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Affective consciousness: Core emotional feelings in animals and humans

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Abstract

The position advanced in this paper is that the bedrock of emotional feelings is contained within the evolved emotional action apparatus of mammalian brains. This *dual-aspect monism* approach to brain–mind functions, which asserts that emotional feelings may reflect the neurodynamics of brain systems that generate instinctual emotional behaviors, saves us from various conceptual conundrums. In coarse form, primary process affective consciousness seems to be fundamentally an unconditional "gift of nature" rather than an acquired skill, even though those systems facilitate skill acquisition via various felt reinforcements. Affective consciousness, being a comparatively intrinsic function of the brain, shared homologously by all mammalian species, should be the easiest variant of consciousness to study in animals. This is not to deny that some secondary processes (e.g., awareness of feelings in the generation of behavioral choices) cannot be evaluated in animals with sufficiently clever behavioral learning procedures, as with place-preference procedures and the analysis of changes in learned behaviors after one has induced re-valuation of incentives. Rather, the claim is that a direct neuroscientific study of primary process emotional/affective states is best achieved through the study of the intrinsic ("instinctual"), albeit experientially refined, emotional action tendencies of other animals. In this view, core emotional feelings may reflect the neurodynamic attractor landscapes of a variety of extended trans-diencephalic, limbic emotional action systems—including SEEKING, FEAR, RAGE, LUST, CARE, PANIC, and PLAY. Through a study of these brain systems, the neural infrastructure of human and animal affective consciousness may be revealed. Emotional

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feelings are instantiated in large-scale neurodynamics that can be most effectively monitored via the ethological analysis of emotional action tendencies and the accompanying brain neurochemical/electrical changes. The intrinsic coherence of such emotional responses is demonstrated by the fact that they can be provoked by electrical and chemical stimulation of specific brain zones—effects that are affectively laden. For substantive progress in this emerging research arena, animal brain researchers need to discuss affective brain functions more openly. Secondary awareness processes, because of their more conditional, contextually situated nature, are more difficult to understand in any neuroscientific detail. In other words, the information-processing brain functions, critical for cognitive consciousness, are harder to study in other animals than the more homologous emotional/motivational affective state functions of the brain.

Keywords: Emotions; Affect; Consciousness; Animals; Brain; Seeking; Fear; Anger; Panic; Sadness; Play; Care

1. Toward a science of animal consciousness

Do other animals have internal experiences? Probably, but there are no mindscopes to evaluate the existence of consciousness in either animals or humans. If we are going to entertain the existence of experiential states (i.e., consciousness) in other animals, we must be willing to work at a theoretical level where arguments are adjudicated by the weight of evidence rather than definitive proof. Such approaches are easier to apply for certain aspects of animal consciousness than for others. My focus here will be on primary-process affective consciousness, many aspects of which may be homologous in humans and other animals. I will proceed from the premise that progress in achieving a deeply scientific human psychology lies in our ability to specify which neuropsychological tendencies evolution constructed within the genetically dictated brain organization and psychobehavioral potentials of the intrinsic neurodynamics of ancestral species (Panksepp & Panksepp, 2000). A detailed neuroscientific understanding of basic human emotions may depend critically on understanding comparable animal emotions.[1] As I have noted many times "As long as psychology and neuroscience remain more preoccupied with the human brain's impressive cortico-cognitive systems than subcortical affective ones, our understanding of the sources of human consciousness will remain woefully incomplete" (Panksepp, 2004a, p. 58).

I will advance the case that one widely neglected form of animal/human consciousness—one that creates internally experienced emotional feeling states—is now sufficiently well understood to permit an affirmative answer to my opening question. Other mammals do have affective experiences. Such states may be a common denominator for a detailed cross-species analysis of relevant brain functions because scientific variants of anthropomorphism can guide the study of integrative mind–brain functions in other animals. I will explore the possibility that basic emotional feelings—a primary process type of phenomenology—may be grounded on instinctual action systems that promote unconditional emotional behaviors. Although such "ancestral voices of the genes" (Buck, 1999, p. 324) undergo a great deal of elaboration epigenetically, the

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[1] Humans are animals, but it is tedious to continually use the qualifier "other animals" when making contrasts to non-human animals. Whenever "animal" is used without the qualifier, it is simply for stylistic grace. At times the term "animalian" is also used when referring to human brain functions, and this is intended to mean the kinds of brain systems that are strikingly homologous in all mammals that have been studied.

fundamental similarity of core affective processes across mammalian species may permit neuroethological work on animal-models to reveal the bedrock of human consciousness. My own work proceeds from a Spinozan-type *dual-aspect monism* premise—namely that primary-process affective consciousness emerges from large-scale neurodynamics of a variety of emotional systems that coordinate instinctual emotional actions (Panksepp, 2001a, 2001b, 2004b).

Before proceeding, let me provide a few terminological clarifications. I use the term *emotion* as the ''umbrella'' concept that includes *affective*, cognitive, behavioral, expressive, and a host of physiological changes. *Affect* is the subjective experiential-feeling component that is very hard to describe verbally, but there are a variety of distinct affects, some linked more critically to bodily events (homeostatic drives like hunger and thirst), others to external stimuli (taste, touch, etc). *Emotional* affects are closely linked to internal brain action states, triggered typically by environmental events. All are complex intrinsic functions of the brain, which are triggered by perceptions and become experientially refined. Psychologists have traditionally conceptualized such ''spooky'' mental issues in terms of *valence* (various feelings of goodness and badness—positive and negative affects), *arousal* (how intense are the feelings), and *surgency* or *power* (how much does a certain feeling fill one's mental life). There are a large number of such affective states of consciousness, presumably reflecting different types of global neurodynamics within the brain and body. Even though there is currently no agreed upon taxonomy of affective states (Ostow, 2004; Panksepp & Pincus, 2004), in this essay I will largely focus on the *emotional*, action-oriented affects, as opposed to sensory pleasures and displeasures, and the various background bodily feelings of satisfaction and dissatisfaction. I will continue to advance the view that specific emotional affects largely reflect the operations of distinct emotional operating systems that are concentrated in sub-neocortical, limbic regions of the brain (MacLean, 1990; Panksepp, 1998a).

For present purposes, the term consciousness refers to brain states that have an experiential feel to them, and it is envisioned as a multi-tiered process that needs to be viewed in evolutionary terms, with multiple layers of emergence. *Primary-process consciousness* may reflect raw sensory/perceptual feelings and the types of internal emotional/motivational experiences just discussed. *Secondary-consciousness* may reflect the capacity to have thoughts about experiences, especially about how external events relate to internal events. Although animals surely do not think about their lives linguistically, they may think in terms of perceptual images. Finally, there are *tertiary forms of consciousness*—thoughts about thoughts, awareness of awareness—much of which is unique to humans and requires expansive neocortical tissues that permit linguistic–symbolic transformation of simple thoughts and remembered experiences.

Those who are not willing to give animals any consciousness are probably thinking about the tertiary human-typical linguistic variants. They may also be generalizing too readily from human perceptual consciousness, which is clearly dependent on neocortical functions, to an affective consciousness whose locus of control is largely sub-neocortical (Liotti & Panksepp, 2004). There are reasons to believe that affective experience may reflect a most primitive form of consciousness (Panksepp, 2000b, 2004b), which may have provided an evolutionary platform for the emergence of more complex layers of consciousness.

Core emotional affects may reflect the neurodynamic attractor landscapes of a variety of extended trans-diencephalic ''energetic'' action systems—e.g., SEEKING, FEAR, RAGE, LUST,

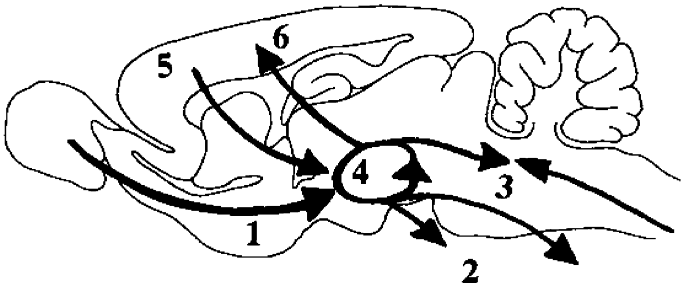

Fig. 1. A cartoon depiction of the various neural interactions that are defining characteristics of all major emotional systems of the brain: (1) various sensory stimuli can unconditionally access emotional systems; (2) emotional systems can generate instinctual motor outputs, as well as (3) modulate sensory inputs, promoting incentive salience. (4) Emotional systems have positive feedback components which can sustain emotional arousal after precipitating events have passed, and (5) these systems can be modulated by cognitive inputs, and (6) these systems can modify and channel cognitive activities, again modulating incentive salience. Also, the important criterion that emotional systems create affective states is not included, but it is assumed that arousal of the whole executive circuit for each emotion is essential for getting feelings going within the brain, perhaps by interacting with other brain circuits for self-representation that may arise from midbrain systems such as the PAG (Panksepp, 1998b). Reprinted from Fig. 3.3 of *Affective Neuroscience* (Panksepp, 1998a) with permission of Oxford University Press.

CARE, PANIC, and PLAY—which need to be defined in neural terms (Fig. 1).[2] These highly overlapping state functions share many neuropsychological components (e.g., biogenic amines), and they energize and are reciprocally regulated by cortico-cognitive activities (information-processing systems that perceive and discriminate environmental events). Through such reciprocal interactions and embeddings, secondary and tertiary forms of extended consciousness emerge. However, attempts to utilize work on animal affective states to understand the corresponding human feelings remain a revolutionary activity in consciousness studies. This is because affects cannot be unambiguously visualized or well operationalized, unless one is willing to take the emotional actions of other organisms as the necessary starting points of empirical inquiries (Panksepp, 1998a).

Many human investigators believe that human consciousness, affective and otherwise, emerges from higher brain functions that most other mammals do not have, and that all we can really study in animals are emotional behaviors (Craig, 2003a, 2003b; Damasio, 2003a, 2003b; Dolan, 2002), with no possible further inferences about mind-dynamics. Many behavioral neuroscientists (e.g., LeDoux, 1996; Rolls, 1999) are not yet ready to conceptualize the neuro-mental lives of animals in psychological terms. This is because for a whole century we have not had the disciplinary will to move beyond the safe harbor of logical positivism in animal brain research, to seek those broader organizational principles that may grant other animals psychological capacities which, in

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[2] Capitalizations are used for designating emotional systems, as in Panksepp (1998a). This convention serves two purposes: (1) it highlights that the referents are specific neural systems of the brain, all of which are only partly understood, (2) it hopefully minimizes the likelihood that by using the vernacular, we will be accused of promoting part–whole confusions (i.e., a slice does not the whole pie make)—see Bennett and Hacker (2003) for a full analysis of such endemic problems in functional neuroscience. Our research aim is to identify the necessary neural components of basic emotions, without suggesting that this provides a sufficient explanation for all of the attributes that such emotions connote in the human mind.

the tradition of dualism, have been at times reserved, arbitrarily, for humans. Such views often ignore the substantial databases, sampled herein, that suggest how raw affective experiences may reflect an ancient form of consciousness, with a sub-neocortical locus of control, where relevant animal–human homologies abound.[1] Accordingly, a brief historical perspective is also shared on why straightforward cross-species monistic strategies have not been energetically implemented in Anglo-American behavioral neuroscience.

Although no argument in this area can be definitive, I will seek to coax some skeptics to be a bit more open-minded, which is most difficult once ontological biases have taken root. Indeed, I asked a friend who is a rigorous neuro-behaviorist, to read a draft of this paper, but the response was: ''Thanks for the invitation to comment… however, I have sworn off any effort to discuss consciousness with any neuroscientists—it is a bad habit of mine, and I'm convinced it comes to no good.'' I responded shortly with my own synopsis of what needs to be done: ''Tis understandable, especially if one believes such issues can't be addressed empirically. I suspect that on the cognitive-learning side that is most difficult (even though at least one solid behaviorist, Tony Dickinson at Cambridge, thinks they now have compelling data). My own take is that neuroscience advances make it an especially workable topic on the affective-emotional side, but only if one is willing to subscribe to radically monistic ideas, such as my preferred *dual-aspect monism*, with the *coup de grace* being predictions at the human level that can be falsified. But if one still subscribes to any variant of dualism, including the 'neuro' or 'speciest' varieties, then it is quite impossible. But even in the best of circumstances it is a difficult task, fraught with conceptual and empirical problems, and ultimately based on theoretical inference and the weight of evidence. Why bother? Because if that is a true aspect of mammalian brain functions, as I suspect it is, who better to deal with it than us neuroscientists?'' The area needs critical dialog. Otherwise, it will remain a topic that is suitable only for tavern-talk.

It is perhaps regrettable that the emerging community of scholars who do favor the acceptance of consciousness in animals still relies so heavily on anecdotal evidence that generates no new predictions concerning the underlying neuro-causal processes. Comparative neuro-psycho-behavioral analyses offer the needed bridging strategies. The anecdotal approach, taken alone, allows critics to remain reflexively dismissive about the critical importance of consciousness studies in other animals. The present essay constitutes an elaboration of previous efforts to redress the intellectual imbalance that has emerged in behavioral neuroscience (Panksepp, 1982, 1998a, 2004a, 2004b), which is reflected all too commonly with a failure to engage with the topic.

2. Anecdotal approaches to animal emotions

At present, as was popular during earlier eras (e.g., Lindsay, 1879; Romanes, 1897), there is a growing animal behavior literature that vigorously seeks to affirm that other animals do have emotional lives. Naturalistic observations offer an invaluable perspective on what animals can do when they are reared in the real world as opposed to artificial laboratories where they often become psychologically constricted (e.g., ''kennelized''—see Panksepp, Conner, Forster, Bishop, & Scott (1983)). A recent collection of anecdotes, many from scientists, makes a compelling modern case for considering animal feelings openly once more (*Smile of a Dolphin*, edited by Bekoff, 2000; to which I was pleased to contribute). Another recent ''popular'' offering is Jeffrey Masson's

(2003) *The Pig Who Sang to the Moon*, which focuses on the emotional lives of farm animals. Masson, a psychoanalyst, has written three other popular books on the emotional lives of domestic dogs, cats, and some wild animals, as have many other animal lovers. This type of literature is based on evidence that most scientists would consider, at best, *only* a prelude to rigorous experimental work. Although anecdotal efforts do offer thought-provoking testimonials about animal abilities which need to be systematically considered and studied, they contribute little to a neuroscientific understanding of the underlying causal processes.

Without a neuroscientific analysis, animal stories must remain forever in the pre-scientific stage of observations, even as they help promote a new respect for other creatures that can encourage better behavioral work on the existing capacities of other animals. My goal here is to summarize brain work on animal feelings, in the hope that some institutional devotion eventually emerges that can promote high-quality work on the underlying neural principles of primary-process affective consciousness. This does not yet exist on the Anglo-American science scene, and only partly because a robust "never-mind" neuro-behaviorist movement retains power over disbursement of funds in this research arena. Credible research on such topics is difficult, but a great deal of insightful work could be conducted if funds were available. For various historical and epistemological/ontological reasons, that is not the case. Recall that the cognitive revolution, ascendant some 30 years ago, did not kill radical behaviorism, at least the animal research part of it. Behaviorists survived and thrived in other fields, especially the emerging neurosciences that became a haven for methodologically rigorous positivists of earlier eras.

The current neuro-behaviorist agenda, ascendant in the 1980s, led to a psychologically impoverished view of "emotions" in behavioral neuroscience, while yielding an enriched understanding of how emotional learning occurs in limited areas of the brain such as the amygdala (LeDoux, 1996). Most emotional processes that actually exist in animal brains have been disregarded (see Blanchard et al., 2001a for a sampling of modern behavioral neuroscience views of emotions). The failure of neuro-behaviorists to accept a diversity of emotions and the corresponding *affective experience* as a key aspect of animal brain functions has reduced the likelihood of useful cross-fertilization between animal and human studies.

Joseph LeDoux, the best funded animal emotional–memory researcher in America, publicly related how he failed to obtain approval for his initial grant applications until he extracted the term "emotion" from his proposed work to study classical-conditioning of fear and replaced it with learning and memory terms (see Panksepp, 2002). Other neuroscientists interested in emotions had comparable, but more sustained, funding problems throughout the last quarter century. Since there were good reasons to hypothesize that emotional feelings emerge from specific, evolutionarily dictated brain operating systems, I chose not to succumb to peer-pressure. Rather, I focused my efforts largely on the unconditional aspects of animal emotionality, largely on my own dime.

From my ontological perspective, an understanding of the neurobiology of raw affective experiences, from pain to joy, remain problems of foremost importance for understanding the evolution of human consciousness as well as for the construction of a solid base for psychiatric theory. I assume that the evolution of consciousness was based on the ability of neural tissues to encode biological values, and that at its core, many psychiatric disorders reflect imbalances in such intrinsic value systems of the brain (Panksepp, 2004c). Practically all of psychology now agrees that affect is a very important scientific topic. But is it something that only humans experience? In behavioral neuroscience, the affective structures of mind remain unrecognized.

3. Experimental strategies for studying experienced feelings in animals

A critical dimension commonly missing from non-neuroscience discussions of animal emotions is what type of data should be deemed sufficiently compelling, one way or the other, for agreeing on the general nature of the brain mechanisms by which affective feelings are generated. This, of course, remains one of the great problems in all consciousness studies, doubly difficult in the analysis of animal brains. In the study of human cognitive aspects of consciousness (e.g., perceptual awareness), leading thinkers are emphasizing that good evidence can only be obtained if one makes levels of consciousness an independent variable in experimental studies (Baars, Ramsoy, & Laureys, 2003). This can be achieved by concurrently studying stimuli that are presented both unconsciously and supraliminally, and then determining differences in how brains respond during the two modes of information input. This "cognitive strategy" is not as workable when it comes to the study of *affective states* in humans, and even less so in other animals whose experiences can only be evaluated through their actions.

Let us briefly consider the difficulties entailed in studying *human* affective experience. Although emotion-provoking cues could potentially be presented subliminally or masked with blocking stimuli (e.g., Morris, Öhman, & Dolan, 1998), that is not the same as having effectively manipulated emotional feelings. When it comes to affective states of consciousness, such as anger or hunger, it is hard to imagine that time-locked delivery of external information can be used as a cogent variable. Such internal states of the brain–mind, whose time-scales are not well suited for modern brain imaging, must be manipulated by other means. Brain stimulation and pharmacological challenges, at several levels of "dosing," could be envisioned, and this has been done with drugs of abuse, albeit the persistent "unconscious reinforcement" interpretations of the few relevant published studies (e.g., Lamb et al., 1991) remain problematic because of the neglect of all relevant experiential issues (for critique, see Panksepp, Nocjar, Burgdorf, Panksepp, & Huber, 2004b). A bigger dilemma for human studies is that we often have no adequate pharmacological tools to manipulate many of the specific neurochemistries of emotional systems, many of which are neuropeptidergic (Panksepp & Harro, 2004). Further, new knowledge about these systems still emerges almost exclusively from animal brain–behavior research—where discussions of affect are rare. Before one can make deep neuroscience predictions in humans, one must infer how homologous processes are changed in animals. This highlights why the study of the neurobiological nature of affect in humans and other animals needs to go hand in hand. The animal work leads the neural analysis, and relevant human work must focus on whether predictions derived from the animal work hold true (Panksepp, 1991, 1999; Solms & Turnbull, 2002).

A psycho-neuro-ethological "triangulation" solution to this problem is as follows: since most now accept that humans do have various affective feelings, we can utilize animals that seem to exhibit outward indicators of emotional states as experimental models for decoding the underlying neural systems. If we discover critical brain variables that regulate animal emotional expressions, such as distinct neurochemical regulators, then we can evaluate the credibility of our provisional affective conclusions by doing the converse experiments—predicting and evaluating the types of affective changes that should result in humans. For instance, if we evaluate certain neurochemical agents that increase or reduce playfulness or separation distress vocalizations in animals, and humans exhibit the predicted increases or decreases in feelings of joy or sadness, then by the criterion of *weight of evidence*, a concrete neural hypothesis concerning the nature of affect would be provisionally supported for all relevant species (i.e., ones that have homologous neural systems). Such conclusions could be reinforced if animals exhibit the predicted behavioral choices, such as conditioned place-preferences, and aversions and the re-valuation of external rewards and punishments (Bardo & Bevins, 2000; Dickinson & Balleine, 2000). Indeed, it is only through such behavioral measures that we can infer that animals have affective experiences. If we are not willing to accept such measures as potential indicators of internal affective processes, then the doors to the experimental study of animal affective consciousness will forever remain sealed, and we must continue to talk in terms of affect-free reinforcement principles. Thereby we may remain ignorant of neuropsychological issues of great philosophical and psychiatric importance.

At present, there is only a modest flow of psychobiological knowledge between human and animal research because few animal investigators consider experiential issues to be relevant. Few investigators of sensory affects (such as the pleasure of taste sensation) are willing to *explicitly* cultivate the working hypothesis that animals do have affective experiences (e.g., Berridge & Robinson, 2003).[3] Of course, animal behavioral analysis has always relied on the concepts of 'rewards'

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[3] My reading of this paper was that the authors advocated the position that animals only exhibit affective behaviors, while humans have true affective experiences because of their cortical enrichments. Within a few days of publication of the Berridge & Robinson piece, I submitted the following letter (references deleted) as a letter to the editor. The authors declined to respond (I assume because taking a position on such topics can leave you branded with the Scarlet letter of Anthropomorphism), and the editor wrote back about half a year later: "Please accept my sincere apologies… for your monumental patience… I do not feel that a letter exchange in TINS is the right place for expression of your ideas… I think that your ideas on this matter need to be raised in the discussion section after a relevant conference talk or in the bar." For archival purposes, what I argued in my "tavern-talk" letter was that:

"Berridge & Robinson's re-conceptualization of dopamine-facilitated "brain reward" into 'wanting' (unconscious desire?) vs. 'liking', have been welcomed memes. They correspond to classic appetitive approach and consummatory reward concepts long accepted by psychologists. A complementary solution to paradoxes associated with brain stimulation 'reward' was the conceptualization of a dopamine driven appetitive SEEKING/expectancy emotional system—a "goad without a goal" that energizes foraging and mediates anticipatory states. Such emotional/motivational urges have many attributes, including sensory-perceptual biasing and cognitive linkages. 'Incentive salience' may reflect conditioned cues getting easily into both the emotional action as well as cognitive *channel-control* components of this widespread *instinctual–emotional-learning* system.

Comparable emotional action systems are critical for diverse feelings states, helping to clarify the multi-dimensional concepts of 'reward' and 'punishment,' which encapsulate our meager understanding of the intrinsic value structures of the brain. To properly clarify affect, we must psychobiologically study many emotions, sensory 'rewards' as well as bodily regulatory/motivational urges (e.g., thirst and hunger). Affective feelings in animals—issues that B&R have strategically, perhaps neo-dualistically, minimized—are likely to be true aspects of animate nature.

A key ontological question, finally neuro-epistemologically workable, is the extent to which arousal of core emotional systems, like arousal of the 'SEEKING/Wanting' system, is experienced in humans and other animals. Since Freud, it has been increasingly recognized that felt experience stews within an enormous unconscious neural caldron. However, is it culturally and scientifically wise for us to deny, ignore or minimize the probable existence of neuro-affective states in other mammals when so much evidence suggests that they have such experiences? All humans affirm that affective experiences are critical for quality of life. Considering the *weight of relevant evidence*, there is no principled reason (only our desire for *proof*—which exists not in science), to marginalize affective experience in the neuro-mental lives of animals. Considering the abundant data from bodily expressive, place-preference, and vocal and ‘punishments’ but these are used strictly operationally (i.e., items which fulfill the “law of effect” in learning studies), thus intentionally leaving the concept of affect out of the conceptual equation. If affective states are the underlying psycho-neural substrates for many behavioral choices (Panksepp, 1998a), perhaps even the fundamental nature of reward and/or reinforcement, a behavior-only analysis is surely discarding critical scientific dimensions from active consideration. My own version of Spinoza’s *dual-aspect monism* has invested in the simplifying assumption that affective consciousness does reflect the actions of the widely ramifying neural “command” networks that control corresponding emotional urges (e.g., the rough-and-tumble play of rats reflects a form of social joy). In short, emotional affects may be thoroughly embedded within the extended activities of brain operating systems that orchestrate certain instinctual action patterns (Fig. 1).

If such central states can serve as rewards and punishments in learning situations, and if we artificially activate the underlying brain systems, as with localized electrical and chemical brain stimulation, and animals exhibit value choices (e.g., place-preferences or aversions), then the weight of evidence supports the existence of affective processes in the animals being studied. In other words, this is a straightforward strategy that can be validated or disconfirmed in various ways, and the gold-standard will be predictions concerning human affective changes following similar manipulations (Panksepp, 1999). The strategy can also be used in reverse, using new, neurochemically induced affective changes in human to make concrete predictions about animal behavior.

Obviously, we should be alert to false-positives emerging from the animal work; there are bound to be some. For instance, in humans we know that pathological laughter and crying are not always associated with feelings of hilarity and sadness (Poeck, 1969). If it turned out that certain drugs only change behaviors but not experienced feelings in humans, we would have a rationale for suspecting that the same agents are *not*, in fact, modulating affective states in animals. Hopefully, such false-positives arising from low-level motor output generators in the caudal

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measures, a scientifically coherent working hypothesis, quite capable of generating testable predictions, is that other mammals do have affective feelings *functionally* similar to our own. Even though we have no ready access to the precise nature of their associated cognitions and qualia, for optimal progress, it is reasonable to entertain a role for core neuro-affective processes for scientifically understanding what animals do.

If basic affects arise largely from evolutionarily conserved core neurodynamics in all mammals, we can finally fathom the nature of homologous value structures that move humans. This critically important step may allow us to better conceptualize brain–mind imbalances in psychiatric disorders. Concepts like ‘SEEKING/wanting’ are promising starts, but let us not make subcortical affect-generating networks unconscious prematurely. The evidence for that remains weak. In fact, studies like that of Lamb and colleagues say little about unconscious motivations. Why re-affirm, even implicitly, the Cartesian sin of granting so little experienced life to the other animals?

Abundant evidence indicates that raw affective experiences are critically linked to the neurodynamics of sub-neocortical limbic networks (homologous in all mammals), and not to neocortical re-representations which abundantly regulate and refine emotions. At what level of the neuroaxis do the deeply unconscious aspects of many brain functions blend with those that are experienced? We do not know. Affectively, the neocortex *may* be more unconscious than sub-neocortical limbic regions! Essential as learning is for navigating complex environments, well conceptualized by B&R, it is unparsimonious to speculate that core values are only experienced when read out by higher cognitions. Despite our disciplinary aversion to ‘spooky’ neuropsychological constructs, feelings may arise more directly from brain emotional, motivational, and sensory systems in action, even in rats. Finally, it should be noted that psychological processes may emerge as much from motor-action processes (SEEKING) as from sensory-cognitive processes (‘wanting’ and ‘liking’).” (*References deleted from above letter; they are available on request*).

brainstem will constitute only a small subset of findings, which can be winnowed using traditional hypothetico-deductive methods. Also, the deployment of multiple measures, with convergent manipulations, will be invaluable in increasing the weight-of-evidence for affective, as opposed to mere reinforcement, interpretations of behavioral data.

Even though animals cannot provide rich verbal feedback about the experiential/cognitive details of their feelings, as humans can, our own endeavors have led us to consider that various emotional vocalizations of other animals may be indicators of affective states (Panksepp, Normansell, Herman, Bishop, & Crepeau, 1988) and to invest in the development of such "self-report" methods in laboratory rats (Knutson, Burgdorf, & Panksepp, 2002; Panksepp, Knutson, & Burgdorf, 2002). Of course, having a feeling is quite different than intentionally communicating about that feeling, which surely requires secondary consciousness, perhaps tertiary consciousness. However, certain animals, such as chimps and even parrots may be able to pick up enough human-type linguistic ability to provide more symbolic self-reports of their emotional experiences (Cabanac, 2005). All this is not to suggest that human feelings may not be dramatically transformed by our superb linguistic abilities.

Animals, just like humans, probably have several distinct levels of consciousness, and unless we have a clear vision of the type of consciousness that we are aspiring to understand, confusions and needless controversy may prevail. My focus here is restricted to *primary-process emotional feelings*, as opposed to the many sensory-based affects (e.g., taste) and background bodily feelings (e.g., tiredness), or thoughts about feelings. I assume that a neural understanding of ancient action-centric emotional feelings may be essential for understanding more recent cognitive forms of consciousness. I think such scientific issues can finally be dealt with in more sophisticated intellectual ways than mere "tavern talk."[3]

4. Evolutionary levels of consciousness

If we believe consciousness is a single type of brain process, we can easily conclude that animals are unconscious. Certain ontological positions assume that consciousness is based upon the superb language and abstract/logical reasoning capacities of the human mind. When investigators of animal brain functions assume such positions (e.g., Macphail, 1998; Rolls, 1999), then they close the book too abruptly on the topic of animal consciousness. Perhaps, these views simply fail to differentiate between primary and tertiary forms of consciousness. At their most extreme, such positions would have to assert that massive left hemisphere damage that produces global language failure would also compromise our ability to be conscious. That is an absurd position. Even after massive left-hemisphere strokes, damaging both expressive and receptive areas of the brain, people can still think in images, and if anything they become more emotional. They feel fully conscious, even though their toolbox of cognitive skills has been seriously compromised. For present purposes, I will simply assume such radical anthropocentric views, focusing on the impressive linguistic abilities of our species as the bedrock of consciousness, are fundamentally wrong with respect to primary-process affective states. Even though our capacities for semantically mediated thought add delicious levels of complexity to our emotional feelings, that should not be taken to marginalize the here-and-now affective states of creatures with more modest neocortical endowments.

It is likely that primary-process conscious abilities based on perceptual images and core affective states are much more common in nature than those based on linguistic capacities, but this also highlights the central dilemma for the study of consciousness in other animals. Since there are few highly discriminating behavioral indicators of animals operating with respect to perception-type conscious *experiences*, as opposed to blind-sight type brain mechanisms, those aspects of animal mentation remain more closed to neuroscientific analysis (but see Cowey & Stoerig, 1995). However, other types of experiences do *appear* to have robust and direct (i.e., instinctual) behavioral indices, for instance basic emotions (Panksepp, 1982, 1998a), and hence they are excellent targets for illuminating cross-species neuropsychological analyses. Taste responsivity measures can serve a comparable role in the analysis of gustatory affects (Berridge, 2000).

A critical concern for cross-species consciousness studies is the degree to which any specific type of psychobehavioral process in animals is homologous to outwardly similar human mind function, and hence open to rigorous comparative analyses (Panksepp, 2003c). Because of our woefully incomplete knowledge about relevant neural mechanisms, that is a troublesome issue at the outset of relevant inquiries. Only the end results of abundant research, yet to be conducted, can help round out conclusions. However, our first order of business must be to conceptualize the varieties of consciousness that *may* have emerged in brain evolution. As already noted, "primary" and "secondary/tertiary" mentations have long been distinguished (Hilgard, 1962), and repackaged for modern use as "core" and "extended" consciousness (Damasio, 1999). Even though evolutionary continuity of basic emotions seems obvious (Darwin, 1872/1998), investigators of human emotional feelings commonly do not explicitly recognize that the deep causal analysis of the primary-processes variants (e.g., the neural nature of raw affective states) is more readily pursued in animal models than human beings (e.g., Russell, 2003; but also see, Buck, 1999; Reddy, 2003).

From a slightly different conceptual trajectory, viewpoints emerging from modern cognitive science also find it useful to distinguish between "first-order phenomenology" and "second-order awareness" (Lambie & Marcel, 2002). For instance, even though people can often repress awareness of their emotional feelings at the level of second-order awareness, they may retain affective feelings at the level of first-order phenomenology (Kaplan-Solms & Solms, 2000; Lambie & Baker, 2003). My own preferred way to make such two-tiered distinctions is between *affective consciousness* and *cognitive consciousness* (Panksepp, 2003a, 2003b, 2003c, 2003d, 2003e).[4]

Within the cognitive science tradition, the temptation to conflate emotional feelings and cognitive processes remains rather too prominent (e.g., Lane & Nadel, 2000). Obviously, affects and cognitions are massively inter-penetrant, but scientifically important distinctions can be made through in-depth consideration of various neural and psychological criteria (Ciompi & Panksepp, 2004; Panksepp, 1999, 2003a), including detailed analysis of neurodynamic changes (Freeman, 2001, 2003a, 2003b; Lewis, 2005; Panksepp, 2000c).

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[4] In addition to cognitive and affective consciousness, we may also need to recognize *conative* variants, each with levels of *first-order phenomenology* and *second-order awareness*, in addition to several levels of unconsciousness processing as well (cognitive, dynamic, and neural). Each major form of consciousness may have distinct primary loci of control within the brain/mind, even though they may also share many components such as the ascending midbrain and thalamic reticular arousal and sensory gating systems.

5. A historical retrospective: The behavioristic denial of animal consciousness

We all understand how difficult an epistemological problem any variant of consciousness is for neuroscience, especially in animal brain research. Let us briefly revisit why the topic was discarded in animal behavioral research throughout the 20th century. For almost a whole century, the discipline of behaviorism, which prevailed in animal experimental psychology, denied that a study of inner mental causes could ever become a workable scientific topic; indeed, the most positivistically hard-nosed insisted that there was nothing real to be understood. The most radically behavioristic asserted, persistently and destructively, that attempts to understand the underlying neural and mental puzzles—the intrinsic dynamics of the ‘‘black box’’—were not necessary for a full and satisfactory understanding of what organisms do (e.g., B.F. Skinner’s monumental work). A study of inputs and outputs of a ‘‘black box’’ would suffice. After one understood the physiology of sensory systems, many investigators pretended everything else emerged from learning. That was a profoundly anti-evolutionary stance (see critique by Panksepp, 1990a).

Many neuroscientifically inclined descendants of those hard-liners continue to advance the view that everything organisms do can be explained simply by an ultra-reductionistic neural analysis with no need for the psychological issues that are part-and-parcel of the more globally operating neuro-mental apparatus (e.g., Bickle, 2003; Blumberg & Wasserman, 1995). Within radically neuro-reductionistic paradigms, talk about emergent neuro-mental causes, including the efficacy of affective experience, has remained as unwelcome as ever (Panksepp, 2002). Largely, this is because mental constructs supposedly do not allow any novel and useful predictions, an assumption that neglects how useful such views are in real life when we try to deal with emotionally aroused animals (Hebb, 1946) and emotionally disturbed humans (Panksepp, 2004c). The acceptance of an experienced affective life in animals, as indexed by uncensored emotional actions, may permit neuro-behavioral research to clarify some basic human psychological concerns (Panksepp, 1998a), psychiatric disorders (Panksepp & Harro, 2004) as well as to illuminate unrecognized emotional capacities of other species (Panksepp & Burgdorf, 1999, 2003).

Regrettably, neuro-behaviorists who have traditionally had little tolerance for the ambiguities that are inherent in all experiential constructs continue to advocate variants of terminal agnosticism that prevent most investigators from making the successive theoretical approximations that are essential for progress in this difficult intellectual arena (for a recent critique, see Panksepp, 2002). Various opinion leaders (e.g., LeDoux, 1996, 2002) continue to assert that the existence of animal experiences is empirically unknowable (as they were before the advent of modern cross-species neuroscience and molecular biology), and hence, argue such brain functions should continue to be disregarded—at best, as insubstantial epiphenomena that surround our growing nest of strictly positivistic and radically reductionistic neuro-causal knowledge. However, even ruthless psycho-neural reductonism (Bickle, 2003) recognizes how important psychological concepts are in framing brain processes that need to be explicated. Still, only a minority explicitly accept, as a working hypothesis, the high probability that certain psychological constructs reflect facets of large-scale neurodynamics that emerge from evolved, epigenetically refined, brain activities, better conceived in terms of *global network dynamics* (Freeman, 2003a, 2003b) than *eliminative micro-neural reductionism*.

An intellectual stance affirming that certain aspects of mind, brain, and behavior are fully interpenetrant (i.e., a Spinozan *multi-aspect monism*) opens up possibilities for a much deeper understanding of affective feelings than can be achieved through the rigors of reflexive and conditioned behavior-only analyses. It also gets around all manner of philosophic quandaries (e.g., homuncular readout fallacies), and it can reduce troublesome explanatory gaps. For instance, if neurodynamics of emotional feelings in animals are even partly isomorphic with the behavioral and neural dynamics of instinctual emotional responses, a host of productive predictions could be generated at the human level (Panksepp, 1998a, 1998b, 1998c, 1999; Panksepp & Harro, 2004).

In lieu of any inner affective causes, behaviorism advanced the position that the systematic application of "rewards" and "punishments" "reinforced" everything animals do, without much in-depth discussion of what those broad concepts may mean either in neural or psychological terms. Pursuit of such a discussion would have required a head-on confrontation with the varieties of brain emotional and motivational processes, as well as the evolved neuro-affective nature of the mental apparatus. But there was, and still is, a profound disregard of such concerns. Such traditions were solidified by the long-standing battle for dominance between Anglo-American animal-learning psychology and European animal-behavior, ethological traditions (i.e., the Lehrman–Lorenz debates of the 1950s; see Lehrman, 1953). As a result, to this day behavioral neuroscience remains more devoted to working out the details of learning and memory than the ancestral instinctual "misbehaviors" of organisms (Breland & Breland, 1961). Obviously an integration of both viewpoints is the only rational way to proceed. Analysis of the instinctual–emotional processes can tell us much about primary-process affective experiences while learning-memory tells us much about second-order awareness. Without such integration, the key behavioral concept of "reinforcement" may remain a phlogiston-like glue between environmental stimuli and response patterns, rather than a concept that is closely linked to the dynamic emotional attractor landscapes of animal brains that allow exteroceptive cognitive events to become experientially coupled to the core affective concerns of organisms.

Only a few revolutionaries from the animal-learning camp, thanks to clever experiments that strongly suggest animals do maintain brain representations of reward value in mind, are currently ready to entertain the proposition that laboratory rats have conscious experiences (Dickinson & Balleine, 2000). This is a major positive step in the right direction, even though they still need to consider how we may get empirical evidence about the evolved nature of affective processes in brain/mind evolution. There is no sound intellectual reason that such sophisticated behavioral analyses should disregard the equally robust evidence for the existence of emotional feelings long available from the studies of affective choices (place-preferences and avoidance) and other natural behavior patterns of animals (e.g., Bardo & Bevins, 2000; Panksepp, 1982, 1998a).

Since discussion of emotional feelings in animals among neuro-behaviorists remains practically non-existent, prominent neurologists, working strictly on humans, are emboldened to assert that while we can study emotional behaviors in other animals, the study of emotional *feelings* has to be reserved for studies of our own species (Damasio, 2003a; Dolan, 2002). Although such ontological disagreements continue to be debated (see Damasio, 2003b; Panksepp, 2003a, 2003b, 2003c, 2003d, 2003e; Panksepp & Watt, 2003), the central dilemma remains: to what extent do affective experiences play a part in the many things organisms do? Some insist that affective dimensions of mind are irrelevant for a scientific understanding of animal brain functions (e.g., Blumberg & Sokoloff, 2003). Others are convinced that a study of the instinctual emotional responses of other animals must be the bedrock for understanding the nature of primary-process affective consciousness of humans (Panksepp, 1998a, 2003a, 2003b, 2003c, 2004a, 2004b).

A graceful synthesis of such divergent points of view is possible, but that will require different camps to begin respecting each other's terminologies and world-views. It will require neuro-behaviorists to accept the high probability of affective experience being part of animal life, and hence of their behavioral equations. It will require those who advocate for the existence of experiential states in animals, to be conversant with the mass of evidence for how behavior is molded by past experiences available from learning studies. Of course, an acceptance of affective concepts has the potential to enliven learning theory. If there is an unwillingness to engage mutually and substantively on such topics, we may have "another century of misunderstanding" (Panksepp, 2000a) and an impoverished understanding of the deep neural nature of affective experience in both animals and humans.

6. Evidence for internal affective states in animals

So what causes behavior? How could something outside of us cause our muscles to move in coherent ways? Is it merely the power of environmental stimuli, as behaviorism long asserted, or must we also consider the nature of internal events? Obviously, it is not possible to achieve a coherent explanation without considering the evolved integrative functions of the brain (Panksepp et al., 2002). Surely there have to be critical processes inside our brains, and it is increasingly unlikely that they can be encapsulated by the concept of *reinforcement* or even more subtle variants such as "reward prediction errors" (Schultz, 1998, 2000, 2002).

There is, in fact, substantial experimental evidence supporting an emotion systems and affectively centered view of animal mind. Emotion systems are clearly evident in the many instinctual behavior patterns organisms exhibit. The existence of affective feelings is premised largely on behavioral neuroscience evidence that: (i) other mammals are attracted to the same environmental rewards and drugs of abuse as we humans, as monitored by a large number of measures including conditioned values (e.g., place-preferences, see Bardo & Bevins, 2000), (ii) to the best of our knowledge, our human emotional feelings are dependent on very similar subcortical brain systems situated in deep brain regions where evolutionarily homologous "instinctual" neural systems exist (Damasio, 1999; Liotti & Panksepp, 2004), and (iii) artificial activations of the deep brain systems that promote emotional actions are liked and disliked by animals, as measured by a host of approach and avoidance measures (Panksepp, 1998a). Let us consider these points in turn.

(1) Perhaps, the most robust evidence for affective states in animals comes from the studies of drugs of abuse in humans and animals. Many humans find drugs that activate opiate receptors in the brain, and those that facilitate dopamine activity, to be pleasurable or euphoria-producing. The types of brain changes that correlate with these effects have been documented (Drevets et al., 2001; Volkow, Fowler, & Wang, 2002). The fact that animals exhibit strong desires for similar agents, and since those attractions are mediated by similar brain systems, is impressive, there should be little doubt that affective states do exist in other animals (Panksepp, Burgdorf, Beinfeld, Kroes, & Moskal, 2004a, 2004b). Indeed, one can predict drugs that will be addictive in humans quite effectively from animal studies of *desire*. Rats show anticipatory positive affective vocalizations (50 kHz "self-reports") in environments where they have received drugs that are hedonically positive to humans, and negative vocalizations (22 kHz "complaints") when placed in locations

where they have received aversive drugs (Burgdorf, Knutson, Panksepp, & Ikemoto, 2001a, 2001b; Knutson et al., 2002).

(2) The second major line of evidence comes from neurological data suggesting that the major loci of control for affective experiences in both animals and humans are subcortically situated in very similar regions of the brain (Panksepp, 2003a). It is within these deep and very ancient circuits of the brain, where neuroanatomical and neuro-functional homologies abound across species, that emotional responses can be triggered. Even though there is a reticence to accept that a primitive affective form of consciousness could be elaborated far below the cerebral mantle, the evidence is quite robust for such a subcortical locus of control in humans (Liotti & Panksepp, 2004). Even though fMRI human brain-mapping studies of various emotions have yielded only modest differentiation of the various basic emotional systems (Murphy, Nimmo-Smith, & Lawrence, 2003; Phan, Wager, Taylor, & Liberzon, 2002), the most extensive PET study has yielded striking differences between sadness, anger, fear, and happiness (Damasio et al., 2000), yielding patterns that often match animal maps based on localized brain stimulation (Panksepp, 1982, 1998a, 2003a). In sum, although higher cognitive functions add an enormous richness to human emotional life and surely that of animals as well, the "energetic" engines for affect are sub-neocortically concentrated.

(3) The third and perhaps most scientifically compelling line of evidence comes from brain stimulation studies. Localized electrical stimulation of the brain (ESB) can evoke several coherent emotional responses, with accompanying affective feelings (Panksepp, 1998a). The fact that electrical "garbage" applied to specific sites in the brain can yield psychobehavioral *coherence* (distinct emotional expressions) indicates that various affect-generating emotional operating systems do exist in deep subcortical regions of the brain. The areas that generate behavioral indicators of positive and negative affective states in humans and animals are remarkably similar, and the most powerful affects are obtained from subcortical brain areas where homologies are striking (Heath, 1996; Panksepp, 1985). A most reasonable conclusion follows: not only are many affective states related to such deep brain system arousals, but the resemblances between basic animal and human emotions are truly remarkable. Indeed, localized brain stimulation of specific brain areas, whether electrical or neurochemical, is a compelling scientific way to specify the types of emotional systems animals have inherited as ancestral gifts (Panksepp, 1982, 1998a, 1998b, 1998c).

Many still prefer to envision these systems as psychologically vacuous "output" components. The matter was well presented by Walter Hess (1957, p.23), who received the Nobel prize for his work on brain stimulation induced autonomic and behavioral changes in cats from the hypothalamus, including the first descriptions of brain stimulation induced anger responses. In considering such subcortical brain functions, including the rage facilitated by decortication, he noted that "American investigators label this condition 'sham rage.' In our opinion, the behavior that we find manifested here should be interpreted as true rage, and its appearance is aided by the suppression of inhibitions that go out from the cortex." Because of behavioristic anti-mind biases, this reasonable perspective never became a mainstream hypothesis on the Anglo-American scene, and there is little discussion of the varieties of affective states in animals among behavioral neuroscientists to this day.

Some neuroscientists may be in denial about such aspects of brain function because of the philosophical concern that we may never have "mindscopes" that can tell us about the qualia of other animals or humans. However, the search for affective consciousness in animals should not be characterized as a search for the qualia that animals experience, but rather the neural principles for the various types of positively and negatively valenced affective processes they can experience. Thus, we may not be able to monitor the specific types of taste qualia a cow experiences when eating high or low quality hay; we may never know whether their experiences are of delightful sweetness or bland starch, or something else quite unimaginable to us. However, with approach and avoidance measures, we can determine that certain experiences are aversive and others pleasant, and that there are many distinct forms of positivity and negativity, with some experiences being more positive or negative than others. With enough experimental finesse, we could also analyze how certain distinct affects, such as anger and anxiety, are differentially processed psychological states in the brain (for one discriminative strategy using ESB, see Stutz, Rossi, Hastings, & Brunner, 1974). Thus, the goal of brain research into the nature of affective consciousness in animals is not a search for perceptual qualia, but rather for more general varieties of feelings that I have previous called *equalia* or evolutionary-qualia (varieties of positive and negative feelings) that are not simply created by our perceptual interfaces with the world but by the nature of emotion/motivation orchestrating brain systems we have inherited (Panksepp, 1998b). There are rough-and-ready evolutionary ‘‘instinctual memories’’ ingrained in our genetically promoted neural organizations, which are *retrieved* and *refined* as we interact with the especially challenging aspects of the world. Because of their intrinsic nature, these systems can be activated and sensitized by unknown internal processes, leading to free floating feelings and intrinsic personality dimensions which are supplemented and molded further by life experiences. Every emotional system exhibits some use-dependent plasticity (Panksepp, 2001a, 2001b).

Thus, the empirical criteria for determining the existence of such subtle mental phenomena as emotional feelings are at least threefold: (1) neural circuits should exist that can activate coherent emotional behaviors (which can be interpreted as affectively expressive indices), (2) artificial arousal of such systems should be sufficient to generate *conditioned* approach, escape, and/or avoidance responses in animals, (3) the key neurochemistries and brain activation patterns of these systems (e.g., neuropeptide modulators of global state dynamics) should be correlated with (and, if causally related, to promote) the predicted types of affective changes in humans. These criteria have been fulfilled or approximated for a variety of brain systems that exist in all mammals studied so far (Panksepp & Harro, 2004). By this line of reasoning, such animals are highly likely to have emotional feelings.

Once we recognize that affective states of the nervous system can arise unconditionally and conditionally from various distinct emotional action urges, then behavioral science also has excellent reasons to consider various instinctual psychological dynamics to be reasonable components within their pervasive learning theory schemes. The neural systems which generate fluctuating affective states may be the same as those that help mediate reinforcement (Panksepp, 1986a). These views promote the acceptance of a more ‘‘active organism’’ view of behavior than has been traditional in learning theory-based behavioral science (Panksepp, 1990b). The whole issue of how learned behavioral change is reinforced may hinge on the dynamic nature of these systems interacting with incoming sensory/perceptual cognitive processes that parse the world into differences. The wide-scale neurodynamic attractor landscapes of the core emotional systems may have properties that facilitate learning and the construction of meaning. As Freeman (2001) has emphasized, each level of neural activation reinterprets its inputs. Information does not simply get passed on within the brain, but different levels of organization within the brain may speak their own functional languages. The experience of affect may be an intrinsic "language" of the brain, one that allows value-laden internal guidance of behavior. Thus, higher brain cognitive processes provide information about the external world, but affects provide internal value codes (various forms of "goodness" and "badness") that guide and sustain ongoing behavior, and affects presumably could not do their job if they were unfelt, deeply unconscious, even though they can easily lead to habit structures that become streamlined and largely unconscious. Let me now focus on a few emotional systems that are pregnant with such synthetic possibilities.

7. The SEEKING/expectancy/wanting system of the brain: Its not just "reward prediction error"

The spectacular discovery of electrical self-stimulation from electrode sites along extended areas of the lateral hypothalamus set the stage for understanding the behaviorist concepts of "reward" and "reinforcement," and perhaps even "pleasure" (Olds, 1977; Wise, 2002). Unfortunately, there were shortcomings to all of these concepts (reviewed in Panksepp & Moskal, in press), and to the present day, it remains unresolved as to what function this psycho-behavioral system of the brain serves in brain organization (even though a new "reward prediction error" learning-theory is ascendant: Schultz, 1998, 2000, 2002). My own struggles with the various paradoxes of self-stimulation reward contributed to a unified incentive motivational model (Trowill, Panksepp, & Gandelman, 1969), which culminated in the conception that this complex neuronal system for appetitive "desire" mediates a coherent organismic urge to explore the environment and seek resources in response to bodily needs and external incentives (Ikemoto & Panksepp, 1999; Panksepp, 1971, 1981, 1982, 1986a, 1986b, 1986c, 1992a, 1992b). I now conceptualize this psycho-ethological pattern of behaviors as arising from the SEEKING/Expectancy system—an energizing, hedonically positive functional system of the brain (Panksepp, 1981, 1998a)—which has been further developed into a dopamine-centered "wanting" or "incentive salience" model by Berridge and Robinson (2003).[3]

With regard to the criteria mentioned above, (i) animals exhibit a coherent emotional response pattern when the system is stimulated—in a word "foraging" or seeking (Panksepp, 1981, 1986a, 1992a); (ii) they show unconditional and conditional approach to this type of brain arousal (Olds, 1977); (iii) a key chemistry of this system, dopamine, is euphorgenic in humans (Volkow et al., 2002). However, dopamine does not appear to be as essential for the discrete consummatory pleasures of the world—food, water, warmth, etc. (Ikemoto & Panksepp, 1999), even though dopamine is certainly necessary for other types of good feelings (Panksepp, 1986b;Wise, 2004). Still, there seems to be widespread resistance to conceptualizing this system in emotional–ethological ways as opposed to simply traditional learning-system terms. I will not here attempt to unravel the many conceptual subtleties and historical strands relevant to unraveling these issues; they are detailed elsewhere (Panksepp & Moskal, in press).

Let us first envision this SEEKING system in relatively straightforward psycho-ethological terms: most of us readily recognize that animals actively do many things "energetically." Many emotional behaviors seem outwardly purposive (they reflect evolved "intentions in action"), and given just a little experience with the reward contingencies of the world, such instinctual tendencies become intensely goal-directed in a "magnetized" sort of way. Animals also seem to show every indication that they have some second-order comprehension of their goals (expectancies), and if barriers to success are imposed, they persist in quite flexible but insistent ways. If nothing works, they often exhibit frustration and anger, and eventually they give up and "extinguish" (but rarely forget). Although their well-integrated behavior patterns seem to make good sense in terms of the apparent cognitive goals, it is the energized nature of their riveted attention to tasks and their focused movement toward engaging objects that seem to indicate that they have coherent brain operating systems to help actualize a diversity of internal wants and desires. Indeed, such behavior patterns are the ones that are activated by electrically or chemically stimulating the trajectory of this SEEKING/Expectancy system (Ikemoto & Panksepp, 1999; Panksepp, 1981, 1982, 1992a).

Feelings of environmentally engaged aliveness—positive excitement or euphoria—accompany such seeking urges in humans. It seems outwardly implausible that such flexible goal-directed patterns could occur in other complex organisms without any corresponding inner experiences, although a clever robotician or cartoonist could surely manufacture good simulacra. It is more straightforward to think about such behavior in terms of what animals are aspiring to find or achieve (the active organism perspective) than simply in terms of the guidance provided by stimuli that have impinged on them in the past (passive receivers of information). However, for ontological reasons (i.e., mental processes do not exist; only neurons fire), behaviorists deemed the latter option to be the more scientifically attractive way to view the causes of animal behavior, and hence are forced to use convoluted concepts to explain dopamine functions such as "reward prediction error" (Schultz, 1998). They seem not to have considered that a dual-aspect monism is a viable scientific option, and not just a circular argument (especially when we can make many novel cross-species, psychobiological predictions about affective changes that simply cannot be achieved with a general-purpose "reinforcement" concept—e.g., Leyton et al., 2002; Panksepp, 1999; Volkow et al., 2002). In any event, the neuroscience evidence indicates that all mammalian brains do contain a general-purpose SEEKING system designed to actively engage the world, especially its life-sustaining resources. The active and automatized urge to energetically interact with the world and to help integrate associated information about environmental events, increases the future efficiency of behaviors through the emergence of cognitive maps, expectancies, and habit structures (Panksepp, 1986a, 1992a, 1998a).

As brain dopamine system analysis moved to the forefront of the field (see Wise, 2004 for a recent summary), the neuro-ethological expectancy/SEEKING concept was largely ignored as the area shifted to more delimited questions concerning the functions of dopamine in reward-learning behaviors (for history, see Ikemoto & Panksepp, 1999; Panksepp & Moskal, in press). With the identification of the exquisite neuroanatomies of brain dopamine circuits and as techniques were perfected to study activities of dopaminergic neurons, learning-system views prevailed in the field (Schultz, 1998, 2000, 2002). Indeed, the evidence is now impressive that neurons in this system are more responsive to the anticipation of rewards rather than the receipt of reward: the evidence is based on the consistent tendency of dopamine neurons (i) to fire selectively in response to unexpected rewards and novel, attention-grabbing events, followed by a rapid diminution of responding with repeated stimulus presentations; (ii) the tendency of these cells to stop responding to predictable rewards, as they gradually become responsive to stimuli that predict rewarding events, and (iii) to be inhibited by the omission of rewards (which may lead to renewed foraging urges). These impressive correlative findings were so compelling that the learning-theory "reward prediction error'' model prevailed. However, this viewpoint fails to deal effectively either with the instinctual or hedonic-emotional aspects of appetitive behaviors. It has moved rapidly to the forefront of theoretical thinking in the field, even as it neglects an abundance of earlier data indicating that appetitive motivational neurons, that behave similar to dopamine neurons, exist in widespread regions of the brain (Olds, 1977; see Panksepp, 1998a, Fig. 8.3).

Perhaps, an elementary mistake is being made in this neo-behavioristic conception of brain dopamine function. All the data for the ''reward prediction error'' model are strictly correlative. There may be no causal dopamine ''reinforcement'' or ''instruction signal'' for learning, even as dopamine permits animals to learn about their environments. The dopamine SEEKING system may merely set the animal up for higher learning processes to be engaged (Ikemoto & Panksepp, 1999). As discussed extensively elsewhere, the termination of the foraging sequence (i.e., when activity in the system rapidly diminishes because the animal encountered a desirable consummatory reward) may engage what has traditionally been called ''reinforcement'' processes (Panksepp, 1992a, 1986a). It could just as well reflect an internal emotive attractor landscape that becomes coupled to exteroceptive perceptions via life experiences. In this context, the well-documented inhibition of frontal cortical glutamatergic inputs to the striatum by ascending dopamine systems makes sense (for the most recent finding at present, see Brady & O'Donnel, 2004). Learning mediated by fluctuating glutamate activity may help solidify and channel prior foraging/SEEKING patterns (e.g., Fig 4.4, Panksepp, 1986a).

What we can confidently conclude from the electrophysiology data is that dopamine neurons are indeed ''listening'' to a great deal of associative information processing in other areas of the brain. However, it may be unwise to assume that the message passed on by dopamine neurons actually retains the information that the cells have been listening too. It is just as likely that instead of a ''reward prediction error'' being passed on, dopamine cells actually pass on an urge to behave in certain characteristic appetitive ways—to approach, explore, investigate—in a word to seek resources, or if unpredicted rewards emerge, to re-energize seeking urges. If so, the ''reward prediction error'' function, abstracted from a study of the inputs to the system, may be a fantasy, and not as good a guide to our thinking as the types of unconditional psychobehavioral states dopamine arousal promotes. In other words, it may be inappropriate to extract a specific dopamine function based merely on conditional neuronal firing patterns from the larger psychobehavioral puzzle within which these firings are embedded. Even though the diverse neural activities (i.e., much of the rest of the brain) to which the dopamine cells are ''listening'' certainly allow expectancy learning to proceed—perhaps largely by interactive effects with corticofugal glutamatergic inputs to the basal ganglia (e.g., Kelley, Smith-Roe, & Holahan, 1997; Panksepp, 1986c)—the primitive integrative function of this system still seems better conceptualized as a broadly ramifying psycho-emotional state that is well characterized as foraging and appetitive eagerness. How such straightforward emotive functions interface with pervasive expectancy-learning processes have been conceptualized (Berridge & Robinson, 2003; Olds, 1977; Panksepp, 1981, 1986a; Toates, 2004). In pursuing such learning-system perspectives, which allow us to understand how specific ''desires'' are constructed, investigators need not ignore the experiential, affective contributions to such learning.

The positively valenced SEEKING/Expectancy urge links up with a host of brain learning processes, which at the highest psychological levels may reflect wants and desires. This affectively valenced core system helps generate a positively valenced psychological state that is closer to an invigorated and generalized positive engagement with the world at large rather than any specific type of consummatory pleasure/reward. This SEEKING concept provides a coherent multi-dimensional psychobiological framework for understanding what this system provides for organismic psychobehavioral coherence (Panksepp, 1986a, 1992a, 1998a). It does not neglect the abundant evidence for the affective states this system helps create, nor is it incommensurate with strictly behavioristic-learning analyses. It provides a natural bridge to ethological studies as well as human psychological and psychiatric issues (Panksepp & Moskal, in press). It provides a gateway to understanding important human feelings.

Attempts to conceptualize the affective attributes of brain activities enrich our capacity to pursue productive cross-species (especially to human) theorizing. They illuminate important psychiatric concerns, including delusional behavior in schizophrenia (Panksepp, 1998a), psychostimulant addiction (Panksepp et al., 2004b), and the anergia, dysphoria, and other unpleasant feelings humans exhibit when this system is pharmacologically dampened (Voruganti & Awad, 2004). A "reward prediction error" hypothesis says little about such psychological and psychiatric topics, and it never deals cogently with the simple fact that dopamine is secreted in a mass-action way to external as well as internal prompts, suggesting it truly mediates global affective/motivational "state control" functions rather than narrow information-processing "channel control" computations (see Panksepp, 2003a, 2003e for a discussion of such distinctions). Obviously, appetitive state control systems must remain attuned to the perceptual information-processing channels of the brain, explaining the intriguing single-unit data (e.g., Schultz, 2002), but they do not simply transmit those detailed messages onward in the control of behavior. Thus, we have a classic dilemma of artificially delimited scientific views—in their ability to exquisitely describe a small slice of pie, investigators may be misilluminating the whole (Bennett & Hacker, 2003).

In sum, mesolimbic dopamine systems are more influential in helping mold psycho-behaviorally coherent action tendencies than in directly mediating "reinforcement" in the brain. Indeed, affective changes in the brain may be critical for understanding what the concept of reinforcement actually means (Panksepp, 1982, 1986a, 1986b, 1986c, 1990b). As long as emotional states remain remote from the interests of brain scientists, we are bound to have a schizoid imbalance in the field that does not serve comprehensive understanding well. Various ways can be conceptualized in which this system links up with cognitive processes, and the variety that have recently been advanced from slightly different perspectives are not all that different from each other (for summaries, see Ikemoto & Panksepp, 1999; Panksepp & Moskal, in press). In any event, the affectively experienced aspects of emotional brain functions are best conceptualized as large-scale neurodynamics of the brain (Freeman, 2003a; Tononi & Edelman, 2000). They are not easily resolved in single-cell recordings.

It is easy to envision how such seemingly divergent views could be blended, but until recently there has been little incentive to include the evolutionary view that an emotive system for resource acquisition is an intrinsic part of the nervous system, and that it entails an affective feel—an invigorated positive feeling of engagement with tasks that can border on euphoria. All psychostimulants promote such feelings, helping explain the addictiveness of certain drugs, and also indicating why goal-directed behaviors have such a persistent quality. Put simply, obsessive persistence may be a direct outcome of sustained affective desires.

Learning is obviously an enormous part of the equation, but a clear recognition of the emotional and motivational evolutionary tools organisms possess to initiate the learning process is equally important, but is still typically ignored in animal behavioral research. Behavioral, reinforcement-based learning theories without any affective concepts resemble "geocentric" Ptolemaic worldviews that become convoluted in their attempt to deal with inconsistent observations (Breland & Breland, 1961). They could become more "heliocentric" as investigators begin to consider the many affective processes that lie at the core of behavioral and cognitive existence.

8. FEAR systems of the brain: Of low roads, high roads, and royal roads

The study of fear learning has been one of the great success stories of behavioral neuroscience, to a point where the details of associative classical-conditioning have been worked out in considerable detail within prominent cognition–emotion interface zones such as the amygdala (e.g., LeDoux, 1996, 2002). It is now recognized that conditional information that predicts pain can reach the amygdala via "low roads" from the thalamus, and "high roads" from the cortex. The only aspect of the equation that has been largely ignored by learning-oriented investigators is the possibility that evolution constructed a "Royal Road"—a trans-hypothalamic FEAR system—which courses between the amygdala the periaqueductal gray (PAG) of the midbrain (for overviews, see Panksepp, 1990c, 2004d). Stimulation of this system at various points along the neuroaxis can generate a coherent fear response, that is imbued with anxious feelings. In short, descending information from the amygdala is involved more about the stimuli in the world that organisms should avoid, while FEAR action systems of the brainstem are more integral to generating the intrinsic actions and feelings of fear.

This system was postulated on the basis of experiments showing that localized electrical stimulation of the brain (ESB) along this trajectory could generate coherent fear responses (Panksepp, 1971, 1982, 1990c, 1998a). Perplexingly, this alternative conceptualization has been almost totally ignored, until recently, as a potential source for the highly aversive affective feelings that accompany traditional fear learning tasks (e.g., Rosen & Schulkin, 1998). This system has been largely treated as a psychologically vacuous "output" system by neurobehaviorists, which would make study of the system of second-rate importance for understanding anxiety disorders. In fact, the evidence indicates that the system integrates ethologically coherent fear responses including: (i) freezing and flight, (ii) that animals find such stimulation aversive, and (iii) that drugs that modulate human anxiety modulate arousal of the FEAR system (Panksepp, 2004d, 1990c).

Critical evidence for the affective properties of this system is reflected in the fact that animals consistently *escape* ESB applied to such brain sites, although their failure to avoid the ESB was problematic (Panksepp, Sacks, Crepeau, & Abbott, 1991). However, when we first evaluated conditioned fear using place-preference paradigms (Sacks & Panksepp, 1987), there was no ambiguity that environmental locations where animals received ESB to such brain sites are avoided (Fig. 2). Although many distinct components of this coordinated system can be discriminated with neuroscience tools, such dissections do not mean that the system does not work normally in a coordinated fashion. Neuroscience tools are ideally designed for dissecting systems that are not fractionated in their coordination of real-life behaviors, a dilemma rarely addressed by investigators. To understand fearful affect, we must study the neurodynamics of evolved systems that allow organisms to unconditionally get out of harm's way. Although there is comparatively little work on the lower parts of the FEAR system in the Anglo-American research scene, such work has flourished in Brazil (for a summary see, Blanchard et al., 2001a; Panksepp, 2004d).

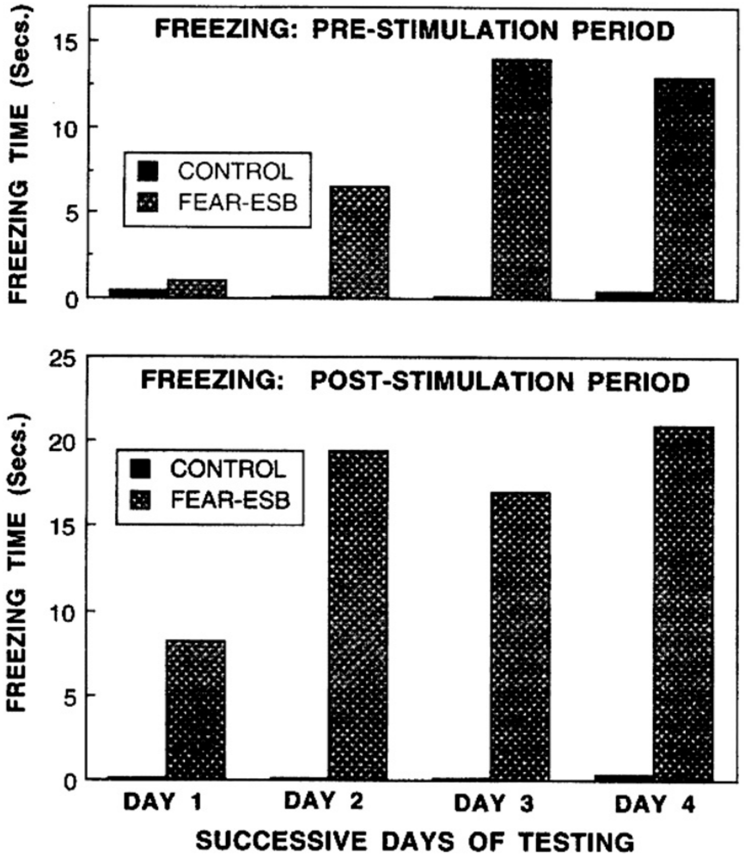

Fig. 2. Freezing time during the minute prior to (top) and right after (bottom) electrical stimulation brain (ESB) within the anterior hypothalamic trajectory of the FEAR system in rats on four successive days of testing. The top graph indicates how contextual conditioning increases during the first 3 days of retention testing (days 2–4). Reprinted from Fig. 11.3 of *Affective Neuroscience* (Panksepp, 1998a) with permission of Oxford University Press.

9. The core emotional systems for social affects

In addition to FEAR and SEEKING circuits, there is sufficient evidence to postulate at least five other basic emotional networks shared by all mammals. Of course, as already noted, there are a larger variety of non-emotional affects based on our bodily needs (e.g., hunger and thirst) and various background states of the body (e.g., fatigue and feelings of well-being) but they will not be covered here. The five remaining *emotional* systems are ones devoted to anger-RAGE, sexuality-LUST, nurturance-CARE, separation distress-PANIC, and joyful PLAY (detailed in Panksepp, 1998a). The last two systems, ones that we first started to investigate 30 years ago, will be used to exemplify how a focus on the instinctual emotional action apparatus may deepen our understanding of human experiences that promote social bonds and attachments. The psychological perspective on the anger-RAGE system has recently been shared (Panksepp & Zellner, 2004), and comprehensive neuro-behavioral monographs on sexuality and maternal behavior are available (e.g., Numan & Insel, 2003; Pfaff, 1999).

9.1. The PANIC/Separation-distress system

To be a mammal is to become socially dependent and bonded to others who can enhance survival. John Bowlby (1972) was the first to bring this concept to the psychiatric forefront, and it is only recently that research programs attempted to clarify the neural underpinnings. We initiated the study of such an intrinsic social-emotional system in the mammalian brain. The systematic analysis of the separation-distress system was enabled by the fact that all young children, as well as the young of other mammals, show powerful and coherent emotional responses such as "crying" when they are isolated from their parents. The guiding psychobiological idea was that severance of social bonds leading to painful feelings of separation distress could be monitored by such distress vocalizations. The guiding evolutionary concept was that neural systems that elaborate social attachments have evolutionary relations with those that mediate the affective qualities of physical pain, including modulation by the same chemistries such as endogenous opioids. This heuristic assumption now has intriguing implications for the clinical management of pain and sadness in both humans and other animals (Panksepp, 2005a, 2005b).

This effect of opioids on the emotional response were more robust than on physical pain (Panksepp, Herman, Villberg, Bishop, & DeEskinazi, 1980; Panksepp et al., 1988). Along the way we also discovered other important chemistries that robustly quelled separation distress, such as oxytocin (Panksepp, 1988, 1992b) and prolactin (Panksepp, 1998a), as well as brain chemistries that intensify feelings of distress, such as corticotrophin-releasing factor and glutamate (Panksepp et al., 1988). It was reasonable to postulate that all these chemistries figure heavily in the genesis of social attachments and regulation of depressive responses (Panksepp, Yates, Ikemoto, & Nelson, 1991), and a large literature supports such views (for reviews, see Nelson & Panksepp, 1996; Panksepp, 2001a). These chemistries help create inter-subjective psychological spaces with others, which permit animals and humans to learn the emotional ways of their kind (Reddy, 2003). Others detailed how oxytocin regulated social dynamics in various species of voles (Carter, 2003; Insel, 2003a, 2003b) and cholecystokinin has also emerged as a regulator of social anxieties and bonding (Weller & Feldman, 2003). Many social neurochemistries remain to be found, but we already have abundant new ideas to help humans whose social emotional "energies" are more or less than they desire (Panksepp & Harro, 2004).

These findings have now converged so that an integrated social emotional system is coming to be an accepted mammalian brain function, although the associated emotional feelings are not as widely discussed. However, the simple fact that mother and infant, in practically all mammalian species, persistently aspire to achieve reunion when forcibly separated, is consistent with the existence of such feelings (although such data are also consistent with the attractive effects of pheromones and the potential influences of other non-social rewards). Still, a straightforward point of view is that other animals do feel the power of their social needs intensely, even though they do not, as we humans can, re-symbolize social needs within tertiary levels of consciousness. Such ancient primary-process emotional controls we share with other animals may play an essential role in the construction of human feelings. Pursuant to the demonstration that prosocial activities such as play and grooming release brain opioids (Keverne, Martensz, & Tuite, 1989; Panksepp & Bishop, 1981), human brain imaging has now highlighted that opioid activity is reduced during the experience of sadness (Zubieta et al., 2003). The resonance of such social-emotional circuits among individuals offers new ways to conceptualize the emotional basis of altruism and empathy (Panksepp, 1986c, 1989/2004).

The clinical implications of this knowledge are many. For instance, children with imbalances of such chemistries may exhibit autistic symptoms (Insel, 2003a, 2003b; Panksepp, Lensing, Leboyer, & Bouvard, 1991). Gentle, loving touch (Fig. 3) can alleviate both psychic and physical pain, partly by activation of brain opioid and oxytocin system (Panksepp, 2004c; Uvnas-Möberg, 1998). If young animals are left alone, they appear to experience a psychic pain that is so strong that it affects many other life regulatory systems, and they exhibit anaclytic depression and usually die (Panksepp, Yates et al., 1991). Such findings attest to the power of affect in animal lives. In domestic animals, the mere proximity of friendly and caring others provides substantial relief from pain (for a review, see McMillan, 2005). Likewise, a growing human psycho-social literature now suggests that the social environment can modulate the affective intensity of pain (e.g., Brown, Sheffield, Leary, & Robinson, 2003; Leary & Springer, 2000; MacDonald & Leary, 2005), which is concordant with the fact that social isolation can increase behavioral indices of physical pain in animals (e.g., Panksepp, 1981).

In diverse human cultures, people talk about the loss of a loved one in terms of painful feelings. This seems to be more than a semantic metaphor (MacDonald & Leary, 2005; Panksepp, 2005a, 2005b). Although we have no time capsule to return to the evolutionary origins of brain emotional systems, close analyses of animal brains do offer important clues. So far, the strongest evidence for the evolutionary relations between social and physical pain systems has come from the fact that localized electrical stimulation of subcortical brain areas that have been implicated in the regulation of pain can provoke separation cries, and these responses are regulated by endogenous opioids (Herman & Panksepp, 1981; Panksepp et al., 1988). Additional areas of control include the anterior cingulate, the bed-nucleus of the stria terminalis, the ventral septal and dorsal preoptic areas, the dorsomedial thalamus, and the periaqueductal gray (PAG) of the brain stem. Recent human brain imaging has highlighted similar trajectories of brain activation on humans experi-

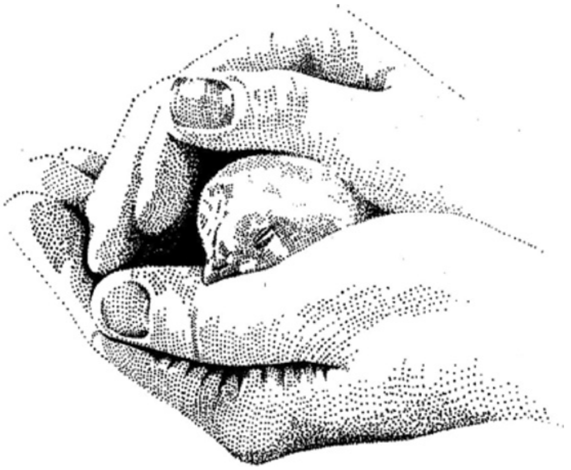

Fig. 3. When held gently in human hands, newborn chicks exhibit a comfort response consisting of the cessation of vocalizations and eye closure. These effects are attenuated by opiate receptor blocking agent naloxone, indicating internal opioids help mediate contact comfort responses. Figure is adapted from photograph in Panksepp (1980), as reprinted from Fig. 14.9 of *Affective Neuroscience* (Panksepp et al., 1980) with permission of Oxford University Press.

encing intense sadness (Damasio et al., 2000; for schematic, see Panksepp, 2003b). Some of these areas, especially the last two, are known to control feelings of physical pain. Indeed, the PAG is the brain area from which emotional distress can be most readily evoked in humans and animals with the lowest levels of brain stimulation. Similarly, the "pain" of social exclusion and depression activates anterior cingulate regions that are known to regulate pain within the human brain (Eisenberger, Lieberman, & Williams, 2003; Mayberg, 2004), even though for multi-functional brain areas such as this, many alternative explanations remain to be winnowed.

The above connections would not have been made without openly entertaining the reasonable possibility that all mammals have similar basic emotional experiences. Such inter-disciplinary thinking can also help us better understand many psychiatric problems. For instance, since social loss is one of the most robust precipitants of depression (Panksepp et al., 1991, 2002), we could anticipate that opioids and perhaps oxytocinergic facilitators should be effective treatments of sadness and depression. Of course, such effects have been well known to physicians and opiate addicts through the ages. Before the advent of modern anti-depressants, opiates were widely recognized as anti-depressants, but rarely used medically because of potential addiction (but in those days self-use was legal). Now that there are mixed agonists/antagonists such as buprenorphine, which are medically approved and have only modest addiction liability, there is a role for off-label use of such agents in treating refractory depressions, an effect that can occur promptly as opposed to over several weeks (Bodkin, Zornberg, Lucas, & Cole, 1995; Callaway, 1996). Parenthetically, opioids are one of the few drugs that have been found to intensity playfulness (Panksepp et al., 1985), which is a potential model system for development of novel anti-depressants (Panksepp, 2000d).

9.2. The PLAY system

Young animals play with each other in order to navigate social possibilities in joyous ways. The urge to play was also not left to chance by evolution, but is built into the instinctual action apparatus of the mammalian brain (Ikemoto & Panksepp, 1992; Panksepp, Normansell, Cox, & Siviy, 1994; Vanderschuren, Niesnik, & Van Ree, 1997). We know less about this emotional system than the others, partly because so few neuroscientists are willing to recognize that such gifts could be derived as much from our neuro-evolutionary nature as our kindest nurture. Soon after our laboratory discovered the locations and cardinal chemistries of separation distress (Panksepp, 2003c; Panksepp et al., 1988), we sought to consider the opposite side of the social coin, that is, the profound desire of animals to interact with each other in energetic, playful ways. We focused on rough-and-tumble play as the foundational process for many other social skills, a brain process almost totally neglected in behavioral neuroscience (Panksepp, Siviy, & Normansell, 1984).

Play is easy to study in the laboratory. It is a powerful positive incentive and many functional attributes have now been clarified (for summaries, see Panksepp, 1998a and Vanderschuren et al., 1997). The underlying brain systems have been harder to identify, but we can be confident such social engagements are critically dependent on sub-neocortical circuitries. The behavior survives radical decortication; animals without any neocortex play vigorously (Panksepp et al., 1994). This work has implications for psychiatric disorders such as Attention Deficit Hyperactivity Disorders (Panksepp, Burgdorf, Turner, & Gordon, 2003).

Our analysis of sensory systems regulating play has highlighted both somatosensory and auditory systems (Siviy & Panksepp, 1987). Most recently, we have been especially intrigued by "play sounds" (Knutson, Burgdorf, & Panksepp, 1998). These abundant 50 kHz chirps resemble laughter, which is further affirmed by our ability to intensify the response by playful, manual tickling. There are now a dozen good reasons for open-minded scientists to entertain the possibility that such sounds reflect a positive affective process which, in its most intense forms, can be emotionally characterized as a playful, social joy (Panksepp & Burgdorf, 1999, 2003).

We would not have spent the past 6 years of laboratory effort to study the laughter-type 50 kHz vocalization, if we did not have the working hypothesis that rat chirps have some kind of ancestral relationship to the playful laughter of the young of our own species (Scott & Panksepp, 2003). We currently know so little about human laughter despite Robert Provine's (2000) seminal efforts. We now know that placing psychostimulants such as amphetamine into the ventral striatum (nucleus accumbens) promotes vigorous 50 kHz chirping (Burgdorf et al., 2001). It is intriguing that mirth provokes robust arousal of this same brain area in humans (Mobbs, Greicius, Abdel-Azim, Menon, & Reiss, 2003). Perhaps, there is a homology here that will give us some lasting information about human joy (Panksepp, 2000d; Panksepp & Burgdorf, 2003). We know that young animals we have tickled become remarkably friendly toward us—apparently socially bonded. They actively chirp when we approach their cages. They unambiguously choose to spend time with older animals that chirp a lot compared to those that do not (Panksepp et al., 2002). The response can be readily bred for (Panksepp, Burgdorf, & Gordon, 2001; Burgdorf, Panksepp, Brudzynski, Kroes, & Moskal, 2005) providing opportunities to identify genes that promote happiness and sadness (Panksepp, Moskal, Panksepp, & Kroes, 2002).

9.3. Social dependence, bonding, and attachments

A fundamental affective neuroscience question is, what are the core neuropsychological dimensions of social attachments that evolution has provided all mammals as birthrights? Our own work on the topic emerged from the recognition that separation distress, and hence crying circuitry, might be the inroad to this problem (Panksepp, 1981; Panksepp, Bean, Bishop, Vilberg, & Sahley, 1980). As already indicated, the key chemistries discovered were opioids that stimulate μ receptors, as well as oxytocin and prolactin sensitivities of the brain (Nelson & Panksepp, 1998; Panksepp, 1998a, 1998b, 1998c). The oxytocin story has received extensive experimental attention because of field mice, such as the prairie voles, that exhibit adult pair-bonding. Sue Carter (1998, 2003) and Tom Insel (2003a, 2003b) have been at the forefront of research programs that have highlighted how important oxytocin (and also vasopressin in males) is to the formation of social friendships and allegiances. Others have shown that oxytocin is critical for facilitating mother–infant bonding in sheep, maternal urges in many species, and solidification of social memories in rats (for details, see Panksepp, 1998a and many papers by Carter or Insel). Our own laboratory was the first to demonstrate that oxytocin was even more effective than opioids in reducing separation distress in birds (Panksepp, 1988, 1992a, 1992b). We proceeded to demonstrate that social bonding from the infant's perspective was also oxytocin-facilitated in rats (Nelson & Panksepp, 1996, 1998).

Although it is well established that opioids are hedonically positive by hundreds of self-administration and conditioned place-preference (CPP) experiments (Bardo & Bevins, 2000), the evidence for oxytocin is still ambiguous. In our hands, *centrally* administered oxytocin only promoted socially induced place-preferences, without having hedonic effects of its own (Panksepp, Nelson, & Bekkedal, 1997). However, others have obtained CPP effects with *peripheral* oxytocin without the use of social facilitation (Liberzon, Trujillo, Akil, & Ytoung, 1997). There is no work on the hedonic effects of prolactin in mammals, but prolactin-induced CPP is evident in domestic chicks (Bekkedal & Panksepp, 1997).

As highlighted in the previous section, our initial work into the neurochemistry of social attachments a quarter of a century ago was motivated by the possibility that the loss of a loved one—the painful grief occasioned by sudden loss of social support—could be alleviated by the same brain chemistries that regulate our feelings of physical pain. The resulting findings with crying measures confirmed that there are fundamental similarities between the brain dynamics of narcotic dependence and social bonding. The role of opioids in maternal–infant attachments in sheep has recently been documented (Shayit, Nowak, Keller, & Weller, 2003). Some of these ideas are ripe to be evaluated in humans, for instance, by evaluating pharmacological manipulations such as the influence of low opiate stimulant and antagonist drugs and intranasal oxytocin on loving feelings. Another peptide that is ready for human evaluation is cholecystokinin, which modulates social preferences in rats (Weller & Feldman, 2003). Many of the needed functional dissections cannot be achieved with human studies, and progress will require investigators to entertain the proposition that various hedonic processes, some of which can be operationalized through a study of instinctual emotional behaviors, do exist in the brains of other animals.

The vigorous social bonding that all infants and mothers of mammalian species show for each other, along with the prolonged signs of distress in isolated young animals, clearly reflects profound affective states. Alternative positions, such as animals exhibiting social conditioning without any feelings, seem increasingly improbable. Philosophic and empirical resolution of such issues may eventually have enormous benefits for broadening and deepening our knowledge about both ourselves and other organisms.

10. Species differences in emotions: Research costs and benefits

It should go without saying that there will be abundant species differences in the details of all brain emotional circuits, and hence the associated affective proclivities. Variety is a cardinal characteristic of life, but practically all that variety is based on patterns of generalizable principles. Thus, although rats and mice differ dramatically in their social responsivity and general intelligence (Whishaw, Metz, Kolb, & Pellis, 2001), they share quite similar molecular mechanisms for learning, with many resemblances to learning in invertebrates. Rabbits may have more vigorous FEAR circuits than lions, and surely only part of that is due to their differential life experiences. Rats are intrinsically scared of cats (especially their odor) and they love the dark; humans are not afraid of the smell of cats, but many fear darkness. Different intrinsic sensory/perceptual inputs and different cognitive processes can access the same type of emotional system in different species. Although different species may fear different things, the core processes for FEAR may be quite similar in their brains. The same could be said about the other emotional systems. A cross-species analysis will provide general principles that may apply to all relevant species (i.e., those having homologous brain systems), while the detailed differences will need to be worked out species by species.

Continuing in this same vein, some animals have robust separation distress systems (e.g., dogs, guinea pigs, and primates) while others do not (e.g., laboratory rats and mice) and the use of the latter can lead to misleading findings if one is interested in the class-general aspects of true social separation distress processes (Panksepp, 2003c). On the other hand, rats (albeit not most strains of laboratory mice) exhibit vigorous social play while guinea pigs do not. Although each species has strengths and weaknesses when it comes to seeking knowledge about basic emotional systems that *may* apply to humans, so far we are pleased that so much of our neurochemical work on separation distress in young dogs, guinea pigs, and chicks (Panksepp, 2003c; Panksepp et al., 1980, 1980) translates to primates (Kalin, Shelton, & Barksdale, 1998; Zubieta et al., 2003). I would note that criticisms of our opioid hypothesis of social affect arising from work with infant rats (Winslow & Insel, 1991) are not as relevant as it has been made out to be (Panksepp, Newman, & Insel, 1992). Since ongoing work on separation distress (our PANIC system) was brought into question again recently (Blumberg & Sokoloff, 2001), I have gone to some length to discuss why infant rats may not be as fine model for *social* separation distress as species that develop robust social-bonds (Panksepp, 2003c). However, recent genetic work does affirm the importance of opioids in regulating rodent social desires (Moles, Kieffer, & D'Amato, 2004).

Obviously, we should be as interested in the emotional lives of animals as we are in how they may serve understanding of our own species, and failure to pay attention to the emotions of other animals may have left a trail of bad data in many rat behavioral studies of the 20th century. One example is pregnant with implications, especially for every rat-runner who has pet cats or ferrets at home, but has not paid attention to the fear evoking smells they may have carried into the laboratory on their hands and clothes. Laboratory rats and mice are dramatically more sensitive to olfactory cues than we are, and they have intrinsic olfactory-based fear systems (Blanchard, Yang, Li, Gervacuio, & Blanchard, 2001b; Panksepp & Crepeau, 1990). Thirty years ago we discovered that some of our pharmacological effects were being biased by the fact that our rat lab was situated three rooms down from a small cat lab. Once the cat lab was closed, some of the drug effects we had seen with anxiolytic drugs diminished dramatically. Only years later did we figure out why—simply returning some cat smell back into the environment was sufficient to resurrect our original findings.

We, as many others, have now evaluated the fear-evoking effects of predatory odors, such as those of cats, foxes, and ferrets, on rodent behavior, and the effects are striking (Blanchard et al., 2001b). Fig. 4 highlights the prolonged effects of a single exposure to cat hair on the play of rats. This contextual fear effect, in a totally clean cage, substantially outlasted the acute effect of that olfactory threat. This unconditional fear effect is mediated via the vomeronasal systems as opposed to the main olfactory apparatus (Panksepp & Crepeau, 1990), presumably by direct effects on amygdaloid/hypothalamic/PAG FEAR circuitry. The smells of mice, chickens, and guinea pigs (and my dog) had no effect on the play behaviors of our young rats, but simply hanging a shirt polluted with cat smell next to an open field where the exploratory behavior of rats was being evaluated, had marked effects on behavior. To argue that these effects were due to other factors than internally experienced neuro-affective changes stretches credulity.

Those who have maintained cat labs right next to their rat labs must consider why their findings may not be replicable in labs that have employed more sensible housing procedures. I know at least one prominent fear researcher, not terribly interested in the emotional feelings of his animals, who had just that type of animal husbandry arrangement. I raise such issues because the failure to consider the possibility that animals do have emotional feelings has led to research practices

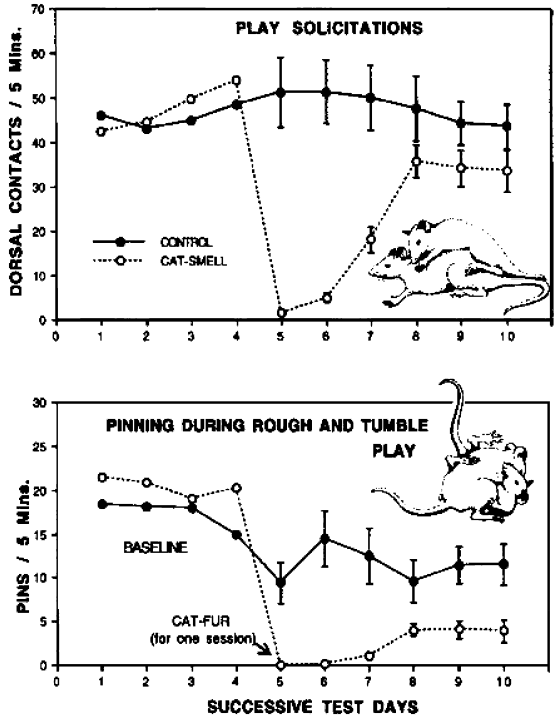

Fig. 4. A single exposure to a small ~20 mg sample of cat hair on the 5th day of testing inhibited rat rough and tumble play completely, and this contextual fear response continued for up to 5 subsequent test days, at higher levels with the measure of pinning (bottom) and less with the dorsal contact measure of play solicitation (top). Reprinted from Fig. 1.1 of *Affective Neuroscience* (Panksepp, 1998a) with permission of Oxford University Press.

which, from a scientific control perspective, are simply unacceptable for obtaining clean data, no matter how compulsive one is about other features of experimental design. Likewise, investigators need to recognize that rodents can be scared by ultrasonic sounds, and on cage-cleaning days (at least if metal cages are used) one can expect animals to be more timid than on other days (Sales, Wilson, Spencer, & Milligan, 1988; note one instance of this in Panksepp & Burgdorf, 1999, Fig. 3, day 5). There are many ways we could improve our research if we considered the affective feelings in our animals.

11. A recognition of affective states may improve our animal research

An important issue in animal research seeking practical answers to human problems must always be which findings from animals may apply to humans. In such endeavors, affective change must be a key concern. Obviously, if there are inadequate homologies in the underlying neural control mechanisms, then the animal work will not give us credible clues about the substrates of core affects in humans. Under those circumstances, the classical sin of anthropomorphic reasoning would be as severe as many behaviorists are routinely eager to emphasize. Still, it must be acknowledged that certain species can serve as excellent models for certain emotional responses that may relate to human issues. Others may not. For instance, rats may be an excellent model for human rough and tumble play (Panksepp et al., 2003; Scott & Panksepp, 2003), and perhaps even infantile human laughter (Panksepp & Burgdorf, 2003), but because of their weak social attachments, they may not be an ideal model for separation distress and social bonding (Panksepp, 2003c).

Can we use animal models of affective change to help sift drug effects that may be of potential bio-medical use in treating human medical problems? Obviously, the drug firms have invested heavily in animal models not only in the development of medicines for bodily ailments but also psychological ones as well. As investigators pay more attention to the affective lives of their animals, the models should become even more useful. Let us consider the present feverish search for medically effective appetite control drugs. How do we sift those that simulate normal satiety from those that simply reduce food intake because they make animals feel bad? Considering how sensitive play is to many psychologically disruptive variables, it can be used to evaluate whether pharmacological agents promote normal feelings of satiety in hungry rats. Hunger dramatically reduces the urge to play, which is restored rapidly by a single meal (Siviy & Panksepp, 1985). Of the many drugs that can reduce food intake, perhaps only those that can restore hunger-reduced play should be deemed reasonable candidates for exerting natural satiety influences on human appetite. Without considering many negative affects—including anger, disgust, fear, sadness, and feelings of sickness—we can stumble upon innumerable significant findings in feeding control research, without having found much of regulatory importance. This is an endemic problem in the field.

Because of the failure of most investigators to acknowledge affective issues, the field is now littered with facts that may tell us little about ''normal'' appetite *regulation*. Let us just consider one of many potential examples. The ability of opioid stimulation of the bed-nucleus of the stria terminalis to reverse anorexia was induced by administration of Corticotrophin Releasing Factor (CRF) into various brain areas to reduce food intake (e.g., Ciccocioppo et al., 2003). This appetite effect may not reflect induction of ''satiety'' but rather emotional distress evoked by the CRF. This ''side effect'' has been well recognized. However, related agents such as urocortin which also reduces food intake but has a different profile of brain effects (via action on a different CRF receptor) were touted not to have those disruptive emotional effects (Spina et al., 1996). In fact, both agents markedly reduce play and just like CRF, urocortin dramatically elevates separation distress in newborn chicks (Panksepp & Bekkedal, 1997) (Fig. 5). Thus, misleading behavioral interpretations of data may easily arise by not taking animal emotional feelings seriously. The field of learning is also littered with hard to interpret findings, because changes in emotions could easily masquerade as learning effects. Motivational changes often produce effects similar to learning changes. To interpret how many new psychopharmaceutical agents truly modify behavior in animals, it is essential to have a better understanding of their affective lives.

The only way we have to conceptualize such effects is by talking about human-type emotional feelings in other mammals. However, anthropomorphism continues to be regarded as a major sin in preclinical research. The attribution of mental states to animals is commonly deemed unparsimonious and dangerously inferential. However, Lloyd Morgan, whose canon of parsimony raised this issue to scientific prominence, never meant it to be used as ammunition against the likelihood that animals have mental lives (see Costall, 1998).

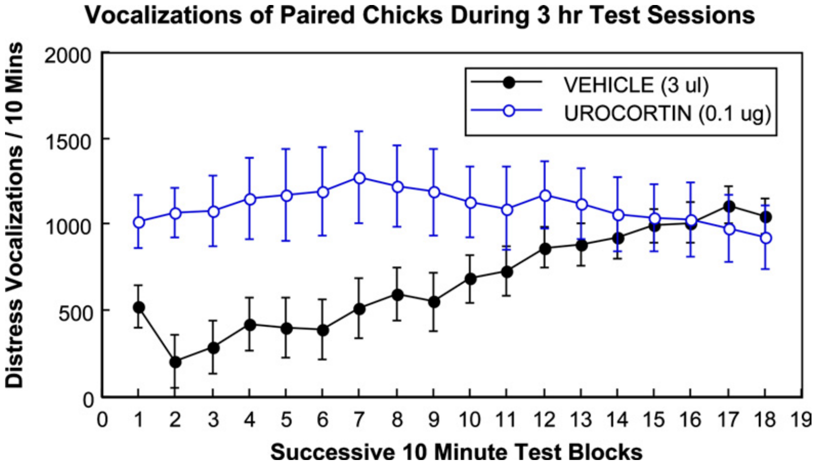

Fig. 5. A small 0.1 μg dose of urocortin administered into the fourth ventricle region of 5- to 7-day-old domestic chicks dramatically facilitates separation distress calls for an hour and a half in pair-tested animals (which serves to reduce baseline separation-distress vocalizations). This is essentially the same effect as observed with CRF, and the effect is dose dependent. After a 1 μ injection, a significant facilitation of vocalizations lasts for up to 6 h following either urocortin or CRF, although the CRF effect was slightly bigger. Unpublished data, Panksepp (1996).

12. The sin and salvation of anthropomorphism (or how Lloyd Morgan's canon misfired!)

The suggestion that human feelings may have substantive parallels in animal brains (zoomorphism) and that animals may have some emotional feelings akin to those of humans (anthropomorphism)—remain sins in various intellectual communities, even though modern variants of such reasoning can be based on the deep functional homologies in mammalian brains which arise from a massively shared genetic heritage. If humans have consciousness, as they surely do, and if one accepts an evolutionary point of view, anthropomorphism is not necessarily as big a sin as it has traditionally been made out to be. There are more disciplined scientific forms of anthropomorphism (Burghardt, 1997; Panksepp, 1998a, 2003c) than those evident in Disney cartoons. As I noted when I first started to cultivate this scientifically credible mode of reasoning for studying primary-process emotions: "Recent advances in brain research may permit anthropomorphism to become a more useful strategy for understanding certain primitive psychological processes in animals than it has been in the past. Although its application may be risky under the best of circumstances, its validity depends on the degree of evolutionary continuity among brain mechanisms that elaborate emotions in humans and other animals. Hence the degree of anthropomorphism that can have scientific utility in mammalian brain research should be directly related to the extent that emotions reflect class-typical mechanisms as opposed to species-typical ones" (Panksepp, 1982, p. 407).

Our analysis of opioid control of separation distress in animals is one of many examples, where a conceptualization of the human psychological effects of a pharmacological agent has led to clear predictions of behavioral change in animals. And now, 30 years later, it is finally evident that human brain opioid activity is reduced during experiences of sadness (Zubieta et al., 2003). There are a large number of comparable affective predictions to be evaluated from considering emotional changes in animals to potential affective changes in humans (Panksepp & Harro, 2004). However, few investigators are willing to voice such possibilities frankly and straightforwardly, for fear of being branded with the "scarlet letter" of anthropomorphism by neuro-behavioristic colleagues, and tarred with accusations of zoomorphism by investigators of human cognitions.

An anthropomorphic–zoomorphic strategy for understanding the neurochemistries of affective processes in humans might be deemed pointless if other animals did not have any emotional feelings that were neuro-evolutionarily continuous with our own brain–mind mechanisms (Panksepp, 2003c). However, there is an intrinsic safeguard built into the psycho-neuro-ethological triangulations strategy I have advocated (Panksepp, 1998a). Even if some affective conclusions drawn from the work should prove wrong, the behavioral facts obtained would remain of undiminished value, since the analysis is based on careful ethological analysis of the spontaneous behaviors of animals.

Still, the borderland between conscious and unconscious processes is hard to define, especially so in animal research (Berridge & Robinson, 2003). Certain core emotional systems can be studied even in fully anesthetized animals (Panksepp et al., 1991; Rossi & Panksepp, 1992), indicating that much of the underlying neural machinery for affects can operate unconsciously. Obviously, consciousness requires the concurrent activities of many widely ramifying neural networks, and it must be studied in animals that are awake, and tested in sufficiently complex and interesting environments so their full capacities can be systematically revealed. In this context, it should be recognized that behavior in the laboratory is often a caricature of what animals can actually do in real-world situations which support their neuro-mental development. Restricted rearing conditions during early development can permanently impoverish organismic capacities (e.g., the "kennel syndrome" which laboratory housing promotes; see Panksepp et al., 1983). The harvesting of anecdotal evidence concerning animal abilities in the real-world offers a fuller picture of the psychobehavioral abilities various species possess (Bekoff, 2000), and some neuroscientific analysis is possible (e.g., psychopharmacological interventions) in such situations (Overall, 1997).

13. Neural substrates of conscious and unconscious emotions, and cognition–emotion interactions

No discussion of consciousness can be complete without a consideration of unconscious brain processes. Just as there is no single type of consciousness, there is surely no single type of unconsciousness. It is unlikely that either conscious or unconscious brain processes reflect singular types of neural mechanisms. I suspect we can all agree that conscious neural processes are constructed from unconscious neural components. Each functioning nerve cell is probably deeply unconscious. Networks of neurons together, working in behavior supportive environments, are essential to generate the full richness of consciousness. Based on what we already know about various brain functions, probably those that generate emotional feelings are quite different from those that generate cognitive perceptions (Liotti & Panksepp, 2004; Panksepp, 2003a). No one knows where the dividing line between affective and cognitive processes, and conscious and unconscious processes, should be drawn, but there are several credible ways to differentiate them (Ciompi & Panksepp, 2004).

Some, including myself, believe it is a category error to call affect, which probably reflects a widespread network function of the brain, unconscious either in animals or humans. Even though many components in the relevant circuits cannot sustain consciousness on their own, it is currently important to specify the key components (e.g., specific neuroanatomies and neurochemistries) that are necessary for emergence of specific types of affective feelings (Panksepp & Harro, 2004) so that one can gradually aspire to clarify the comprehensive system properties (Edelman, 2004). We may also need to consider that what was a consciously experienced process at one evolutionary or developmental stage may become peri-conscious at a later evolutionary or maturational stage (in the case of emotions, perhaps becoming dynamically unconscious in humans, as in repression; Lambie & Baker, 2003). For instance, adults may be generally less emotional than children, because epigenetic emergence of a sophisticated cortico-cognitive apparatus can regulate and dampen the intensity of core emotional experiences (Liotti & Panksepp, 2004). Also, as behavior becomes automatized, it tends to become unconscious unless it is affectively engaging.

There are many reasons emotional feelings within modern consciousness studies have been demoted to second class status. Despite great advances in brain imaging (Murphy et al., 2003; Phan et al., 2002), many of these imaging studies tell us more about emotional information processing than emotional feelings. Affective processes are more difficult to visualize, in any neuroscience detail, using current brain imaging approaches (but see Damasio et al., 2000).

Of course, emotions without cognitions are rather coarse tools of mind. It is when our primary-process emotional feelings get embedded in our secondary and tertiary cognitive processes, that new levels of complexity emerge that have yet to be illuminated by animal brain research. Many of our ''cognitive'' decisions are regulated by a deep self-awareness of the potential affective consequences of our actions. When we actively try to rein in our passions, our restraint may itself be motivated by affect. For instance, our tendency to hold off smacking someone when we are angry is surely partly premised on our cognitive ability to avoid the negative affect that could arise from being socially excluded from future activities, being attacked in return or legally charged with assault. The reason we may avoid eating the whole half-gallon of just opened ice cream is because we know it can make us feel ill or perhaps promote feelings of guilt, shame, and embarrassment at putting ourselves at risk of becoming overweight and another coronary statistic. And, of course, many of us have just been appalled by a presidential campaign in the USA that used primal fear and socially constructed shame as political tactics. Likewise, the manipulation of emotions for economic gain has become a routine part of our cultural landscape.

Such cognitive complexities may make the basic animal research even more important in our attempts to decipher the underlying nature of affect that governs so much of our cognitive lives. It is doubtful that other animals deliberate on their feelings in ways that we humans do. However, we should not underestimate the mental skills that animals do have. For instance, re-valuation of reward in one situation translates to changing behavioral tendencies in another situation that uses the same rewards (e.g., Dickinson & Balleine, 2000; Krieckhaus, 1970). These conditioning and generalization effects probably require higher cortical functions that may not be essential for the generation of raw affective states.

However, even in animals there will be an enormous number of cognitively mediated affective effects to be documented. For instance, certain drugs with mild arousal properties can promote or inhibit social tendencies, depending on whether the animals have previously experienced the drugs in affectively positive or negative environmental contexts (Bekkedal, Rossi III, & Panksepp, 1999). Clearly, there is a mountain of interesting work to be done if we take affective consciousness seriously in the animals we study.

With clever experiments we can presently determine where in the brain certain types of emotion–cognition interaction occur (LeDoux, 2002). However, I suspect that a cross-species understanding of primary-process affective consciousness is much easier to achieve at the present time (e.g., through, for instance, CPP experiments with various drugs and ESB administered at various levels of the neuroaxis) than an equally sophisticated understanding of cognitive consciousness. Indeed, from an evolutionary perspective, secondary and tertiary forms of consciousness may be built integrally on more primary process variants. If so, a sophisticated neural understanding of cognitions may be critically dependent on understanding the nature of affect. If affect (i.e., felt biological values) came first onto the consciousness scene, one could even envision neural scenarios whereby cognitive-perceptual *qualia* remain critically dependent on affective *equalia* (Panksepp, 1998b).

14. How is affect created in the brain? Levels of control in emotional/affective processing along the neuroaxis

Obviously, the mind, just like the brain, is a multilayered system that works in hierarchical bottom-up and recursive top-down ways. There are pre-ordained reflexive emotional responses very low in the brain that are, in and of themselves, deeply unconscious (e.g., startle reflex). However, there are many reasons to believe a solid neural foundation for affective consciousness was laid down in emotion-coordinating systems situated a little further up in the brainstem, in areas such as the PAG of the midbrain (Panksepp, 1998a, 1998b; Watt, 2000). At such low levels of the brain, the concept of "cognition" would have to be stretched to its limits to make much sense. Still, many scholars of consciousness do not consider the likelihood of any kind of consciousness being elaborated at such low levels of the neuroaxis. The existence of *blindsight*, mediated by superior collicular systems of the midbrain tectum, has primed investigators to reject any form of consciousness existing below the neocortex. They might pause to consider the affective richness of human infants and children, even those with massive higher cerebral damage (Shewmon, Holmes, & Byrne, 1999). Damage like this typically produces unconsciousness in adults, leading to a persistent vegetative state (Watt & Pincus, 2004).

Because of the long-standing bias, most views of affect assume that some type of "readout" of unconscious emotional information into higher regions of the brain is the way *all* forms of consciousness must work. For instance, LeDoux (1996, 2002), who has extensively analyzed the synaptic mechanisms of classical conditioning of fear responses within the amygdala and written popular books on emotions and learning, has consistently expressed skepticism over views like my own that argue for the existence of emotional feelings in other mammals. He believes animals do not have affective experiences and suggests that such feelings arise in humans from higher working memory mechanisms concentrated in dorsolateral prefrontal cortical tissues. Rolls (1999), who has done wonderful work in animals and humans on how brain areas respond to pleasant and unpleasant gustatory qualities, has advanced the position that conscious experience requires linguistic re-symbolization of behavioral states. If so, the non-speaking animals would not be expected to have internal subjective experiences, which from my point of view would have been a puzzling way for brain–mind evolution to have proceeded. Damasio (1999, 2003a, 2003b) has championed a multi-tiered affectively embodied view of mind, with which I largely agree. However, he has typically situated our capacity for emotional feelings quite high in somatosensory body representation areas of the cerebral cortex, a view that seems to me flawed, at least for *emotional* feelings (Panksepp, 2003d).

Such neocortical views of affect lead to conceptual conundrums that remain empirically unresolved: what is it about those higher systems that allow translation of subcortical neuronal information into an emotional feeling? The only general possibility is that affective feelings represent a re-symbolization of more primary-process brain activities. Not only is there no good evidence for this, but it promotes an unparsimonious neuro-dualistic view of emotional feelings. In other words, it leaves most other mammals outside the circle of affect. Such "readout" views also tend to make affect a mere information-processing function of the brain, similar to hearing and vision, as opposed to a *state* control function (for discussion of distinctions, see Panksepp, 2003a, 2003e).

At present, the evidence is most consistent with the conclusion that our core *emotional* feelings (e.g., fear, anger, joy, and various forms of distress), motivational experiences (e.g., hunger and thirst), and sensory affects (pain, taste, temperature, etc.) reflect activities of massive subcortical networks that establish rather global states within primitive body representations that exist below the neocortex (Panksepp, 1982, 1998a; for additional recent summaries, see Sewards & Sewards, 2000, 2003). This is not to suggest that there are no relevant cortical influences. Obviously there are, ranging from how cognitions precipitate emotional states, and emotional states channel and energize emotion–congruent cognitive activities (Ciompi & Panksepp, 2004). Also, certain *sensory affects*, such as taste and disgust, clearly have important loci of control in mesocortical regions of the insula. However, there is little to suggest that neocortical functions create *emotional* feelings.

The dual-aspect monism perspective I prefer leads to the parsimonious premise that raw (unconditional) emotional feelings require no "readout" by a higher cognitive apparatus. They largely reflect the neurodynamics of emotional operating systems and associated brain mechanisms in action (Fig. 1). This of course leaves open the mystery of how neurodynamics actually create experienced emotional feelings, but there is abundant complexity in the massive, longitudinally arranged core emotional systems to provide abundant hypotheses (Panksepp, 1982, 1998b; Panksepp & Harro, 2004). For instance, emotional feelings may arise from various poorly understood interactions of core emotional command circuits with primordial somatic and visceral self-representation systems situated deep in midline areas of the brain (Panksepp, 1998b) reaching the very rostral pole of the upper brainstem (i.e., the septal area; see Sheehan, Chambrs, & Russell, 2004). In this view, affective states are critically linked to the dynamics of the instinctual emotional action apparatus, which can be regulated, but not created, by higher cortico-cognitive activities. This points to various concrete neural processes, which are essential for raw feeling but certainly not sufficient for the fully cognitivized spectrum of emotional experiences.

Obviously, the rest of the brain and body cannot be left out of the equation, for the full emotional feeling state ramifies throughout the organism. It includes many hormonal controls (e.g., Van Honk et al., 2004; Viau, 2002). However, the specification of key brain systems points investigators toward new and potentially productive neurodynamics inquiries (Freeman, 2001, 2003a, 2003b; Lewis, 2005; Panksepp, 2000b, 2000c). The neuro-psycho-behavioral affective neuroscience triangulation strategy provides a straightforward empirical approach to the study of the basic organization of human emotional feelings. It also readily allows sensory-based learning-theories of behavioral neuroscience to link up with the basic evolutionary tools that organisms possess as genetically based birthrights. Thus, the increasing interest in affective processes among human investigators (Lambie & Marcel, 2002; MacDonald & Leary, 2005; Russell, 2003) must also lead to increasing interest as to how such psychological constructs are instantiated in brain activities. Very briefly, let me sketch how the various affective states may be created by neurodynamics.

Emotional feelings may largely reflect the brain activities that control spontaneous emotional action tendencies. Although the motor system has typically been conceptualized as an unconscious output system of the brain, this disregards the evolutionarily dictated action systems that generate emotional behaviors, and there is a great deal of data to suggest that those systems do have a raw-feeling aspect when they are aroused (Panksepp, 2000b). Even though this view does not neglect the likelihood that many sensory and perceptual inputs, from below and above, regulate the intensity of these dynamics, it places a motor-action homunculus at the center of emotional life rather than any sensory homunculus. This shift of emphasis (toward "motor/action coordinates" in generating consciousness) helps solve a variety of troublesome philosophical problems (e.g., the infinite regress of sensory-based "observers").

Sensory affects may reflect how various brain neurochemistries regulate internal homeostatic affects (e.g., hunger, thirst, thermal, and hormonal imbalances). Those that bring those neural imbalances back toward homeostatic equilibrium are perceived as pleasant, and those that cause deviations from bodily homeostasis are perceived as unpleasant (Cabanac, 1992). Much of the raw affect in these systems is subcortically mediated (e.g., urges to defecate and micturate), even though ancient limbic cortices, most prominently the insula, are essential for many exteroceptively as well as interoceptively induced sensory affects (Augustine, 1996; Craig, 2003a, 2003b).

Background bodily feelings and moods may reflect the overall status of the various neurochemistries of affects (Panksepp, 1993) which interact with primitive self-representations (Panksepp, 1998b). All of these vast chemistries, many of them neuropeptidergic (Panksepp & Harro, 2004), are under genetic controls which are responsive to environmental events, especially those that are emotionally and homeostatically challenging (e.g., see Panksepp et al., 2004a for our most recent efforts in this area). Let us consider one complex example: depression. Even though there are abundant neurochemical theories, the one straight forward possibility is that many forms of depression simply reflect chronic depletion of various prominent brain chemistries that can mediate positive affect. Presently, the most prominent molecules in that arena are dopamine and endogenous opioids. I would predict that one common form of depression, perhaps that arising from social loss, is characterized by low endogenous opioid, and perhaps oxytocin, synthesis or utilization.

The bottom line in all of these views may be that a primordial body representation in the brain can be disrupted by emotional and homeostatic imbalances, and that pleasure is the capacity of various neurochemistries to reduce those deviations in the neurosymbolic, virtual representations of the body. I have taken the position that this virtual body image is concentrated in dorsal mesencephalic regions of the brain, with the visceral components concentrated in the PAG and somatic ones in surrounding tectal areas, which are strongly connected with a variety of paramedian brain systems reaching up to the anterior cingulate and medial frontal cortices (Panksepp, 1998a, 1998b).

Many higher regions of the human brain are specialized for the epigenetic emergence of emotion–cognition interactions and those brain functions are more readily studied in humans than animals (Berridge, 2003). The evidence that limbic cortices such as anterior cingulate, medial frontal, and insular are essential for many emotional states, including many affective feelings (MacLean, 1990), is now supported by a mass of brain imaging evidence (Murphy et al., 2003; Phan et al., 2002). However, it is proposed that such higher brain regions cannot support affective states on their own. They need various brainstem functions, especially an intact PAG. Even widely touted emotion regulating areas such as the amygdala may be more important in linking external events to emotional arousal, than for actually generating affective states. Bilateral amygdala damage, indeed quite extensive higher limbic damage, does not robustly diminish internally experienced emotional feelings in humans (Adolphs, Tranel, & Damasio, 2003; Zald, 2003), even though the ability of such individuals to decode static fearful and angry faces, and other external signs of such emotions, is severely compromised. The many well-established laterality effects (i.e., right brain being more negativistic than the left) may also be critically dependent on subcortical functions, and the hemispheric difference could reflect many psychological aspects beside affect such as motivational styles (e.g., Harmon-Jones, 2003). Indeed, when the neocortical apparatus is removed completely soon after birth, rats grow up with seemingly normal basic emotions and motivations (Panksepp et al., 1994), even though they certainly are not very smart. Also, as already noted, human children with higher brain damage that would clearly produce unambiguous persistent vegetative states in adults do exhibit rich affective lives as long as they have been reared in loving environments (Shewmon et al., 1999).

In sum, emotional feelings appear to reflect ancient brain functions. The apparent psychic power of such functions appears to diminish with higher cortico-cognitive maturation, especially among the most over-intellectualized and autistic members of our species. Perhaps for many individuals emotional arousal becomes part of their dynamic unconscious, as they come to rely largely on their cognitive resources.

15. Five reasons to take animal consciousness seriously

In sum, there are at least five substantive reasons to cultivate the study of affective consciousness in animal models more intensively than it has in the past: (1) the triangulation affective neuro-psycho-behavioral strategy may be an effective way to decode how affect is generated in mammalian brains, (2) such work may reveal the very foundations of human consciousness, (3) the study of affect may be essential for coherent progress in understanding the nature of many psychiatric disorders, (4) the study of emotional affects may also help close the explanatory gap between objective observations of brain functions and the quality of at least one category of experience (i.e., the global neurodynamics of emotional systems in action may be isomorphic with the felt dynamics of basic emotional feelings), (5) last, but not least, an understanding of affect in the lives of other animals may be critical for making informed choices on how we ethically treat other creatures (Broom, 2001; McMillan, 2005). By failing to study such issues, we may continue to deny animals the respect they deserve. Of course, pursuit of this kind of knowledge is, by necessity, a highly theoretical enterprise, with many potential errors to be worked through.

A stumbling block to future scientific progress in mind sciences interested in the fundamental nature of consciousness is the modest amount of ongoing work on brain-affect linkages in animal models where the neural foundations of emotional experiences can be studied in some detail. This state of affairs persists because the very existence of affective experience in animals remains a contentious issue. Some experts, to this day, are willing to claim that most other mammals do not even experience pain. One prominent investigator recently asserted that anatomical "evidence indicates that they cannot, because the phylogenetically new pathway that conveys primary homeostatic afferent activity direct to thalamocortical levels in primates… is either rudimentary or absent in non-primates" (Craig, 2003b, p. 501). Although anatomical evidence surely suggests that many other species do not have the sophisticated, high-order forms of reflective self-awareness common in humans, such views ignore vast amounts of behavioral data on the role of many primitive brain systems in the generation of pain (Panksepp, 2005a, 2005b) and raw emotional experiences (Panksepp, 1998a). In fact, the behavioral data are quite compelling that all mammals experience pain and that, just as in humans, the anterior cingulate participates in the genesis of those experiences (Johansen, Fields, & Manning, 2001). The many other basic emotions discussed here also rely on specific brain circuits to concurrently organize the enactive and the affective aspects of emotional life. It is no wonder that animals like to self-pace their sexual activities (Martinez & Paredes, 2001) and the many other sensorially centered affective experiences (Berridge, 2000, 2003).

I suspect the extended behavioral neuroscience community would readily accept affect as a major topic of study if funding policies changed. Right now it remains unlikely that grant applications seeking explicitly to clarify affective processes through animal brain research could get funded. I, as well as many colleagues, know this from frustrating personal experiences. It is time to encourage such inquiries, but for now, one has to pursue such scientific pursuits on their own dime. Scientific administrators are encouraged to change such policies.

Let me close this section with an anecdote. When I first presented our work on rat "laughter" (as summarized in Panksepp & Burgdorf, 2003) at a NIMH symposium in 1998 (entitled "It's Not Just Context") aimed at encouraging more emotion research, there was not a single question from a seemingly stony-faced audience of neurobehaviorists. One of the organizers of the meeting took me aside after my session and essentially said, "This research is wonderful. It could be used as a simplified model for positive emotions the way classical conditioning of freezing and startle potentiation is used to study fear... but would you please call it something other than laughter." I replied, "Yes I could, but then I might be lying, for we do believe this response may be the ancestral source of infantile laughter." It is a pity when dedicated scholars are discouraged from considering the affective dimensions of brain functions in their study of animal behavior and that they are routinely and strongly encouraged to restrict their discussions to mere behavioral descriptions and learning theory terminologies.

I have had more than my share of difficulty publishing our seminal work on separation-distress, rambunctiously joyful social activities, and most recently rat tickle-induced chirping, because we used words such as "crying," "playing," and "laughter." Of course, the problem is how do we agree to speak about things that we cannot clearly see and define. Meanings of affective terms must remain rather vague until we know much more about the brain complexities that generate these brain states (Fig. 1). In any event, more of my papers have been rejected for publication because of what I said about the nature of animal affect than what I failed to do in my experiments or data analyses (for a recent explicit example, see Panksepp & Burgdorf, 1999).

Thus, I would share a modest proposal: to help encourage more flexible thinking about the varieties of animal consciousness, premier brain–behavior journals might encourage dual discussion sections in which investigators are encouraged not to only discuss their behavioral findings but also the psychological implications of their work. One discussion would be devoted to the traditional focus on just the positivistic facts without any mention of psychological concepts. A second segment would allow investigators to theorize (or as many prefer to phrase it: "to speculate") how their findings may relate to experiential aspects of mental life. For instance, instead of just talking about amounts of food intake, investigators would be encouraged to talk about feelings of hunger and satiety in animals. Instead of just measuring sexual behaviors (e.g., numbers of intromissions and lordosis responses) some talk about sexual feelings that might be permitted. Instead of just discussing aggressive attack behaviors, investigators may also be permitted to focus on anger. And isn't it an intellectual tragedy that we have so little basic animal brain research on the nature of anger—such a pervasive problem in so many individual lives as well as our society as a whole (e.g., Panksepp & Zellner, 2004)?

Let me share one specific example, related to a study already noted, where administration of CRF into the BNST (an area rich with separation distress circuitry) reduces food intake that can be reversed with concurrent opioid administration to the same brain sites (i.e., Ciccocioppo et al., 2003). From a psychological point of view, the CRF induced reduction in feeding may have little to do with the good feelings of satiety, but rather the evocation of negative affective feeling, perhaps those resembling separation distress, which is known to reduce feeding behavior. Thus, the opioids may simply have been alleviating the separation type of distress caused by the CRF. An enormous number of behavior-only analysis could be enriched substantially through the more flexible use of emotional/affective terms. Few who study behavior indulge in this practice, even though this more flexible psychological language could easily lead to a variety of novel predictions, especially at the human level, thereby promoting interdisciplinary integration of all relevant levels of analysis.

If we want to make progress on subtle mental issues that may actually transpire in the brains of animals, we have to liberalize our attitudes in this arena. Why should we continue to unnecessarily censor our thinking about potentially relevant issues? I suspect that once we cultivate such new ways of looking at our findings, from the perspective that there are internal affective realities in all mammalian brains, we will eventually develop intellectual skills to do research in new and ever more productive ways. And in doing that, we will open up the field once more to subtle but important mind issues that have long been neglected for outdated historical reasons (Panksepp, 1990a; Rollin, 1998). This will be a challenge for many members of our species, since some have been all too willing to marginalize the emotions of fellow humans. Only a century and a half ago, slaves in America were envisioned as brutes—as lower animals—who had no feelings (Thomas, 1996).

16. Coda

When we observe certain emotional activities in animals that resemble our own, are we justified in inferring that they also have feelings? If the pat answer is no, as it has long been, then the problem of animal consciousness is probably insoluble. Those who are committed to such conservative views will probably assert that the strategy advanced here is little more than a scientifically cultivated opinion. But if we can generate new animal behavior predictions and/or make credible predictions about human emotions, it is much more than that. It is an evolutionary window into the nature of our own minds and thereby of other animals as well. In such neuro-psycho-ethological research endeavors, we can also keep our behavioral observations separate from the inferences we draw from them. Accordingly, the behavioral observations will be of undiminished value even if the psychological hypotheses are not.

If we are going to take the study of affect in animals seriously, we have three options: (i) to share our impressions about what animals must be feeling, (ii) to try to experimentally analyze the first-order phenomenology that accompanies unconditioned emotional behaviors (Panksepp, 1998a), or (iii) to study second-order awareness as indexed by learned (conditioned) behaviors of various kinds, especially those that indicate animals are sensitive to incentive re-evaluations (Dickinson & Balleine, 2000). The first approach, interesting and important as it is, is not typically deemed to be scientifically compelling. The other two strategies are both, by necessity, indirect approaches. There is no mindscope, and may never be, that can directly monitor any psychological process. This problem, not that different from the one physicists were confronted by a hundred years ago, should lead us to respect the importance of substantive theoretical inference and the power of the resulting predictions. Physicists were forced to recognize that certain aspects of nature must be approached from seeming incommensurate but complementary perspectives (e.g., *particle* and *wave* views of certain sub-atomic phenomena). For now, neuroscientists can study emotional behaviors and affective state dynamics in comparable ways. Through the gradual refinement of methods and procedures, we can achieve substantive understanding, one empirical step at a time.

In a long historical tradition (e.g., Darwin, 1871, 1872/1998; Hess, 1957; MacLean, 1990), my position is that the weight of evidence indicates that human emotional feelings are critically dependent on primitive neural systems of the mammalian brain that coordinate instinctual actions, and that these systems are quite comparably represented in the brains of all mammals. Basic emotions may need to be defined in terms of such neural system attributes (Fig. 1). Although we should not mistake these critical neural parts—the natural or *practical* kinds (Zachar & Bartlett, 2001)—for the entire emotional response (Bennett & Hacker, 2003), there will be brain areas, such as the PAG, that are evolutionary epicenters for affective "gravity" around which many other complexities revolve (Panksepp, 1998a, 1998b; Watt, 2000).

Our cognitive abilities are channeled dramatically during emotional arousal. The basic emotions represent essential tools for living and learning, and the higher brain systems with which they are intimately related provide the perceptual and learned guidance that organisms must have to fulfill their primitive urges (Davidson, Scherer, & Goldsmith, 2003; Manstead, Fridja, & Fisher, 2004). From a behavioral perspective, investigators are accustomed to looking at their organisms from the outside in. From an evolutionary perspective, it is as wise to also envision organisms from the inside out—to try to fathom the foundations from which the more recent, and cognitively more apparent, psychological complexities emerge (Panksepp & Panksepp, 2000; Panksepp, Moskal, et al., 2002).

An emotion-systems view of the brain can also generate new perspectives on affective issues that are hard to study in animals, such as the nature of altruism and empathy, that are currently hot topics in human brain imaging (Singer et al., 2004). There are many ways to conceptualize how such processes emerge in the brain, but presumably such affective tendencies could not exist without basic emotional circuits interacting with higher cognitive structures. One way to envision such processes is through the developmental emergence of mirror-neuron systems that are attuned to emotional signals (Gallese, 2003). Another is the possibility that we have higher regions of the brain, perhaps situated more in the emotionally sensitive right hemisphere, that have special skills in thinking non-verbally about emotional situations. Another factor, perhaps compatible with aforementioned dynamics, is that the basic emotional systems can establish perceptually induced affective resonances between nearby animals. As we consider the potential dynamics of the PANIC/Separation distress system, we can envision how helping behaviors might emerge. With regard to such low-level brain interactions, several key questions still need to be addressed empirically: "(1) Does the activation of distress circuits in young and relatively helpless animals generate resonant evoked activity in the same circuits of nearby adults who could provide care? (2) If such perceptually induced resonance does exist, is the evoked activity especially strong between bonded individuals? (3) Does such brain activity arouse caregiving behaviors in adults?" (Panksepp, 1989/2004). In considering such issues, we must remember that core emotional systems have low-level, subcortical perceptual inputs as well as high-level cortico-cognitive ones (Fig. 1). It is as possible that our lower level, sensory-induced resonances of emotional systems contribute substantially to the affective substrates of empathy.

Also, the core emotional operating systems may be essential in the construction of long-term cognitive and temperamental structures as they interact with the perceptual processes of higher regions of the brain. It could be argued that much of human personality is based on the emotional strengths and weaknesses of individuals. Because of such considerations, we recently constructed an *Affective Neuroscience Personality Scale* (see www.anps.de) to evaluate such core emotional processes in humans (Davis, Panksepp, & Normansell, 2003) and we are pursuing genetic linkages (Reuter et al., 2004). This kind of knowledge can also suggest new ways of solving long-standing philosophical quandaries (e.g., DeLancey, 2002; Griffiths, 1997).

The fact that these systems were evolutionarily designed to be centers of gravity for the emotional concerns of animals also provides a clear rationale for addressing animal welfare issues (Broom, 2001; Dawkins, 1980; McMillan 2000, 2005; Thomas, 1996). Just as with Pascal's famous wager concerning the existence of a God, we are surely less likely to partake in ethical travesties if we provisionally accept the mind-affirming position that animals do have emotional feelings rather than that they do not. And to understand the nature of animal feelings, as well as our own, we have to pursue neuroscientific work with a sense of cross-species sensitivity that was not a striking feature of 20th century behavioral research.

I encourage all concerned scientists to carefully consider such difficult issues. By empirically entertaining such neuro-ontological options, we need not grant our lab animal any form of tertiary consciousness (e.g., awareness of awareness) that humans can have in such splendid abundance. The existence of secondary-awareness—low-level imagery based cognitive consciousness—remains an important, empirically approachable issue, perhaps even in other animals, despite continuing skepticism (Wynne, 2004). At the very least, I think we must be gracious enough to grant other mammals primary-process consciousness—first-order phenomenological experiences that bring them back into the "circle of affect"—as most thinking people do both graciously and spontaneously as they interact with many other creatures. As Robert Burns related in his eight verse poem *To a Mouse* after he overturned a nest while plowing in November 1785:

Verse 2

I'm truly sorry man's dominion
Has broken Nature's social union
An' justifies that ill opinion
Which makes thee startle
At me, thy poor, earth-born companion
An' fellow mortal!

Verse 8
Still thou art blest, compar'd wi' me!
The present only toucheth thee
But och! I backward cast my e'e
On prospects drear
An' forward, tho' I canna see
I guess an' fear

Although animals may not have the neocortical brain power to look forward and backward in time the way we do, they apparently live the moments of their lives as vibrantly full of simple affects, as we live with feelings having more cognitive depth. Perhaps, just perhaps, our studies of their emotional and other affective systems will shed profound light on the nature of our own feelings. Since our research approaches and attitudes do have societal consequences, acceptance of such a stance can only increase the recognition of our scientific integrity in the eyes of the extended community of interested human beings. Although some of our more conservative scientific colleagues may call us sinners or dreamers, it is more likely they are simply impeding progress on topics of ultimate concern. My own commitment to good scientific methodology, and reasoned argument, remains complete, even as I seek to open doors of inquiry to some of the more profound questions that still face neuroscience. As more investigators commit themselves to new levels of critically open thinking about such issues, we may be making a substantial positive investment in the long-term intellectual health of our field. By so doing, we can again be on the same page as most other reasonable people who think about such things. It is long past time for many of us, working in behavioral neuroscience labs, to deal more forthrightly with the potential complexities of neuro-mental life that exists in the brains and bodies of the animals with whom we are still fortunate enough to share the earth.

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