Laughing Rats?
Playful Tickling Arouses High-Frequency Ultrasonic Chirping in Young Rodents

•

Jaak Panksepp and Jeffrey Burgdorf

In this reprint of a seminal article, once considered quite controversial, the authors discuss their radical claim that rats laugh. Even more provocative, the authors found that this rat-joy sound, especially evident during play, could be amplified dramatically by what they formally call heterospecific (cross-species) handplay (tickling). The authors tickled rats during the most playful juvenile period of their development (older rats sometimes resisted tickling), then studied the ultrasonic chirping the rats produced in response. When analyzed, these vocalizations, occurring during playful rough-and-tumble bouts, suggested analogies to human laughter. The authors also found that fear inhibits playfulness and precludes laughter in rats: sudden, startling bright lights and rough handling reduces the chirping, but even more than these, the smell of a predator's urine suppresses rat "laughter." The similar positive emotional responses evident in humans and rats suggests a shared brain anatomy and similar neurochemistry, which, in turn, suggests new ways to investigate the ancient origin of human laughter. This article was the first publication to summarize the full set of groundbreaking experiments that changed the way many researchers and scholars consider animal feelings, human nature, and the field of play.

Prologue: On the Discovery of "Laughter" in Rats

Laughter is a simple and robust indicator of joyful social affect. All too commonly, it is considered to be a unique emotional capacity of humans and, perhaps, a few other higher primates. If more primitive mammals also exhibit such emotional responses, it would suggest that joyful affect emerged much

earlier within mammalian brain evolution than is generally believed. In this article, we summarize the discovery of a primitive form of "laughter" in rats, and we provide convergent evidence and argumentation that a study of this response may help us decipher the neural basis of joy and positive emotional consciousness within the mammalian brain.

The stylistic approach used in this article is somewhat unique—namely, a traditional scientific report sandwiched between a short prologue and epilogue. We do this to share the full text of the manuscript of our initial discovery—a contribution that was rejected by the journal *Nature* in September 1997, leaving us concerned, once more, over the scientific openness of our present era. One reviewer did enthusiastically support our efforts (accepting this contribution with no major changes as a "scientifically sound" set of studies), while another rejected it outright on the basis of minor methodological concerns. At the conclusion of a harsh review, he asserted that "This is an interesting idea accompanied by some rather bad experiments. So even though the authors' conclusions may be right, it doesn't get a lot of help from the data. I am not sure that even better- controlled experiments would be more convincing to all readers." Even after we pointed out that most of our "flaws" were largely misinterpretations, the editor refused to reconsider his decision. Now, after a year of additional work and the worldwide broadcasting of our findings in the popular press following the Tucson III meeting (e.g., see *New Scientist,* May 2, 1998 [14] and *People* magazine, June 15, 1998 [105], as well as cameo appearances in *Believe it or Not* and *News of the Weird)*, we continue to believe that our interpretation of this robust tickling-induced vocal phenomenon in young rats is on the right track. Accordingly, we now share our initial results for the first time, and we wish to do it in essentially the form that the work was originally submitted for peer review.

Our Original Findings as Submitted to *Nature*

Abstract: In humans, laughter and giggling are objective indicators of joyful positive affect, and they occur most abundantly during playful social interactions. An understanding of such positive emotions has been hampered by the lack of simple measures of joyful social engagement in "lower" animals. Since the simplest way to induce laughter in children is tickling, we sought evidence for a comparable phenomenon in young rats by studying their ultra-

sonic "chirping" during vigorous bodily stimulation. Such vocalizations are common during juvenile play (Knutson, Burgdorf, and Panksepp 1998), and they can also be evoked by rapid manual stimulation (i.e., tickling). Stimulation of anterior body areas, which are especially important for arousing playfulness (Siviy and Panksepp 1987), yielded more chirping than stimulation of posterior zones, and full body stimulation with the animals in a supine position yielded the most. Analyses of these vocalizations suggest relationships to primate laughter: Tickling is a positive incentive state, as indexed by classical conditioning induced sensitization and instrumental approach tests; it is also correlated to natural playfulness and is inhibited by fearful arousal. These data suggest that a primal form of "laughter" evolved early in mammalian brain evolution and provide a new way to study the neural sources of positive social-emotional processes (i.e., joyful affect) in other mammals.

Although laughter is a prominent behavior of the human species, reflecting our ability to experience joy and humor, only fragments of data suggest that other species have similar brain functions. Certain vocal patterns of chimpanzees (Jurgens 1986; Berntson, Boysen, Bauer, and Torrello 1989) and some lower primates (Preuschoft 1992) appear to reflect the existence of homologous processes, but credible evidence for other species is marginal (Douglas 1971; Masson and McCarthy 1996). However, considering the clinical evidence that the neural mechanisms for human laughter exist in ancient regions of the brain, including thalamus, hypothalamus, and midbrain (Arroyo et al. 1993; Black 1982; Poeck 1969), the existence of such processes in common laboratory species seems feasible, at least in principle. We now report evidence congruent with the presence of analogous, perhaps homologous, responses in domesticated rats.

Adult rats commonly exhibit two distinct types of ultrasonic vocalizations (USVs): Long, distress USVs in the low-frequency range (peaking at around 22 kHz) reflect negative emotional arousal related to fear, social defeat, and the postcopulatory refractory period (Haney and Miczek 1993; Sales and Pye 1974). On the other hand, short, chirping-type USVs in the high-frequency range (peaking at approximately 50 kHz) appear to index more positive forms of arousal that occur at high rates during desired social interactions (Knutson, Burgdorf, and Panksepp 1998; Sales and Pye 1974).

Human and chimpanzee laughter tends to emerge most readily in playful contexts (Rothbard 1973; Sroufe and Waters 1976; Van Hooff 1972), and the rough-and-tumble play of young rodents is accompanied by an abundance

of short, high-frequency USVs (Knutson, Burgdorf, and Panksepp 1998). Although such high-frequency USVs have typically been studied in the context of adult sexual and aggressive encounters (Adler and Anisko 1979; Barfield and Geyer 1975; Tornatzky and Miczek 1995), they have also been noted during routine handling (Sales and Pye 1974). In the following experiments, we determined whether the type of chirping seen during play has any resemblances to human laughter which may suggest a degree of evolutionary kinship between the two phenomena.

The easiest way to induce primal laughter and joy in young children is through tickling. This response conditions rapidly (Newman, O'Grady, Ryan, and Hemmes 1993). After a few tickles, one can provoke social engagement and peals of laughter by provocative cues such as wiggling a finger (Rothbart 1973). We have now found that chirping at around 50 kHz is increased markedly in young rats by manual tickling, and converging evidence suggests the response has more than a passing resemblance to human laughter.

First, we determined whether tickling different parts of the body leads to different levels of chirping and whether the response varies as a function of previous social experience and gender. Thirty-one Long-Evans hooded rat pups (thirteen males, eighteen females) were weaned and individually housed at twenty-four days of age. Half the animals were assigned to pairs and allowed two half-hour play sessions daily (alternately, in each other's home cages), while the remaining fifteen animals were handled an equal number of times but always left solitary in their own cages. At forty-one and fifty-five days of age, all animals were left undisturbed for forty-eight hours and then observed during a two-minute standard dyadic play encounter, during which the frequencies of two objective play activities of each animal—namely pins and dorsal contacts—as well as the number of 50 kHz chirps, were monitored (Panksepp, Siviy, and Normansell 1984). Counting of chirps in all experiments was always done by a listener who was blind to experimental conditions. All testing, except as indicated, was carried out under dim (25 lux) illumination.

The next day, all animals were given standardized tickling tests. Animals were transported quietly in their home cages and placed for observation in a quiet observation enclosure. High-frequency USVs were monitored with a Mini-3 Bat Detector (Ultra Sound Advice, London), tuned to detect the high USVs. High USVs were recorded during six successive twenty-second test periods: 1) an initial no-stimulation baseline, 2) vigorous tickling-type manual stimulation of either the anterior or posterior dorsal body surfaces, 3) a second

baseline, 4) vigorous manual stimulation of the dorsal body surface that had not yet been stimulated (i.e., the sequence of anterior and posterior target areas being counterbalanced), 5) a final baseline, followed by 6) vigorous whole-body playful tickling (focusing on the ribs and ventral surface), with animals being repeatedly pinned four to six times, throughout the fifteen-second interval. For all animals, the tickling was done with the right hand and consisted of rapid finger movements across their respective body parts. Even though the stimulation was brisk and assertive, care was taken not to frighten the animal. Chirping typically started immediately at the onset of tickling.

As summarized in figure 1, tickling differentially invigorated chirping during all conditions, and the effects were similar at both ages [$F(1, 56) = .52$]. Full stimulation was more effective than anterior stimulation, which was more effective than posterior stimulation, which was more effective than no stimulation [overall $F(2, 56) = 86.8$, $p < .0001$ for the three types of tickling, with all successive p's $< .001$]. This effect was larger in males than females [$F(1, 56) = 19.1$, ps $< .0001$], but only marginally more effective in the socially isolated animals than in the play-experienced ones [$F(1, 28) = 4.39$, $p < .05$, on day forty-four, but
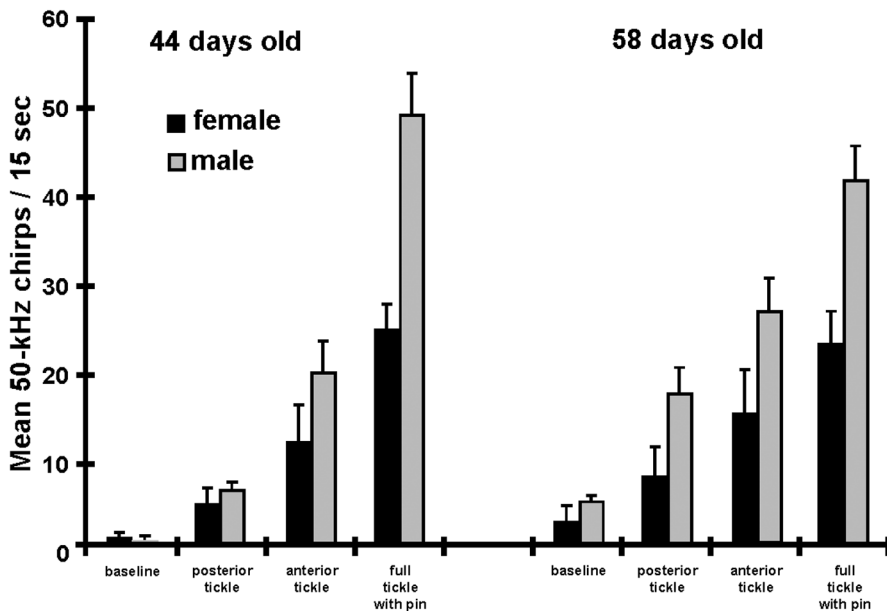

Figure 1. Mean (± SEM) levels of 50 kHz chirping in 44- and 58-day-old rats as a function of type of body stimulation and gender.

not significant on day fifty-eight; data not shown]. The levels of dorsal contacts during the above play sessions on day forty-four were correlated with levels of tickling-induced USVs on day forty-five during posterior stimulation ($r = .47$, $p < .01$), anterior stimulation ($r = .50$, $p < .01$), and during the full simulation ($r = .50$, $p < .01$), suggesting that playfulness predicts responsivity to tickling prior to puberty. The respective correlations to number of pins were .45 ($p < .1$), .38, and .20. There were no significant correlations to the recorded behaviors of the play partners. All correlations at the older test age were negligible, potentially because of the slight decline and increasing variability/seriousness in playfulness that occur after puberty (Panksepp 1981). The test-retest correlation between succeeding tickling tests separated by the two-week interval was $r = .41$ ($p < .05$) for anterior, $r = .45$ ($p < .02$), posterior, and $r = .57$ ($p < .01$) for full-body stimulation. Correlations in other tests using successive daily test days are typically above .75 for this measure.

An additional age comparison contrasted responses of six seventeen-day-old males and six seven- to nine-month-old males during five successive daily tests employing full-body tickling. The young animals exhibited much more chirping than the old ones during the tickle periods [48.3 (±6.9) vs 15.1 (±3.7) chirps / 15 sec, with $F(1, 10) = 17.87$, $p < .002$] as well as during the intervening no-tickle periods [22.6 (±2.6) vs 0.7 (±0.4) with $F(1, 10) = 70.93$, $p < .001$].

To evaluate the conditionability of the chirping response, another group of eleven male rats was weaned at twenty-one days of age and housed individually for ten days prior to the start of testing. After two brief sessions to acclimate them to human handling and following five minutes of habituation to the test arena (a 48 x 38 x 30 cm high, open-topped chamber with corncob bedding on the floor), half the animals underwent systematic classical conditioning, consisting of four trials as follows: 1) a fifteen-second base-line recording period, 2) a fifteen-second conditional stimulus (CS) period, 3) a fifteen-second unconditioned stimulus (UCS) period consisting of full-body tickling with repeated pinning (i.e., identical to the final condition of the previous experiment), 4) followed by a fifteen-second post-tickling period. For the six experimental animals, the conditioning procedure was conducted for five successive trials during three test sessions separated by at least eight hours. The CS was the experimenter's hand, which had a distinctive odor because of brief immersion in dry coffee grounds. The hand was used dynamically to follow each test animal around the observation chamber, with gentle touching of the face and the sides of the animal. A bout of vigorous tickling commenced fifteen seconds thereafter. For the remaining control animals, the experimenter wore a leather

glove dipped in the coffee grounds, but during the ensuing fifteen seconds, the glove was left immobile in the corner of the test chamber.

Significant conditioning was evident during the very first training session (figure 2). The level of vocalization increased systematically during both the CS and UCS periods, but only for the experimental animals, as indicated
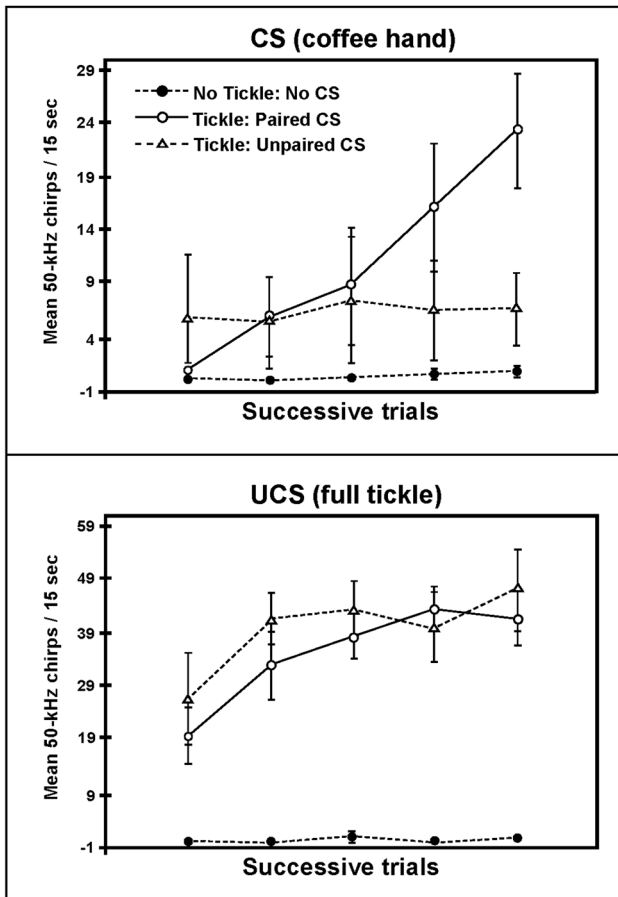

Figure 2. Mean (± SEM) levels of 50 kHz chirping during the first day of conditioning as a function of 5 successive training trials during conditioned stimulus (Top: CS—coffee hand) and the unconditioned stimulus (Bottom: UCS—full tickle) trials. The animals receiving paired CS-UCS trials exhibited clear acquisition of a conditioned response, while those receiving the unpaired CS-UCS conditions only exhibited sensitization. Both groups exhibited much more chirping than the untickled controls. The CS presented alone also does not provoke chirping.

by a significant group by trial interactions during both CS and UCS periods [F's(4,9) > 7.0, p's < .001]. This pattern was sustained during the subsequent two sessions (figure 3): Although there was no differential chirping during the fifteen seconds prior to the CS, elevations were evident during the CS period [t(9) = 3.4, p < .01], even more marked elevations during the tickling period [t(9) = 9.2, p < .0001], and a modest differential excitement remained during the fifteen-second poststimulation period [t(9) = 2.49, p < .05]. To further evaluate the nature of the conditioning, an additional sensitization control group of six rats was added which received the CS unpaired with the UCS (namely with a fifteen-second interval between CS and UCS), and as is evident in figures 2 and 3, this group of animals did not show a clear acquisition curve, even though it did exhibit a reliable elevation of chirping over the no-CS group, indicating that part of the elevation of chirping to the CS is due to sensitization rather than associative conditioning.

To determine whether animals would seek tickling, twenty-one, seventeen-day-old, group-housed animals were individually placed in one corner of the
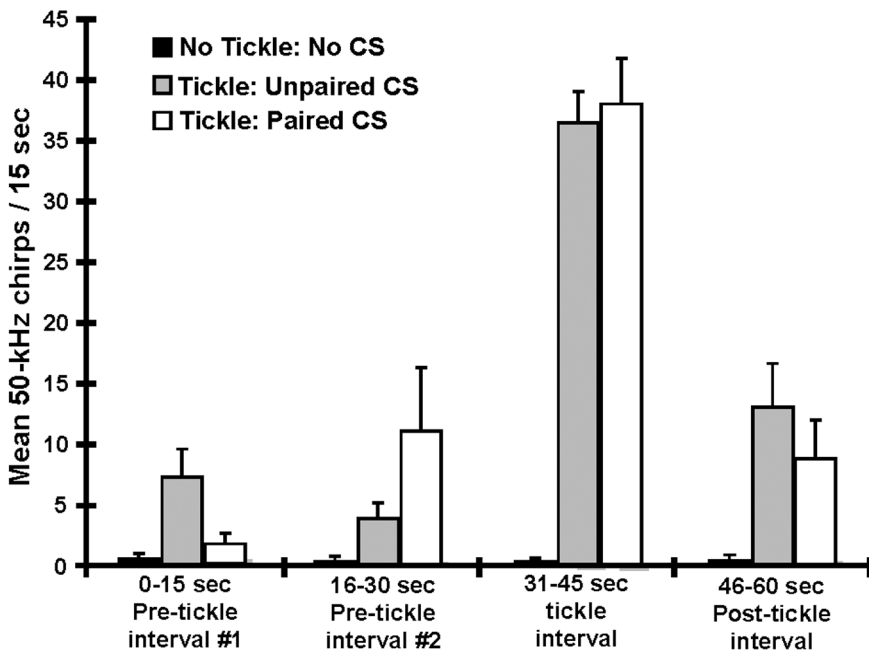

Figure 3. Mean (± SEM) levels of 50 kHz chirping during the four phases of conditioning averaged across the second and third conditioning sessions. First session for these animals is in figure 2.

$48 \times 38 \times 30$ cm high open-topped test chamber, with the experimenter's hand placed palm up in the diagonally opposite corner. When an animal approached to within two inches, it was given fifteen seconds of tickling. Five sequential trials were conducted with ten-minute inter-trial intervals (during which animals left individually in holding cages). Animals showed significantly faster running times during this training session [$F(4,20) = 4.68$, $p < .002$], with the mean latencies being 19.2 (± 3.5) seconds for the first trial and 6.9 (± 1.1) seconds for the fifth trial.

To determine how negative emotional arousal would affect tickling-induced chirping, ten thirty-seven-day-old, tickle-habituated animals were tested successively using four fifteen-second test periods (baseline, full-body tickle, baseline, tickle), contrasting three pairs of successive counterbalanced conditions: 1) hunger (eighteen hours food deprivation) vs satiety, 2) dim (25 lux) vs bright (1000 lux) ambient illumination, and 3) exposure to predatory odors (30 mg of cat fur mixed into the bedding of the test cage) compared to unadulterated bedding. As summarized in figure 4, tickling elevated chirping
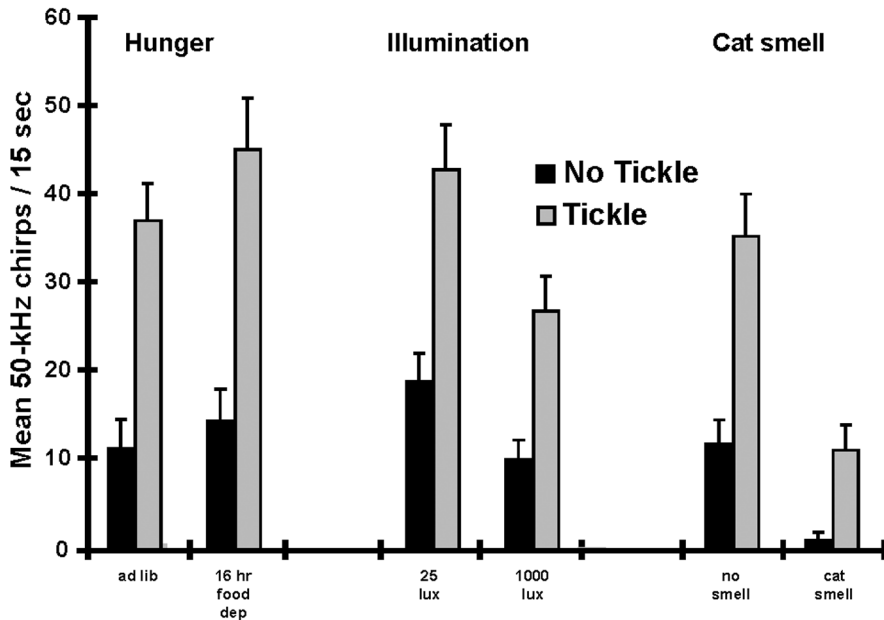
Figure 4. Mean ($\pm$ SEM) levels of 50 kHz chirping during three successive counterbalanced experiments evaluating three types of negative emotional/motivational arousal: mild hunger, bright illumination, and the presence of cat smell.

under all conditions compared to the nontickle periods. Mild hunger marginally increased chirping [$F(1, 18) = 3.80$, $p < .07$]. Bright light significantly reduced chirping [$F(1, 18) = 60.82$, $p < .0001$], with the effect being slightly larger for tickle than no-tickle periods as indexed by an interaction of the two test variables [$F(1, 18) = 4.80$, $p < .05$]. Exposure to cat smell had an even larger suppressive effect on chirping [$F(1, 18) = 71.56$, $p < .0001$], but under this condition, a significant interaction indicated that behavioral suppression was greater during the no-tickle period [$F(1, 18) = 10.28$, $p < .005$]. We would note that chirping during such no-tickle period is largely a contextually conditioned response. Without prior tickling, chirping typically remains close to zero levels (see figure 2).

In additional control studies (data not shown), we determined that gentle touch did not provoke the vigrous chirping evident in figures 1–4, nor were static forms of somatosensory stimulation effective. Negative touch, such as holding animals by the scruff of the neck or by their tails, strongly inhibited chirping. We have also monitored 22 kHz USVs, and they are rare during tickling. Finally, we determined whether this type of manual play would substitute for the satisfactions derived from dyadic play, as measured by the satiety that normally occurs during a half-hour play period (Panksepp, Siviy, and Normansell 1984). Manual tickling play for fifteen minutes significantly reduced the ensuing amounts of social play exhibited by pairs of young rats. On the other hand, sustained, artificial somatosensory stimulation (animals' bodies restrained snuggly in a hollowed foam pillow connected to a vibrator) had no such effect.

These studies support the possibility that the chirping induced in young rats by manual tickling may be homologous to, or at least functionally akin to, human laughter. This conclusion is warranted because of the many similarities between the two phenomena. First, in humans, certain parts of the body are more ticklish than others (Ruggieri and Milizia 1983), and in rats, chirping was intensified more by anterior than posterior body stimulation, which corresponds to the differential play reductions following anesthetization of dorsal body areas (Siviy and Panksepp 1987). In addition, just as the human tickling response conditions rapidly, so does tickle-induced chirping in rats. Laughter typically occurs during natural play episodes in human children (Rothbart 1973; Humphreys and Smith 1984), and in the present work, as in previous work (Knutson, Burgdorf, and Panksepp 1998), the level of tickling-induced chirping was strongly related to playful tendencies. Tickling was also a positive incentive

as measured by a variety of approach and conditioning tests. Although we have yet to evaluate the hedonic qualities of the tickle-induced chirps in animals listening to such vocalizations, we note that comparable high-frequency, sex-related USVs in adult hamsters have been found to be attractive to conspecifics and to facilitate their sexual responsivity (Floody and Pfaff 1977).

That none of our animals seemed to interpret the tickling stimulation as aggression is indicated by the fact that, during the more than one thousand distinct tickling episodes that we have so far conducted, no young animal has become outwardly defensive. No rat has threatened or sought to aggressively bite the bare hand of the experimenter. However, there have been abundant, nonharmful, play bites. The animals that chirp the most play the most; and they also exhibit the highest levels of play biting. To all appearances, young animals are aroused by and enjoy this type of bodily stimulation. They readily approach the hand that does the tickling, and they exhibit lots of squirming during the tickling. Many begin to react to the hand as if it were a play partner, exhibiting playful darts and pouncing interactions which appear to fulfill their biological need to play. However, some animals over two months of age have seriously challenged our attempts to tickle them.

It is also unlikely that the tickling provokes much anxiety, even though it can surely provoke some avoidance. In some children, tickling can become so intense as to induce transitory avoidance, and excessive tickling has been used effectively as punishment in behavioral-modification programs (Greene and Hoats 1971). Some subjectively evident approach-avoidance conflict was evident in a minority of the present animals, especially the ones that chirped least during the tickling. On the rare occassion that an animal has exhibited some apparent anxiety, it has invariably stopped chirping. Likewise, anxiogenic stimuli such as bright light and cat odor unambiguously diminish the response. Clearly, young rats do not regard the smell of a predator as anything to chirp about. The fact that this same aversive stimulus can activate 22 kHz distress calls in adults (Blanchard et al. 1990), further highlights the potential functional and neuroanatomical distinction between high and low USVs in rodents (Brudzynski and Barnabi 1996; Fu and Brudzynski 1994). The present work lends support to the idea that high and low USVs may index distinct affective states in rats.

In sum, the chirping emitted by tickled rats is a robust phenomenon. More than 95 percent of the young animals we have studied so far have unambiguously exhibited the response, but there are a few animals that chirp rarely dur-

ing the stimulation. Thus, as in humans (Provine 1996), tickling responsivity appears to be traitlike, suggesting the genetic underpinnings of this reponse may be analyzed in animals. The overall responsivity of animals tends to remain stable throughout early development and is strongly related to playfulness. The slightly elevated levels of chirping in males may correspond to the oft-reported elevations of rough-and-tumble playfulness in males, but it may also correspond to the elevated levels of fearfulness commonly seen in females. The onset of puberty does not appear to diminish the reponse, as indicated by the similar responsivities of forty-four- and fifty-eight-day-old animals, although much older animals did exhibit diminished ticklishness.

Since vigorous chirpers were more playful, perhaps one function of chirping is to signal readiness for friendly social interactions. Presumably these vocalizations come to be used in various ways as animals mature, including sexual and aggressive contexts. In the same way, childhood laughter may gradually come to serve several distinct functions in adults, ranging from good-humored social eagerness and communion to displays of dominance, triumph, and even scorn. Whether chirping in rats transmits specific information between animals or simply promotes mood states that facilitate certain interactions remains unknown (Nyby and Whitney 1978). We favor the second option, and believe that the study of rodent chirping could be used to index the ongoing socioemotional states of test animals in a variety of experimental situations.

Although Charles Darwin noted in his *The Expression of the Emotions in Man and Animals:* "Laughter seems primarily to be the expression of mere joy or happiness" (1872, 198), we would note that the motor expressions of laughter and the affective experience of mirth may be elaborated in distinct areas of the brain (Arroyo et al. 1993). Many neurological disorders are accompanied by reflexive laughter that is typically distressing to the patient (Black 1982; Poeck 1969). Accordingly, we would suggest that the rapid learning that occurs in this system (i.e., the conditioned chirping response), may be a better indicator for the neural sources of mirth than the unconditional chirping response. We suspect that brain circuits of human laughter and the neural underpinning of rodent chirping do interconnect with brain areas that mediate positive social feelings, but the locations of those areas remain unknown. In sum, although we would be surprised if rats have a sense of humor, they certainly do appear to have a sense of fun.

Rodent chirping may have evolutionary connections to comparable human emotional response systems. Alternatively, it may simply be a social-engagment

signal that is unique to rodents. Skepticism about the existence of rodent laughter is to be expected as long as we know so little about the organization of social-emotional systems in the brains of animals, but at present we are optimistic that the intensive neurological analysis of the playful chirping of young rats may help clarify the fundamental brain sources of human laughter and joy. We suspect that both of these responses go back in brain evolution to a time when the readiness for friendly social engagment was communicated by simple acoustic signals. In any event, this work highlights the possibility of systematically analyzing friendly cross-species social interactions in the animal research laboratory.

If a homology exists between joyous human laughter and rodent high-frequency chirping, additional work on the topic may yield information of some clinical value. For instance, depressed individuals laugh and play less than normal; the elucidation of neurochemistries that promote chirping and playfulness in rodents may help guide development of new types of antidepressants. Also, the effect of positive emotions on many other bodily processes, such as autonomic reactivity and the vigor of immune responses, can now be studied systematically. If the chirping response has some evolutionary continuity with our human urge to laugh, it could further our understanding human emotions through the study of other animals (Panksepp 1998a).

Epilogue: Relations of this Work to Understanding Affective Consciousness

The objective phenomenon we have discovered is robust. Although the interpretation of the findings is certainly open to other explanations, we have not yet encountered an empirically defensible alternative to the one advanced here. We have shared the above findings with hundreds of colleagues at several scientific meetings, and no one has yet generated an alternative hypothesis that we had not already considered and experimentally disconfirmed. Indeed, all the additional tests we have conducted since completing the work outlined above continue to indicate that rats relish the experiences that evoke high-frequency 50 kHz chirping. To our knowledge, intentional human tickling generates these vocalizations at higher rates than any other social situation.

If there are evolutionary relations between human laughter and this form of rodent "laughter," we may finally have a credible strategy for systematically clarifying the nature of positive emotional consciousness within the human

brain. We are now seeking to specify the brain areas and neurochemistries that mediate this positive affective response, and our preliminary work indicates that circuits situated in the reticular nuclei of the thalamus and mesencephalon are important. Also, glutamate is essential for triggering the response, since the NMDA receptor antagonist MK-801 can eliminate tickle-induced chirping.

We currently remain open to the possibility that many other mammals beside humans experience joyful affect during their playful social engagements. The vocal component of this state may have diminished through negative selection in the young of many other species, especially if it served to alert predators in the evolutionary history. Since ultrasonic calls do not travel far, such evolutionary weeding may not have transpired in burrowing species such as rats. The scenario we prefer is that the fundamental process of joy emerged early in brain evolution, even though the external signs of this central state may have diversified considerably among species. Of course, if the response only reflects convergent evolutionary processes in different species, insight into human joy are less likely to emerge from such work. However, if there is an evolutionary relationship between the joyous chirping of rats and the the joyous laughter of young children, a study of the rodent brain does provide a compelling way for us to try to understand the nature of a joyful form of affective consciousness within the human brain.

Our provisional conclusion is: Rats do laugh, and they certainly enjoy the frolicking that induces them to do so. We suspect that the nature of their positive internal affective experiences is not all that different from our own, even though the cognitive accompaniments (e.g., a sense of humor) are bound to differ markedly. We remain saddened that many of our colleagues in the prevailing scientific establishment are not more open to entertaining such possibilities. We believe that raw emotional experiences and a primitive sense of self, probably created by deep subcortical structures that all mammals share, may constitute the neural ground upon which the more figurative aspects of human consciousness were built (Panksepp 1998b).

REFERENCES

Adler, Norman, and Joseph Anisko. 1979. The behavior of communicating: An analysis of the 22 kHz call of rats (*Rattus norvegicus*). *American Zoologist* 19: 498–508.
Arroyo, Santiago, Ronald P. Lesser, Barry Gordon, Sumio Uematsu, John Hart, Pamela

Schwerdt, Kati Andreasson, and Robert S. Fisher. 1993. Mirth, laughter and gelastic seizures. *Brain* 116:757–80.

Barfield, Ronald J., and Lynette A. Geyer. 1975. The ultrasonic post-ejaculatory vocalization and the post-ejaculatory refractory period of the male rat. *Journal of Comparative and Physiological Psychology* 88:723–34.

Berntson, Gary G., Sarah T. Boysen, Harold R. Bauer, and Michael S. Torello. 1989. Conspecific screams and laughter: Cardiac and behavioral reactions of infant chimpanzees. *Developmental Psychobiology* 22:771–87.

Black, Donald W. 1982. Pathological laughter: A review of the literature. *Journal of Nervous and Mental Disease* 170:67–71.

Blanchard, Robert J., D. Caroline Blanchard, John Rodgers, and Scott M. Weiss. 1990. The characterization and modelling of antipredator defensive behavior. *Neuroscience and Biobehavioral Reviews* 14:463–72.

Brudzynski, Stefan M., and Francesco Barnabi. 1996. Contribution of the ascending cholinergic pathways in the production of ultrasonic vocalization in the rat. *Behavioural Brain Research* 80:145–52.

Darwin, Charles. 1872. *The expression of the emotions in man and animals*.

Douglas, Mary. 1971. Do dogs laugh? A cross-cultural approach to body symbolism. *Journal of Psychosomatic Research* 15:387–90.

Floody, Owen R., and Donald W. Pfaff. 1977. Communication among hamsters by high-frequency acoustic signals: III. Response evoked by natural and synthetic ultrasounds. *Journal of Comparative and Physiological Psychology* 91:820–29.

Fu, Xiao-Wen, and Stefan M. Brudzynski. 1994. High-frequency ultrasonic vocalization induced by intracerebral glutamate in rats. *Pharmacology, Biochemistry and Behavior* 49:835–41.

Greene, Robert J., and David L. Hoats. 1971. Aversive tickling: A simple conditioning technique. *Behavior Therapy* 2:389–93.

Haney, Margaret, and Klaus A. Miczek. 1993. Ultrasounds during agonistic interactions between female rats (*Rattus norvegicus*). *Journal of Comparative Psychology* 107:373–79.

Humphreys, Anne P., and Peter K. Smith. 1984. Rough-and-tumble in preschool and playground. In *Play in animals and humans*, ed. Peter K. Smith, 241–70.

Jürgens, Uwe. 1986. The squirrel monkey as an experimental model in the study of cerebral organization of emotional vocal utterances. *European Archives of Psychiatry and Clinical Neuroscience* 236:40–43.

Knutson, Brian, Jeffrey Burgdorf, and Jaak Panksepp. 1998. Anticipation of play elicits high-frequency ultrasonic vocalizations in young rats. *Journal of Comparative Psychology* 112:65–73.

Masson, J. Moussaieff, and Susan McCarthy. 1996, first published 1994. *When elephants weep: The emotional lives of animals*.

Newman, Bobby, Mairead A. O'Grady, Carolyn S. Ryan, and N. S. Hemmes. 1993. Pavlovian conditioning of the tickle response of human subjects: Temporal and delay conditioning. *Perceptual and Motor Skills* 77:779–85.

Nyby, John, and Glayde Whitney. 1978. Ultrasonic communication of adult myomorph rodents. *Neuroscience and Biobehavioral Reviews* 2:1–14.

Panksepp, Jaak. 1981. The ontogeny of play in rats. *Developmental Psychobiology* 14:327–32.

———. 1998a. *Affective neuroscience: The foundations of human and animal emotions*.

———. 1998b. The periconscious substrates of consciousness: Affective states and the evolutionary origins of the self. *Journal of Consciousness Studies* 5:566–82.

Panksepp, Jaak, Steve Siviy, and Larry Normansell. 1984. The psychobiology of play: Theoretical and methodological perspectives. *Neuroscience and Biobehavioral Reviews* 8:465–92.

Poeck, Klaus. 1969. Pathophysiology of emotional disorders associated with brain damage. In *Handbook of clinical neurology*, vol. 3, ed. P. J. Vinken and G. W. Bruyn, 343–67.

Preuschoft, Signe. 1992. "Laughter" and "smile" in Barbary macaques (*Macaca sylvanus*). *Ethology* 91:220–36.

Provine, Robert. 1996. Laughter. *American Scientist* 84:38–45.

Rothbart, Mary K. 1973. Laughter in young children. *Psychological Bulletin* 80:247–56.

Ruggieri, Vezio, and Maria Milizia. 1983. Tickle perception as micro-experience of pleasure: Its phenomenology on different areas of the body and relation to cerebral dominance. *Perceptual and Motor Skills* 56:903–14.

Sales, Gillian, and David Pye. 1974. *Ultrasonic communication by animals*.

Siviy, Stephen M., and Jaak Panksepp. 1987. Sensory modulation of juvenile play in rats. *Developmental Psychobiology* 20:39–55.

Sroufe, L. Alan, and Everett Waters. 1976. The ontogenesis of smiling and laughter: A perspective on the organization of development in infancy. *Psychological Review* 83:173–89.

Tornatzky, Walter, and Klaus A. Miczek. 1995. Alcohol, anxiolytics and social stress in rats. *Psychopharmacology* 121:135–44.

van Hooff, Jan A. R. A. M. 1972. A comparative approach to the phylogeny of laughter and smiling. In *Non-verbal Communication*, ed. Robert A. Hinde, 129–79.