The Riddle of Laughter: Neural and Psychoevolutionary Underpinnings of Joy

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Abstract

Modest advances are being made in understanding the neurology and functions of laughter. The discovery of tickle-induced "laughter" in animals should facilitate the characterization of this basic emotional response of the mammalian brain. The existence of such vocal activities in species other than humans (e.g., rats) suggests that the fundamental brain processes for joyful affect may have emerged early in vertebrate brain evolution. Here, I summarize the little that we know about the evolutionary and brain sources of laughter, and how the accompanying positive emotions may solidify social bonds within the mammalian brain. Discovery of unique neurochemistries that specifically promote laughter and joy may provide clues for development of new classes of antidepressants.

Keywords

laughter; tickling; play; joy; brain

There is something primitive and something psychologically sophisticated about human laughter. On the one hand, the stereotyped vocal patterns, which first appear in rudimentary form at 2 to 3 months of age, reflect an ancient heritage. On the other hand, the subtleties of adult humor highlight how those primitive emotional processes interact with refined cognitions within higher reaches of the brain-mind. Long regarded as a uniquely human phenomenon, "laughter" is evident in other primates (Provine, 1996), and recently, it has been observed even in laboratory rats (Panksepp & Burgdorf, 1999). A study of the underlying brain systems in other mammals may eventually help clarify the ancestral antecedents of social joy within the human brain.

LAUGHTER IN INFANCY AND ADULTHOOD: FROM TICKLING TO HUMOR?

Laughter is fundamentally a social phenomenon. In young children, it is most easily evoked by playful tickling. The perennial childhood puzzle of why one cannot tickle oneself may simply indicate that the underlying neural systems are controlled by social cues and interactions—perceptions of being wanted or chased, as well as the dynamics of the resulting playful social activities. As might have been predicted from everyday psychological observations, being tickled by another person arouses the brain more than being "tickled" by oneself (Blakemore, Wolpert, & Frith, 1998). This simple fact highlights how subtly our brains have been honed, in part by evolution, to be mindful of social priorities. Tickling and laughter help weave individuals into the social fabric in which they reside, in various hues of position and dominance.

The tickling response conditions so rapidly that after only a few tickles one can evoke laughter simply through gestures that imply threats of tickling (e.g., "coochi-coochi-coo"). Indeed, if one wants to become friends with a young child, there is no easier way to negotiate the social terrain than by gently escalating tickle games (an obvious fact that remains to be experimentally verified, although it can be observed by any sensitive adult who wishes to do so).[2] This type of learned anticipatory response is also evident in rats (Panksepp & Burgdorf, 1999).

An infant's engagements in joyful tickling may pave the way for peek-a-boo games in which the anticipation of sudden social presence and absence can rivet the infant's delighted attentions. These antecedents may gradually give way to children's enjoyment of the many variations in the games, practical jokes, and mischievous pranks they come to cherish.

It is a common but not an empirically firmly established view that the maturing human taste for humor is based, in some foundational way, on the existence of infantile and childhood joy and laughter. It is easy to envision, at least in metaphoric terms, the dynamics that may transpire in such developmental passages: Our emotional responses project affective values onto world events, and in some yet unfathomed way, cognitive and affective processes ensnare (i.e., mutually condition) each other during psychological development.

THE EVOLUTIONARY ANTECEDENTS OF LAUGHTER

Because smiling and laughter are the quintessential indicators of joyful affect across human cultures,

189

feel what suffering people were feeling. In compassion training—sometimes called "loving-kindness meditation"—they were told to direct warm thoughts toward others, but they were not to feel empathy, only positive feelings.

Their brains were scanned while they did this, and it turns out that there was a neural difference in the two cases: Empathy training led to increased activation in the insula and cingulate cortex, the same parts of the brain that would be active if you were empathizing with the pain of someone you care about. Compassion training led to activation in other parts of the brain, such as the ventral striatum, which is involved in, among other things, reward and motivation.

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These studies also revealed practical differences between empathy and compassion. Empathy was difficult and unpleasant—it wore people out. This is consistent with other findings suggesting that vicarious suffering not only leads to bad decision-making but also causes burnout and withdrawal. Compassion training, by contrast, led to better feelings on the part of the meditator and kinder behavior toward others. It has all the benefits of empathy and few of the costs.

These results connect nicely with the recent conclusions of Paul Condon and his colleagues, published in the journal Psychological Science in 2013, who found that being trained in meditation makes people kinder to others and more willing to help (compared with a control condition in which people were trained in other cognitive skills). They argue that meditation "reduces activation of the brain networks associated with simulating the feelings of people in distress, in favor of networks associated with feelings of social affiliation." Limiting the impact of empathy actually made it easier to be kind.

I don't deny the lure of empathy. It is often irresistible to try to feel the world as others feel it, to vicariously experience their suffering, to listen to our hearts. It really does seem like a gift, one that enhances the life of the giver. The alternative—careful reasoning mixed with a more distant compassion—seems cold and unfeeling. The main thing to be said in its favor is that it makes the world a better place.

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a study of the underlying neurobiological substrates may help us decode the fundamental nature of joy within the brain. The fact that common laboratory animals such as rats also exhibit high-frequency (approximately 50 kHz), ultrasonic, laughter-type chirping responses to tickling suggests that the fundamental neural sources of positive social affect may be studied in animal models (Panksepp, 1998). Of course, the success of such strategies will depend on the extent to which laughter responses in humans and animals arise from evolutionarily related brain systems. The probability of that being the case seems high because in both humans and other animals, tickling is rewarding, conditions rapidly, and occurs most abundantly during social play (Knutson, Burgdorf, & Panksepp, 1998; Panksepp & Burgdorf, 1999).

The parts of the body toward which animals normally direct their playful activities (e.g., the nape of the neck) are more ticklish than other body areas. Comparable bodily sensitivities to tickling, although long recognized, have rarely been studied in humans. Just like human children, young rats find tickling to be rewarding, as indicated, for example, by the finding that young rats will seek the proximity of a hand that tickled them rather than one that simply petted them. Young rats also generally prefer to spend time with older animals that chirp abundantly as opposed to those that do not. Rat "laughter" can easily be amplified or reduced by selective genetic breeding, suggesting that it reflects a heritable emotional trait. The trait also predicts playfulness in young rats—animals that chirp most during tickling also solicit play the most (Panksepp & Burgdorf, 1999, 2000). This emotional response may eventually provide a model for the study of learning in positive emotional systems comparable to those simple classical conditioning models that have been developed for the study of negative emotions such as fear (for a summary, see Panksepp, 1998). The response may also be used to index rats' desire for other rewards, even pharmacological ones, as indicated by the ability of this 50-kHz vocalization to index eagerness to obtain rewards (Burgdorf, Knutson, & Panksepp, 2000; Knutson, Burgdorf, & Panksepp, 1999).

If we are willing to accept that such laughter responses may arise from the neuronal infrastructure of joy within the mammalian brain, these data suggest that a positive form of social affect is a fundamental aspect of mammalian brain organization. Although the social facilitation and social bonding associated with shared laughter remains to be empirically evaluated, laughter is most certainly infectious and may transmit moods of positive social solidarity, thereby promoting cooperative forms of social engagement. Presumably, the ultimate evolutionary function of laughter is to help organize social dynamics in support of reproductive success. Such ticklish issues may be best addressed experimentally in animal studies. However, what we need to determine first is whether there are evolutionary continuities between animal laughter and primal human laughter—a project that requires implementation of subtle affective neuroscience methodologies (Panksepp, 1998).

THE NEUROANATOMY OF LAUGHTER

At present, the neural substrates of laughter remain poorly defined. Certain epilepsies and neuropathologies that are commonly accompanied by uncontrollable bouts of laughter provide marginal clues concerning the underlying brain substrates (Black, 1982). However, they may not highlight the brain mechanisms of joy because such forced motor responses are commonly not accompanied by feelings of mirth.

It is generally believed that positive feelings of humor may require higher brain systems such as those of the frontal lobes, where the right side appears to be especially important for the appreciation of humor (Shammi & Stuss, 1999). A striking recent discovery was the induction of hearty laughter, accompanied by true mirth, during presurgical brain stimulation of a specific frontal cortical area. A 16-year-old girl undergoing this procedure to localize the source of her seizures in the brain was repeatedly overcome by laughter that intensified systematically as brain stimulation was increased. Most strikingly, this led to the projection of mirthful feelings onto "whatever external stimulus was present" (Fried, Wilson, MacDonald, & Behnke, 1998, p. 650).

Our laboratory is presently studying the functionality of 50-kHz chirping in rats, and it is clear that it occurs at a modest level in a large variety of social engagements, for instance, during sexual solicitations and some forms of aggression, and even when rats are anticipating other rewards (e.g., Burgdorf et al., 2000; Knutson et al., 1999). Identification of the key neurochemistries for this response may eventually yield new antidepressants—ones that may actively promote positive social affect as opposed to simply dulling the edge of negative feelings and thoughts. Once the brain chemicals that control laughter in animals are clarified, this knowledge could be used to investigate whether joyful mirth is controlled by corresponding processes in human brains.

LAUGHTER AND HEALTH

Studies of the relationships between positive affect and beneficial

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health outcomes have been proceeding on the heels of pioneers like Norman Cousins (1979), who made "the joyous discovery that ten minutes of genuine belly laughter had an anesthetic effect" that allowed him hours of relief from chronic pain (p. 39). Even biblical scholars asserted that "a merry heart doeth good: like medicine" (Proverbs 17:22). Since then, a modest amount of empirical support has emerged to affirm that humor and laughter may ameliorate pain, alleviate stress, and promote functioning of the immune system.[3] Some of these effects could be due to the release of endogenous opioids (natural, morphinelike pain-control systems) in brain systems that are known to be important in mediating social emotions, such as playfulness and social "warmth" (Panksepp, 1998), although many other brain and body chemistries will surely be involved (Berk et al., 1989).

AND THE OTHER SIDE OF LAUGHTER

Of course, there is a dark side to laughter that I have not emphasized: the derisive laughter that arises from feelings of social scorn. All too often, especially in children (although some adults are not far behind), laughter tends to become a psychological tool for teasing and taunting; the establishment of exclusionary group identities can set the stage for finding mirth in misfortunes of other people. Within-group laughter may promote group solidarity, which may then be used to exhibit disdain toward others and to ostracize those outside the group. In short, laughter can be a tool for "roasting" friends and enemies alike.

The various social and socialization effects of laughter need to be studied more thoroughly. One-sided laughter can certainly become an irritant, perhaps because it signals that the person may be seeking dominance. We must also suspect excessive self-involvement in people who laugh too much at their own remarks.

Similarly, too much laughter can become a social problem, not only in well-regulated places like the schoolroom, but also in more private places: Joubert (1579/1980), in his classic treatise, discussed how laughter can lead to incontinence. Although it is mercifully uncommon for modern children to exhibit "giggling enuresis," it is noteworthy that such eliminative urges can be treated effectively with amphetamine-like drugs like methylphenidate (Sher & Reinberg, 1996). This is the same agent commonly used to treat attention deficit hyperactivity disorder (ADHD). Because such medications are "beneficial" for ADHD partly because they reduce playfulness (Panksepp, 1998), we may wish to inquire what such pharmacological agents do to children's sense of humor.

In sum, one of the great mysteries of laughter and mirth, indeed of emotions in general, is how we project them onto objects and events of the world, and how our affectively skewed cognitions feed back to regulate the intensity of emotional feelings. When one is anxious, everything in the world looks bleaker. When one laughs, everything appears brighter. It seems that joy lowers the neural threshold for perceiving life events as being positive and hopeful, while raising the threshold for perceiving events as negative and hopeless. These simple psychological observations suggest the existence of rather subtle processes and dynamics within mammalian brains—processes about which brain scientists, until quite recently (e.g., Panksepp, 1998), had remarkably little to say. Clearly, incisive research in this area has only just begun.

FUTURE RESEARCH

The mind-body dichotomy that has characterized much of modern psychological thought is eroding as we increasingly appreciate the powerful relationships and interpenetrations between emotional states and bodily functions. Because feelings of mirth may not elaborate fully in the brain without accompanying laughter, the mere study of laughter without a study of the accompanying affect could easily lead to faulty conclusions.

Because of the importance of the topic for understanding our basic emotional nature as well as our sophisticated love of the comic, experimental work on laughter is beginning to attract the attention of investigators who agree that a careful scientific understanding of laughter is a reasonable way to fathom the nature of one form of positive affect and its lubricating effects on social interactions (Provine, 1996). Unfortunately, the amount of substantive research in the field remains meager. It is most difficult to bring such potent experiences into the laboratory, and much of the research may need to be done in naturalistic settings.

What we need to determine now is precisely when laughter occurs in the midst of rough-and-tumble play and other social interactions. What behaviors does it predict? What behaviors does it follow? How does tickling laughter become conditioned in children and other young organisms? How does laughter come to be used for subsidiary social goals? Is shared laughter a potent factor in establishing friendships and social bonds? What is the precise relationship between natural laughter and feelings of mirth? Can laughter and feelings of mirth really change bodily functions and promote health? Where are the neural circuits for laughter and what are

their cardinal neurochemistries? In general, it will be most interesting to know how the readiness to laugh and play are related to the development of psychological resilience, mental health outcomes, and various dimensions of personality, especially in children. The unraveling of the underlying neural circuits in rodent brains may help us address some of these important questions at a basic neuroscience level. *Let* the research begin!

Recommended Reading

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Notes

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2. During the past few years, I have tested this proposition informally with a half dozen children from 3 to 5 years of age. Within their home environments, with their parents present, I was able to make friends with all within a few minutes by gradually escalating tickle games. There are obvious problems, not insurmountable, in trying to replicate such observations in laboratory settings with all the necessary controls.

3. Because of restrictions on the number of citations, please contact the author for relevant references on these topics.

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