

Hard Heads and Open Minds: A Reply to Panksepp (2003)

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In the authors' original article (M. S. Blumberg & G. Sokoloff, 2001), they provided evidence that the ultrasonic vocalizations of infant rats are acoustic by-products of a physiological maneuver. In J. Panksepp's (2003) comment, he sidestepped the authors' empirical findings and focused on his concern that their perspective might prevent progress toward his ultimate goal of understanding the neural substrates of emotion in mammals. In this reply, the authors question the reliability of J. Panksepp's strategy for studying emotion on the basis that anthropomorphism has yet to prove itself an effective research tool. In addition, the authors believe that J. Panksepp's anthropomorphic–zoomorphic strategy defeats the goal of building a comparative psychobiology of behavior and cognition that does not reify false distinctions between humans and other animals.

Animals produce a dizzying array of sounds. Animals sneeze, cough, belch, wheeze, moan, sigh, whine, whimper, scream, screech, growl, bark, howl, yowl, wail, chirp, and sing. Humans talk. Some animals cry.

The causes and functions of these sounds are as diverse as the sounds themselves. Some sounds, like sneezes and coughs, are merely acoustic by-products of physiological processes; such inadvertent sounds may provide information about the physiological state of an animal, but they do not appear to have communicatory functions per se. Other animal sounds that do have clear communicatory functions, like birdsong and human speech, are relatively independent of the physiological state of the animal and, moreover, have become designed through evolutionary pressures to maximize their communicatory effectiveness. Although researchers typically attribute such communicatory design to senders, the vital role of receivers in shaping features of signals has become increasingly appreciated (Guilford & Dawkins, 1991). For example, in the domain of visual signaling, although it might be said that moths use eyespots on their wings to deter predation by birds, it was selective predation by birds that selected for the very eyespots that birds find aversive. Thus, it may be that all communicatory systems can trace their origins to inadvertent signaling by senders, selective behavior by receivers, and persistent bidirectional interactions among senders and receivers that, over time, result in highly complex and even elegant communicatory relationships, both within and across species (Blumberg & Alberts, 1997).

Another dimension of animal signaling that has garnered increasing interest among biopsychologists is that of affect. Al-

though there is no a priori reason to believe that communicatory behaviors should be motivated by emotion any more than other behaviors such as walking, eating, drinking, or writing, there are several communicatory behaviors that, for some investigators, require an affective explanation. One such behavior is crying, including the cries emitted by infant mammals during maternal separation. In our article published last year in *Psychological Review* (Blumberg & Sokoloff, 2001), we specifically addressed the ultrasonic distress vocalizations of infant rats, one of the most well-studied putative animal models of human separation anxiety. Our focus, however, was neither on the emotional bases of the vocalization nor on the communicatory effects of the vocalization (e.g., stimulating maternal retrieval). Rather, we focused our review on evidence that bears on the hypothesis that the vocalization is, like a sneeze or a cough, an acoustic by-product of a maneuver that serves a physiological function. Specifically, this hypothesis states that perturbations of the cardiovascular system that reduce the return of venous blood to the heart elicit a maneuver (i.e., the abdominal compression reaction, or ACR) that serves to enhance venous return. This reflexive response in turn results in the production of sound. The concordance between physiological cause and physiological consequence is the cornerstone of our contention that the vocalization is an acoustic by-product and not primarily an act of communication. That the mother responds appropriately to the vocalization by retrieving her pup to the nest does not, we argued, require us to situate communicatory intent inside the mind of the pup. With regard to the affective state of pups as they vocalize, our hypothesis was decidedly and intentionally mute.

In his comment, Panksepp (2003) has produced a wide-ranging and often sharp critique of our approach and the "broader theoretical agenda" (p. 376) in which that approach, as he sees it, is embedded. Because of Panksepp's self-proclaimed "unabashed" interest in "understanding the basic emotions of the human brain–mind" (p. 379), he has presented our work largely within a context that reflects his, rather than our, interests. Furthermore, Panksepp presents a picture of psychologists as fearful of anthropomorphic methods, methods that he believes can now be resurrected without the risks that originally led to their banishment from scientific

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Preparation of this article was supported by National Institute of Mental Health Grant MH50701 and National Institute of Child Health and Human Development Grant HD38708 to Mark S. Blumberg.

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psychology. Ironically, he seems unaware of the hostility that has met the idea that infant rat ultrasonic vocalizations are perhaps not cries of emotional distress. If Panksepp's depiction of the proclivities of psychologists with regard to emotional behaviors among animals is correct, then our approach should have meshed seamlessly with this supposed antiaffect zeitgeist. On the basis of numerous experiences, we can report that this simply has not been the case.

Beginning in the late 1980s, interest in the infant rat's vocalization had moved beyond its modulation by sensory stimuli (Hofer & Shair, 1978, 1980) to its neurochemical basis (Carden, Davachi, & Hofer, 1994; Kehoe & Blass, 1986; Kehoe & Harris, 1989; Vivian & Miczek, 1991; Winslow & Insel, 1991a, 1991b). The predominant paradigm for these studies was, and continues to be, a method in which pups are extracted from the nest and placed in a novel environment for 3–6 min. In experiments in which a pup is pretreated with a drug, that drug's ability to modulate ultrasound production during the isolation test is considered evidence of that drug's involvement in the distress–anxiety system. It cannot be overemphasized, however, that this paradigm is used to examine the ability of drugs to modulate ultrasound production, not evoke it.

As we discussed in the original article, although it has been known for many years that temperature is one of the primary controlling parameters of ultrasound production by pups (Allin & Banks, 1971; Okon, 1971), investigators using the transfer paradigm test their subjects at any of a number of air temperatures. This inattention to methodological detail reflects the prevailing attitude that the proximate mechanisms responsible for emission of the vocalization are not to be found in such mundane issues as temperature or, for that matter, any other physiological parameter. For these investigators, temperature is simply one sign to the pup that it is no longer in the nest. Thus, even today, the implicit assumption among pup-vocalization researchers is that this vocalization serves a communicatory function and is mediated, in a causal sense, by the negative affect triggered by separation from the home nest.

The first challenge to this prevailing view entailed a reconsideration of the causal role played by temperature in emission of the vocalization as well as the adoption of a testing paradigm that allowed for greater experimental control than the ubiquitous transfer paradigm (Blumberg & Alberts, 1990). One interesting finding arising from this early work was that starvation and hypoxia, two highly stressful conditions, do not evoke ultrasound production, thus calling into question a simple distress hypothesis (Blumberg & Alberts, 1991a). Subsequently, the thermoregulatory capabilities of infant rats were investigated more thoroughly in a series of studies in which the behavioral and physiological responses of pups were examined during what we refer to as *moderate* and *extreme* cold exposure (see Blumberg & Sokoloff, 1998, for a review). During moderate cooling, pups activate brown adipose tissue (BAT) thermogenesis, increase oxygen consumption and respiratory rate, maintain cardiac rate, remain asleep, and do not vocalize. In contrast, during extreme cooling, BAT thermogenesis no longer compensates for heat loss, resulting in hypothermia, decreased cardiac rate, increased blood viscosity, behavioral arousal, and the emission of high rates of ultrasound production. These and related findings helped us to discern the factors that lead infants to emit ultrasonic vocalizations. It should also be clear,

however, that our investigation of this vocalization was only a part of a larger research program aimed at understanding basic biobehavioral processes in infants during thermal challenge.

It may be that our research program does reflect a bias on our part for preferring by-product hypotheses for these particular rat vocalizations. But given the empirical fruitfulness of our approach over the last decade and the recent insights generated by the ACR hypothesis, there seems little for which to apologize. We are disappointed, then, that Panksepp (2003) has chosen to look past these successes and has focused instead on what he sees as a "broader theoretical agenda" (p. 376). As Panksepp pointed out, Mark S. Blumberg has promoted similar by-product hypotheses for the long-duration 22-kHz vocalization of adult rats (Blumberg & Alberts, 1991b) as well as for the short-duration 50–70-kHz chirp vocalizations of adult rats (Blumberg, 1992). Much more work needs to be done to clarify the physiological and biomechanical causes of these vocalizations, and they may very well turn out to be emitted independently of the physiological state of the animal. If so, that would be fine with us. After all, despite Panksepp's suspicions, our goal here is not to peripheralize all animal vocalizations but merely to ask reasonable and testable questions about the physiological and behavioral contexts in which these sounds are emitted.

Although Panksepp (2003) stated repeatedly, and emphatically, that he does not consider the infant rat to be a good model of separation distress, he appeared to be sincerely disappointed that our work has forced a reconsideration of the causal antecedents of infant rat ultrasound production. Specifically, he stated

Unfortunately [italics added] . . . it presently does seem likely that infant rats' [ultrasonic vocalizations] reflect a generalized form of distress rather than specific socioemotional distress based on the severance of discreet social bonds. As Blumberg and Sokoloff (2001) emphasized, the *worst case scenario* [italics added] is that they largely reflect epiphenomenal by-products of respiratory reflexes. (Panksepp, 2003, p. 379)

It is revealing that he uses such value-laden words and phrases as *unfortunately* and *worst case scenario* to describe the possible conditions under which the infants of one species emit sound. Does Panksepp also feel that it is unfortunate that sneezes and coughs have a physiological, rather than an emotional, foundation? Of the many points raised by Panksepp in his comment, this is one of the crucial ones for revealing the chasm that exists between our and Panksepp's two approaches to the scientific study of animal behavior.

To examine this chasm in detail, we need to step back and look at the twin tenets that undergird Panksepp's (2003) comment. These twin tenets—what he calls *anthropomorphism* and *zoomorphism*, or *A-Z reasoning*—are explicitly defined as follows: "*Anthropomorphism*, in the present scientific context, is the recognition of certain human psychological qualities in other animals, and *zoomorphism* refers to the recognition of psychobehavioral qualities of animals in human nature" (p. 376). Because he notes parenthetically in the next paragraph that "humans, after all, are animals" (p. 377), it is quite clear that Panksepp's twin tenets fail to accomplish what definitions are supposed to accomplish, that is, to clarify. Specifically, if one's aim is to blur the line between human and nonhuman animals, then why promote an explicit form of reasoning that reifies that line? Furthermore, what does Pank-

sepp mean by *psychobehavioral qualities* and *human nature*? Finally, what is the significance of the asymmetry in the two definitions if Panksepp truly considers these two concepts to be “opposite sides of the same coin” (p. 377)?

It is striking that someone who seems committed, as we are, to knocking the human species off its pedestal would write that his work is “unabashedly aimed at understanding the basic emotions of the human brain–mind” (Panksepp, 2003, p. 379) and bemoan the fact that many neuroscientists “continue to devalue the utility of animal models for understanding the foundations of human behavior” (p. 385). Panksepp’s focus on the utility of nonhuman animals as models for understanding humans hardly seems an effective strategy for understanding behavior and cognition in all species—including both their similarities and differences—from a truly comparative perspective; after all, rats, guinea pigs, dogs, elephants, dolphins, whales, giraffes, tigers, and dugongs are not models for humans any more than humans are models for them. Of course, we do acknowledge that thinking in terms of animal models can be useful when carefully applied to specific research problems, but the explosive growth and widespread acceptance of animal model thinking is, in our opinion, devaluing the appreciation of comparative analyses of behavior and cognition for their own sake. Regardless, we cannot help but note the irony of being accused of anthropocentrism by someone whose interest in nonhuman animals rests so clearly on their value as models for humans.

Thus, the A-Z reasoning promoted by Panksepp (2003) actually detracts from the basic methods of comparative psychology, anatomy, and physiology that already exist to guide our research (Butler & Hodos, 1996; Harvey & Pagel, 1991; Wasserman, 1993). Indeed, when Panksepp attempted to visualize A-Z reasoning in his Venn diagram in Figure 1, we are immediately struck by the division between humans and animals as depicted in the diagram and enunciated in the recast definitions of anthropomorphism and zoomorphism. It is also striking how arbitrary the characteristics of humans and animals are in that figure. For example, although animals have “species specific abilities,” humans have “rational choice,” “higher emotional faculties,” and “language.” But why, for example, isn’t language classified as a species specific ability? And what is the difference between basic and higher emotional faculties?

What is our view? We believe that humans are animals—nothing more, nothing less. Because of that simple fact, we should be striving to eliminate from our science any words or phrases that perpetuate the idea that our species is in any way subject to different biological constraints than other animals. One will not find in our writings, as one can in Panksepp’s (2003) comment, any reference to lower and higher species (or even “lower” and “higher” species). One will also not find in our writings any references to “human nature,” “primal sources of human emotions,” “the neuroevolutionary foundations of human nature,” “the essential underbelly of human psychological life,” “the deep animalian underpinnings of human affects and motivations,” “essential aspects of reality,” “a powerful heritable ‘nature’ that guides human destinies” (pp. 378, 383, 384, 385) or any other phrases that appeal to unsubstantiable, essentialistic, and quasi-mystical perspectives of human and nonhuman behavior.

Panksepp (2003) repeatedly criticized modern behavioral neuroscientists for their continued fear of anthropomorphism. But to

dissect Panksepp’s view of anthropomorphism, we must first be clear as to what it is. Anthropomorphism is not, as quoted earlier, “the *recognition* [italics added] of certain human psychological qualities in other animals.” Rather, anthropomorphism is, as stated in Panksepp’s Figure 1, “the *attribution* [italics added] of human traits to animals.” But much more can be said. Kennedy (1992), for example, distinguished between two very different forms of anthropomorphism. First, there is *mock anthropomorphism*, which entails the attribution of human traits to animals as a strategy for generating hypotheses about the function of animal behavior. Second, there is *literal anthropomorphism*, favored by Panksepp, which promotes hypotheses concerning the proximate, material causes of behavior. It is this literal form of anthropomorphism that continues, and should continue, to be spurned by behavioral scientists interested in rigorous, testable, and mechanistic explanations of behavior from a comparative perspective.

The dangers and traps of literal anthropomorphism have been exhaustively detailed and reviewed (Kennedy, 1992). We can see these dangers in Panksepp’s (2003) attempt to describe proximate mechanisms for emotion. For example, he wrote that “there are abundant reasons to posit that evolutionary selection created a series of conserved emotional mechanisms that generate affective states within homologous subcortical regions of all mammalian brains” (p. 379). But what exactly is an *emotional mechanism* (is it analogous to a hunger mechanism?) and how do we distinguish it from the affective state that it generates? If affective states evolved and have a function, then are these states themselves emotional mechanisms that influence behavior? And are the affective states a property of the subcortical regions of the mammalian brain, as implied by Panksepp, or of the brain as a whole? These questions are difficult to answer because Panksepp’s poorly defined concepts are so intimately tied to human experience and their implications are, therefore, so difficult to test objectively.

We see similar problems with Panksepp’s (2003) A-Z strategy for revealing the mechanistic foundations of emotions in humans and other animals. First, our reading of the A-Z strategy is that introspection is used to identify humans’ emotional states during particular contexts. Then, through analogy, the strategy aims to identify contexts in which animals are likely to be experiencing the same emotions as humans are; this is the anthropomorphic link. Finally, if and when the neurobiological substrates of these emotions are identified in animals, we can then argue that those same substrates produce those emotions in humans; this is the zoomorphic link. But is this a real experimental strategy? Does Panksepp provide a single example in which this “new and evolutionarily disciplined” (p. 378) strategy has produced an unambiguous advancement in the understanding of emotion? Despite all the words and argument, it seems that the answer is no.

Confronted with such vague concepts and dubious experimental strategies, we find ourselves in agreement with Kennedy (1992) that “our penchant for anthropomorphic interpretations of animal behavior is a drag on the scientific study of the causal mechanisms of it” (p. 5). Indeed, we believe that our explicit conviction to avoid anthropomorphic interpretations of infant rat vocalizations was a critical factor in our ability to discover so many contextual and physiological features of its emission that had been overlooked by others.

Having already defended ourselves against the charge of anthropocentrism, we must also address Panksepp’s (2003) contention

that there is a “radically behaviorist agenda” (p. 384) that drives our research. This accusation was made, in part, because Mark S. Blumberg coauthored an article in *American Psychologist* that was openly critical of cognitive ethology and its commitment to understanding the “animal mind,” using such anthropomorphic and language-dependent terms as *consciousness*, *beliefs*, and *desires* (Blumberg & Wasserman, 1995). However, neither of us is even remotely sympathetic to radical behaviorism as a modern method for investigating animal behavior and cognition (although we do acknowledge the important role that behaviorism played in prying psychology from the grasp of lax conceptual and methodological approaches that, we fear, Panksepp’s approach will resurrect). Turning to Kennedy (1992) once again, animals “are not the stimulus–response automata which anthropomorphists seem to think are the only alternative that anti-anthropomorphists can offer to animals with minds” (pp. 2–3). It is interesting to note that Panksepp falls into this dichotomous trap, stating that many behaviorists, by which we presume he means to include us, “still wish to view other animals as nonconscious zombies” (p. 386). Whatever Panksepp might mean by this statement, we are confident that it does not legitimately apply to us.

We have been placed in the odd position of replying to a critique that seems to take us to task for potentially being too successful in providing an alternative framework for understanding one of the most well studied of all separation-distress vocalizations. Despite his own reservations about the legitimacy of the infant rat’s vocalization as a legitimate example of such distress, Panksepp (2003), nonetheless, challenges us to account for every reported phenomenon of ultrasound production in the literature within the context of the ACR hypothesis. Given that the ACR hypothesis has been around since only 1996, it would perhaps be most fair to judge our progress in relation to investigators who have been committed to the same perspective and performing experiments that reflect that perspective since the 1970s.

It is still too early for us to provide a comprehensive explanation within our framework for every phenomenon associated with ultrasound production or for every drug that has been shown to modulate its emission. Nonetheless, we can say quite a lot.

First, we have examined a number of aspects of social modulation of ultrasound production, most particularly the conditions under which infants vocalize in the presence of other littermates. Thus, we have found that the presence of huddling littermates merely decreases the temperature required to elicit ultrasound production in a way that is consistent with the thermal benefits of huddling (Blumberg, Efimova, & Alberts, 1992b; Sokoloff, Blumberg, & Adams, 2000). In addition, isolation of pups from littermates under conditions in which cold exposure is prevented does not result in ultrasound production (Blumberg, Efimova, & Alberts, 1992a).

Second, we have provided an explanation within the ACR framework for the paradoxical ability of clonidine, an alpha-1 adrenoceptor agonist that has anxiolytic properties in adults, to evoke ultrasound production even in the absence of cold exposure (Blumberg, Kreber, Sokoloff, & Kent, 2000). Then, also using this framework, we have correctly predicted that other antihypertensive drugs, such as sodium nitroprusside and chlorisondamine, should also be able to evoke ultrasound production on the basis of their cardiovascular effects (Blumberg, Sokoloff, Kirby, Knoot, & Lewis, 2002). Notice that here we are referring to the ability of

these drugs to evoke ultrasound production, not merely to modulate it.

Third, it is curious that the distress hypothesis persists in its traditional form despite numerous counterintuitive findings. For example, as already mentioned, infant rats don’t vocalize when starved or when made hypoxic, even when these insults are coupled with cold exposure (Blumberg & Alberts, 1991a). In addition, infant rats do vocalize while still unconscious during recovery from hypothermia anesthesia (Hofer & Shair, 1992). Also, as we have observed numerous times, pinching the tail of an infant rat does not evoke ultrasonic production, even though such tail-pinched pups do kick and squirm as well as emit audible vocalizations (such audible vocalizations are produced by a different vocal mechanism than ultrasonic vocalizations). If separation-distress systems emerged at least in part from systems that mediate responses to pain, as Panksepp has suggested (Panksepp, 1998), then it is difficult to understand why tail pinching is not capable of evoking ultrasound production.

Despite all of this, there are numerous published reports regarding the modulation of ultrasound production by social cues. For example, Hofer and colleagues have investigated the phenomenon of *maternal potentiation*, which occurs when a pup is isolated, reunited with its mother, and then isolated again, resulting in enhanced rates of vocalization (Hofer, Masmela, Brunelli, & Shair, 1998, 1999). These and similar findings of social modulation are typically cited as evidence of a nonphysiological basis for the vocalization. We believe, however, that some caution is warranted here. Social stimuli can modulate nervous system activity in a variety of conditioned and unconditioned ways, and we simply do not yet know how these stimuli influence autonomic nervous system activity and other possible factors that could modulate rates of ultrasound production. In other words, evidence of social modulation does not necessarily negate the physiological basis of a behavior. For example, the fact that we can stifle a sneeze or a cough under different social contexts does not negate the fundamental physiological functions of these maneuvers. Clearly, this is an area in need of further exploration.

Perhaps the most difficult issue to address in Panksepp’s (2003) comment is his discussion of a class of 50-kHz vocalizations emitted by young rats, which he refers to as laughter. In general, these high-frequency vocalizations, or *chirps*, are associated with intense behavioral arousal, as occurs in adult rats during sexual and aggressive behavior (McIntosh & Barfield, 1980; Sales, 1972a, 1972b; Takahashi, Thomas, & Barfield, 1983). Previous investigations in adult gerbils have provided strong evidence that chirps are produced as an incidental by-product of mechanical compression of the thorax as the forepaws hit the ground during intense activity (Thiessen & Kittrell, 1979); this by-product hypothesis was developed further and applied to adult rats by Blumberg (1992). It is interesting to note that Panksepp assumes that any such by-product hypothesis applied to the chirps of adults would also apply to juveniles, although there was no mention of juvenile vocalizations by Thiessen and Kittrell (1979) or Blumberg (1992). Panksepp’s assumption is interesting because it suggests that he views the adult and juvenile rat chirps as similar, a position that places his laughter hypothesis in some jeopardy. Why? Because it is hard to imagine that rats would be laughing during the intense motor activities that accompany male–male aggression as well as the chasing and mounting that occur during copulatory behavior.

At this time, we have no direct information on homologies between juvenile and adult rat 50-kHz vocalizations because Panksepp has not yet attempted an examination of the chirps of adult rats and whether these chirps can be made to fit within his laughter perspective. As he admits, “the final word on these topics is not yet in” (Panksepp, 2003, p. 384).

Our research on the biobehavioral responses of infant rats to thermal challenge has covered a wide range of physiological and behavioral phenomena, including homeostatic regulation, cardiac and respiratory rate, blood viscosity, blood pressure, sleep, and ultrasound production (Blumberg, 2001). We have also examined the interrelations among physiological and behavioral thermoregulation by using comparative methods in individual infant rats and hamsters (Sokoloff, Blumberg, Boline, Johnson, & Streeper, 2002) as well as during huddling (Sokoloff & Blumberg, 2001, 2002; Sokoloff et al., 2000). Our only agenda has been to provide a more cohesive and coherent picture of the many ways that physiology and behavior interact in developing mammals. Moreover, although the infant rat’s ultrasonic vocalization has been an important player in this developing story, the contributions of this program of research to the understanding of biobehavioral development does not rest on the final outcome of the debate in which we are currently engaged.

As with all scientific disputes, acceptance of our interpretation of crying pups and of Panksepp’s (2003) interpretation of laughing rats depends on the critical experiments that these interpretations inspire and the balance that is struck among our and Panksepp’s colleagues between the competing demands and attractions of hardheadedness and open-mindedness. Given the steady progress that has been made over the last few decades in the understanding of the neural substrates of behavior, we are personally most comfortable with the sure-footed approach that builds our science on a strong foundation. Panksepp clearly views this approach as hindering “progress in the understanding of how the brain–mind truly operates” (p. 384). In other words, we and Panksepp seem to be at an impasse. As we each go about our business of performing experiments to test our hypotheses, perhaps the healthiest attitude is simply to acknowledge that each camp benefits from the presence of the other. Neither side may ultimately win the argument, but with any luck, our science will benefit from the interaction.

References

- Allin, J. T., & Banks, E. M. (1971). Effects of temperature on ultrasound production by infant albino rats. *Developmental Psychobiology*, 4, 149–156.
- Blumberg, M. S. (1992). Rodent ultrasonic short calls: Locomotion, biomechanics, and communication. *Journal of Comparative Psychology*, 106, 360–365.
- Blumberg, M. S. (2001). The developmental context of thermal homeostasis. In E. M. Blass (Ed.), *Handbook of behavioral neurobiology* (Vol. 13, pp. 199–228). New York: Plenum Press.
- Blumberg, M. S., & Alberts, J. R. (1990). Ultrasonic vocalizations by rat pups in the cold: An acoustic by-product of laryngeal braking? *Behavioral Neuroscience*, 104, 808–817.
- Blumberg, M. S., & Alberts, J. R. (1991a). Both hypoxia and milk deprivation diminish metabolic heat production and ultrasound emission by rat pups during cold exposure. *Behavioral Neuroscience*, 105, 1030–1037.
- Blumberg, M. S., & Alberts, J. R. (1991b). On the significance of similarities between ultrasonic vocalizations of infant and adult rats. *Neuroscience and Biobehavioral Reviews*, 50, 95–99.
- Blumberg, M. S., & Alberts, J. R. (1997). Incidental emissions, fortuitous effects, and the origins of communication. In D. H. Owings, M. D. Beecher, & N. S. Thompson (Eds.), *Perspectives in ethology* (Vol. 12, pp. 225–249). New York: Plenum Press.
- Blumberg, M. S., Efimova, I. V., & Alberts, J. R. (1992a). Thermogenesis during ultrasonic vocalization by rat pups isolated in a warm environment: A thermographic analysis. *Developmental Psychobiology*, 25, 497–510.
- Blumberg, M. S., Efimova, I. V., & Alberts, J. R. (1992b). Ultrasonic vocalizations by rat pups: The primary importance of ambient temperature and the thermal significance of contact comfort. *Developmental Psychobiology*, 25, 229–250.
- Blumberg, M. S., Kreber, L. A., Sokoloff, G., & Kent, K. J. (2000). Cardiovascular mediation of clonidine-induced ultrasound production in infant rats. *Behavioral Neuroscience*, 114, 602–608.
- Blumberg, M. S., & Sokoloff, G. (1998). Thermoregulatory competence and behavioral expression in the young of altricial species—Revisited. *Developmental Psychobiology*, 33, 107–123.
- Blumberg, M. S., & Sokoloff, G. (2001). Do infant rats cry? *Psychological Review*, 108, 83–95.
- Blumberg, M. S., Sokoloff, G., Kirby, R. F., Knoop, T. G., & Lewis, S. J. (2002). Effects of antihypertensive drugs on ultrasound production and cardiovascular responses in 15-day-old rats. *Behavioural Brain Research*, 131, 37–46.
- Blumberg, M. S., & Wasserman, E. A. (1995). Animal mind and the argument from design. *American Psychologist*, 50, 133–144.
- Butler, A. B., & Hodos, W. (1996). *Comparative vertebrate anatomy: Evolution and adaptation*. New York: Wiley–Liss.
- Carden, S. E., Davachi, L., & Hofer, M. A. (1994). U50,488 increases ultrasonic vocalizations in 3-, 10-, and 18-day-old rat pups in isolation and the home cage. *Developmental Psychobiology*, 27, 65–83.
- Guilford, T., & Dawkins, M. S. (1991). Receiver psychology and the evolution of animal signals. *Animal Behaviour*, 42, 1–14.
- Harvey, P. H., & Pagel, M. D. (1991). *The comparative method in evolutionary biology*. Oxford, England: Oxford University Press.
- Hofer, M. A., Masmela, J. R., Brunelli, S. A., & Shair, H. N. (1998). The ontogeny of maternal potentiation of the infant rats’ isolation call. *Developmental Psychobiology*, 33, 189–201.
- Hofer, M. A., Masmela, J. R., Brunelli, S. A., & Shair, H. N. (1999). Behavioral mechanisms for active maternal potentiation of isolation calling in rat pups. *Behavioral Neuroscience*, 113, 51–61.
- Hofer, M. A., & Shair, H. N. (1978). Ultrasonic vocalization during social interaction and isolation in 2-week-old rats. *Developmental Psychobiology*, 11, 495–504.
- Hofer, M. A., & Shair, H. N. (1980). Sensory processes in the control of isolation-induced ultrasonic vocalization by 2-week-old rats. *Journal of Comparative and Physiological Psychology*, 94, 271–279.
- Hofer, M. A., & Shair, H. N. (1992). Ultrasonic vocalization by rat pups during recovery from deep hypothermia. *Developmental Psychobiology*, 25, 511–528.
- Kehoe, P., & Blass, E. M. (1986). Opioid-mediation of separation distress in 10-day-old rats: Reversal of stress with maternal stimuli. *Developmental Psychobiology*, 19, 385–398.
- Kehoe, P., & Harris, J. C. (1989). Ontogeny of noradrenergic effects on ultrasonic vocalizations in rat pups. *Behavioral Neuroscience*, 103, 1099–1107.
- Kennedy, J. S. (1992). *The new anthropomorphism*. Cambridge, England: Cambridge University Press.
- McIntosh, T. K., & Barfield, R. J. (1980). The temporal patterning of 40–60 kHz ultrasonic vocalizations and copulation in the rat (*Rattus norvegicus*). *Behavioral and Neural Biology*, 29, 349–358.

- Okon, E. E. (1971). The temperature relations of vocalization in infant golden hamsters and Wistar rats. *Journal of Zoology*, *164*, 227–237.
- Panksepp, J. (1998). *Affective neuroscience: The foundations of human and animal emotions*. New York: Oxford University Press.
- Panksepp, J. (2003). Can anthropomorphic analyses of separation cries in other animals inform us about the emotional nature of social loss in humans? Comment on Blumberg and Sokoloff (2001). *Psychological Review*, *110*, 376–388.
- Sales, G. D. (1972a). Ultrasound and aggressive behaviour in rats and other small mammals. *Animal Behaviour*, *20*, 88–100.
- Sales, G. D. (1972b). Ultrasound and mating behaviour in rodents with some observations on other behavioural situations. *Journal of Zoology, London*, *168*, 149–164.
- Sokoloff, G., & Blumberg, M. S. (2001). Competition and cooperation among huddling infant rats. *Developmental Psychobiology*, *39*, 1–9.
- Sokoloff, G., & Blumberg, M. S. (2002). Contributions of endothermy to huddling behavior in infant Norway rats (*Rattus norvegicus*) and Syrian golden hamsters (*Mesocricetus auratus*). *Journal of Comparative Psychology*, *116*, 240–246.
- Sokoloff, G., Blumberg, M. S., & Adams, M. M. (2000). A comparative analysis of huddling in infant Norway rats and Syrian golden hamsters: Does endothermy modulate behavior? *Behavioral Neuroscience*, *114*, 585–593.
- Sokoloff, G., Blumberg, M. S., Boline, E. A., Johnson, E. D., & Streeper, N. M. (2002). Thermoregulatory behavior in infant Norway rats (*Rattus norvegicus*) and Syrian golden hamsters (*Mesocricetus auratus*): Arousal, orientation, and locomotion. *Journal of Comparative Psychology*, *116*, 228–239.
- Takahashi, L. K., Thomas, D. A., & Barfield, R. J. (1983). Analysis of ultrasonic vocalizations emitted by residents during aggressive encounters among rats (*Rattus norvegicus*). *Journal of Comparative Psychology*, *97*, 207–212.
- Thiessen, D. D., & Kittrell, E. M. W. (1979). Mechanical features of ultrasound emission in the Mongolian gerbil, *Meriones unguiculatus*. *American Zoologist*, *19*, 509–512.
- Vivian, J. A., & Miczek, K. A. (1991). Ultrasound during morphine withdrawal in rats. *Psychopharmacology*, *104*, 187–193.
- Wasserman, E. A. (1993). Comparative cognition: Beginning the second century of the study of animal intelligence. *Psychological Bulletin*, *113*, 211–228.
- Winslow, J. T., & Insel, T. R. (1991a). Endogenous opioids: Do they modulate the rat pup's response to social isolation? *Behavioral Neuroscience*, *105*, 253–263.
- Winslow, J. T., & Insel, T. R. (1991b). The infant rat separation paradigm: A novel test for novel anxiolytics. *Trends in Pharmacological Sciences*, *12*, 402–404.

Received April 5, 2002

Revision received May 3, 2002

Accepted May 3, 2002 ■

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