processed and thus maintained. In other terms, cortical elaboration may extend the temporal window of self-relatedness (and consciousness) and may potentially make it more independent of the actual stimulus presence, which in turn allows for higher cognitive abilities like introspection to interact with phenomenal consciousness and pre-reflective self-awareness, resulting in reflective consciousness and reflective self-awareness (see above). We must admit though that this neuro-temporal subcortical-cortical hypothesis remains speculative at this point since the underlying neurophysiological mechanisms for such psychic functions remain to be empirically clarified. Certain lines of thought would implicate medially situated ascending dopamine systems, essential for SEEKING urges in all animals (Alcaro et al., 2007; Ikemoto & Panksepp, 1999; Panksepp, 1998a) which innervate higher brain more extensively in primates than rodents (Berger, Gaspar, & Verney, 1991), to expand and extend spatio-temporal processes within the brain (Previc, 1999).

10. Evidence for a trans-species self and the resting-state "default-mode network"

We now address the question of whether and how the concept of SRP holds across species and how its expression as a trans-species brain function contributes to our understanding of self in general. Although these issues have not been pursued with brain imaging, in general the medial brain structures implicated in SRP are the ones that have long been demonstrated to be essential for a large variety of emotional experiences, and the affective components typically intensify as one goes to lower and lower reaches of this network, with brain stimulation within the PAG having the most powerful effects at the lowest current levels (Panksepp, 1998a, 1998b). Since these lower subcortical reaches of the SCMS are clearly homologous across species and since SRP has been determined to be strongly affective at its core, with these lower cross-species brain regions being positively correlated with affective states in humans and higher cognitive brain regions generally exhibiting reciprocal relationships (Grimm et al., 2006; Northoff et al., 2004, 2007), it is evolutionarily appropriate to postulate that the basic brain mechanisms known to be involved in self-related affective processing in humans are evolutionarily related in all mammals, with diversification in various species-typical details but not general principles. This is consistent with our evolutionary model that the core mechanisms for raw emotional affective states, concentrated in subcortical medial regions of the brain, are homologous in all mammals (Panksepp, 1982, 1998a, 2005a, 2005b).

Still, in each species these emotional operating systems interact with different ecological, cultural, and neocortical environments, and these should dramatically impact how we envision the higher reaches of SRP and interactions with other higher reaches of the brain. Indeed, it is becoming clear that as different animals value many different aspects of the world, their higher SRP processes must remain dynamically environmentally informed. Likewise, since social development of all mammals, as that of humans, is relational, the same external stimuli may be related differently to the organism in different situations depending on the importance and meaning of particular stimuli within environmental contexts. Thus, what becomes represented in our perceptions are not just environmental objects and stimuli, but organism-environment relationships and social interactions that are mediated affectively.

Although the presence of many morphological homologs in similar brain regions of all mammals does not necessarily guarantee fundamental similarities in functions, it is a reasonable working hypothesis that homologous psychological

processes—similar basic tools for living—do emerge from homologous brain networks (Panksepp, 1998a). Indeed, current evidence suggests that the functional similarities in all mammals at midbrain and diencephalic levels are truly remarkable (Denton, 2006; MacLean, 1990; Panksepp, 1982, 1998a, 2005a). Social affiliation tendencies, courtship and mating, maternal care, separation distress, and social bonding tend to be conserved across many species, as do angry and fearful behaviors, as well as playfulness and vocal expressions of social joy (Panksepp, 2005a, 2005b, 2007a, 2007b, 2007c, 2007d, 2007e). The same goes for homeostatic regulatory processes such as thirst, hunger and thermoregulation (Denton, 2006).

Further up, the functions of basal forebrain, extended amygdala and related limbic structures seem conserved. The behaviors dependent on them are similar and suggestive of deep homologies, as mirrored in recognition of conspecifics, potential mates, or competitors, through practically all sensory modalities across species. On the other hand, even though the columnar structure of the neocortex also seems to be conserved across species, this repetitive "columnar" tissue appears to be largely a *tabula rasa* on which experience can transcribe the details of individual lives, partially by traditional associationistic learning principles but probably more intensively by life-long epigenetic engraving of specialized, functional networks (as some like to say, in "modules," albeit that is a concept of dubious neuroscientific value) into the initially general purpose cortical terrain. Strong evidence suggests that even the basic perceptual functions, as in visual cortex, are epigentically created rather than genetically dictated (Sur & Leamey, 2001). In other words, critical neuroscientific experiments have made it clear that the functional parcelation of those regions is much more dependent on the functional parcelation of cortical functions by subcortical innervations and individual experiences than any evolutionarily prescribed "functional modularity." This solves many genetic mysteries—such as how ∼22,000 genes could construct a functionally competent MindBrain. The genes only provide foundational processes—basic tools for living—allowing the developmental landscapes of epigenesis and learning to do the rest. Lateral neocortex is prime neural territory for the gradual development of idiographic selves.

As noted earlier, it is of great importance to determine whether the mirror-neurons found in widespread regions of the neocortex (Iacoboni & Mazziotta, 2007) encode their functions genetically or epigenetically. We favor the latter alternative. Just like the visual cortex gets programmed by more tightly genetically-controlled subcortical circuits, we believe this applies to mirror-neurons as well as most of the "modular" functions of the neocortex that permit a massive variety of culturally-promoted, neocortically-based "conceptual acts" which promote vast variety of individual differences in secondary (learning-based) and tertiary (thought-based) emotions in human beings (Barrett, 2006), but which provides no good empirically relevant reason for denying the existence of cross-species basic emotions (Izard, 2007; Panksepp, 2007e).

More individual variation does occur in these higher brain regions, as life experiences construct epigenetic landscapes, commonly unique-idiographic ones, which are more heavily dictated by cultural and individual learning/ecological constraints. The recognition of the power of epigenetic developmental lanscapes led us to postulate that "most of the higher aspects of the human brain/mind arise largely from the interaction between general-purpose neural systems of the multimodal cortical association areas and the very basic life experiences encoded by more ancestral emotional/mind systems that all mammals share" (Panksepp, 2008b; Panksepp & Panksepp, 2000). Thus, to the extent that certain more primitive levels of SRP are shared among mammals (MacLean, 1990; Panksepp, 1998a), it is reasonable that a core-SELF is also shared among them (yielding a nomothetic infrastructure for mental development). This provides the evolutionary basis upon which we claim SRP to be a trans-species process and postulate that the general principles underlying the neural infrastructure of the SCMS is homologous in all mammals (Northoff & Panksepp, 2008).

Most importantly for our current analysis, the archaic subcortical-cortical midline structures include what traditionally has been described as the limbic system (MacLean, 1990). Because of abundant neural and functional homologies (Panksepp, 1998a), the limbic system, concentrated in medial regions of the brain provides a rationale for postulating remarkable cross-species similarities in the evolutionary construction of a core-SELF. The limbic system and thus the rather ancient subcortical-cortical midline networks may therefore provide a solid foundation for SRP across different species. The mushrooming of neocortical fields, permitting increasingly sophisticated cognitive and memorial capacities, allowed organisms already possessing core-SELF structures to become active agents in the world as opposed to passive ones that survived largely by responding to stimuli. This has forced us to envision, contrary to many prevailing trends in modern neuroscience, a distinct type of emotional action (SEEKING) system (Alcaro et al., 2007; Panksepp, 1998a; Panksepp & Moskal, 2008). Thus, we envision these subcortical-cortical midline systems, interacting with the seemingly random access processors of association neocortex, constrained only by their multimodal connectivities, to provide a credible neural account of "embeddedness" as a way for animals to meld into variable aspects of the environments in which they must live (Northoff, 2004; Varela, Thompson, & Rosch, 1991).

This leads us to another central feature of the subcortical-cortical midline system. A unifying characteristic is the high resting state activity with spontaneous fluctuations in these regions, the so-called default-mode network, which has been observed in both humans (Raichle et al., 2001; Fox & Raichle, 2007; Fransson, 2006; Damoiseaux et al., 2006) and chimpanzees/macaques (Vincent et al., 2007; Rilling et al., 2007). One however has to say that high resting state activity in these studies focuses especially on the cortical midline structures while subcortical midline regions seem to be spared (even though they probably have a different type of resting activity that is currently harder to measure because neurons in those brain regions have very low resting activities). Another limitation is that high resting state activity does not seem to be specific for the subcortical-cortical midline system since to some extent it occurs, indeed must occur, throughout the brain (see Fox & Raichle, 2007). What seems to be specific, however, especially for the cortical midline structures (the default mode network) is that they show predominant deactivation, i.e., negative signal changes, in fMRI (see Fox & Raichle, 2007; Raichle et al., 2001). As observed in a recent study in humans, the degree of self-relatedness engendered by different emotional

pictures modulated predominantly negative signal changes in a variety of subcortical and cortical midline regions (see Northoff et al., 2008). This indicates that the resting state activity in these regions might be rather high and can no longer be elevated by external stimuli, resulting thus in predominantly negative rather than positive signal changes, especially when there is some substantial subcortical emotional arousal. It is possible that the brain does not readily integrate incoming information during such active emotional arousal, and that this tends to occur during resting states, potentially accounting for the high level introspective activity during these periods of time. Based on our own (Northoff et al., 2008) and others' (d'Argembeau et al., 2005; McKiernan, D'Angelo, Kaufman, & Binder, 2006) research, we assume that such high resting state activity in the subcortical-cortical midline network may reflect what we have identified as self-related processing, the continuous process of coding the relation between interoceptive, affective, motor and, if present, exteroceptive stimuli. Such continuously ongoing processing of self-relatedness even in the absence of new streams of exteroceptive stimuli might allow us to maintain a continuous and temporally extended "sense of relatedness" and thus a "core-SELF," homologous across mammalian species (Northoff & Panksepp, 2008).

In other words, we assume that the continuous high resting state activity may be crucial in maintaining our relatedness to others and to potential future changes in the environment and thus what we describe as embeddedness. While high resting state activity may be regarded as "physiological baseline," continuous SRP even in the absence of exteroceptive stimuli may be described as "psychological baseline" (see Northoff & Bermpohl, 2004; Northoff et al., 2006). If this is true, exteroceptive stimuli might only modulate the already existing high-resting state neural activity and the corresponding degree of self-relatedness (see Northoff et al., 2008, for empirical support in humans). What is coded then in neural activity is the relation between the pre-existing degree of self-relatedness, as reflected in the level of resting state neural activity, and the exteroceptive stimulus' degree of self-relatedness. Future investigations in both animals and humans might then focus predominantly on the modulation of high resting activity by exteroceptive stimuli with different degrees of self-relatedness that might reveal what we call the subcortical-cortical midline systems neural reactivity.

To further support this hypothesis, one also needs to develop trans-species studies of self-relatedness employing the same task, thus extending the above-mentioned studies by Vincent et al. (2007) and Rilling et al. (2007). As also noted previously, one potentially neat way to do this in common laboratory rodents, who rely heavily on olfaction for identification of other animals, would be to see how they respond to the odor of either a strange conspecific or an important other species, such as the smell of cats for rats, on their modes of behavior and brain activity along the SRL continuum within SCMS brain regions.

11. Conclusion: ecological trans-species concept of self

A concept of a core nomothetic SELF may be elemental for understanding how brains work so as to represent organisms in their quest for survival. Such nebulous topics have traditionally remained outside the realm of neuroscientific discourse (e.g., of the many fine essays in Gallagher & Shear, 1999, only several address brain issues), but they may need more attention than has so far been common in the discussion of basic brain functions. If animals with limbic systems (MacLean, 1990) do indeed possess "core or mental selves" that have some self-similarity across mammalian species, it opens up new avenues for understanding how the capacity to experience emerged in brain evolution: the first glimmers of experiential states in brain evolution may have been premised on the existence of a proto-SELF that first represented the somato-visceral body (a diffuse autonomic "homunculus" in the upper brain-stem, followed by a core-SELF constituted of basic emotional actions that engender characteristic neurodynamics in the proto-SELF that constitute raw emotional affects.

This more implicit and strictly affective form of selfhood might thus reflect what in humans has been called the "mental or core-self" (Damasio, 1999), "experiential self" (Lambie & Marcel, 2002; Zahavi, 2003), "primitive form of selfhood" (Gallagher & Zahavi, 2005; Legrand, 2005), or "minimal self" (Gallagher, 2000; Gallagher & Frith, 2003; see also Baars et al., 2003; Dalgleish, 2004; Lambie & Marcel, 2002), the lowest mode of the "consciousness of the self" (Pinku & Tzelgov, 2006), the synchronic unity of self (Carruthers, 2007), or simply the SELF (a Simple Ego-type Life Form in the brain), the first self-related construct postulated on the basis of animal neuroscience data (Panksepp, 1998a, 1998b). This basic substrate for self-representation has to be connected to the world, and this apparently occurs as animals become embedded in the world through SRP in the medial subcortical regions and various other cortical structures of the forebrain.

Since SRP allows organisms to become coupled to their environments (to be jointly informed by evolutionary and ecological constraints), we would conclude by speaking of selective-adaptive coupling (see Northoff, 2004). What is selective-adaptive coupling? Generally it allows mutual contact between brain, body, and environment. Accordingly, Noe (2004) speaks of "episodes of contact with the world." However, selective-adaptive coupling goes beyond that since brain, body and environment are not only in contact but also influence and mutually determine each other. For instance, van Gelder and Port (1995, p. 373) speaks of a "matter of coupling, such that both sets of processes (i.e., the inner brain and outer world processes) continually influence each others' direction of change." Edelman and Tononi (2000) highlight "selective matching that occurs between ongoing, distributed neural activity and various signals coming from the world, the body, and the brain itself" (pp. 94–95, see also footnote 2 on p. 238). We postulate that it may be self-related processing as mediated by subcortical-cortical midline networks, which generates a basic nomothetic sense of self, that allows such selective-adaptive coupling in many different species. Of course, humanistic scholars are not wrong when they assert that there exists a diversity of cognitive selves across different individuals and cultures. These diverse idiographic forms of selfhood, we assume, remain

integrally linked to the more universal affective and SRP aspects of the self, concentrated in midline structures, which a cross-species neuroscience is finally well positioned to focus both its conceptual and empirical efforts.

Finally, we would reiterate that in the present relational view, the proto-SELF is envisioned to be a coherent, albeit widely distributed entity in SCMS that is absolutely necessary for the constitution of consciousness; without such a foundational process, reflective self consciousness and awareness may remain impossible. However, this proto-SELF is not sufficient for constituting phenomenal consciousness since for that, as we assume, synchrony between a pure bodily representation that constitutes the core-SELF and many emotional-affective circuitries, to yield a core-SELF whose neural synchrony among various subcortical midline regions is necessary for affective consciousness to emerge. This then, provides a solid foundation for both higher forms of selves and reflective-cognitive forms of consciousness. Because of space and empirical limitations, we cannot go into fine-grained detail, but this suggests that the different levels of self are directly and progressively related to the constitution and increasing epigenetic growth of consciousness, affective complexity and the inextricable blending of emotions and cognitions in higher regions of the brain during early development (Panksepp, 2001).

12. Predictions and opportunities for future cross-species research

To help highlight how some of the ideas advanced above could be cashed out in new research, we share ten general predictions and a few more highly specific ones this view of brain organization generates (in which the key concepts need to be further operationalized):

- Without necessarily being able to specify what form it would take, there should be a *common form of neural coding* across species in subcortical and cortical midline regions in terms of the neural processing of self-relatedness.
- The dorsolateral cortical regions would, in humans, be prominently involved in processing the interactions between cognitions and higher forms of self-relatedness.
- In contrast, subcortical midline regions, in conjunction with medial frontal regions, would be prominently involved in processing the interactions between basic emotions and SELF-relatedness.
- The subcortical midline regions would be more involved in generation of implicit and automatic SELF-relatedness. In contrast, cortical midline regions would be more involved in explicit and more deliberative self-relatedness.
- Extrinsic self-relatedness in cortical midline regions would be more dependent on external stimuli and past life histories, especially in emotionally arousing situations, while intrinsic SELF-relatedness in subcortical midline regions would be more independent of external stimuli and more dependent on the emotional tools evolution built in, as basic tools for living, within lower midline regions of the brain.
- The "resting state of the brain" monitored from cortical midline regions would degrade with damage of subcortical midline regions such as the PAG and medial diencephalons (e.g., especially the diversity of medial forebrain bundle systems).
- Medial frontal cortical damage will impair the ability of individuals to perceive the world with a strong sense of personal meaning.
- Medial frontal cortical damage will promote sociopathic and psychopathic mentation, as self-related processing of information in the context of other selves diminishes, degrading the possibility of empathy.
- There will be more alpha rhythm blocking (i.e., Event-related dysnchronizations) in medial cortical structures when individuals are analyzing situations from first-person points of view, as when dwelling on personally meaningful situations.
- Perhaps most tellingly, we predict that normal brain death will proceed from lateral to more medial brain regions, and the lowest medial regions, such as the PAG, at the interface of proto- and lower core-SELF structures will be the last neural tissues to die, which may help explain various out-of-body experiences accompanying near-death experiences.

13. Coda: toward a neurobiology of the soul?

It has not eluded our attention that ultimately research on the SCMS continuum that integrates lower core-SELF with higher core-SELF processes may have profound implications for understanding the biological nature of the "soul" (Panksepp, 2007d). The classical view that brain-body and soul are distinct and incommensurate entities can finally be countered neuroscientifically (Crivellato & Ribatti, 2007; Dolan, 2007) without necessarily contradicting traditional religious thought (Murphy, 2003). Although there are bound to be abundant debates about the relevance of such cross-disciplinary constructs, as well as what are the most relevant neuroscience perspectives (Panksepp, 2000c; Panksepp & Watt, 2003), we think that it will be healthy for a cross-species integrative neuroscience as well as consciousness studies to conceptualize such foundational issues for the emergence of mind (Watt & Pincus, 2004) using neuropsychologically well-integrated first and third person perspectives (Northoff, 2004; Northoff et al., 2007; Panksepp, 1999, 2000d) that cultivate an active organism view rather than a passive one (i.e., a mere associative learning machine perspective) of how the brain operates. Passive organisms may not need a core-SELF, soul-type neural process. Active ones do.

Let us briefly address the issue of how visions of active vs. passive animals have influenced how we study the brains and minds of animals: A perennial issue in behavioral science has been to decide whether, in our scientific attempts to explain animal behavior, organisms are better conceptualized as active creatures seeking knowledge as they pursue their various

affairs or as passive organisms whose behavior is constituted largely by genesis of information processing and learning. The active organismic view, engendered by ethological analysis, conceives of animals being born with various instinctual action tendencies, so readily observed in natural environments (Burkhardt, 2005). The passive organism view was engendered by behavioristic analysis of animals in artificial environments, with behavioral options constrained by experimenter controlled stimulus-response-reward relationships that animals had to master in order to survive. This approach dominated Anglo-American experimental analysis of animal behavior and more recently behavioral neuroscience. The former approach was advocated by European ethologists, although, in general, it has engendered less experimental attention among neuroscientists. Ethological analysis, since it requires careful monitoring of many natural behavioral tendencies, is considerably more difficult to implement than the study of microswitch closures (e.g., lever presses). Accordingly, it has had less impact in molding neurobehavioral inquiries and theories. However, there is an enormous body of evidence to indicate that the active organism view, where a core-SELF structure may be essential for behavioral coherence, is the correct view of animals' nature (Panksepp, 1998a).

Accordingly, affective neuroscience strategies emphasize that all mammals possess various genetically ingrained, experientially refined, emotional-action systems, each of which can provide state-dependent regulation of learning and memory retrieval. This provides ways to coordinate the best of active and passive organismic approaches to the study of behavior and mind. Brain stimulation evidence indicates that one can evoke various emotional-instinctual action tendencies, that are accompanied by affective states, as evaluated by various choice tasks such as conditioned place preferences and avoidances, as well as the willingness of animals to turn such brain stimulation on or off. The variety of emotional-action patterns, accompanied by affective urgencies built into organisms, are impressive. Distinct behavioral tendencies evoked from stimulation of median upper brain-stem regions include seeking-foraging urges, fearfulness, anger tendencies, sexual eagerness, maternal nurturance, panicy social separation-distress, and social playfulness, all with complex patterns of autonomic and hormonal arousals (Panksepp, 1998a, 2005a, 2005b). The existence of such emotional systems mandates an active organismic view of the affective core-SELF concentrated in medial brainstem regions. These systems energize higher medial cortical regions to evaluate world events in self-referential ways (Northoff et al., 2006), permitting the linking of organismic urgencies to higher brain mechanisms that process information about the world entering through the sensory portals.

Consciousness is severely compromised after extensive damage in these regions, the subcortical midline infrastructure that engenders behavioral and apparently psychological coherence, and constitutes neural foundation for the active organism view of brain organization. Within this view, self-representation becomes a global aspect of the underlying brain organization, helping establish active emotional and motivational ground states for higher brain regions to harvest external information to allow better behavioral choices (see Alcaro et al., 2007 for a recent fine-grained description of how this transpires in the SEEKING urge system). The vision of a core-SELF advanced here allows integration of the abundant learning data, harvested with comparatively passive behavioristic information-processing paradigms, with ethological, active organismic visions of how living creatures, awash with self-referential affective states, evolved to cope with fluctuating environmental demands.

The kind of research that might be engendered by an active-organism perspective would include (i) a focus on how this complex network achieves global integration of a host of specific brain functions, (ii) how the underlying emotional systems regulate various epigenetic developmental landscapes, and (iii) how all of this figures in mental health and distress. There is clearly more ignorance than knowledge in this field, but the heightened enthusiasm to deal with such cross-species brain/mind issues should be both healthy and productive for the field in general, and especially for linking psychiatric and mental health issues to emotional endophenotypes (Northoff, 2007; Panksepp, 2006). With respect to types of specific projects that could be undertaken to address each of the above three issues, let us consider a few:

There may be an ancient viscero-somatic homuncular representation of a primal body schema laid out within the SCMS that provides the neural fabric for the overall integrative activity that is encapsulated in our proto-SELF concept (Panksepp, 1998b, 2000b). It would be important to characterize the bodily autonomic and endocrine changes that result from stimulating throughout this field (where proto-SELF and core-SELF processes interdigitate), and correlating these changes to the instinctual emotional actions and the attending affective changes that can be engendered from these brain regions (Panksepp, 1982, 1998a, 2005a, 2005b) as the neurodynamics become part of the core-SELF that employs the frontal CMS networks to engage in self-related processing of incoming exteroceptive information.

There is abundant evidence that various subcortical emotional systems become sensitized by life experiences (e.g., Ashton-Jones & Harris, 2004; Vanderschuren & Kalivas, 2000), and that they guide integrated learning processes, partly through the auspices of higher CMS regions of the brain (Alcaro et al., 2007; Ikemoto & Panksepp, 1999; LeDoux, 2002). How do these lower systems, interacting with various environmental events, help create life-long epigenetic landscapes in higher regions of the brain, that can decrease or increase resilience for a lifetime (e.g., Meaney et al., 2000; Panksepp, 2000a, 2000b)? This calls for detailed epigenetic studies where chromatin methylation and acetylation studies are conducted on specific genes expressed along the individual emotional command systems (Szyf, McGowan, & Meaney, 2008).

The implications of such long-term changes in the interactions of SCMS functions and the maturation of cognitive landscapes for mental health and emotional disorders should foster symptom-based endophenotypic thinking in psychiatry, which seeks to treat the real-life emotional symptoms of individuals as opposed to conceptual syndromes (Panksepp, 2006).

Acknowledgments

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