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The First Joke: Exploring the Evolutionary Origins of Humor

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Abstract: Humor is a complex cognitive function which often leads to laughter. Contemporary humor theorists have begun to formulate hypotheses outlining the possible innate cognitive structures underlying humor. Humor's conspicuous presence in the behavioral repertoire of humankind invites adaptive explanations. This article explores the possible adaptive features of humor and ponders its evolutionary path through hominid history. Current humor theories and previous evolutionary ideas on humor are reviewed. In addition, scientific fields germane to the evolutionary study of humor are examined: animal models, genetics, children's humor, humor in pathological conditions, neurobiology, humor in traditional societies and cognitive archeology. Candidate selection pressures and associated evolutionary mechanisms are considered. The authors conclude that several evolutionary-related topics such as the origins of language, cognition underlying spiritual feelings, hominid group size, and primate teasing could have special relevance to the origins of humor.

Keywords: humor, evolution, laughter, teasing, language, group size.

Introduction

Evolutionary forces will have shaped, or at least not selected against, any phenotype that has an appreciable connection to genotype and has existed over a number of generations. T. Dobzhansky, the pre-eminent geneticist, emphasized this point in his famous aphorism, "Nothing in biology makes sense, except in the light of evolution" (as cited in Mayr, 2001, p. 39). The ability to generate and perceive humor is a biological process – a cognitive phenotypic trait – almost certainly dependent on a corresponding genetically based neurological substrate. Humor has certainly been around for thousands of years and possibly even a few million years. This article will systematically and briefly review topics that could be germane to the evolutionary origins of humor.

Humor and laughter are closely related; however, they are not synonymous. Humor is the underlying cognitive process that frequently, but not necessarily, leads to laughter. Laughter is a seizure-like activity that can be elicited by experiencing a humorous cognitive stimulus but also other stimuli such as tickling. Thus, one can laugh without a humorous stimulus and similarly one can experience humor without laughter.

The basic ability to perceive humor seems "instinctive" and, thus, likely reliant on genetic machinations. Humor is complex; arguably too complicated to learn without an assemblage of specific neural pathways or an associated cognitive module. Whether something is funny or not is often dependent on nuanced verbal phrasing in combination with a full appreciation of prevailing social dynamics. In fact, humor's inherent opacity yields itself to occasionally be purposely used when ambiguous communication is particularly desired. Humor is ubiquitous and universal, further implicating a genetic substrate. To our knowledge, no culture exists that is unfamiliar with humor. It appears that all healthy individuals reliably comprehend obvious attempts at humor.

Humor has been part of the behavioral repertoire of modern *Homo sapiens* for thousands of years. Ancient Greek texts contain descriptions of "professional" jesters and jokebooks (Bremmer, 1997, pp. 11-18). One of the earliest historical figures to be firmly associated with humor and laughter was the Greek philosopher Democritus. Known as the "laughing philosopher," he not only had a reputation for his mirthful disposition but perhaps also for his tendency to "[laugh] at the stupidity of his fellow citizens" (Bremmer, 1997, p. 17).

Using two pieces of available evidence, a minimum figure for the age of humor can be proposed. First, humorous conversation has been observed by the pioneering anthropologists in first contact with Australian aboriginals (Chewings, 1936; Schulze, 1891). Second, it appears that Australian aboriginals have been essentially genetically isolated for at least 35,000 years (O'Connell and Allen, 1998). If genetic factors dictate the fundamental ability to perceive or produce humor (and barring convergent evolution), then 35,000 years may reflect a minimum age for humor in *Homo sapiens*.

There are several reasons to suppose humor and laughter could be evolutionarily adaptive. As previously mentioned, the complexity of humor implicates an established genetic substrate that in turn could suggest evolutionary adaptiveness. Given that even a simple joke can utilize language skills, theory-of-mind, symbolism, abstract thinking, and social perception, humor may arguably be humankind's most complex cognitive attribute. Despite its ostensible complexity, humor is also paradoxically reflexive – people typically laugh without consciously appreciating all the causal factors. Other human behavioral reflexes such as the corneal reflex or startle response clearly reflect behavioral adaptations. In fact, laughter may perhaps represent an ethological *fixed action pattern*. Supporting this notion are several accounts of runaway pathological laughter originating in various neurological brain insults (Black, 1982; Dabby et al., 2004; McCullagh et al., 1999; Okuda, Chyung, Chin and Waubant, 2005). One could perhaps frame humor in reductionistic ethological terms: exposure to a humorous stimulus induces laughter – a loud multi-second seizure-like signal – that generates a positive emotional state in conspecifics and facilitates further social activity.

Something evolutionarily positive seems to be occurring around humor and laughter – another reason to invite adaptationist thinking. Foremost, laughter is pleasurable and, consequently, a reinforceable behavior. Perhaps, the most overarching use of humorous communication is to help navigate contentious social situations. In addition, humor is widely utilized during courtship (Weisfeld, 1993). Outside the social domain, humor may have modest physiological benefits such as boosting immunity (Bennet, Zeller, Rosenburg, and McCann, 2003, Martin, 2001).

It has been forwarded that there are certain evolutionary costs to humor and laughter - disadvantages that prompt the expectation of countervailing evolutionary advantages. Appreciable physiological energy is spent during vigorous laughter (McGhee, 1983). Almost every culture spends appreciable time communicating in a humorous context. Laughter is noisy and could even attract the attention of predators (Weisfeld, 1993).

If humor and laughter are, in fact, evolutionarily advantageous, a myriad of questions must accordingly follow. How does humor specifically enhance fitness? Which vehicle of selection (individual, kin, or group) most benefits? Invoking the principle of gradualism, how would early or intermediate forms of humor be configured? Which cognitive attributes had to be in place before humor evolved (i.e. language, theory-of-mind)? Have any contemporary cognitive functions been exapted from the neural mechanics of humor?

This article cannot definitively answer all these questions. However, we do intend to methodically explore important areas that could reveal further clues to humor's enigmatic evolutionary history. The first section will review contemporary humor theories including previous evolutionary ideas on humor. The second section will explore a number of topics which could be related to the evolution of humor – 1) animal models, 2) genetics, 3) children's humor, 4) humor in pathological conditions, 5) neurobiology, 6) humor in traditional societies, and 7) cognitive archeology. In addition, the reader is directed to two other reviews, emphasizing different aspects of humor and laughter's evolutionary history (Vaid, 1999; Weisfeld, 1993).

Humor Theories

Because of the multilayered nature of humor, no single humor theory has been completely satisfactory and thus clinched universal acceptance. Plato perhaps expounded the earliest recorded speculations on the subject, although according to Provine (2000, pp. 12-13), he appears to have discussed the effects of laughter rather than humor per se. Aristotle commented on the social effects of laughter (Provine, 2000, pp. 13-14) although evidence exists that one of his lost manuscripts may have "concentrated on humor" (Bremmer and Roodenburg, 1997, p. 4).

Similar to the familiar story about the blind men, each figuring their own unique representation of an elephant, every humor theory seems to reflect a partial truth. Three essential themes, however, are repeatedly observed in the majority of humor theories: 1) humor reflects a set of incongruous conceptualizations, 2) humor involves repressed sexual or aggressive feelings, and 3) humor elevates social status by demonstrating superiority or saving face. These ideas reflect separate cognitive domains and therefore are not necessarily mutually exclusive. Incongruency theories, for example, emphasize the underlying cognitive structure of humor, while the latter two ideas relate putative social purposes to humor. Evolutionary humor theories have emphasized the possible adaptive characteristics of humor and laughter.

1) Incongruity Theories of Humor

Notions that humor involves incongruity can be seen in the writings of Immanuel Kant (LaFollette and Shanks, 1993), Norman Maier (Vaid, 1999), Arthur Schopenhaur (Provine, 2000) and Arthur Koestler (1964). Suls was perhaps the first to formalize the incongruity model of humor by unequivocally demarcating the congruous and incongruous components of humor in his two-stage model (Suls, 1972) According to Suls, solving an incongruity by applying an alternative formulation to the discrepancy forms the basis of humor.

Building on Raskin's (1985) linguistic-semantic theory of verbal humor, T. C. Veatch (1998) has perhaps formulated the most precise and encompassing humor theory. Veatch utilizes the established idea that humor contains two incongruous elements; however in Veatch's formulation, one element is socially normal while the other constitutes a violation of the "subjective moral order." Veatch defines this moral order as the "rich cognitive and emotional system of opinions about the proper order of the social and natural world" (p. 168). Using one of the series of "Mommy, Mommy" jokes as an example:

> Mommy, Mommy! What is a delinquent child?
> Shut up and pass me the crowbar.

The inferred setting is a young child asking his mother an innocent question about a topic the child presumably knows nothing about. The social violation is embedded in mother's incongruous reply – mothers are supposed to disapprove rather than encourage egregious antisocial behavior. The congruency is that it is also natural, to a small extent, to teach your children some non-altruistic strategies in order to more effectively compete with others. Humor is complex and dependent on a myriad of subjective associations. Consequently, its specific makeup is open to subjective interpretation. In this joke, there is arguably a secondary layer of incongruency and an associated resolution. Despite asking, "What is a delinquent child?" it becomes clear that an act of delinquency is precisely what the child is doing. People are supposed to know the essential features of their character and when they don't – that is incongruous. However, children can be exempt from this stringent expectation due to their immaturity and this detail could be the associated resolving element.

There are other factors to consider when determining the funniness of any situation such as how surprised one is by a punch line or the mood of the respective participants. Laughter facilitates laughter in others (Chapman, 1976) and therefore could conceivably cue and enhance humor perception. Also, it has been hypothesized that an optimum state of arousal exists to enjoy humor (Apter and Smith, 1997; Rothbart, 1977). Notwithstanding the lack of clarity around the construct of psychological arousal, entrenched boredom or extreme fear seem to limit laughter.

2) Humor and Laughter originating in repressed expression of sexual or aggressive feelings

The aggressive quality of jokes has been cleverly captured in Mel Brook's amusing characterization of humor, "Tragedy is when I cut my finger. Comedy is when you fall into an open manhole and die." Freud (1905/1963) viewed humor as a release of

excessive sexual or aggressive tension. Framed within his views of the unconscious mind, humor and laughter release the psychic tension related to inhibiting unconscious sexual or aggressive impulses. Expressing laughter is considered anxiety-reducing, pleasurable and healthy. Subsequent researchers have studied various aspects of humor within this framework (Ziv and Gadish, 1990). Although numerous jokes do, in fact, have a hostile edge, many others seem to lack prominent aggressive themes (although it is acknowledged that depending on social context, covert or low level aggression could conceivably be interpreted in any humorous comment).

3) The use of Humor to demonstrate superiority and elevate social status

Several humor thinkers have emphasized how humor is often utilized to demonstrate superiority or elevate social status. Weisfeld (1993) provides several examples such as the Greenland Inuit who "traditionally resolved disputes by engaging in public contests of ridiculing each other" (p. 154). Thomas Hobbes (1651/1981) in Leviathan was the first to clearly articulate this idea, characterizing laughter as an extension of "sudden glory." Critics point out that most jokes do little to boost feelings of superiority.

4) Evolutionary Theories of Humor

In *Expressions of the Emotions in Man and Animals*, Darwin (1872/1920, p. 196) conjectured, "Laughter seems primarily to be the expression of mere joy or happiness." By comparing the behavioral aspects of laughter in "savages," "imbeciles," and apes, Darwin thus implied some evolutionary advantage. He did not address the concept of humor.

Alexander (1986) was one of the first to methodically analyze humor and laughter within an evolutionary context. Advancing an idea clearly rooted in Hobbes' superiority theory, Alexander figured humor led to greater reproductive success by enhancing one's social standing through ostracizing others. Ostracism steers "conflicts and confluences of interest" ultimately altering access to resources. Humor is considered one method of social ostracism. Thus, according to Alexander, the major benefits of telling jokes are varied and include 1) raising one's own status, 2) lowering the status of certain individuals and 3) raising the status of designated listeners and thereby enhancing camaraderie or social unity.

Weisfeld (1993) proposed a general humor theory suggesting humor provides valuable social information to others while laughter provokes pleasurable feelings that positively reinforce the humorist. In return, the humorist gets forthcoming reciprocation by putting an ally in a favorable disposition. It is an interesting hypothesis although difficult to critique given that the mechanics of mammalian cooperation are exceedingly complex and yet unsolved (Wilson, 1975/2000).

Ramachandran's (1998) "false alarm theory" suggests "the main purpose of laughter is for the individual to alert others in the social group that the anomaly detected by that individual is of trivial consequence". The immediate social group would be close relatives who are likely to share similar genes. Ramachandran further speculates that the cognitive perspective necessary to distinguish between trivial and serious could have

somehow evolved into a cognitive framework that classifies congruous and incongruous components of humor.

Noticing that both laughter and social grooming release endogenous opiates, Barrett, Dunbar and Lycett (2002) have speculated that the enjoyment associated with humor eventually replaced the pleasure associated with social grooming in primates. In each case, the feelings of gratification positively reinforce each respective behavior. These ideas are based on the hypothesis that language eventually replaced social grooming as the principal social bonding device between hominids (Dunbar, 1993; Aiello and Dunbar, 1993). In this context, humor and laughter would have facilitated the development of language by maintaining a pleasurable association to conversation.

W. E. Jung (2003) suggests that the fundamental evolutionary purpose of humor and laughter was to facilitate cooperation between people. According to Jung, the ability to attribute mental states to others (theory-of-mind) is humor's most essential feature. His "Inner Eye" theory proposes that "laughter is a signal that facilitates cooperation by transfer of information on the laugher's empathy with attributed mental states and his sympathy levels for others" (p. 245) Ultimately, a laughing response signals that one is both ready and able to cooperate.

Topics Potentially Salient to the Evolution of Humor

1) Animal Models

Perhaps the most primitive ethological behaviour linked to humor and laughter has been contemplated by Van Hooff (1972). He proposed that the possible phylogenetic roots of smiling could reside in the "bared-teeth display" seen in many mammals while laughter could be related to the "relaxed open-mouth display" observed in primates and often associated with playful activities. Panksepp and Burgdorf (2003) have detected a 50 kHz chirp in young rats during social interactions resembling play, and wonder if this positive affective vocalization could be related to human laughter. Certain vocalizations in dogs may also demonstrate parallels to conventional laughter (Simonet, Murphy and Lance, 2001).

When tickled, the higher primates (humans, chimpanzees, gorillas and orang-utans) all display a laughter-like behaviour (Caron, 2002; Fry, 1994). Fry dates the "rudimentary elements of contemporary humor" to 6.5 million years ago - a figure representing the last common ancestor of Homo sapiens and chimpanzees. However, it appears that Fry inadvertently misses the last common ancestor of humans and orang-utans, which is approximately 14 millions old (Dawkins, 2004). This means that the rudimentary origins of laughter could be at least 14 million years old.

Some primate researchers have been struck by the pervasiveness of teasing-like behaviours in captive apes - particularly chimpanzees (Butovskaya and Kozintsev, 1996; De Waal, 1996, p. 114; Gamble, 2001). In contrast, it appears that Goodall (1986) witnessed much less playful teasing behaviour in the wild. Nonetheless, a spectrum of interactions from aggressive confrontations to teasing is apparent in the behavioural repertoire of chimpanzees. Teasing seems more commonly initiated by youngsters in the form of play. For example, young chimpanzees may throw dirt, hit with sticks or jump on

their elders (De Waal, 1996, p. 114). Often, the older chimpanzees will react in a playful manner such as tickling the youngster or engage in a mock chase. De Waal figures that teasing, "serves to gather information about the social environment, and to investigate authority" (p. 114). Butovskaya and Kozintsev frame such teasing as "quasi-aggression". Although the authors are not explicit, the implication seems to be that teasing is a novel mammalian behaviour falling between aggression and peacefulness. The need to readily integrate these two mutually exclusive behavioural states could perhaps have led to the congruous and incongruous elements of humor.

Unlike any other animal, only humans seem to fully possess the cognitive machinations necessary for humor. The use of rich complex symbols within the framework of a universal syntactical structure, in combination with a high-powered working memory invariably leads to intricate conceptualizations. This ability - to quickly manipulate multifaceted symbols in the service of even more intricate conceptualizations - may be an essential distinguishing feature of Homo sapiens (Deacon, 1997). Leaving aside the disputed accounts of the occasional primate combining two words when using sign language, apes undeniably have trouble integrating two juxtaposed conceptualizations (Roberts, 1998).

2) Genetics

The genetics of multifaceted behaviors is just beginning to be systematically investigated. For example, a few twin studies have attempted to parse the relative genetic versus environmental contributions related to humor appreciation (Cherkas et al, 2000; Lichtenstein et al, 2003; Wilson, 1977). These studies have measured personal preferences to various forms of humor rather than humor competence per se. One study found a potential genetic effect for appreciating aggressive jokes (Wilson, 1977).

In the future, various epidemiological characteristics of humor could conceivably point to candidate genes involved in humor perception or production. For example, there may be gender differences in the predilection to laugh, which could implicate sex chromosomes. According to Provine (2000, pp. 27-28) women laugh 126% more than men during conversations with each other. In this particular case, cultural factors such as contemporary gender imbalances in social status are probably more important than genetic differences (it has been observed that persons in higher positions of authority seem to laugh less than those in lower positions).

In a similar vein, bipolar disorder patients (previously known as manic-depressives) clearly have a greater propensity to initiate and enjoy humor during manic episodes (although this too awaits systematic study). Candidate susceptibility genes are being actively investigated for all major psychiatric conditions, however, as of yet, no conclusive chromosomal regions have yet been associated with bipolar disorder. Results from future bipolar genetic studies could conceivably produce a list of genes potentially involved with humor comprehension or production.

3) Children's Humor

Because ontogeny can sometimes recapitulate phylogeny, the maturation of humor in children could perhaps have some evolutionary relevance. It is certainly

conceivable that the various stages of humor development seen in children mimics humor's evolutionary path. In the 1970's, a number of pioneering studies on children's humor were conducted; however, the pace of research has appeared to slacken – perhaps, because these early attempts produced few firm conclusions to build further research upon.

Smiling and laughter occur within the first year of life and are undoubtedly triggered by stimuli separate from the conventional processes associated with adult humor. Laughter in infants could, however, represent an embryonic form of fully developed humor. Using the widest possible definition of humor, Shultz (1976/1996, pp. 11-36) linked four primitive forms of "humor" – smiling in infancy, peek-a-boo, tickling and chase games – to formal incongruity models of humor. Extending Piaget's ideas on the subject, Shultz viewed infant smiling as a pleasurable response to perceived mastery over a situation. Mastery, which brings pleasure, reflects resolution of a previous uncertain and incongruous situation.

The Peek-a-boo game also has possible analogues with conventional humor. Object permanence forms around 6 -12 months and when it is well formed in infants, no explicit anxiety is caused by having items temporarily out-of-view. According to Schultz, it is during this transition en route to object permanence that uncertainty exists during peek-a-boo. Seeing mother's face, for example, solves the incongruency and elicits smiling.

Tickling, chase games, and other forms of play have an intuitive appeal for all children. Darwin (1872/1920) first recognized that the areas most vulnerable to tickling such as the neck, abdomen and soles of the feet are perhaps equally the most vulnerable areas to predator attack. Koestler (1964) framed tickling as a "mock attack" and therefore evolutionary adaptive. According to Shultz, the re-creation of a predatory attack inherently possesses incongruous and congruous parts. Tickling and chase games fall within a certain window of arousal similar to humor (an actual attack would be too arousing and therefore scary and no attack is not arousing at all). Laughter accompanies the reduction in arousal.

By about 7 or 8 years old, children's humor approaches that of an adult although it understandably lacks the same richness. In a series of experiments with children 6, 8, 10, and 12 years, 6 year-olds understood the incongruities in a story but failed to recognize the resolvable elements (Schultz, 1976/1996). Children aged 8 and older appreciated both elements. The timing coincides with the usual advent of concrete operational thought in children. Similarly, theory-of-mind researchers have shown that children under age 6 have a particular difficult time distinguishing lies from jokes (Winner, Brownell, Happe, Blum, and Pincus, 1998).

There have been few cross-cultural studies involving children's humor. Apte's (1985) surveillance of the anthropological literature gleaned two patterns: 1) children mimicking adults in a comical manner may be universal and 2) humor involving ridicule is always more common in children compared to adults.

4) Humor in Pathological Conditions

Because the consequences of brain damage can help connect brain anatomy to function, any deficit in humor perception associated with specific neuropathology has the

potential to be illuminating. It is well known that brain damage, particularly in the frontal lobes, causes deficits of humor appreciation. The precise cerebral areas most closely associated with humor deficits will be reviewed in the next section. The neurological condition most often associated with changes in humor and laughter is epilepsy. For many years, an "epileptic personality" has been described with "humorlessness," a common associated feature (Kaplan and Saddock, 1985). Recent studies have confirmed previous clinical observations – specifically, patients with frontal lobe epilepsy demonstrate deficits in humor appreciation (Farrant et al, 2005). Gelastic seizures, also known as laughter epilepsy, are most commonly associated with hypothalamic hamartomata (benign hypothalamic malformations consisting of heterotopic nervous tissue) but can also arise from the frontal or temporal lobes (Pearce, 2004).

Among psychiatric conditions, only schizophrenia has been systematically shown to be accompanied by humor perception deficits (Corcoran, Cahill, and Frith, 1997; Polimeni and Reiss, 2006). Anecdotal observations of humorlessness in severe obsessive-compulsive disorder have not been methodically investigated.

To our knowledge, humor perception in clinical depression has also not been systematically explored although clinical observation suggests no appreciable deficits. Anyone who has grieved recognizes that although we may be less inclined to laugh, our ability to perceive humor is more or less preserved.

The best documented case of a laughing epidemic originated in Tanzanian schoolchildren in 1962 (Rankin and Philip, 1963). Over two hundred adolescents and young adults were overcome by recurrent bouts of hysterical laughter and crying over a period of a few months. Although no initiating factor was ever discovered, this incident exemplifies the social and contagious aspects of laughter.

5) Neurobiology

An outline of the brain areas responsible for humor appreciation is beginning to emerge (Wild, Rodden, Grodd, and Ruch, 2003). Delineation of the neural pathways responsible for humor could have evolutionary significance, especially if the phylogenic history of the human brain could be precisely retraced. The elucidation of the neurobiology of humor has benefited from two approaches: 1) observing the effects of various brain lesions on humor perception and 2) functional magnetic resonance imaging (fMRI) studies which monitor brain activity in normal subjects while perceiving humor.

Thirty years ago, Gardner, Ling, Flamm, and Silverman (1975) demonstrated humor deficits in both left and right hemispheric damaged subjects. However, subtle distinctions between subjects may not have been possible since all sixty subjects were inpatients and therefore likely to have had considerable cognitive impairment. A study by Dagge and Hartje (1985) using a continuum of simple to complex cartoons showed that patients with right-sided lesions fared worse than left-sided patients and both groups inferior to controls.

Perhaps the most comprehensive study to date utilizing brain lesioned individuals in order to localize humor centers was conducted by Shammi and Stuss (1999). They administered various humor tests to 21 right-handed individuals with focal brain damage documented by CT or MRI, and compared them to 10 controls. In addition, they administered a general battery of cognitive tests. They concluded that right frontal lobe

lesions (particularly Brodman areas 8, 9, 10) most disrupted humor appreciation. However, it was not clear whether subjects with right-sided lesions demonstrated greater general impairment (because the results of the accompanying cognitive battery were not available). Furthermore, only five subjects possessed impairment from singular frontal lesions (R = 3, L = 2). Of note, deficits in working memory, mental shifting and verbal abstraction significantly correlated with poor humor appreciation for all subjects. This study exposes one of the most formidable problems in humor cognitive research –that the integrity of humor perception is subservient to numerous cognitive skills such as working memory, long-term memory, executive functions, emotional expression and language skills.

Three functional magnetic resonance imaging (fMRI) experiments involving humor in unimpaired participants have been published to date. FMRI is an especially appealing new technology because it allows non-invasive measurement of localized brain activity during various cognitive-behavioral tasks. However, fMRI is characterized by low signal-to-noise ratios and other potential confounding variables, which can easily produce inconsistent results between various research groups.

Using event-related fMRI, Goel and Dolan (2001) observed differences in neural activations between semantic and phonological jokes – the former preferentially activating bilateral temporal lobes while the latter predominantly accessing a left hemispheric network centered around speech production regions. Activation in the medial ventral prefrontal cortex (MVPFC) bilaterally correlated with how funny a joke was rated. The authors suggest their results indicate "the affective appreciation of humor involves access to a central reward system in the MVPFC" (p. 238).

Moran, Wig, Adams, Janata, and Kelley (2004) monitored humor detection versus humor appreciation using *The Simpsons* and *Seinfeld* comedies in an event-related fMRI experiment. They found significant activations in the left posterior middle temporal gyrus and left inferior frontal gyrus, with additional activations in the bilateral anterior temporal cortex, left inferior temporal gyrus, right posterior middle temporal gyrus and right cerebellum. Of note, the authors point out that the left inferior frontal cortex has been previously associated with "reconciling ambiguous semantic content with stored knowledge" (p. 1058).

Mobbs, Greicius, Abdel-Azim, Menon, and Reiss (2003) event related fMRI study used captioned funny cartoons versus non funny ones and showed that humorous content primarily activated, the left temporal-occipital junction, left inferior frontal gyrus, left temporal pole, left supplementary motor area, left dorsal anterior cingulate and bilateral subcortical structures including ventral striatum, nucleus accumbens, ventral tegmentum area and amygdale, which are key components of the mesolimbic dopaminergic reward system. The authors point out a similar pattern is commonly observed in "monetary and video-game reward tasks" (p. 1043).

Consolidating the results of all neuroanatomical humor perception studies reveals two general patterns: 1) the integrity of humor may rely more heavily on right-hemispheric structures (although recent fMRI results are not entirely in accordance with the brain lesion studies pointing towards greater right-side involvement) and 2) the prefrontal cortex seems intimately involved (the involvement of the temporal lobes is probably related to the language component of humor). The natural question that follows

is what can these two tentative conclusions tell us about the evolution of humor in human beings?

The right hemisphere appears to be preferentially involved in the "interpretation of emotional material presented linguistically" or more broadly, the "expression and comprehension of emotion" (Edwards-Lee and Saul, 1999, pp. 310- 311). In addition, the right hemisphere may be more instrumental in maintaining "global attention to the environment" (Edwards-Lee and Saul, 1999, p. 306). Both characteristics could be essential to humor appreciation and may explain why right-sided lesions seem to disrupt humor perception more than left-sided pathology. Cerebral asymmetry is most pronounced in humans compared to any other animal and this may perhaps be due to the need to accommodate language (Banyas, 1999. p. 97; Deacon, 1997, p. 309). The possible evolutionary relationship between language and humor will be addressed in a subsequent section.

The prefrontal cortex is a part of the brain consistently associated with higher cognitive functions. Attentional tasks, executive functions, cognitive flexibility and incorporation of emotional behavior are higher cognitive functions generally affiliated with the prefrontal cortex (Fuster, 1997, p. 251; Grady, 1999, p. 197). Semantic memory retrieval, episodic memory, working memory and theory of mind are more specific cognitive skills also repeatedly linked to prefrontal cortical structures (Grady, 1999, pp. 203-205). Additionally, the subcortical dopaminergic reward system projects to the prefrontal cortex (Schultz, 2000).

The prefrontal cortex appears to be a distinguishing cerebral feature in the evolution of man. In primates, the prefrontal cortex consists of 3 major regions (but only 2 regions in other mammals) (Streidter, 2005, p. 307). The "lateral prefrontal region, namely area 10 is almost twice as large (percentagewise) in humans as in other apes" (Striedter, 2005, p. 329). It is therefore not surprising that such a seemingly complex mental activity like humor would be anatomically affiliated with the prefrontal cortex.

6) Humor in Traditional Societies

Modern culture has a remarkable ability to transform adaptive behaviors so completely that it makes it difficult to comprehend why certain behavioral propensities exist at all. Listening to music alone through headphones for hours couldn't possibly be adaptive; however, witnessing a ceremony of song and dance in preparation for tribal warfare puts an entirely different perspective on the potential evolutionary functions of music. Similarly, can the use of humor in traditional societies provide any insight to the possible evolutionary purposes of humor?

Despite language and cultural barriers, humor in traditional societies is generally comprehensible to visiting anthropologists (Schiefenhövel, 1984). For example, Wulf Schiefenhovel, who spent a number of years in the highlands of West New Guinea, had no significant trouble comprehending humor in the Eipo (personal communication, March, 2005). This seems to be the prevailing perspective whenever anthropologists comment on humor in traditional societies (Turnbull, 1961/1968).

Two humor phenomena especially standout in the anthropological literature: joking relationships and clowns. Since the turn of the century, various anthropologists have noted certain kinships ties are accompanied by greater joviality and humor. Despite

the lack of a satisfactory operational definition, Mahedev Apte's (1985) synthesis of joking relationships, nevertheless, reveals several interesting patterns. First, joking relationships in preliterate societies are most commonly observed between extended relatives. Nuclear families do not typically communicate extensively in this manner. Siblings-in-law and cousins, particularly of the opposite sex, seem to most readily demonstrate humor in their conversations. Second, there are definite customary expectations associated with some joking relationships. The most common expectation is that the participants not take offense. Third, a variety of topics are typically involved in joking relationships although sexual humor between sibling-in-laws of opposite sex is commonly witnessed. Reducing potential conflict and aggression is the usual explanation for this type of communication.

Tribal clowns, from several different continents, are described in a variety of cultures. Turnbull noted, for example, that each Mbuti band seemed to have an unofficially designated clown. "His function is to act as a buff between disputants, deflecting the more serious disputes away from their original sources, absolving other individuals of blame by accepting it himself" (Turnbull, 1965, p. 183). The tribal clown, typically male, can also have a more formalized position, particularly in native North American tribes. Apte (1985) refers to them as "ritual clowns" and some descriptions cross over with shamanism. Since shamanistic experiences can resemble psychotic symptoms, one naturally wonders whether this reflects underlying mania in the individual. Ritual clowns have been known to act in an exaggerated feminine manner, spoof neighboring tribes, mock formal religious ceremonies and utter sexual or obscene humor (Apte, 1985).

In an attempt to methodically assess humor in traditional societies, our group had three independent raters judge 95 humorous situations from ten hunting and gathering societies. Using the eHRAF (Human Relation Area Files) database, we searched ethnographic texts for 30 words (laugh, joke, humor, funny, tease, giggle, etc…) that could perhaps reveal humorous situations. The eHRAF Collection of Ethnography is an online cross-cultural database containing over 350,000 pages of information about many world-wide cultures, including numerous accounts of the first Western contact with a number of hunting and gathering societies. The ethnographic search was confined to ten hunting and gathering cultures (Bororo, Mbuti, Aranda, Assiniboine, Copper Inuit, Trobrianders, Tlinglit, Chukchee, Kapauka and Yanomamo) chosen because of the authors' familiarity with literature related to these cultures. For a humorous account to be included, at least one native participant had to laugh or acknowledge the humorous situation. Accounts that were incomprehensible (uncommon) or humorous situations directly involving the ethnographer were excluded. For each humorous account, we explored nine possible functions of humor: 1) expressing superiority, 2) indirect expression of anger, 3) indirect expression of sexual feelings, 4) desire for approval or diverting attention from a misdeed (saving face), 5) signaling affiliation to a specific subset of individuals, 6) enhancing group cohesiveness or settling differences in a positive manner, 7) signaling to others that a discrepancy or anomaly is trivial (Ramachandran, 1998), 8) expressing an idea that is simultaneously normal but also violates a social or moral expectation (Veatch, 1998), and 9) play. Inter-rater reliability was poor (52% with random chance being 33%) and, therefore, no firm conclusions

could be drawn. This substandard data exemplifies how difficult it is to analyze something as indistinct and ambiguous as humor.

Reviewing the 95 humorous situations led us to the same broad conclusions as previous anthropologists – that humor in traditional societies grossly appears similar to our own. Examples involved such varied situations as laughter at the antics of children, lewd comments, sexual jokes, teasing, mocking others who were too serious or in positions of authority, spousal jibes, slapstick maneuvers, uncomfortable laughter to save face, and humor to quell conflicts within a tribe. One particularly unsettling example of humor involved the brutal but perhaps necessary Inuit custom of occasionally sacrificing one twin infant to save the other. Resembling the Freudian concept of reaction formation, "One woman laughed over a baby girl she had killed two or three years before, and said that it had provided the foxes with a good meal" (Jenness, 1886/1969, p. 166).

7) Cognitive Archeology

a) Humor and Language

There is no way to know with certainty when humor evolved relative to language although it would appear that at least sophisticated humor must have succeeded language. The credible range for the origins of language lands between a few hundred thousand years to about 2-4 million years ago. The authors tend to side with those linguists who date the origins of language to coincide with the first appreciable increase of brain size about 2 million years ago (Deacon, 1997). For example, one Homo habilis brain cast (2.4 – 1.5 MYA) shows a bulge which seems to represent Broca's area (Banyas, 1999, pp. 95-99). The precise syntactical evolution of protolanguages are, for now, indeterminate.

In our view, larger brains seem to be fundamentally related to language because the majority of higher cognitive functions appear to have been "designed" specifically to support language functions. Working memory, long-term memory, executive functions and rich associative thinking make significant demands on neural networks and are simultaneously integral to language function. Capacity for theory-of-mind and other enhanced social abilities may also necessitate significant cerebral computing power. Other plausible but less convincing candidates responsible for the initial enlargement of ancient human brains are visual-spatial skills (to hunt) and fine motor control of hands (tool use, hunting).

One does not need words to convey humor; however, conversation greatly enhances the opportunity for humorous expression. Consequently, humor usually utilizes a string of complex symbols (words). If incongruency based humor theories are on the right track, the vast majority of humor shared between people must involve, at minimum, several intricate symbols (words) and two concepts (incongruous and congruous). Disparate words can be similar but never truly identical in meaning. Each word has its own unique fingerprint of manifold connotations (associations) which slightly changes its meaning. Remove one subtle connotation and you can significantly lessen the humor of any given statement – this explains why comedians choose their words carefully and why so many jokes cannot withstand translation. At the risk of stating the obvious, at the very least, the full expression of humor in contemporary humans is fundamentally contingent on language.

"A concept or category is said to have been learned when an organism responds to a group of stimuli in the same way because these stimuli have common properties" (Roberts, 1998, p. 356). Within this definition, even pigeons have demonstrated rudimentary concept recognition. Using American Sign Language, the famous chimpanzee, Washoe, seems to have "invented" 2 or 3 word combinations to describe singular objects such as "water bird" after spotting a swan and "candy fruit" after tasting watermelon (Roberts, 1998). An alternative explanation would be that Washoe was just describing various aspects of her experience without any significant sense of the relationship between the two ideas. In any case, Washoe's sporadic and simple juxtaposition of 2 or 3 word combinations would probably reflect an upper limit of a chimpanzee's ability to instantly manipulate more than one abstract concept.

In a recent article, Hauser, Chomsky and Techumseh Fitch (2002) hypothesize that syntactical recursion is a defining feature of Homo sapiens. In simple terms, linguistic recursion is the ability to construct a phrase within a phrase indefinitely (only limited by the constraints of memory) to create an almost limitless number of ideas. Again, using incongruency based humor theories as our framework, there could be similarities between syntactical recursion (the ability to form a concept within a concept) and humor's apparent juxtaposition of a congruous and incongruous idea. If recursion is a truly special cognitive ability, it could have conceivably been co-opted by other evolving cognitive traits, like humor.

b) Milestones in Human Evolution

In addition to language, are there any other milestones in human evolution that must have either come before or after the advent of humorous thinking? The complexity of various tool technologies (Oldowan, Mousterian, Acheulean and Upper Paleolithic) has improved through human evolution. However, the enhanced appreciation for causality or visual spatial skills presumably necessary for more sophisticated tool development (Geary, 2005; Povinelli, 2000) does not readily lend itself to be compared with humor skills. The betterment of social intelligence through such "cognitive modules" as theory-of-mind or cheater-detection would also seem integral to humor development; however, the evolutionary timing of various social skills is, as of yet, undetermined.

There is increasing evidence that a new level of symbolic thought was achieved around 50,000 years ago. A figurine integrating the head of a lion with the legs of a person dated around 32,000 years old is among the earliest evidence for symbolic art (Mithen, 1996). Placing importance on items that integrate complementing facets (human legs and lion head) from two disparate categories (lion and person) does bear a certain resemblance to the postulated integration of the congruent and incongruent aspects of humor.

Evidence for spirituality also begins around this time through archeological depictions resembling contemporary shamanistic art. Because of the presumed fluidity in thinking involved, the cognitive innovation behind spirituality could also somehow be related to humor. Interestingly, Pascal Boyer's (2001) theory on the cognitive mechanics of spirituality bears a striking resemblance to Veatch's hypothesized cognitive structure of humor. Boyer's theory says that all magico-religious thinking consists of a direct

violation of an ontological category - the five most basic ontological categories are person, animal, plant, tool and natural object. For example, a zombie or ghost is a spiritual idea because being dead is a direct violation of an essential quality related to being a person. In contrast, a person with five arms may be unusual but the concept would not be a spiritual thought because it does not violate the essence of a living person. Boyer's theory broadly applies to all forms of spirituality and magico-religious thinking, including shamanistic spirituality, magic rituals and modern religions.

Humor can perhaps be framed as an incongruent social concept "violating" the essence of a congruent social concept. Recall, that in Veatch's humor theory, acting in a socially bizarre or "incongruent" manner is not enough to be funny – the incongruency must violate the "subjective moral order". Therefore, the term "incongruent" so often used in humor literature may be analogous to Boyer's term "violation" and Veatch's "subjective moral order" may be akin to an ontological category.

If humor and spirituality are related, which trait is phylogenetically older? Assuming animal models for humor have some merit, spirituality could be an exaptation succeeding humor. The similarities between humor and spirituality are certainly intriguing and worthy of further analysis.

c) Humor and Group Size

Dunbar (1993) has put forward a theory that, in primates, neocortical size is proportional to group size and that language ultimately replaced grooming as the primary social bond (Aeillo and Dunbar, 1993). Furthermore, laughter could have been the affirming social "bonding agent" which replaced the positive reinforcing experience of physical touch (Barrett, Dunbar and Lycett, 2002, p. 346). Dunbar could well be on the right track since there appears to be a richer rationalization behind his proposition.

Nicely captured in Frans De Waal's (1982) phrase "chimpanzee politics," primate life is characterized by constant negotiations between empathic and aggressive tendencies. Grooming engenders pleasurable feelings that countervail aggressive tendencies. But with language replacing grooming, what mitigates aggressive tendencies between lesser-related individuals? Humor seems to inject positive feelings while hierarchal competition and other minor social quarrels are being worked out. Humor can't control pernicious disputes but for the more mundane disagreements, it diminishes the risk of a contentious issue deteriorating to violence. Much has been written about the anthropological study of violence within tribes because of its potential relevance to hominid evolution - humor may be an essential part of the story.

Another reason why humor may be linked to group size is because humor and laughter are candidate group-selected traits (Gervais and Wilson, 2005; Wilson and Sober, 1994). Humor is a form of complex communication - a trait only seen when animals aggregate with lesser related individuals. Laughter is preferentially shared by lesser related individuals and non-kin. Humor is not deceptive in nature – in fact, it is just the opposite. Although humor can be used to probe social issues or advance personal agendas, the bulk of information revealed by humor is shared by the community and therefore can be considered altruistic. Although humor perception appears to be quite uniform, greater variability is observed on the production side (greater variability in a trait could suggest a group selected trait through adaptive specialization). Clowns (or

other funny people) could represent "humor specialists," evolved to reduce tense social situations through humorous injections.

Conclusion

Humor is a fascinating cognitive function. The relative ease in how we use it belies its considerable complexity. Humor appears to be a function of Homo sapiens' augmented social abilities and as an extension of language, could perhaps be the most complex cognitive function in the animal kingdom. We have reviewed the major structural and evolutionary theories of humor, in addition to a number of topics potentially relevant to deciphering the origins of humor – animal models, genetics, children's humor, humor in pathological conditions, neurobiology, humor in traditional societies and cognitive archeology. In our view, the origins of language, spirituality, hominid group size and animal teasing may have particular relevance to humor. A number of humankind's higher cognitive functions could well be inextricably rooted in humor's evolutionary history, thus making this subject worthy of further exploration.

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