

# What is an emotional feeling? Lessons about affective origins from cross-species neuroscience

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**Abstract** Cross-species affective neuroscience aspires to provide an evidence-based foundation for understanding the *primary-process* emotional networks that concurrently control instinctual emotional actions and affective feelings—direct emotional circuit mediated ‘rewards’ and ‘punishments’. In humans and other mammals, the ancestral subcortical regions of the brain are central to such affective BrainMind functions (a monistic term, here used synonymously with MindBrain, depending on stylistic needs). Although these circuits cannot be ‘identical’ across species (that would be incompatible with evolutionary principles) they are sufficiently similar, anatomically, neurochemically and functionally, to allow animal brain research to illuminate (yield testable predictions) about homologous human mind functions. Primal emotional feelings (affects) are inbuilt value functions of the brain that energize and inform the rest of the mental apparatus about basic survival values, thereby promoting *secondary-process* learning/memory functions and *tertiary-process* cognitive thinking-ruminative functions, yielding bottom-up evolutionary controls that ultimately allow top-down regulatory controls. As we envision how such “nested” hierarchies—two-way paths of causality—reflecting both bottom-up and top-down functions—we will need disciplined distinctions between cognitions and emotions at the primary-process level, while also accepting total interpenetration of cognitions and affects at the tertiary-process level of MindBrain organization. This allows full and synergistic integration of basic and dimensional approaches to emotions. Here the primal

emotional networks, so critically important for understanding ‘human-nature’ and psychiatric disorders, are discussed didactically in ways that can minimize dilemmas that non-evolutionary, non-hierarchical perspectives are subject to in modern emotion research.

**Keywords** Primal affects · Emotions · Cognitions · Neuroevolutionary layers · Hierarchical controls · Psychiatric disorders

## Introduction

William James (1842–1910) published a famous essay with the title “*What is an Emotion?*” in *Mind*, 1884, that led to a fanciful, counterintuitive theory that was essentially wrong at the evolutionary foundational level, but remained influential in psychology for over a century (Ellsworth 1994), and still has its proponents. Robert Solomon (1942–2007) creatively summarized classic pre-neuroscientific theories of emotions in a collection of philosophical and cognitive essays on emotions by that same name in 2003. Both of these scholars had a deep appreciation of the diverse facets of human emotional experiences—multi-layered phenomenal states of mind—but they knew essentially nothing about how emotions arise from brain activities. Neither of these philosophers knew what emotions really are evolutionarily and neuroscientifically. Philosopher Paul Griffiths, better versed in the experimental evidence than his predecessors, came closer to a defensible experimental view in his heralded 1997 book, *What Emotions Really Are*, and we can now come even closer by paying attention to the increasingly abundant neural evidence, that unfortunately remains to be well-integrated into traditional psychological and philosophical perspectives. The aim of

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this essay is to clarify why the vast multi-tiered landscape of adult human emotional experiences is not as good a guide to understanding the fundamental nature of emotionality as brain research on other animals.

To be human is to have had innumerable emotional experiences, where certain forces of mind can seem overwhelming, driving our thoughts, reflections and outbursts in directions that, without emotional wisdom (Aristotelian *phronesis*, a higher cognitive function), seem beyond our control—with both the positive emotions (desire and lust) and negative ones (fear and rage) often leading to prolonged suffering. Apparently emotions have a mind of their own, and in Freudian theory, such forces were conceptualized as the “dynamic unconscious” since consciousness was, and often still is, conceptualized as “knowing one is experiencing something” rather than simply raw subjective “experience” itself. Most humans are enthralled, and perhaps most psychologists remain confused, by the power of emotions over human lives. A key question of emotion research is “What are these forces?” We simply cannot understand their ‘nature’ psychologically. Because of deep evolutionary roots, a cool-headed cross-species neuroscientific analysis may take us there more rapidly than any human research that we can presently conduct. Psychological science may be wise to accept those cross-species neurobiological foundations for its own phenomenological thinking and research. And theoretical disagreements should be premised on current cross-species evidence, rather than long-standing historical belief systems.

By necessity, our search has to be initially guided by our own emotional experiences. But a full scientific understanding must include, to a substantial extent, neuroscientific hypotheses based on emerging understandings of the primal sources of the diverse affective experiences of the brain that make emotional arousals so incredibly powerful and interesting. Perhaps many psychologists would still like it to be some other way—that feelings just like our ideas are simply conceptual acts. But few are willing to probe this well hidden underbelly of mind in animals. Thus, most psychologists are happy to pass on the responsibility for doing the necessary brain research to some other discipline, leaving psychologists to continue what they do best, weaving fairly complex conceptual-cognitive understandings from psychology-only experiments, now often supplemented by human brain-imaging correlates. That is useful, but no more so than a biological understanding of the primordial emotional-affective circuits of the brain in animals.

The question “What is an emotion?” requires us to combine, with conceptual grace and empirical rigor, the best of mental, neural, and peripheral psychophysiological analyses. There really is no other way. But there are modern resistances, not dissimilar to those that “the

behaviorists” promoted concerning the supposed irrelevance of emotions and other hidden entities within “*The Black Box*” for controlling, predicting and understanding behavior, and hence as accepted dimensions of their advocated curriculum for psychology. The classic behaviorist bias was only reversed by a funding crisis some 40 years ago—certainly not by the accumulating weight of evidence that neuroscience was providing. Obviously, behavioral techniques are incredibly powerful for controlling behavior, and also for understanding how behavior is controlled when combined with neuroscientific analyses.

In the 1970s, the shifting priorities in research funding in the USA, fostered by the emerging neuroscience revolution as well as a newly-minted “Cognitive Revolution” in psychology, led to a transformation of emotion studies. Funding dried up for behavior-only research, and many behaviorally oriented investigators, using exceptionally rigorous experimental approaches, shifted their work toward psychopharmacological and neuroscientific perspectives, with no more interest in animal minds than existed before. Thus, the new field of behavioral neuroscience sprouted and thrived. But to this day behavioral neuroscience has little taste for mental constructs in the animal-models that most investigators pursue. This has led to emotional research strategies (e.g., fear conditioning) where the affective feelings of animals are rarely discussed or experimentally analyzed. Their capacities to experience the world are still commonly denied, or simply ignored, since they are still outside the scientific Zeitgeist.

Concurrently, a few decades after the onset of the Cognitive Revolution, spurred on by the invention of new human brain-imaging technologies, mainstream psychology rapidly learned to integrate brain research with higher-order mental analyses that could be easily studied in humans. And a vast amount of research on higher neuromental functions is now being published in journals like the *Cognitive, Affective and Social Neurosciences*, *Emotions*, *Social Neuroscience* and many other journals devoted largely to human research. In these new intellectual endeavors, rich discussions of the neural nature of affective processes have failed to emerge. And this has impoverished a foundational understanding of both human and animal emotions and motivations. For instance, to this day, behavioral neuroscientists interested in emotions have difficulty talking about anger in animals, and those interested in feeding motivation have comparable difficulties discussing hunger.

Thus there is currently a large ontological/epistemological gap in both modern behavioral neuroscience and to a lesser extent cognitive neuroscience. The experiential (mental) properties of neural activities are generally not discussed or recognized even though it is a self-evident fact that all other mammals are profoundly emotional creatures

(Darwin 1872/1998), and not just behaviorally but also affectively (for recent discussion, see Panksepp 2011). The affective components of certain neural activities, as emphasized through this essay, can be systematically studied by the capacity of artificial arousal of brain emotional networks, with both localized electrical and chemical brain stimulations, to serve as rewards and punishments in a variety of learning tasks.

Cross-species affective neuroscience has now clarified the outlines of a variety of coherent emotional networks built into ancient subcortical regions of mammalian brains. To the best of our knowledge, we humans share these brain functions homologously with all other mammalian creatures (Panksepp 1998, 2005a, b; Panksepp and Biven 2011), perhaps many other vertebrates as well. There are reasons to believe that consciousness itself, in the form of raw phenomenal affective experience, is grounded on such brain mechanisms (Panksepp 2005a, b, 2009a, b). If we do not understand these primary-process aspects of human consciousness, it seems self-evident that we will not understand the ‘real-life’ emotional “wholes” that intrigue every thoughtful human being. Although all experimental work on the seemingly infinite complexities of biological brains must focus on the many component parts, the natural affective emotional-behavioral coherence of organisms allows us to envision reconstructions of the various parts back into the integrated wholes. The animal work can now make many specific affective predictions on the proclivities of our own species.

Without cross-species neuroscience, neither psychological nor cognitive neuroscience analyses are well suited for understanding the mechanisms that generate affective experiences. This essay will address a series of critical issues that are too commonly neglected when philosophers and psychologists think about the higher-order complexities of our emotional lives which, unlike primary process affects, are intimately related to the complexities of our cognitive lives.

The aim is to provide an essential foundation for the current patchwork of emotion research. In psychology, we are still in an *era of phenomenology*—describing the vast complexities of life—resembling that which existed in biology before the discovery that DNA was the hereditary material. Without an understanding of genetics, biologists were satisfied to catalog the complexities of nature, with no understanding of their sources. Likewise, without clear neuro-evolutionary approaches to the affective mind, our causal neuroscientific understanding of human emotionality will remain chaotic—focusing more on the diverse cognitive “shadows” of affect as opposed to the core underlying processes. As Nietzsche (1885/1996, p. 100) reflected “moralities are also merely a sign language of the affects.” When one looks at the mind closely, much of the

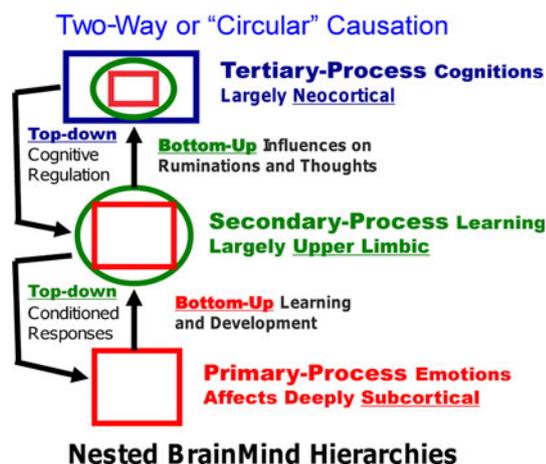
cognitive apparatus revolves around our primal affective concerns.

### Levels of evolutionary emergence in emotional control systems

Emotions are pervasive in the behavioral repertoires of other mammals, as Darwin (1872/1998) and most other ethologists have long recognized. For any constitutive (i.e. mechanistic) understanding of emotional behaviors and the associated feelings, we need homologous animal models where the needed neuroscientific work can be done in the needed detail. And the lower we go in the brain, the more assurance we can have that the findings will have substantive cross-species relevance, even up to the human condition. Of course, such comparative translational work is only as robust as the evolutionary homologies in the underlying brain mechanisms. But it does look like diversification has occurred much more at higher BrainMind levels than lower ones.

We now have abundant data to conclude that cross-species translational work will illuminate the human condition (e.g., Alcaro et al. 2010; Panksepp and Biven 2011). Unlike other bodily organs, mammalian brains exhibit clear evolutionary layering, if one knows how to read the existing neuroanatomical and neurochemical patterns (MacLean 1990; Panksepp 1982, 1998). The most ancient brain mechanisms remain situated more medially and caudally within brains—in their ancestral locations—with more recent developments added laterally and more rostrally, yielding interpenetrating “stratifications” that can inform us about distinct levels of control within the BrainMind. It is evident now that what emerged earlier not only remains in its original location, but is foundational for later developments. But it is not known exactly how. Perhaps lower emotional-affective functions are in some presently unknown way re-represented, perhaps in nested-hierarchies within the higher levels (Fig. 1). That is a reasonable way for the internally motivated brain to be organized, with more recent neural developments still being solidly grounded in what emerged earlier.

This does not necessarily mean that the brain is a strictly “hierarchically” organized organ, with just bottom-up controls. There are many top-down regulations. No doubt, in immature individuals the former routes of control prevail, and among mature ones, the latter. But each level brings new principles of organization into the overall equation. During development this kind of ‘hierarchical emergence’ leads to two-way (or circular) causality, whereby levels of control get integrated. Some psychopathologies may reflect specific problems at the various levels while others reflect failures of integration. Conceptually, there can also be



**Fig. 1** Schematic conception of nested-hierarchies where primary process affects are foundational and re-represented at higher levels of MindBrain processing. Adapted from Northoff et al. 2010

excesses of integration, as when psychologists, most interested in the higher levels, argue there are no meaningful distinctions between cognitive and affective processes. Such confluences fail to recognize key issues. At the lowest levels of affective organization, one is hard pressed to find any distinct functions that deserve to be called cognitive, unless one is willing to call those “unconditioned stimuli” (in behavioral parlance, “sign-stimuli” in the parlance of ethology) that trigger emotionality as being “cognitive”.

At these subcortical levels of affective organization, it is the so-called emotional “output” apparatus that is critical for organismic coherence. Here we have diverse emotional unconditioned responses and fixed-action patterns (e.g., freezing, flight, etc.). Perhaps surprisingly for some, these important “parts” of the overall emotion equation, already have feelings built into their neuronal infrastructures. Clearly, the higher emotional apparatus is built upon a solid foundation of “instinctual” *primary-processes*—genetically encoded network functions that provide organismic and emotional coherence to animals. These ‘emotional memories’—arising from genetically ingrained brain circuit functions—allow organisms to face key environmental challenges with little need for individual learning. However, these systems do provide a critical infrastructure for life-long learning to occur.

It is clear that all mammalian brains contain such “basic” emotional networks (Panksepp 1982, 1998, 2005a, b), but they probably are the least studied, and understood, foundations of our affective life by investigators of emotions. This should not be as surprising as it may initially seem to be. The nature of affect is one of the hardest mental entities to study experimentally in humans. In contrast, it is among the easiest to pursue neuro-scientifically in animal

models. But why is that not happening? There are more than a few historical flies in current conceptual stews that prevent integrative understanding. Among the biggest is the resistance of many in the behavioral neuroscience community to deploy affective concepts. Another is the understandable attraction for cognitive psychologists to focus on the higher levels of emotional controls that are full of psychologically attractive regulatory nuances. Thus, on the one hand behavioral neuroscientists recuse themselves from affective discussions. On the other, this encourages psychologists interested in higher mental functions to neglect the cross-species affective foundations of emotional life within the brain. Why even consider issues that your own experimental approaches do not have the power to illuminate?

There is also outright deception, because funding is non-existent for anyone wishing to understand human affective experiences by studying emotions of animals. Cognitive-behavioral scientists who study the neurology of *secondary-process* emotions—namely behavioral changes arising from neural mechanisms of learning and memory (e.g., LeDoux 1996, who claimed that emotional feelings are just icing on the cake, p. 302)—effectively use primary affective processes as essential *unconditioned stimuli* (UCSs) and *unconditioned responses* (UCRs) in their learning paradigm, without acknowledging that UCSs and UCRs may already elaborate affective mentality within the underlying neuronal infrastructures. It serves some well to pretend that UCSs and UCRs are presumably unconscious. Of course, the acceptance of such views necessarily neglects the robust and abundant evidence that direct electrical stimulations of the brain (ESB), applied to emotional UCR networks, routinely yield ‘reward’ and ‘punishment’ functions indicative of the arousal of diverse *emotional affects*. This indicates that raw affects are closely linked to the inbuilt (instinctual) functions of UCR networks. And surely this applies to commonly used UCSs as well, such as sugar water and foot shocks—albeit they also probably generate different species of feelings, namely *sensory affects*).

With investigators best situated to clarify primary-processes tending to obfuscate issues, most psychologists are satisfied to study *tertiary-process* emotions in humans, namely the full emotional complexities of sapient Brain-Minds as they confront the many aspirations and vicissitudes of social-cultural life—the joys and woes of living among the complexities of the world. Understandably, psychologists are well prepared to assimilate the wonderful data generated at the secondary-process level, since everyone agrees on the importance of learning and memory. But psychologists have no “disciplined” experimental approaches to study primary-process levels of the Brain-Mind. Thus, a seemingly consensual silence concerning

existence of affective experiences in animals continues to be implicitly accepted. Psychologists have little empirical access to those ancestral brain memories—the “instinctual-affective” tools of our nervous system—except perhaps through facial and phenomenological analyses, which can be endlessly debated (Ortony and Turner 1990; Barrett 2006). How we credibly integrate the primary process level of affective analysis into “the whole” remains a challenge for psychologists interested in mental life.

### **Conceptual dilemmas: emotions are not just a variant of cognitive activity**

Emotions are widely considered to be completely interpenetrant with the cognitive activities of the brain. This is of course psychologically quite obvious at the tertiary-process level. However, this assumption has become so pervasive that few pause to consider the credibility of such beliefs from the primary-process level of control. While whole issues of journals are devoted to extolling the total interpenetration of emotions and cognitions (e.g., see the 2007 special issue of *Emotion & Cognition* focused on that topic), few pause to consider whether such conclusions are justified at the primary process level. At the secondary-process levels, the automatic and largely unconscious mechanisms of learning and memory could be considered “cognitive” with some imagination. However, to consider the various “state-control” BrainMind functions generated by primary-process emotional systems as being “cognitive” is less than a reasonable stretch of the imagination. Surely primal emotions can be triggered by the various UCSs that promote learning. But is that cognitive? Such an oversimplification yields no unique predictions, only an empty sense of intellectual satisfaction for those already committed to the complete interpenetration of emotions and cognitions.

The more reasonable perspective is that evolutionarily “conditioned” subcortical emotional systems have a mind of their own, generating coordinated emotional responses as well as raw feelings. The minimal environmental triggers that can activate such systems (e.g., the smell of certain predators in rats) do not make the emotional reactions cognitive; such unconditioned emotional states can be evoked by epileptic foci in those brain regions as well as localized experimenter imposed brain stimulations. At these low levels of the ancestral BrainMind, where emotional, and other basic affective issues loom large there are no “cognitive” controls. The cognitive regulation of emotional arousals (Goleman 2006), arise from higher brain regions, yielding at their very best, Aristotelian *phronesis*: For example learning who to be angry with, for how long, and with what intensity, and how to regulate

irritability in body and mind. At their worst, they lead to psychopathic behaviors.

There are other reasons for accepting the classical, and not misguided, distinction between affective and cognitive processes. For example, although all organs of the body are highly interactive, a physiology that does not make disciplined distinctions among them is not a science. The same principle should apply to cognitive and affective concepts. Thus, all psychologists need to consider that there is practically no evidence that affective feelings can arise independently from brain regions that are accepted as the most cognitive regions of the mind, such as neocortex.

With various hierarchical affective-cognitive MindBrain complexities, we really do need special nomenclatures for the various levels of organization to communicate clearly. Our use of vernacular emotional languages, derived obviously from tertiary-level brain abilities, will not suffice for clear communication, most especially at primary-process levels. That is why I have long chosen to use a special nomenclature for the primary-process level of analysis, using full capitalizations of common emotional words as designators for the various emotional primes—SEEKING, RAGE, FEAR, LUST, CARE, PANIC/GRIEF and PLAY—all identified with ESB techniques (i.e. Electrical Stimulation of the Brain at discrete subcortical neural loci, to produce coherent emotional behaviors, which can routinely serve as rewards and punishments in learning paradigms), that not only engender emotional instinctual behaviors of the kind that Charles Darwin discussed, but also raw feelings as can be demonstrated by the fact that artificial arousal of such brain networks engenders affectively positive ‘rewards’ and negative ‘punishments’ in various learning tasks.

More work is needed to determine how well animals discriminate these central affective states, but little work has been done at that level (for first study, see Stutz et al. 1974). It is a pity that the critically important primary-process level of analysis, which provides a solid neuroevolutionary foundation for understanding higher emotional processes, remains rather neglected in modern emotion studies. This neglect may lead to many errors in conceptualizing how both emotional behaviors, feelings and accompanying bodily arousals arise from brain activities.

### **Mammalian brains have many affects beside emotional feelings**

There is a menagerie of inbuilt affective proclivities in mammalian brain. One can surely cut that pie of complexity in various ways, including making the grand, but neuroscientifically unsupported, assumption that there is a singular Core Affect (Russell 2003; for full discussion, see

Zachar and Ellis in press), which is the staging ground for cognitive processes to label locations in the underlying affective space laid out in generalized arousal and valence coordinates. This vision is neither based on nor consistent with available neuroscience evidence. For a full discussion of basic emotion approaches, see the special forthcoming *Emotion* edited by James Russell (2011). Primary-process affects are the intrinsic barometers by which animal brains automatically gauge survival issues: If it feels good in a certain way, continue doing whatever you were doing. If it feels good in a different way, continue that type of behavior. If it feels bad, cease and desist from continuing the ongoing behavior, and shift to escape, hiding and avoidance modes.

How might we subcategorize affects to have some relationship to the distinct types of diverse affective networks—the valuative BrainMind ‘organ systems’. As a first pass, we should distinguish (1) the *sensory affects*—the pleasures and displeasures aroused by low-level exteroceptive inputs (Berridge 2004), from (2) the *homeostatic affects*, such as hunger and thirst, which arise from interoceptors of the brain and body about which much is known (Denton 2006). Further, both of those surely need to be distinguished from the main concern here, (3) the *emotional affects* which were evolutionarily created as intrinsic (instinctual) BrainMind states. Abundant evidence indicates that emotional affects arise concurrently with the arousal of intrinsic emotional instinctual behavior generators, each of which deals with distinct survival issues. And those affects can be rapidly interfaced with world events through learning (secondary-processes), and gradually through higher cognitive abilities also (tertiary-processes). If we do not make such distinctions, and conflate all affective feelings under the category of emotions, then we have a bit of a semantic mess on our hands.

### **Are human emotions unique? and Why one simply can’t understand emotions without animal models**

Of course, human emotions are unique at the tertiary process levels. Presumably so are the emotions of guppies, if they have any tertiary process emotions at all (almost impossible to study). Our uniqueness is evident in our capacity for language, thought, art, dance, music, poetry, theater, not to mention the differential values placed on higher emotional traits across human cultures—for instance, family-centered interdependences fostered abundantly in Buddhism-oriented countries of the far east, while emotional independence and individuality are cherished in Judeo-Christian quarters of western civilizations.

But can those levels of analysis tell us how our brains construct affective feelings? At those levels, do we not still

need to ground our understanding of human emotions on evolutionary perspectives (Dunbar and Barrett 2007)? Causal neuroscience research, achievable via an affective neuroscience triangulation strategy—integrating brain, behavioral and psychological evidence (Panksepp 1998)—is critical for scientific understanding of emotionality. Likewise, modern human brain imaging can facilitate understanding of the neural correlates of higher emotional functions in the human brain. Indeed, a recent meta-analysis of brain imaging of human emotions, contrary to two earlier meta-analyses, has strongly supported the existence of various “basic emotions” (Vytal and Hamann 2010). In my estimation, the PET studies have provided the most compelling evidence (e.g., Damasio et al. 2000), with fMRI probably providing more false-positives and false-negatives, at least in terms of the affect generators of the brain. Such approaches often cannot parse the massive underlying levels of “dark energy” that sustain diverse endogenous brain functions (Raichle 2006).

An especially troublesome aspect of brain emotional processing, as one moves from primary- to tertiary-levels of analysis, is that activities at the lower and higher levels of brain integration are often reciprocally related; for instance, higher cognitive activities typically suppress lower affective activities (Liotti and Panksepp 2004; Northoff et al. 2009). This creates problems for many brain imaging studies where cognitive-affective judgments are made *during* scanning sessions: The tertiary-process cognitive judgments may inhibit the primary-process emotional feelings, leading to biased results. Investigators that have sought to disentangle such confounds, by evaluating affective changes after, rather than during, brain-scanning sessions, have found that affective intensity is correlated positively to subcortical network arousals implicated in primary-process emotions, and negatively related to neocortical activity changes induced by emotional stimuli (Northoff et al. 2009). This is bad news for the many emotion researchers working at tertiary process levels, many of who tenaciously sustain the myth that human affective feelings *largely* reflect neocortical “read-out” functions of the brain.

If all this is true, perhaps human emotional *feelings*—the *affects* that lie at the heart of our emotional lives—may not be as unique as associated cognitions. How might we evaluate this conjecture? One possibility is to consider where in the human brain ESB produces the strongest emotional responses. The evidence is consistent—from the brain areas that mediate animal instinctual-emotional processes. The strongest affects are obtained from the lowest levels, such as the periaqueductal gray (PAG), where stimulation can produce feelings of being “scared to death” (Nashold et al. 1969). For summaries of the classic work, see Heath (1996) and Panksepp (1985), with more

recent reflections in Coenen et al. (2011). As predicted from the animal work, stimulation of the shell of the nucleus-accumbens can yield anti-depressant effects in humans (Bewernick et al. 2010; Schlaepfer et al. 2008).

Likewise, modern Diffusion Tensor Imaging (DTI) reconstructions of shared brain connectivities from historical brain-lesion anti-depressant therapies suggest neural convergence onto the medial forebrain bundle (MFB), which is the heart of the reward SEEKING system (Schoene-Bake et al. 2010). Those that have stimulated such human brain regions get profound and rapid mania responses on the one hand (Coenen et al. 2009), and profound depression in other nearby areas (Bejjani et al. 1999).

In sum, although the cognitive manifestations of emotions are unique in humans, many of the affective underpinnings are shared, namely homologously organized. Thereby, neuroscientific approaches that respect the evidence-based existence of affects in other animals will eventually inform us about the way in which subcortical brain dynamics promote affective experiences in human brains. And thereby, pre-clinical animal research will become a linchpin for neuroscientific understanding of psychiatric disorders and the discovery of new treatments (e.g., Krishnan and Nestler 2010; Nestler and Hyman 2010; Panksepp and Watt 2011).

### Can animal behavior be explained without affective feelings?

Resistances against some of the above views are pervasive in psychology. That is understandable for a science that has not developed the needed linkages to neuroscience approaches that provide paradigms for understanding the proximal causes that engender emotional feelings. This is implicitly supported by behavioral neuroscientists and ethologists who have neglected the emotional feelings of the animals they have studied because such issues are presumably scientifically unfathomable. The classic era of denial of animal emotions yielded infamous claims such as B.F. Skinner's (1953) dictum that "The "emotions" are excellent examples of the fictional causes to which we commonly attribute behavior" and Niko Tinbergen's assertion (in his classic *Study of Instincts*, 1951, p. 4) that "Because subjective phenomena cannot be observed objectively in animals, it is idle to claim or deny their existence." Those days are not gone. Even though great progress has been made in the development of models that access some of the higher emotional functions in the 'lowly' laboratory rodents (Mendl et al. 2010), the hesitation to consider experiential levels was highlighted up-front, with the qualification that they are not "discussing

animal emotions as states that may or may not be experienced consciously". This attitude still pervades animal behavior studies, even among those intensely interested in emotionality.

In a fine paper on primate emotionality, by an eminent ethologist, that I reviewed as I wrote this paper (late Sept 2010), the following assertions were made, and I include my reflections on their short-sightedness: (1) "the actual experiences of animals remain inaccessible"—not if one accepts 'reward' and 'punishment' functions of specific brain networks to highlight positive and negative affects; (2) "we may never be able to assess the experiential side of animal emotions"—I doubt it, but those assessments do require functional brain research; (3) "emotions are always felt, but perhaps not consciously"—if *experience* is the *sine qua non* of consciousness, that phrase makes no sense at all. This prominent scholar suggested ethologists can study emotional behavior patterns but they should "stay away from the unanswerable question of what animals feel"—but if we do that, we are staying away from the most interesting aspect of emotions and discouraging neuroscientists, who have the requisite tools, so they also avoid the topic, as most have done for a century, to the detriment of psychological science. My overall recommendation was to stop this historically encouraged wavering and equivocation that may seem appropriate for a behavior-only level of analysis, while not being cogent when it comes to neuroscientific causal analyses.

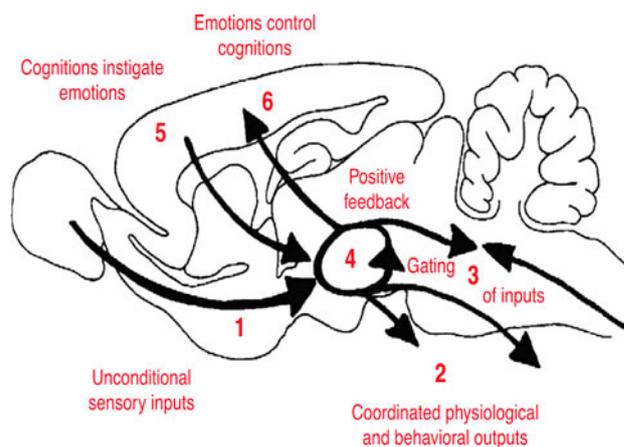
The field at large will be illuminated and enriched when psychologists and neuroscientists begin to learn how to discuss the affective functions of animal minds, which are much easier to neuroscientifically analyze than the cognitively experienced associates of the ancient affective processes. Indeed, affective thinking, barely apparent in modern behavioral neuroscience—even among those developing pre-clinical models of psychiatric disorders (where talk about affective processes of animals has long been discouraged and marginalized)—can actually strengthen the weak bridges that currently exist between animal and human research traditions. The great recent success story of intranasal oxytocin effects in humans, guided largely by animal studies, is one fine exemplar (Panksepp 2009b). There are others. For instance, our early work on brain control of separation-distress in young animals (first summaries in Panksepp et al. 1980, Panksepp et al. 1982), has been confirmed by human brain imaging (e.g., Freed et al. 2009; Swain et al. 2007; Zubieta et al. 2003). The opioid mediation of social-comfort, is consistent with recent findings that human depression is a low brain-opioid state, and studies of human social feelings have been enriched by the preceding animal work (Depue and Collins 1999) and continues in the analysis of opioid

receptor subtypes in humans (Copeland et al. 2011). Abundant work on steroids highlights how rapidly they can modify affective states (Schutter and Van Honk 2010). There are an enormous number of such linkages that can enrich the intellectual commerce that needs to be promoted between human emotion studies and the work on proximal causal processes that can only be conducted in animals.

Coherent progress on understanding affective states will emerge once the field begins to understand how animal brains operate. To achieve such knowledge, human brain-imaging may be less useful than is currently widely believed. The unbelievably high correlates of brain changes, both metabolic and in blood flow, to ongoing psychological processes, are often laden with statistical artifacts and misinterpretations (e.g., Vul et al. 2009). Although such empirical techniques tell us something useful about the brain, we cannot be confident that they are as applicable to the affective functions as the cognitive functions of the MindBrain. After all, these techniques are ultimately related to changing firing rates of neurons. One problem is that both inhibitory neurons and excitatory neurons, convey their messages to synaptic-terminal regions by the generation of essentially identical action potentials, which can lead to 180 degree shifts in functional interpretations of what a brain region is doing, and if there is a balance of excitatory and inhibitory inputs to a nucleus that does something important in emotions, the brain region may appear invisible to brain-imaging techniques. Other false-negatives can arise from the simple fact that higher more perceptual-cognitive functions commonly operate with neurons that fire up to hundreds of times a second, while the deep subcortical systems where primary-process emotions are integrated largely fire at more than 10 times a second, and often neurotransmitters and neuromodulators are released by a change in the patterning of action-potentials with no overall rate changes. For instance, reward-SEEKING dopamine (DA) neurons of the ventral tegmental area commonly have a background firing of about once per second, which does not effectively lead to abundant DA release in terminal fields. What reward opportunities do is to increase the bursting of these cells (clusters of two or three quick firings one after the other, with slightly longer pauses between clusters); changes in firing *patterns*, rather than overall rates that most effectively release DA. Thus, from metabolic and blood-flow perspectives, these neurons may be invisible during human brain scanning, not to mention the background haze provided by the massive “dark-energy” stores that sustain the internal “housekeeping” functions of the brain (Raichle 2006)—some of them perhaps affective. Such issues need to be more deeply considered in the interpretation of brain-imaging studies.

## So how shall we define emotions?

The dilemma of generating a coherent definition of emotions and motivations has long haunted the field. At the primary-process level, a general solution to that problem simply has to include neural criteria. To a substantial extent, emotionality is an endogenous BrainMind function, carried on by intrinsic within-brain dynamics, whose externally directed, environmentally enriched manifestations are multifarious. As intrinsic affective brain network activities interact with emerging cognitive brain functions, through general capacities for learning and memory, and yield higher brain functions traditionally deemed to be ‘cognitive’, the complexities multiply. A definition of emotions has to respect evolutionary levels of control, and make disciplined distinction between those aspects of the BrainMind that are evolutionarily intrinsic and those that are acquired. The intrinsic functions need much more attention in current scientific definitions of emotions, than the culturally acquired ones, but they should highlight how levels of control are integrated. My own attempt is summarized in Fig. 2.



**Fig. 2** A neurally-based definition of emotional systems, highlighting the types of neural functions that characterize all major emotional operating systems: (1) A limited number of sensory stimuli can unconditionally access emotional systems and this is increased substantially by learning; (2) emotional systems can generate instinctual somatic and visceral outputs; (3) emotional arousals gate sensory/perceptual inputs; (4) emotional systems reverberate longer than precipitating circumstances; (5) These systems can be modulated by learning and higher cognitive inputs; (6) emotional arousals can modulate and guide cognitive activities; (7) the operation of the lower parts of these emotional networks engender primary-process affective states, and higher parts modulate, combine and channel affects cognitively. Adapted from Panksepp 1998, Fig. 3.3, p. 48, with permission

### **In sum: What is the most important question in emotion research? Surely not “Do Rats Laugh?”**

There will be diverse answers to that question. My own is the biological nature of experienced affective processes; I don't think this question can be answered without animal research. However, few in behavioral neuroscience, not to mention the rest of psychology, have started to consider the possibility of ever scientifically addressing such aspects of mind, especially in species that do not talk. I think that is a rather narrow view of what science can accomplish, and reflects the language-based, human-focused parochialism of so much of current psychological science. We should not forget that language was perhaps the latest brain function to emerge, largely under the influence of cultural evolution rather than genetic selection. It is full of idiosyncrasies and peculiarities, as is the left-hemisphere that serves understanding much less effectively than is commonly believed (McGilchrist 2009).

Let me close this essay with a call for more open minds concerning the emotional lives of other creatures. With few exceptions, psychologists and neuroscientists have been lost in solipsistic denials and outdated skepticisms for too long. In behavioral neuroscience and ethology, the topic of emotional feelings in other animals has barely been broached. In contrast, many with practical concerns, such as veterinarians and animal-rights advocates, have to be concerned by such practical issues, and some have been probed deeply (e.g., McMillan 2005).

Of course, science has all too many constraints in dealing with mental complexities, so animal feelings have traditionally not been on many lists of urgent projects. Indeed, the eminent ethologist, noted above, who is intensely interested in animal emotion research suggested that we must “stay away from the unanswerable question of what animals feel” as if that was *fait accompli*. But that question has been on top of my list of key questions ever since I shifted from majoring in clinical psychology to physiological psychology in the mid 1960s (see Panksepp 2010, for my perspective in taking on such issues), at the time I was most interested in the nature of psychiatric disorders, and still am (e.g., Panksepp et al. 2003; Panksepp and Watt 2011). But faced with the profound ignorance about emotions 50 years ago, indeed the general absence of any open conversation in science, I decided that the bedrock of human emotionality could only be studied in detail through animal brain research. Was this a useful insight or a delusion? One of my esteemed colleagues Richie Davidson (2003), in response to my many efforts to go where human research cannot go (Panksepp 2003), has implied it is the latter. I am more convinced than ever that it is the former, even though that view has not yet taken root in the minds of many animal behaviorists, ethologists,

psychologists, and philosophers, albeit there are an increasing number of exceptions.

With this insight, we have often asked seemingly silly questions. For example, in the mid 1990s, we seriously considered “Do rats laugh?” After a mountain of research, consisting mainly of tickling rats in playful ways and focusing on their ultrasonic vocalizations, we concluded that they do have a robust ancestral form of laughter (50 kHz chirps, with considerable sub-types). The data were incredibly reliable and robust. We could not negate this wild idea no matter how hard we tried. And we tried hard. Even though the findings were initially distinctly hard to publish (see Panksepp 2010 for the first submission: the main critique was “even if this phenomenon is true, you would never be able to convince your colleagues”), we persisted (for an overview of the many empirical findings and interpretations, see Panksepp 2007). I only note one finding that is especially germane to the present discussion: Every ESB site that triggers laughter-type “chirps” (all subcortical except for medial frontal cortex, along the MFB—reward SEEKING circuitry) sustains self-stimulation reward (Burgdorf et al. 2007)! Indeed, mania, laughter and smiling have been evoked by electrical stimulation of parts of this system in humans (Coenen et al. 2009; Okun et al. 2004).

Why would we pursue a line of research that was first announced in “*Believe it or Not*” and “*News of the Weird*” with a cameo in *People* magazine (June 15, 1998, p. 105)? Because to develop better pre-clinical models, we simply must have better and more direct measures of the affective states of animals, both positive and negative, that we can use to monitor affective changes that accompany all major forms of emotional imbalances in humans (Panksepp 2010; Panksepp and Watt 2011). Having specific neural-circuit manipulations and measures, that modify and reflect internal affective states, allows investigators to develop ever more focused strategies for understanding the neural underpinning of various psychiatric problems, including anxiety, depression, mania, addictive urges, and many others. This direct measure of positive social affect in lab rats is currently one of the most promising ways to directly understand their urge to socialize (Burgdorf et al. 2008) as well as to pursue addictive drugs (Browning et al. 2011; Panksepp et al. 2002, 2004). And it has been increasingly realized that our social needs are highly addictive brain processes, through both animal research (Panksepp 1981, 1998) and more recently human investigations (e.g., Copeland et al. 2011; Zubieta et al. 2003).

And as we study such evolved emotional systems, shared homologously by all mammals, we may eventually be able to clarify what emotions really are, at rock bottom. Sound answers to such primary-process questions can enliven our understanding of learning and memory (secondary emotional processes) as well as our understanding

of why our emotional thoughts and ruminations are so narrow and insistent (tertiary-process emotion-cognition interpenetrations). It allows us to envision the BrainMind in terms of novel ‘nested-hierarchies’ (Fig. 1) where higher functions remain rooted in lower functions, which is surely one way evolution worked in constructing the sophisticated cognitive potentials of human minds. But we should be wary of believing there is much that is genetically coded in the higher regions of our minds, namely neocortex, where most of what gets modularized, does so through our life experiences, rather than by a vast array of functional specializations provided by our evolutionary heritage. There is hardly any good genetic evidence that what we cherish most about our higher cognitive abilities was premised on cortical modularization (McGilchrist 2009).

A neuroscientific knowledge of our primary-process emotional foundations does not oversimplify the vast complexity and richness that emerges within each of our emotional lives, as Robert Solomon, the great modern philosopher of emotions, repeatedly insisted (see the memorial issue of *Emotion*—2010, vol. 10, to see the reach of his influence). Bob needled me about my “oversimplified” research program whenever we spoke, but I know in certain corners of his mind he grew ever increasingly enchanted by the prospects of an affective neuroscience that returned the other creatures into the “circle of affect” which many scholars of emotion, from Descartes onward, have arrogantly reserved for mankind. What a blunder! Cross-species affective neuroscience can enrich our understanding of the higher aspects of humans’ emotional lives, in which we are all so personally interested, but which cannot be neuroscientifically penetrated without a clear understanding of the evolutionary foundations.

The future should be bright for further developments as new neurochemical approaches are developed, and new and more specific brain stimulation approaches emerge (Ikemoto 2010) including optogenetic procedures that allow selective stimulation of discrete neuronal populations (e.g., Zhang et al. 2007), and new electrophysiological measures are developed for analyzing large scale neural network dynamics which have the potential to capture distinct types of emotional arousals and distinguish top-down and bottom-up controls (e.g., Kenemans and Kähkönen 2011).

Primary-process emotions were bequeathed to us from our ancestral past. And they are here to stay. They emerged long before the Pleistocene. They are essential for our conscious lives. They can make life hell. They can make life wonderful. This is the case in all mammalian species that have been studied. In the Freudian era, they were conceptualized as part of the dynamic unconscious, because consciousness was defined as the ability to be aware of the fact that you experience life. Now, we should

recognize that the foundation of conscious life must be defined in terms of being able to subjectively *experience* living, than to be aware of the fact that you are, unlike rocks and vegetables, a conscious being. If we do not pursue the foundations of emotions in neuroscientifically credible animal models where the underlying primary-processes are situated, can we ever know what emotions really are?

Primal emotional networks enact a variety of action schema that have proved useful in promoting survival. These action systems also elaborate feeling states in the brain, which can serve as diverse rewards and punishments for refining behavior patterns through learning and memory. Through such intrinsic action-feeling systems, certain animals eventually became capable of representing their needs and desires through higher cognitive activities. However, all higher animals are fundamentally “active” motor-centric creatures rather than “passive” sensory-centric ones. As soon as we recognize that psychological processes can arise from the primal emotional-action processes of brains, we can create visions of the BrainMind that are more coherent than the scientific visions of the past.

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