



Review

The basic emotional circuits of mammalian brains: Do animals have affective lives?

Jaak Panksepp*

Department of VCAPP, College of Veterinary Medicine, Washington State University, Pullman, WA, USA

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ABSTRACT

The primal affects are intrinsic brain value systems that unconditionally and automatically inform animals how they are faring in survival. They serve an essential function in emotional learning. The positive affects index “comfort zones” that support survival, while negative affects inform animals of circumstances that may impair survival. Affective feelings come in several varieties, including sensory, homeostatic, and emotional (which I focus on here). Primary-process emotional feelings arise from ancient caudal and medial subcortical regions, and were among the first subjective experiences to exist on the face of the earth. Without them, higher forms of conscious “awareness” may not have emerged in primate brain evolution. Because of homologous “instinctual” neural infrastructures, we can utilize animal brain research to reveal the nature of primary-process human affects. Since all vertebrates appear to have some capacity for primal affective feelings, the implications for animal-welfare and how we ethically treat other animals are vast.

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Contents

1. Introduction.....	1791
2. Historical antecedents to the study of emotional affective states of the brain.....	1794
3. Primal affects and the cognitive revolution.....	1795
4. The varieties of raw affects: the unconditioned response and stimulus processes of the brain.....	1796
5. The basic affective circuits of mammalian brains.....	1797
6. A neuroscience of the affective mind and ethical implications.....	1800
7. What difference does it make whether animals have emotional feelings?.....	1801
8. Conclusion.....	1801
References.....	1802

1. Introduction

I thank my colleagues Casey Cromwell and Vern Bingman (2011) for organizing this Festschrift celebrating some of the achievements of a cross-species Affective Neuroscience at Bowling Green State University and elsewhere. This essay provides a synopsis of key

ideas and findings that have guided that intellectual journey. I appreciate that so many former students, present colleagues and friends returned for this intellectual celebration of mammalian emotional systems, and that so many crafted summaries of the kinds of work and thinking that may allow us to finally answer the perennial question “What is an Emotion?” asked by Darwin (1872), James (1884) and hopefully innumerable future investigators of the human mind.

A closely related and equally important question is how the brain generates *affective feelings*—the valenced phenomenal experiences (qualia) that come in desirable (positive) and undesirable (negative) forms and varieties. Until recently *emotions* had to be

* Corresponding author at: Baily Endowed Chair of Animal Well-Being Science, Department of VCAPP, College of Veterinary Medicine, Washington State University, PO Box 646520, Pullman, WA 99164-6520, USA. Tel.: +1 509 335 5803.

E-mail address: jpanksepp@vetmed.wsu.edu

addressed behaviorally and physiologically in animals, but my claim is that we now can also understand the affective (subjective feeling) component of emotions through close and sensitive studies of the underlying brain mechanisms in other creatures. I will passingly incorporate all of the published contributions to this special issue of *Neuroscience and Biobehavioral Reviews* into the following essay—“passingly” because they speak loudly for themselves. And I thank all the participants for constructing so many fine scientific overviews and especially fine philosophically edged contributions (e.g., Davies, in this issue).

My entry into the field in 1965 was motivated by a desire to understand human emotions (for relevant interview, see Panksepp, 2010a). My simple research premise and claim, during the past 40 years of a cherished professorial life, has been that a close study of the emotional networks of our fellow creatures may give us a more lasting answer to the evolutionary foundations of this devilishly complex question, so important for psychiatric issues, than any human research can achieve. This is because our emotional feelings are grounded on “instinctual-behavioral” neural networks that evolved long before humans walked the face of the earth. Although the animal work cannot tell us much about how we cognitively dwell on our emotions and how we use them to mold culture, it can provide a solid primary-process understanding of how the affective mammalian BrainMind—a term affirming monism, here used synonymously with MindBrain, depending on stylistic needs—emerged in evolution.

Thus, clear dialog in this area requires a disciplined distinction between the affective-emotional aspects of experience and the widely studied cognitive and emotional-behavioral aspects of human and animal BrainMinds. This distinction remains especially muddled in current psychological research, where most investigators work at the tertiary-process level of the MindBrain. The primary-process emotions—and their psychological emissaries, the affects—can be called “cognitive” only by a stretch of the imagination (see Cromwell and Panksepp, in this issue). Thus, it is useful to divide evolved brain functions in terms of primary-processes (tools for living provided by evolution), secondary-processes (the vast unconscious learning and memory mechanisms of the brain), and tertiary-processes (the higher order functions of mind permitted largely by the cortical expansions that allow many thought-related symbolic functions).

Primal emotions are among the most important aspects of our mental lives—they bring us great joys and sorrows, and intrinsically help anticipate the future—but behavioral neuroscientists have offered few hypotheses about how experiences emerge from brains, especially those of other animals. Indeed, to a large measure they have long avoided one key question: Do other animals experience their emotional lives? Most intelligent people, not concerned with the rules of scientific evidence, and nuances of scientific limits, would surely respond, “Obviously they do!” and some courageous investigators of the past framed their empirical inquiries in this way (e.g., MacLean, 1990; Young, 1966, 1968). But they had regrettably little impact on modern neuroscience, except for a few recent pioneers (e.g., Berridge, 2003, 2004; Cabanac, 1992). Paul MacLean’s contributions have been actively and regrettably marginalized in the past decades (for a pithy critique, see Panksepp, 2002).

In contrast, most neuroscientists who study animal behavior (i.e., behavioral neuroscientists and neuroethologists) remain skeptical of such conclusions, and generally prefer to sustain an agnostic silence on such issues. They prefer to use generic general-purpose traditional terms such as “reward” and “punishment”, with little consideration of what such key brain processes that control learning mean in psychological terms. It is now quite reasonable to envision that external rewards and punishments actually control learning by modulating the affective neural substrates of the brain, but that is a view that has hardly been addressed. The dilemma

is that such brain functions can only be well studied in animal models, and a sustained conversation about how affects are generated by the brain has never been engaged. Most would claim that anthropomorphic reasoning is an inappropriate starting point for our most pressing scientific questions about emotions. Since affects are fundamentally subjective experiences, they have been the prime targets for critique of the kinds of brain processes we should never discuss in animals. This type of stance, still pervasive in the modern neurosciences, automatically and autocratically precludes the study of how affective feelings are generated within animal brains.

Many choose to ignore the likelihood that raw affective experiences—primal manifestations of “mind”—are natural functions of mammalian brains (perhaps other species too, see Huber et al., this issue; Ritters, this issue; Normansell and Panksepp, this issue), which could serve as key empirical entry points for understanding the experienced reward and punishment functions of the human mind. To proceed on this tack, investigators would need to accept one grand but empirically robust premise—that higher aspects of the human mind are still strongly linked to the basic neuropsychological processes of “lower” animal minds.

To this day, many neuroscientists would assert, in line with longstanding traditions, that troublesome dilemmas such as the internal experiences of other animals are not questions that science can ever answer. And with no direct empirical access to their subjective states—i.e., us experiencing what they are experiencing—we are left forever in the unenviable position of merely speculating. That may still be the case with regard to subtle cognitive issues, but not for primal affective ones. Since there are many psychological predictions about human feelings that can be generated from existing cross-species animal BrainMind databases, the “sin of anthropomorphism” is no longer a view that should garner much support, at least in basic emotion studies (Panksepp, 1998, 2005a; Panksepp and Biven, in press). And perhaps with homeostatic and sensory affective issues as well (Berridge, 2003; Cabanac, 1992; Denton, 2006).

Our failure to more explicitly entertain the obvious, namely that other animals have affective feelings, can have invidious consequences. For instance, currently a form of “ruthless reductionism” (behavior and brain count, but experience does not) rules among the functional neurosciences—among scientific practitioners who have the best empirical tools to address questions concerning the causal infrastructure of subjective experience. First of all, we should agree that the assumption that animals have no emotional feelings has no greater intrinsic logical truth-value than the claim that they do. Second, a key issue is whether we can make reasoned choices based on the evidence, especially causal evidence. Since we cannot see into the mind of other creatures, some will say there is no relevant evidence. They are wrong.

Were it not for the “neuroscience revolution”, the dilemma of not being able to see into the mind of other creatures would, of course, be the path of perpetual agnosticism, with different philosophical camps arguing for their beliefs or simply deciding to disregard the issue. Despite the progress of neuroscience, the latter has transpired historically: in general, behavioral neuroscientists have traditionally remained satisfied with careful behavioral analyses of animal behaviors and their neural correlates and causes, guided by the operationalism of logical positivism, leading to beautiful research, but regrettably weak bridges to human concerns. Many still suppose that is as far as we can go, and should go. But this proscription dramatically weakens our ability to provide important insights for understanding especially pressing psychiatric issues such as affective disorders.

At this moment in our intellectual history, the alternative is becoming ever more attractive, as long as we consider an underlying “dual-aspect” ontology (see Panksepp, 2005b), not unlike

the one physicists had to confront a century ago. At the beginning of the “quantum era”, led by pioneers like Niels Bohr, Louis de Broglie, Albert Einstein and Max Plank, to name a few, those interested in the nature of light and subatomic particles had to accept wave-particle duality: Early in the 20th century, physicists revealed how photons have both wave and particulate characteristics and how energy is related to matter, just about the time that neuroscience was taking its fledgling steps with inspiration from pioneers like Ramón y Cajal, Charles Sherrington, and many others. Perhaps we neuroscientists will also one day agree (and reveal), how mind is a manifestation of brain activity, using similar dual-aspect strategies. If so this may first happen, at a causal level, with animal models used to study the nature of affects, especially emotional rewards and punishments. Thus, the main goal of this essay is to encourage more open-minded discussions about the variety of primary-process affective processes in mammalian brains—emotional, homeostatic and sensory feelings—and to motivate young scholars to avoid the grand mistakes of the 20th century, which in a sense were similar to those bequeathed to us by Rene Descartes.

A cross-species Affective Neuroscience (Panksepp, 1982, 1998, 2005a) has chosen to develop the theme that we can scientifically understand the foundations of the human mind by studying the basic subcortical emotional systems that can be well studied in animals. Partly, this initiative was taken because understanding the affective aspects of mind are critically important for human and animal welfare issues, and hence should not be left in limbo (see McMillan, 2005; Panksepp, 2010a). The evidence for various types of affective feelings in other mammals is now rather overwhelming. The key facts are as follows: Wherever in the ancient subcortical reaches of the mammalian brain we evoke coherent emotional behaviors with electrical stimulation of the brain (ESB), we can also demonstrate that the central states evoked can serve as rewards and punishments (Panksepp, 1982, 1998, 2005a; Panksepp and Biven, in press). This also provides a potentially cogent answer to one of the great dilemmas of behavioral science: What is the fundamental nature of “reinforcement” as a brain process. One credible hypothesis is that shifting tides of neuro-affective processes are critical for instantiating the concept of “reinforcement” within the brain. Perhaps most neuroscientists might envision this to *merely* reflect the strengthening of synapses via glutamate-based “long-term potentiation” type mechanisms, but one only need point out that every emotional system of the brain has glutamatergic transmission at its core (e.g., see Normansell and Panksepp, in this issue). Hence the “conceptual glue” of “reinforcement”—which has remained the key concept of behavioral analysis—is actually a reflection of brain affective systems in action.

Of course, it could be claimed that the conceptual and methodological problems we face on that road to returning *experience* back into brain, as key types of neural processes, especially in other animals, remains truly huge. Indeed, we have no semi-direct access to the minds of other humans, unless we believe what they say. The other animals cannot even symbolically communicate their feelings, expect perhaps for “talking” parrots and linguistically adept great apes, species that are unlikely to be used in routine brain research. Thus, it is self-evident that to proceed, we have to use other strategies to probe emotional feelings in other animals—for instance their *natural* emotional behaviors, especially their emotional vocalizations (see Riters, in this issue; Normansell and Panksepp, in this issue)—and we have to empirically validate such measures as behavioral proxies for the generation of novel affectively related animal behavior predictions, and thereby also provide novel, testable hypotheses about the neural nature of human feelings (who obviously can provide symbolic self-reports).

This type of new dual-aspect epistemology is critical since detailed and comprehensive neuroscientific work on such issues is typically impossible to do in humans, unless there are compelling medical reasons (see Coenen et al., this issue). As a result, we have crafted innumerable falsifiable hypotheses in animal models. Just consider some recent ones: Frequency-modulated (trill type) tickle-induced 50 kHz chirps in rats reflect positive affect (Burgdorf et al., 2007; Burgdorf et al., this issue) with evolutionary relations to human laughter (Panksepp, 2007a). Human depression can be understood by the study of imbalances in specific affective systems in animal brains (Panksepp and Watt, 2011; Watt and Panksepp, 2009; also see Wright and Panksepp, in this issue as well as Zellner et al., in this issue). And there are many, many others (for some, see Panksepp and Harro, 2004).

Thus, the situation is not so bleak that we cannot make solid predictions, and thereby make rigorous experimental-inductive progress toward understanding certain internal affective states of both humans and other animals. Although “ruthless reductionism” currently still thrives in most animal neuroscience work, there are signs of implicit change (with too many wonderful lines of thinking to integrate into this short essay). But our conversations would be richer, and more realistic, if we lifted the restriction to use primary-process mental concepts in animals work. We do need much more research and discussion using indirect dual-aspect approaches that fully respect the hypothetico-deductive methods of modern science (see Bernroider and Panksepp, in this issue).

In other disciplines, most investigators recognize that if certain processes in nature (e.g., gravity) cannot be observed with direct objective measures, they must be studied using indirect measures. That is the time-tested scientific tool for evaluating most theoretical predictions in ‘deep science’ where different views have to be resolved by the weight of evidence for one position or another, based on the differential predictions they make. Would physicists be searching for Higgs bosons if they did not value indirect measurement procedures? These procedures can range from rather general hedonic tests like conditioned place preferences (CPPs) and aversions (CPAs) for various neurochemical agents (Tzschentke, 2007), to the evaluation of the rewarding and punishing properties of emotional response circuits (Panksepp, 1982, 2005a), to the use of emotional vocalizations as proxies for corresponding feeling states (for overviews, see Brudzynski, 2009). I am especially pleased to have been among the first to study subtle social-emotional processes neuroscientifically, with much of our work during the past 30 some years having been devoted to the study of maternal separation-distress (the PANIC/GRIEF system) as the key foundation for social bonding, and the neural mechanisms for rough-and-tumble PLAY being critically important, not only for development of social skills, but for social joy and even laughter (Panksepp, 1998). The implications for psychiatric issues are bound to be substantial (Panksepp and Biven, in press).

Clearly, it is only because of advances in brain research that credible *scientific* arguments can finally be advanced for the thesis that other mammals do have emotional and other affective feelings. Indeed, those findings already appear to illuminate the sources of human mind, providing even new visions for how we may conceptualize human personality (see Davis and Panksepp, in this issue) as well as many other multi-tiered aspects of mind (Northoff et al., in this issue). Comparable behavioral tests can be conducted in other vertebrates and invertebrates (see Huber et al., this issue). Although the weight of scientific evidence may have been insufficient in the 19th century, and even the first half of the 20th century, the second half yielded wonderful discoveries about emotional circuits that changed the ballgame (Hess, 1957). But historically, ultra-conservative ways of thinking in science typically take a rather longer time to adjust to new realities.

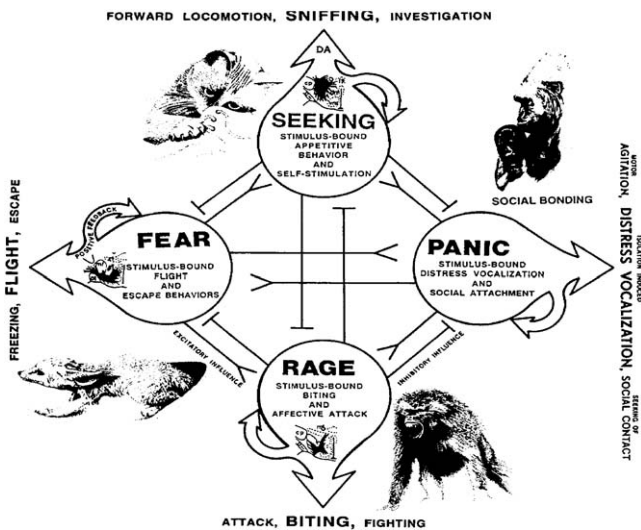


Fig. 1. The major emotional operating systems are defined primarily by genetically coded, but experientially refined neural circuits that generate well-organized behavior sequences that can be evoked by localized electrical stimulation of the brain. Representative behaviors generated by the various systems are indicated, and the approximate locations of the SEEKING, FEAR, and RAGE systems are depicted on small frontal section inserts through one side of the hypothalamus. The PANIC/GRIEF system courses through the medial thalamus rather than hypothalamus. There is abundant overlap and interactions among the various systems; some excitatory and inhibitory interactions are suggested by the various lines linking the systems in this cartoon depiction.

Adapted from Figs. 3.5 in Panksepp (1998) *Affective Neuroscience*, with the permission of Oxford University Press.

2. Historical antecedents to the study of emotional affective states of the brain

In brief, the discovery of emotional networks in ancient subcortical brain regions that can mediate various feeling of 'goodness' or 'badness' as monitored through behavioral choices grew steadily more robust from the early 1950s (Delgado et al., 1954; Heath, 1954; Olds and Milner, 1954) through the 1970s (e.g., Panksepp, 1971, 1981), with no major negations to this day. A synthetic diagram of the state of emotion systems research by 1982 is depicted in Fig. 1. The state of the field by 1998 is depicted in Fig. 2. This could be considerably refreshed for specific systems such as the mesolimbic dopamine (DA) reward SEEKING circuitry (see Alcaro and Panksepp, this issue; Nestler and Carlezon, 2006).

The most compelling and most informative evidence about discrete emotions has come from the study of emotional responses to specific kinds of brain manipulations such as electrical, and more recently localized chemical stimulation (CSB) of specific parts of the brain. All mammals that have been studied, typically exhibit distinctly similar (yet, species-specific) types of instinctual emotional responses to localized ESB and CSB applied to homologous brain regions. In other words, direct stimulations of certain brain circuits can serve as rewards and punishments in various simple learning tasks (for respective summaries, see Panksepp, 1998; Ikemoto, 2010). When given control of the stimulation—to turn it on or off—animals clearly indicate that they either like or dislike such forms of brain stimulation, findings well affirmed by CPP and CPA studies, both with ESB and relevant psychopharmaceuticals (Tzschenke, 2007). Such robust evidence is now supplemented by evocation of the diverse emotional vocalizations animals make in various emotional situations, mapped to specific brain circuits, which are not all that different from primitive emotional sounds made by humans in affectively intense situations (Bishop, 1984; Herman, 1979; Jürgens, 2009; Brudzynski, 2009; Burgdorf et al., 2007; Normansell and Panksepp, this issue). To put it bluntly, the

experience of pain can cause shrieking and crying in all mammals, and the stronger the pain stimulus, the stronger the vocal response. If we dull the feelings of pain (properly called *sensory affects*) with opiates, all behavioral indices of pain diminish in all mammalian species, just as in humans. However, there are also wonderfully positive sounds, such as those of social play related to brain SEEKING circuits (Burgdorf et al., 2007), and wonderful courting songs in birds, which are modulated by social neuropeptides such as endogenous opioids (see Ritters, in this issue).

When we artificially activate brain emotion-behavior generating circuits, animals rapidly learn to turn off ESB that evokes fear- and anger-type responses, and they turn on brain stimulation that generates playful sounds, exploration, sexual eagerness and maternal care. Just as humans laugh when they experience joy, so do rats chirp when aroused to PLAY—namely they make positive affective sounds that match our children's playful laughter (Scott and Panksepp, 2003) rather well, including maximal responses during tickling (Burgdorf and Panksepp, 2006; Panksepp, 2007a). Are we fooling ourselves that we have captured something very important about human experiences of pain, anger, fear and joy through such animal research? There is no empirical line of research that suggests such a dismal conclusion. Indeed, such research is already leading to the development of many new mind medicines, including novel anti-depressants and perhaps medications to minimize the impact of autistic disorders (see Burgdorf et al., in this issue; Moskal et al., in this issue; Panksepp, 1998; Panksepp and Watt, 2011). It is also providing a coherent rationale for the efficacy of older, officially un-condoned medications with robust antidepressant effects such as buprenorphine (Bodkin et al., 1995; Panksepp and Watt, 2011; Watt and Panksepp, 2009; also see Zellner et al., this issue).

Further, all other mammals learn to vigorously self-inject drugs that are addictive in humans, probably because they produce similar desirable feelings, and this eagerness can be monitored in at least some species of rodents by their enthusiastic euphoric, SEEKING-indicative ultrasonic vocalizations (Browning et al., 2011; Burgdorf et al., 2007). Such findings would be hard to explain if animals had no feelings. Surely we can conclude that the only reasons addictions occur is because drugs produce desired feelings, in both mice and men (Panksepp, 2010b; Kassel, 2010; Zellner et al., this issue). In short, the brain mechanisms for psychological experiences are very important guides for what humans and animals do. The resulting "Law of Affect" is that 'rewards' and 'punishments' would not work unless they changed the way animals feel affectively.

With this principle, we can readily make cross-species predictions, even to humans. At the primary-process level (i.e. the *primal* unconditioned emotional response systems of the brain), the study of all other mammals is relevant to the human condition—even laboratory rats and mice, not just primates. The primal affective mechanisms exist in some of the most ancient regions of the brain, where evolutionary homologies are striking. Thus, in order to understand how the human BrainMind operates—especially our affective emotional mind—it is essential to cultivate neuroempirically based, as opposed to speculation-based, evolutionary perspectives (Panksepp and Panksepp, 2000). The brain seems to be the only organ of our bodies that is clearly evolutionarily layered, albeit all levels functionally interdigitate. What came first remains low and medial in the brain; what came later was added on the outside (more laterally) with the vastest recent expansions rostrally.

In order to make sense of the 'whole', one has to respect and understand the ancient 'parts' and levels of BrainMind organization (see Northoff et al., in this issue for how nested-hierarchies may achieve that). If we don't understand the foundational level—the *primary-process* mechanisms of BrainMind—then we will never have a clear image of how our emotional feelings evolved and

Basic Emotional Systems	Key Brain Areas	Key Neuromodulators
General Pos. Motivation SEEKING/ Expectancy System	Nucleus Accumbens – VTA Mesolimbic and mesocortical outputs Lateral hypothalamus – PAG	DA (+) , glutamate (+), opioids (+), neurotensin (+) , orexin (+) , Many other neuropeptides
RAGE/ Anger	Medial amygdala to Bed Nucleus of Stria Terminalis (BNST). Medial and perifornical hypothalamic to PAG	Substance P (+) , Ach (+), glutamate (+)
FEAR/ Anxiety	Central & lateral amygdala to medial hypothalamus and dorsal PAG	Glutamate (+), DBI, CRF, CCK, alpha-MSH, NPY
LUST/ Sexuality	Cortico-medial amygdala, Bed nucleus of stria terminalis (BNST) Preoptic hypothalamus, VMH, PAG	Steroids (+), vasopressin, & oxytocin, LH-RH, CCK
CARE/ Nurturance	Anterior Cingulate, BNST Preoptic Area, VTA, PAG	oxytocin (+), prolactin (+) dopamine (+), opioids (+/-)
PANIC/ Separation	Anterior Cingulate, BNST & Preoptic Area Dorsomedial Thalamus, PAG	opioids (-), oxytocin (-) prolactin (-), CRF (+) glutamate (+)
PLAY/ Joy	Dorso-medial diencephalon Parafascicular Area, PAG	opioids (+/-) , glutamate (+) Ach (+), cannabinoids, TRH?

Fig. 2. General summary of the key neuroanatomical and neurochemical factors that contribute to the construction of basic emotions in the mammalian brain. The online version shows positive emotions in red and negative emotions in blue. Data summarized in Panksepp (1998). For summary of abbreviations used, see Panksepp (2000, p. 144).

how higher brain mechanisms work—how the *secondary-process* mechanisms of learning and memory, deeply unconscious brain processes, are regulated by more primal emotional systems and how *tertiary-process* substrates for various higher brain functions remain tethered to what came before. In other words, the secondary and tertiary functions of the brain rely critically on unconditional networks that evolved earlier. This resembles the *anoetic, noetic*, and *autonoetic* levels of consciousness proposed by Endel Tulving (2002).

It is only the tertiary process level that cannot be well fathomed scientifically through current animal brain research—our cognitive thoughts and emotional ruminations, the sources of our art, beliefs, creativity, dance, fantasies, literature, music, theater. . . the cognitive aspects of schizophrenias, obsessions, manias, and depressions. All are constructed from our vast capacity for learning and working memory, and our ability to learn languages (see Vandekerckhove and Panksepp, in this issue). In contrast, our primal emotional urges can be best understood through animal brain research.

3. Primal affects and the cognitive revolution

Our cognitive lives are vastly enriched by our subcortical affective powers, with major, although poorly understood implications for human welfare (see Bernatzky et al., this issue) and happiness (Sheldon et al., 2011). However, we should avoid mixing up affective and cognitive issues within the brain, even though they are so intimately blended in our higher brain functions (Cromwell and Panksepp, in this issue).

Since so many of our cognitive complexities remain linked and tethered to our primordial affective values, there will be a growing interest in this kind of psychologically oriented neuroscience in the humanities. All the higher MindBrain riches are profoundly impaired or destroyed by substantial damage to the medial subcortical affective state-control networks (Bailey and Davis, 1942, 1944; Parvizi and Damasio, 2003). In contrast, our basic affective lives sur-

vive vast destructions of our more recently evolved upstairs brain. These are robust BrainMind facts. Why would anyone still believe that the *sources* of our emotional feelings arise from the neocortex, the way William James and many psychologists for the past century surmised (including famous neuroscientists, neurologists and psychiatrists: for a vivid portrayal of uniform agreement see the 12th show, on emotions, in the Charlie Rose/Eric Kandel Brain Series, aired first on PBS in 2010)? This is a puzzling residue of an era where open and frank scientific discourse about the neural nature of consciousness and emotions was rare during the second half of the 20th century. It has been clear for a long time that the most powerful affective experiences in humans are evoked by stimulating deep subcortical regions of the brain from where emotional behaviors can be evoked in animals (Heath, 1996; Panksepp, 1985). Of course the older cortices, such as insula and orbitofrontal regions, contribute much to sensory and homeostatic feelings (Craig, 2003), but so do many other brain regions (Denton, 2006).

In sum, diverse primal affective feelings, homologous in all mammals, have their origins in subcortical structures, and our working hypothesis is that they are re-represented, in nested-hierarchies, in higher brain regions, and that basic learning, like classical conditioning, is dependent on such bottom-up hierarchical controls. For instance, fear-conditioning (LeDoux, 1996) may depend on the ability of primal FEAR circuits to “captivate” associated external information, perhaps through primary-process emotion induced NMDA receptor-mediated glutamatergic amplification of AMPA receptors at various cognitive emotional interfaces of the brain, especially the amygdala and other basal ganglia (Panksepp et al., 2011; Panksepp and Biven, in press).

In the beginning, our higher neocortical brain, for all intents and purposes, is a *tabula rasa* of seemingly endless fields of self-similar columnar “chips” that are programmed by subcortical processes. Thus, practically everything that emerges in our higher neocortical apparatus arises from life experiences rather than genetic specializations. Simply consider the wondrous fact that surgi-

cal elimination of the occipital “visual” cortex before birth in mice hardly impairs their ability to develop visual competence in adjacent cortical areas (Sur and Rubenstein, 2005). William James guessed that our emotional feelings arise from the higher somatosensory cortical regions that harvest our bodily sensations (as Damasio (1994) also later surmised), leading first to a century of misunderstandings (Ellsworth, 1994), and now another decade or two. But that conjecture is simply not true, at least not as the major cause of our feelings. If anything, the frontal executive regions of the brain, especially in the midline (medial prefrontal cortex) are much more important than sensory regions in controlling emotions, but they largely do so through cognitive ruminations as well as mindful regulation of the subcortical emotional arousals that often overwhelm the mind from below.

Comparable mistakes are currently being made in many human neuropsychological studies of emotions where many investigators feel that emotional feelings arise from our higher cortical capacities for noetic (knowing) conscious “awareness” as opposed to our subcortical anoetic affective consciousness, which elaborates raw affective *experiences without knowing*. To avoid such errors, we need to make disciplined distinctions between tertiary-process cognitions and primary-process emotions/motivations (Panksepp, 2003; Panksepp and Biven, in press). Indeed, in modern human emotion-affect studies, we must question the excessive weight of explanatory power that has been placed on poorly defined “cognitions” in lieu of a full consideration of the primal nature of our emotions and motivations (see Cromwell and Panksepp, this issue). It is very difficult to get clear signals of emotion-specific processing from direct neuronal recordings of cortical activities (see Bekkedal et al., in this issue). We must descend to the subcortical realm for more robust signals (Damasio et al., 2000; Damasio, 2010).

4. The varieties of raw affects: the unconditioned response and stimulus processes of the brain

Within the subcortical terrains of raw *affective experience*, there are many varieties of affects. There are (i) the *emotional affects*, which arise from the same neural circuits that integrate and orchestrate the emotional action and autonomic responses of the brain-body continuum (Panksepp, 1998), (ii) the *homeostatic affects* that arise from intero-receptors that gauge a variety of bodily states from air-hunger to thirst (Denton, 2006), and (iii) the *sensory affects* that arise rather directly through our various sensory portals, especially taste, touch, smell and sound (Craig, 2003; Peciña et al., 2006; Rolls, 2005). These affects are the same “unconditioned stimuli” (UCSs) and “unconditioned responses” (UCRs) that behaviorists used to train their animals. The *procedure* called *reinforcement* (sensory cues followed quickly with sensory rewards and punishments) can be very effectively used to bring brain-learning processes under “stimulus-control”, but that ghostly *process* of “reinforcement” remains to be empirically demonstrated within brain dynamics to anyone’s satisfaction.

As already noted, that overused concept of “reinforcement”—a presently very mysterious *process* of the brain—may simply turn out to be a shorthand way of talking about how brain affective networks promote learning.

One can easily envision that, perhaps through neuropsychological UCR and UCS based “attractor landscapes”—which may help sensitize glutamatergic channels from temporally associated conditioned stimuli (CSs)—new conditioned response (CR) pathways are opened up to brain emotional operating systems (which originally engendered the affective attractor neurodynamics in the first place). This potential shortsightedness, of not recognizing the role of UCR systems (e.g. the FEAR circuitry) in the establishment of

conditioning, may arise from the fact that most behavioral investigators have not envisioned that the emotional UCR generating systems of the brain can also generate emotional feelings. It is traditional to believe that only the UCS systems might have psychological attributes. It requires a shift in perspective to consider that certain UCR systems, such as the primary-process emotional circuits, can also have psychological properties.

Before causal neuroscience studies of the early 1950s (e.g., self-stimulation and escape from aversive ESB) investigators had no real basis for evaluating whether animals experienced their emotional arousals—whether they felt their emotions—but learning mediated by ESB induced reward and punishments solved that problem a long time ago; we just chose not to modify well-established ways of speaking (behavior-only lingo) and related neuroscientific ways of thinking (ruthless reductionism). During the current era, only the most affect-sensitive kinds of human brain imaging, mainly PET scans, can visualize the ghostly tracks of primal affective experiences in the deepest areas of the human brain (e.g., Damasio et al., 2000; Denton, 2006; but also see Northoff et al., 2009). But it is now noteworthy that these regions have long been implicated in engendering emotionality in animals (MacLean, 1990; Panksepp, 1982). And ESB studies in humans have been quite consistent in generating intense affective experiences during stimulation of such brain regions (Heath, 1996; Panksepp, 1985). Never have such profound emotional states been provoked by stimulating neocortical regions. Although some emotional responses have been recently evoked by cortical microstimulation (Stepniewska et al., 2009), the rewarding and punishing properties of such brain sites remain to be evaluated.

Are the various affects—diverse feelings of positive and negative valences (‘good’ and ‘bad’ feelings in the vernacular)—identical across species? Of course not! Evolution persistently generates abundant differences, but always on top of conserved-homologous foundational principles at genetic, neural and primal psychological levels. Natural selection is adept at constructing vast diversities of forms and functions with profound similarities in underlying controls. Within the evolved BrainMind, the potentials for variety get ever greater as one ascends the various levels of control, with perhaps the greatest species variability in neocortical specializations, most of which are developmentally/epigenetically created (Sur and Rubenstein, 2005), even if they exhibit very high location concordance in the neocortex (from auditory to speech cortices so to speak). Those cross-species standard patterns are probably dictated by genetic controls that promote subcortical systems to innervate the nearest cortical regions—surely an energetically efficient strategy for brain construction. There need be no intrinsic cortical specializations before such genetically specialized innervations into what is initially general-purpose “computational” space (aka, neocortex).

Could such a scenario also apply to subcortical attentional, emotional and homeostatic motivational systems? Perhaps. But that may be pushing evolutionary plasticity a bit too far. Long-term energy balance (i.e., hunger) registration systems are well situated in the arcuate nucleus of the ventromedial hypothalamus (see Panksepp, 1974, and all the great work on neuropeptides that mediate body energy regulation, all studied with hardly a word about the affective properties of hunger and normal satiety: see Panksepp, 2010c), just above the pituitary, which is essential for proper distribution of nutrients in the body. Just like our energy, water, and other regulatory systems, which are self-similar across species (Denton, 2006), the weight of evidence currently indicates that many other animals do possess quite similar primary-process brain mechanisms that mediate at least seven basic emotions easily recognized in humans.

Because of evolutionary diversification and the complexities added by levels of control, we would be foolish to call these primary-process emotional systems simply with the vernacular

terms that are common in human conversations. For various reasons, too long to summarize here (see Zachar and Ellis, *in press*) we need a specialized language for the primary MindBrain processes. To try to achieve such a needed terminology, we have long chosen to fully capitalize the emotional primes that are strongly supported by cross-species neuroscience evidence. The full capitalizations I chose to use as designators for primal emotional feelings are intended to recognize this dilemma, while not allowing us to be semantically immobilized in addressing some of the most momentous neuroscientific issues.

In sum, the most compelling scientific evidence about the foundational nature of animal emotions comes from behavioral brain research, where specific brain systems are manipulated. So how did such lines of inquiry begin? Walter Hess, who received the Nobel Prize in 1949, initiated his most influential work starting in the 1930s. He was the first to find that localized hypothalamic ESB in cats could transform them from friendly animals into intensely angry creatures (full summary in Hess, 1957). Eventually various distinct forms of attack were identified, the main two being an angry-emotional attack and a methodical stalking-predatory attack (Flynn, 1976). Hess regretted calling the former behavior “sham-rage”; as he confessed late in life, he only chose to use a non-affective lexicon, rather than emotional terms, because he feared his work would be marginalized by the seemingly all powerful behaviorists (Hess, 1964).

As already noted, when investigators finally inquired whether animals “cared” about such stimulation, by asking whether they would turn the stimulation on or off, the answers were clear. Animals would turn off ESB that provoked “affective attack”, but self-activate sites that provoked predatory attack (Panksepp, 1971). Likewise, animals would terminate ESB that produced fearful behaviors, and would self-stimulate SEEKING sites that could generate exploratory and various consummatory behaviors (e.g., feeding, drinking and sexual) which, to practically everyone’s surprise, were completely interchangeable (Valenstein et al., 1970). Activation of many of these emotion provoking brain sites also promoted CPPs (animals returning more frequently to places where they had those neurochemical experiences) or CPAs if RAGE, FEAR or PANIC/GRIEF had been provoked. One of my fine students/collaborators, Satoshi Ikemoto, has pursued brain self-administration of diverse neurochemicals with more diligence than anyone before (he shared findings from Ikemoto, 2010, at this Festschrift).

Taken together, these studies confirm that affective states are organized within primitive regions of the brain that anatomically and neurochemically resemble each other closely in all mammals. Important general principles have emerged from this kind of work. To re-iterate a few key points:

- (1) A diversity of brain networks for basic emotional instinctual behaviors, homologous across vertebrate species, are situated in ancient brain regions evolutionarily similar in all mammals.
- (2) The lower regions of the brain are more important for generating emotional feelings than the higher regions of the brain (this has been verified by both ESB and brain damage studies, including in humans—eg., Heath, 1996; Merker, 2007). Damage to lower regions of each network are more disastrous for emotional competence than damage to higher regions, and as one maps ESB thresholds, one consistently needs lower currents to evoke emotional behaviors and indices of affect as one descends into the midbrain along any primal emotional network—for instance in FEAR and RAGE systems, as one moves from amygdala, to hypothalamus to the Periaqueductal gray (PAG). And higher functions are always dependent on the lower functions (Fig. 3).

- 1) PAG: Lowest ESB energy to obtain powerful emotional changes
- 2) PAG: Smallest brain damage compromising consciousness
- 3) PAG: Most massive convergence of brain emotional systems

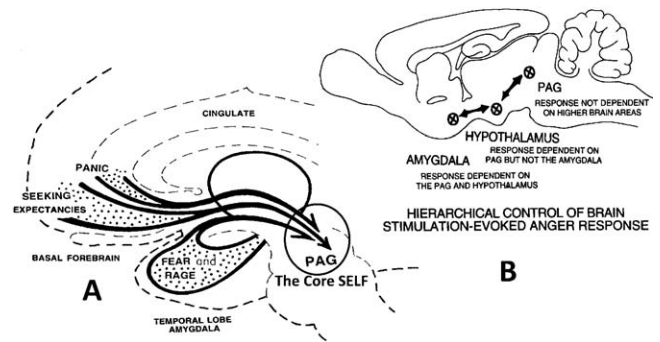


Fig. 3. (A) Overview of forebrain zones that are devoted to elaborating higher manifestations of basic emotional processes. Each of the emotional systems has higher spheres of influence, with FEAR and RAGE concentrated in the lateral and medial temporal lobes, SEEKING in the ventromedial frontal lobes, and various social emotional processes such as separation distress or PANIC in the anterior cingulate. All of these systems converge on the most highly concentrated emotional and core-affective SELF representation zones of the midbrain. Three properties of the PAG are highlighted which indicate its critical importance for core-emotional processing in the brain, compared to higher brain areas. (B) A schematic depiction of the hierarchical control within brain emotional systems, with the best worked out system being RAGE. Clearly lesions of higher areas do not diminish the emotional responses from lower areas, while damage to lower areas can dramatically compromise emotional actions generated from higher areas.

Adapted from Figs. 15.2 (A) and 10.4 (B) in Panksepp (1998) with the permission of Oxford University Press.

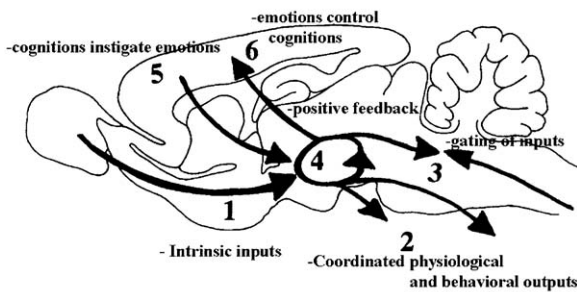
- (3) There is a tight correspondence between brain loci (and hence presumably networks) that generate emotional instinctual behavioral responses and the feelings that accompany those states.
- (4) The basic neurochemistries for emotional feelings, as far as we presently understand them, are essentially the same in all mammals (Panksepp and Harro, 2004).

5. The basic affective circuits of mammalian brains

Current evidence supports the existence of at least seven distinct forms of emotional arousal in all mammalian brains that have been sufficiently studied (see Panksepp, 1998, for fuller anatomical, neurochemical and behavioral descriptions of these systems, with a skeleton summary in Fig. 1). They are not completely “independent” but surely interact massively with each other. . . see hypothetical controls in inter-systemic controls in Fig. 2, including the facilitation of SEEKING by FEAR and RAGE responses. Again, the names of these emotional systems are capitalized to emphasize the existence of such functionally dedicated primal emotional processes within mammalian brains. There are no comparable nomenclatures for the secondary and tertiary manifestations of these systems, but it is easy to imagine how they diversify “into the vernacular” so to speak (i.e., cultural designation of emotional nuances), and examples are provided below for each system.

Neuroanatomically, all primal systems are situated subcortically, and consist of large transverse networks that interconnect midbrain circuits concentrated in midbrain regions such as the PAG and ventral tegmental area (VTA), with various basal ganglia nuclei, such as amygdala and nucleus accumbens as well as cingulate and medial frontal cortex, via pathways that run through the lateral and medial hypothalamus and medial thalamus (Fig. 3). Each system has abundant descending and ascending components that work together in a coordinated fashion to generate various instinctual emotional behaviors as well as the raw feelings nor-

Emotional “Command” or “Operating” Systems



7. Affect reflects the full operation of such systems Neural Definition of Emotional Systems

Fig. 4. A schematic summary of the defining characteristics of basic instinctual emotional systems: They all have a few (1) intrinsic inputs, which behaviorists called *Unconditional Stimuli* (UCSs); (2) various instinctual behavioral and bodily, especially autonomic-visceral, outputs, which behaviorists called *Unconditional Responses* (UCRs); (3) the input of various other stimuli into higher brain regions—potential *conditional stimuli* (CSs)—if they predict rewards and punishments, is controlled by emotional systems (yielding what some people call ‘incentive salience’); (4) emotions outlast the stimuli that activated the systems, whether external (UCSs) or internal ruminations, such as those that arise from, (5) higher cortical areas, especially in the frontal cortex activating or inhibiting emotions, and (6) emotional systems clearly have the power to control and modify higher brain functions—the affective feeling of an emotion largely produced by an internal brain process summarized by attribute 4. Still, as highlighted by attribute #7, all the other aspects of the system can modify and regulate the intensity, duration and patterning of emotional responses. Thus, the final affect is a consequence of the interactions of all the BrainMind attributes that define each primal emotional network.

Adapted from Fig. 3.3 in Panksepp (1998) with the permission of Oxford University Press.

mally associated with those behaviors. The raw affects engendered by these systems are ancestral memories (instincts) that promote survival—they anticipate the kinds of survival needs that all organisms require to successfully navigate the world. They also help mediate the poorly understood brain processes called “reinforcement” in traditional behavioristic learning theory, based upon the temporal association of external stimuli with the unconditioned affective responses of the nervous system.

Through an understanding of these primary-process systems, we may eventually be able to craft a scientifically sound general definition of emotions (Fig. 4). These systems sustain their integrity in decorticated animals (Merker, 2007; Panksepp et al., 1994), but they probably control and are controlled by various higher brain processes that are hard to analyze psychologically in animal models, just like the lower subcortical systems are almost impossible to study, ethically, in any detail in humans. There is so much functional work left to be done on these systems, especially with regard to preclinical modeling of emotional distress, but relatively little is being conducted. This could be deemed regrettable because a cogent argument is readily made for the likelihood that these systems are of critical importance for all psychiatric disorders characterized by affective turmoil (Panksepp, 2006). Indeed, by taking these affective systems seriously, we may be heading toward more precise animal models of psychiatric disorders (Wright and Panksepp, in this issue). Here are thumbnail sketches of the seven *emotional* systems, more fully described in many of the contributions to this Festschrift issue, but also in Panksepp (1998, 2005a) and Panksepp and Biven (in press). I will not focus on the *homeostatic* and *sensory* affects in this short essay.

(1) **The SEEKING System.** For literature overviews, see Alcaro et al. (2007), Ikemoto and Panksepp (1999) and Panksepp and Moskal (2008). This is a vast, general-purpose appetitive motivational

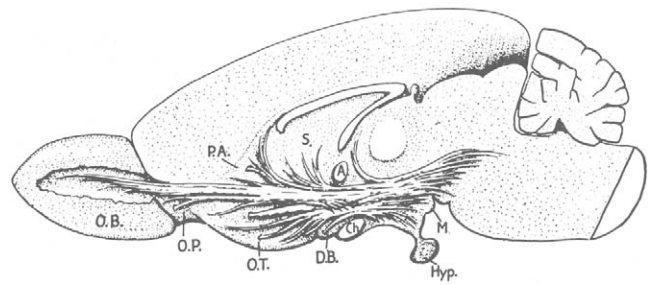


Fig. 5. A schematic summary of the Medial Forebrain Bundle (MFB)—namely “The Brain Reward” system or better, the “SEEKING” system, connecting central regions of the midbrain with higher brain regions, that runs through the Lateral Hypothalamus (LH) situated just above and to the right and left of the optic chiasma (Ch), with the remaining anatomical nomenclature highlighting Olfactory Bulbs (O.B.), Olfactory Peduncle (O.P.), Paraolfactory Area (P.A.), Olfactory Tract (O.T.), Diagonal Band of Broca (D.B.), Anterior Commissure (A), pituitary gland or as it used to be called, the hypophysis (Hyp.), and Mamillary Bodies (M). In the midbrain, parts of the descending branches of the MFB project to medial regions such as the Periaqueductal Gray.

This classic figure comes from LeGros Clark (1938).

system with a magnificent and ultra-complex anatomy of the medial forebrain bundle (MFB)—the first fine anatomical depiction is shared in the classic image of Fig. 5 (for trajectories in the human brain, see Coenen et al., in this issue). This system engenders an enthusiastic affective-‘energy’ that has at times been called “libido” in the psychoanalytic tradition, and “euphoria” within modern drug addiction research. It provokes animals to become intensely energized to explore the world and also promotes learning, with the useful but logically faulty principle of *post hoc ergo propter hoc*—what comes after was caused by what came before, leading to the feeling of causality when an important event such as a UCS follows a cue, a CS. But even without learning, it leads animals to become excited about the mundane, and the system conditions rapidly to yield vigorous approach, exploration and, eventually, various consummatory behaviors when there are predictable associations between external events and the things animals need to survive.

It should be emphasized that this system “wants” to learn, is designed to learn automatically, and as a result has an enormous number of acquired behavioral manifestations (Valenstein et al., 1970). But this system does not “want” anything specific before learning; it just wants opportunities to explore the world, which is critical for survival. Indeed, predatory behavior is one manifestation of this system in action (Panksepp, 1971). Ultimately this SEEKING urge *spontaneously* allows animals to explore and to find and eagerly anticipate all kinds of resources they need for survival. It is a general-purpose “go-get-it” system—the epitome of “intentions in action”—a philosophical term for primary-process intentionality, that may be foundational for our higher-order (cognitive) “intentions-to-act” (Searle, 1983)—which, as it interacts with the world, comes to facilitate learning and thought, because it also engenders curiosity, interest, enthusiasm and cravings. The arousal of this system is diminished in psychiatric disorders such as depression (Nestler and Carlezon, 2006) and is excessive in mania and in paranoid schizophrenia, where it promotes delusional psychotic thinking patterns (Kapur, 2003), perhaps through increased ‘incentive salience’ (Berridge, 2007), a neat new term for the old concept of “secondary reinforcement”.

All animals readily ‘self-stimulate’ this dopamine facilitated MFB circuitry (Fig. 5) “addictively”, both electrically and chemically, in diverse brain locations as this extensive network courses from the VTA, to various basal ganglia nuclei, upward to the medial frontal cortex (Ikemoto, 2010). This system,

long misconceptualized as “The Brain Reward, Pleasure and/or Reinforcement System”, is more cogently conceptualized as a general-purpose reward SEEKING system, at least at the primary-process level. At the secondary-process learning level it may promote learned ‘incentive salience’, and perhaps at the tertiary process level it can be readily discussed in terms of engendering specific expectancies (Panksepp, 1981), ‘wantings’ (Berridge, 2007), desires and a host of other related concepts. This system permits learning by readily promoting the perception of predictive stimulus-reward relationships in the world, but a fundamental error is being made (mixing levels of analysis) if one just restricts their vision to concepts like ‘reward prediction error signaling’ or any very narrow behavioristic concept such as approach.

SEEKING is a very broad *action* system of the brain that should convince us that the motor urges of our ancestral brain could generate feelings, just like all the other major emotions. Most neuroscientists are beginning to agree that this dopamine-energized network helps coordinate many MindBrain functions from anticipatory eagerness to feelings of purpose and persistence, all the while promoting planning, foresight and dreams through its multiple normal manifestations, but addictions and psychotic delusions when the system is dysregulated. To some extent, the SEEKING system participates in the tasks of every other primary-emotion (helping explain why stressful circumstances release dopamine) as well as practically everything we do, and this highlights a general subcortical principle: All primal emotional systems interact with each other in primal inhibitory and excitatory relationships that no one has yet mapped empirically (Fig. 1).

- (2) **The RAGE/Anger System.** For literature overview, see Flynn (1976), Guerra et al. (2010), Panksepp and Zellner (2004) and Siegel (2005). Working often in opposition to SEEKING is a system that mediates anger, but no doubt also aspects such as dopamine release are facilitated by anger. RAGE is normally aroused by frustrations and attempts to curtail animals’ freedom of action, but it can be evoked by stimulating brain networks that lie close to and interdigitate with the trajectory of the FEAR system (discussed next). The RAGE system invigorates aggressive behaviors when animals are irritated or restrained and also helps animals defend themselves by arousing FEAR in their opponents. Human anger presumably gets much of its ‘psychic energy’ from arousal of the RAGE system. How can we find out? Perhaps by modulating key chemistries in this system—e.g., reducing rage with receptor blockade of the best studied neuropeptide, Substance P, that arouses this system, and by monitoring the anti-aggressive effects of opioids, which among many other BrainMind functions, can inhibit RAGE. The kinds of vernacular words that relate to higher brain functions that accompany arousal of this system may be anger, irritability, explosiveness, resentment, and many others.
- (3) **The FEAR/Anxiety System.** For literature overview, see Panksepp (1990), Panksepp et al. (2011) and Davis et al. (2009). A coherently operating FEAR circuit was designed during brain evolution to help animals escape and avoid the many dangers of the world that could result in severe injury and death. When stimulated intensely, primary-process FEAR circuits running from amygdala to PAG motivate animals to freeze and flee in apparent frights. At low ESB current levels, freezing is promoted and from many brains sites rats exhibit 22 kHz “complaint” type vocalizations, while at high current levels flight is precipitated, often without vocalizations, which return when the ESB stops. These responses are the same as when animals are placed back into environments where they were previously hurt. Humans stimulated in these same brain loci, especially from the PAG, report being engulfed by intense anxiety (quote: “scared to death”) with no environmental cause (Nashold et al., 1969). Key chemistries that regulate this system are Neuropeptide Y and Corticotrophin Releasing Factor (CRF); specific anti-anxiety agents such as the benzodiazepines inhibit this system.
- (4) **The LUST Systems.** For literature overview, see Pfaff (1999) for mammals and Ritters (in this issue) for birds. Sexual urges are mediated by specific brain circuits and chemistries that are overlapping but also quite distinct for males and females. They are aroused by male and female sex hormones, which regulate various neuropeptides: Brain oxytocin transmission, facilitated by estrogen, promotes sexual readiness in females, while male assertiveness (“pushiness”?) is regulated by vasopressin, a neuropeptide that is invigorated by testosterone. These brain chemistries help create gender specific sexual tendencies. Although distinct male and female sexual proclivities are constructed into LUST networks early in life, they are brought to full bloom by the hormonal tides of puberty. Because brain and bodily sex characteristics are independently organized, in all mammals, genetically male animals may exhibit female sexual urges, and genetic females can exhibit male typical urges. Certain ancestral chemistries of sexuality, for instance oxytocin, have been re-deployed for crafting maternal CARE—nurturance and social bonding—suggesting evolutionary continuities between female sexual rewards and maternal satisfactions.
- (5) **The Maternal Nurturance CARE System.** For detailed overviews, see Numan and Insel (2003) for mammals and Ritters (this issue) for birds. Brain evolution has provided safeguards to assure that parents take care of offspring, with mammalian mothers generally more devoted than fathers. The massive hormonal changes at the end of pregnancy (declining progesterone, and increasing estrogen, prolactin, and oxytocin) set the stage for the activation of maternal urges a few days before the young are born. These hormonal and neurochemical tides, facilitate maternal moods and promote social-bonding with offspring. Similar neurochemicals, especially oxytocin and endogenous opioids, promote infant bonding to the mother. These changes are foundational for a fundamental love: mother–infant bonding.
- (6) **The Separation Distress PANIC System.** For literature overview, see Nelson and Panksepp (1998) and Panksepp (2011) for animals, and Freed and Mann (2007) and Swain et al. (2007) for human psychological implications. All young mammals and birds are dependent on parental care, especially maternal care, for survival. Distinct emotional powers that engender crying, allow young animals to signal their desperate need for care, especially when lost or isolated from caretakers by experimenters. These separation calls alert caretakers to seek out, retrieve, and attend to the needs of the offspring. The alleviation of separation distress in young animals can be easily achieved simply by holding them. The PANIC system has now been electrically and chemically mapped in several species (see Normansell and Panksepp, this issue). Separation distress is powerfully inhibited by endogenous opioids, oxytocin, and prolactin—the major social-attachment, social-bonding chemistries of the mammalian brain. PANIC circuits are also aroused during human sadness, which is accompanied by low brain opioid activity. The clinical implications for understanding depression are summarized in Watt and Panksepp (2009) and by Zellner et al. (in this issue). Beautiful examples of environmental modulation of genetic endowments have been revealed in primates (Suomi, 2006).
- (7) **The PLAY/Rough-and-Tumble, Physical Social-Engagement System.** For literature overview, see Burghardt (2005), Pellis and Pellis (2009), Sivy and Panksepp (this issue) with some clinical implications in Panksepp (2007b). Young animals crave

physical play. When made hungry for play, rats pounce on each other, engendering bouts of chasing and wrestling, all accompanied by joyful 50 kHz chirps signaling an intense social joy. Wherever in the brain one can evoke these chirps with ESB, the animals eagerly self-stimulate the circuitry, suggesting one motivation for play is the dopamine energized SEEKING system (Burgdorf et al., 2007, *this issue*). If humans tickle rats, these vocalizations become very intense but when any negative affect is induced, these vocalizations cease. A key function of the social PLAY system is to help young animals to acquire the social knowledge and refinement of subtle social interactions that they will need to thrive. Thus, PLAY may be one of the major emotional forces that promotes the epigenetic construction of higher social brain functions, perhaps even mirror-neurons. It may be the primary brain process that promotes all kinds of social communication, which can be quite subtle even in rats and birds (see Arakawa et al., *in this issue*; Panksepp and Lahvis, *in this issue*; Ritters, *in this issue*).

We can be confident that all of these emotional networks are concentrated in highly interdigitating brain regions far below the cortex. Radical neo-decortication (surgical elimination of the whole dorsal cerebral mantle) leaves all of the above emotional-instinctual urges intact, even as the capacity of such animals to learn new instrumental behavior patterns is severely impaired, although many forms of classical conditioning survive. Again, the existence of feeling states during such arousals is based on the observation that animals are never neutral about such kinds of physical stimulation of their brains. The almost infinitely complex neural mechanisms that undergird these emotions can finally be understood through the increasing powers of neuroscience techniques. Regrettably, they are still all too rarely used to understand the nature of mind.

By understanding the neurochemistries that control these systems, I and many of my colleagues assume that a new generation of more potent and affectively more specific psychiatric medicines can be developed to help control excessive and diminished emotionality and mood in humans and in our fellow animals (Panksepp and Harro, 2004; Panksepp and Watt, 2011; and see also Zellner et al., *in this issue*), with even more radical possibilities emerging from human brain stimulation (Coenen et al., *this issue*).

Although many dedicated behavioral neuroscientists still resist the use of neuro-emotional concepts illuminated by affective neuroscience, that is more by force of habit than the force of evidence. In any event, since raw emotional feeling states are closely linked to the natural emotional behaviors that animals exhibit, we can utilize a Spinozan *dual-aspect monism* strategy, which accepts that unconditioned emotional behaviors and certain intrinsic emotional feelings arise from the same brain substrates. To the best of our knowledge, raw feelings do not need to be ‘read-out’ by higher brain regions, although they obsessively interact with higher mental functions.

This is what the evidence indicates: we can use the natural emotional behaviors of animals to serve as proxies for their emotional feelings. This view can be advanced to the degree that brain networks that mediate unconditioned emotional responses control reward (and conditioned approach) and punishment (along with conditioned avoidance) in animals, also generate corresponding types of positive and negative feelings in humans. Such findings have profound implications for biological psychiatry (Panksepp, 2004, 2006), including new therapeutics for depression (see Burgdorf et al., *this issue*; Coenen et al., *this issue*; Zellner et al., *this issue*). We are even using positive emotional vocalizations as natural self-report measures of addictive craving for cocaine in rats (Browning et al., 2011), as well as ways to develop circuit-based preclin-

ical models of psychiatric disorders (Harro et al., *in this issue*; Wright and Panksepp, *in this issue*).

6. A neuroscience of the affective mind and ethical implications

If the ancient brain mechanisms for affective feelings are evolutionarily related in all mammals, we can finally begin to understand the deep neural nature of human feelings by studying the homologous neuroanatomies and neurochemistries of these systems in animal models. This could greatly advance our understanding of the human brain and mind. But this transition from Cartesian skepticism, and denial of mind in other animals, to neuro-mental realism is bound to be a slow process, at least among neuroscientists who have built their careers and belief systems on the behaviorist “never-mind” tradition. And of course there are other issues to consider.

The existence of internal feelings in other animals is also rich with ethical implications. The ways in which we treat animals are surely based, in part, on their abilities to experience fear, pain, hunger, thirst, etc.—the major sources of suffering. If the experiences of affects resembling our own anger and despair, desire and joy do exist in other animals, then these issues must figure in our treatment of experimental animals. To treat animals as if they had no such feelings, if they do, is an ethical mistake, and hence a dilemma that investigators need to consider frankly. For my part, I think scientific knowledge about our shared affective heritage can justify the sacrifices that are required. But we should not deny the dilemmas involved, and often such considerations may lead to better research. For instance certain aversion-creating systems can be studied under full anesthesia (Panksepp et al., 1991), just like certain positive affect systems (Rossi and Panksepp, 1992). Many of the properties of these systems can be studied using *in vitro* systems; for instance, we could imagine studying the conditioning of emotional systems using simplified preparations such as brain slices sustained *in vitro*.

It is important for scientifically informed people to consider all the relevant evidence in order to determine where they should stand on such important animal mind and well-being issues (McMillan, 2005). Basic animal research raises other ethical issues too subtle to consider here, such as the potential presence of raw affective states in people with brain damage leading to persistent vegetative states (Panksepp et al., 2007). At the same time the existence of phenomenal affective states in animals does not automatically mean that they have the mental wherewithal to have reflective awareness—namely higher forms of consciousness that humans cherish as a foundation for our forms of community and culture.

Whether other animals also emotionally suffer, or have more subtle emotional feelings such as jealousy, shame, guilt or a sense of humor—feelings that are created by the interrelations of basic emotions with higher cognitive processes—remains an open issue. Subtle analyses of animal behavior in natural environments, especially our primate cousins and domesticated companion animals, certainly suggest that other animals do have more subtle emotions, and even episodic memories and degrees of cognitive reflections, built upon the basic seven systems described above (e.g., Clayton et al., 2003). There are now abundant behavioral demonstrations of remarkably subtle choice behaviors in other animals—from crows to dogs—and that behavioral literature is growing rapidly. However, our neuroscientific methods to study such higher emotional processes are not well developed, even though behavioral interest in such issues is rapidly growing, but sophisticated behavioral methodologies are being developed to monitor higher emotional issues (McMillan, 2005; Mendl et al., 2010; Panksepp and Lahvis, *in this issue*).

7. What difference does it make whether animals have emotional feelings?

The simplest answer to this question is that it surely makes a difference to the animals having such experiences. Just as we care about how we feel, animals surely care whether they feel good or bad. Since affective feelings are the source of most of our satisfactions and sufferings, as well as many of our behavioral choices, the scientific resolution of the existence of primary-process feelings in other animals and the brain mechanisms for those feelings is of momentous importance for understanding the basic psychological processes and well-being issues of our own species. Such feelings promptly inform animals where they stand in terms of health and other survival issues. The resulting practical and philosophical implications for understanding human behavior are complex and pregnant with possibilities (see [Davies, in this issue](#)).

Through a study of the subcortical brain systems in animal, and development of better animals models of social behaviors that do not disregard their feelings (see [Colonnello et al., in this issue](#); [Cromwell and Panksepp, in press](#); [Cromwell, 2011](#); [Panksepp and Lahvis, in this issue](#)), we can generate a solid understanding of the basic emotional systems of human beings. This work is also important for the next generation of scientific developments in biological psychiatry and psychotherapeutics ([Coenen et al., in this issue](#); [Zellner et al., in this issue](#)). Once we begin to psychologically appreciate primary-process affective systems, and to study them more precisely, we will surely, as already noted, be able to develop better treatments for the various psychiatric-affective disorders. We will also have a much better understanding of the nature of the core-self and the constraints over our cognitive processes ([Panksepp, 2007c, 2009](#); also see [Bernroider and Panksepp, in press](#); [Vandekerckhove and Panksepp, in this issue](#)).

Some sympathetic critics of the above views may suggest that many investigators are already committed to such an affective neuroscience agenda. To see if there is some evidence for that, I popped onto Pubmed to simply inquire about number of papers that have worked on the topic of “emotions”—142,392 hits was not bad. There is an “Emotion Revolution” going on for sure. When I added “affects”, the hits dropped precipitously to 27, 227. So feelings are still a bit dicey? And when “brain” was included, the drop was disconcertingly low at 4293. When the most commonly used species (rats) was included, only 616 remained. With mice, it was only 205. With the proverbial “guinea pig” only two showed up (one was ours). Substituting “dogs” fared little better at 5. And “monkeys” zoomed up to 3550—suggesting that the closer we get to humans, the more willing we are to use “emotion, affect, brain” concepts. In any event, I suspect the bottom line is that affect-related brain issues have not yet penetrated mainstream neuroscience. Considering their importance, the above scan of penetrance is disappointing. The Cognitive Revolution prevails: “Learning” yielded 323,494 hits, albeit adding the product of learning, “memory”, dropped the number of hits to 43,897, but adding “brain” did not lead to the 84% drop but a more modest 48% decline.

By such rough estimates, it looks like affective issues are only about half as popular in neuroscience as memory related ones, but I expect that in psychiatry, the nature of affect is considerably more important. Of course, one would have to do a content analysis of all those papers to get a more meaningful estimate of where we currently stand in the study of how affects arise from brain activities. It is pretty clear that many people still subscribe to the James-Lange view that emotional affects reflect a “read-out” of bodily commotions by higher regions of the brain. That viewpoint has very little causal neuroscientific support from the modern era of causal neuroscience, albeit it is understandable why the many brilliant reflections of William James remain very popular. In this context, it is worth remembering his less known theory of emotions—that

emotional feelings are intimately intertwined with the instinctual processes of the organism. He just did not know how those instincts were organized in the brain.

8. Conclusion

It has become increasingly clear during the past half century that primary-process affective mechanisms are concentrated in ancient subcortical midline brain regions that are anatomically and neurochemically, and hence, evolutionarily, similar in all mammalian species. However, we do not know how members of different species cognitively respond to such feelings. There are no instinctual indicators for higher mental processes. One must use more subtle behavioral tests. Thus it will be much harder to decipher the cognitive contents/infrastructure of animal minds than it is to decipher their emotional feelings. That will require more subtle behavioral analyses of more complex behavior patterns, as is being pursued by many investigators around the world, who monitor self-recognition in animals, mirror neurons, empathy, concerns about the perceptions of others, and so forth. In the arena of emotions, investigators are developing techniques to monitor higher-level affective valuations ([Balleine, 2005](#); [Mendl et al., 2010](#)).

The future looks promising for those who never gave up hope of deciphering the affective (and hopefully cognitive) minds of other animals. The dramatic affective similarities across mammals, concordant with neurological work in humans, highlight the conserved, primary-process emotional mechanisms of the brain that can engender reward and punishment functions in learning tasks. Indeed, those all-important UCSs and UCRs that were essential for any cogent analysis of learned behaviors, although widely used, were never a major subject of either behavioral or psychological inquiry. Those issues were too difficult to pursue in human research. Hence they were neglected. In animals, their pursuit required some serious neuroscience. Also, since the major question in psychology was the nature of learning and memory, the affective faculties of the BrainMind never attracted the attention they deserved in mainstream psychology.

It now seems pretty clear that primary-process emotions are experienced within the deep neural circuits that generate unconditioned emotional behaviors. This is a blessing for a dual-aspect monism epistemology as well as for the hope that we can decipher the foundations of human mind by studying the affective infrastructures of animals' minds. Indeed, if one simply considers the troublesome concept of “self”, it may need, at a primary-process level, to be anchored in the bodily emotional action coherences that characterize all organisms. We may even begin to make progress on such scientifically problematic concepts ([Northoff and Panksepp, 2008](#)) and come to realize that a primary-process core-SELF may not only be the ground for organismic motor coherence but affective-psychological coherence as well ([Panksepp and Northoff, 2009](#); [Panksepp, 2007c, 2008, 2009](#)).

But there are bound to be some who will suggest that affects are merely dynamically unconscious aspects of brain functions, and mind only arises from the cortical sophistications that surround the ancient and necessary subcortical system for existence. Perhaps the affects are *just* ‘read-out’ by some higher brain networks, such as neocortex (James-Lange type theories) or those in higher limbic structures. But there is no solid stream of data for that conclusion, even though higher limbic structures clearly participate in generating distinct emotions ([Vytal and Hamann, 2010](#)). In contrast there is abundant evidence that the brainstem is needed for mental existence ([Damasio, 2010](#); [Merker, 2007](#); [Parvizi and Damasio, 2003](#); [Shewmon et al., 1999](#)). And there is abundant evidence that higher brain regions can add something very special to experience—vast varieties of autobiographical memories as well as the awareness of what one is experiencing. And cognition has a vast domain of inte-

grative and regulatory functions that are very hard to study in other animals (Cromwell and Panksepp, in this issue; Northoff et al., in this issue; Vandekerckhove and Panksepp, in this issue). However phenomenal affective consciousness is not simply a 'read-out' function of the neocortex. That view of emotional feelings is only a small part of the story, and hence deeply flawed as a major explanation (Panksepp, 2008).

The primal affective "tools for living" are very ancient brain functions, intimately integrated with instinctual behavioral capacities, and ancestrally related in all mammals. There is abundant room for "core-self" type concepts in the subcortical emotional terrain of animals that engenders an "organismic coherence", for lack of a better term, that makes us all active creatures of the world, as opposed to mere information-processing automata. The remarkable evolutionary continuities, seen so clearly in the primal emotional attitudes of animals, provide a coherent scientific approach for understanding how some very powerful feelings are created in human brains. Such knowledge provides new and robust pre-clinical models for psychiatric research that take the experienced aspects of brain network functions ever more seriously (e.g., Arakawa et al., in this issue; Panksepp and Lahvis, in this issue; Wright and Panksepp, in this issue; Zellner et al., in this issue).

As we leave behind the transitional era between rigorous brain/behavior-only research traditions and the current ruthlessly reductionistic neuroscientific hubris that has little room for "mind"—the experience of oneself in the world—we can develop robust empirical approaches to illuminate the neural roots of human affective experience through the sensitive study of other animals (Panksepp, 2008). For major future advances in psychiatry, using preclinical (animal) models, we must put behavior and affective experience on an equal footing. That form of neuroscience does not yet exist. So far, affective neuroscience has aspired to do that. It could be a very exciting era for future neuroscience.

But some progress is being made and I deeply appreciate all the wonderful colleagues I have had the opportunity to work with during the past half century, many of whose work is represented here, but regrettably not all. It is long past time for discussions of animal affective experiences to be reinitiated in earnest by behavioral neuroscientists, at the very least. The claim is not that we have procedures to study reflective consciousness ("awareness") but raw phenomenal affective consciousness (i.e., emotional qualia). Let the conversation begin.

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