
Male Production of Humor Produced by Sexually Selected Psychological Adaptations

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Influenced by Hollywood and the theatrics of a beauty pageant won by her mother, a former Mrs. Los Angeles, a young girl decided she would become an actress when she grew up. Years later, while making her first steps into show business, the aspiring actress, imbued with her mother's sense of style and independence, was about to audition for a role in a new play on Broadway, a big opportunity to launch her acting career. The little known clumsy-looking playwright, who was also the director and the lead actor in the play, was conducting auditions to find the leading female role, his onstage companion. This was only his second play, and he was waiting to make a breakthrough of his own. The actress auditioned successfully for her role as Linda Christie, a performance that earned her a Tony nomination. The play, *Play It Again Sam*, was a big hit and was turned into a film, starring her, Diane Keaton, and Woody Allen, the writer, director, and actor. And just as the two insecure characters on the stage fall in love, the two actors also fell for each other in real life (Keaton, 2012).

What attracted Keaton to Allen, who by most accounts is not considered a physically attractive man? In her autobiography, Keaton, who is 11 years his junior (and 2 in. taller), attributed her enchantment with Allen to his sense of humor.

Upon meeting Allen for the first time, she wrote to her mother: "Woody Allen is cute, and of course very funny" (p. 61), and what really got her was that he was "...looking down in a self-deprecating way while he told jokes like... 'I'd rather be with a beautiful woman than anything else except my stamp collection.'" She was charmed by him, captivated by his jokes, recalling "I was a good audience. I laughed in between the jokes. I think he liked that..." (pp. 86–87).

Keaton's attraction to Allen's sense of humor and personality and Allen's successful endeavors to woo her with his wit are a good example of the importance of humor creativity in mating. The story about Allen, whose self-deprecation and funniness allure Keaton, might be only one anecdote, but nonetheless, it reveals a larger truth about how humor is used to attract mates. As we will see, humor plays an important role in mate choice, a role in which males and females are not equal partakers. Men and women view humor differently, and their motivations, experiences, usage, and consumption of humor are not the same. These differences might be best understood in light of sexual selection theory and by looking at the distinct evolutionary forces that shaped the psychological adaptations of men and women.

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What Is Humor?

Before delving into the evolutionary roots of humor, it is important to discuss the notion

of humor. Developing a comprehensive theory of humor poses a challenge because any attempt at framing such a broad topic often results in more questions than answers. Is humor a distinct concept that can be easily recognized and defined? What does it mean to say that someone has a good sense of humor? What is the quality that he or she possesses? Is there even agreement of what constitutes a humorous event and what does not? Philosophers and researchers have been debating the definition of humor for centuries and searching for an ultimate and complete theory of humor, one that explains all humor formations and occurrences and elucidates what makes things funny (Martin, 2007; Morreall, 1987; Schmidt & Williams, 1971). One of the main difficulties in defining humor or finding a comprehensive theory of humor is that humor can be seen as a personality trait, a habitual behavior, a temperament, an ability, or an attitude (Feingold & Mazzella, 1991; Greengross & Miller, 2011; Martin, 2003, 2007; Ruch, 1998, 2004). Humor appears easier to recognize than define, and most people have some intuitive sense of what humor is. But people also use the term to refer to many different experiences and usages and do not always agree about what comprises a humorous episode. It is outside the scope of this chapter to introduce a complete review of humor theories, but I will highlight a few key features pertaining to the understanding of humor, especially as a social phenomenon. These will help illustrate the complexity of the humor experience and assist in evaluation of any theory which tries to explicate humor.

Sense of humor also largely depends on the context in which it is used and the interactions between the participants in the situation. What is funny and what is not largely depend on the individual assessing the humor and the context in which humor is used. The best example is the contagious nature of laughter. Most laughter takes place in spontaneous social situations, usually in response to other people's sayings or actions. The presence of other people, and their audible laughter, increases the amount of

laughter produced by an individual (Martin & Kuiper, 1999; Provine, 2000; Provine & Fischer, 1989). This contagious laughter effect is well known to comedy show producers, who use laugh tracks to boost audience laughter (Graziano & Bryant, 1998; Smyth & Fuller, 1972). Different moods also affect our perception of humor and can increase or reduce the amount of laughter produced (Deckers, 1998; Martin & Lefcourt, 1983). These effects underline the notion that to some degree, humor is a subjective experience, depending on external and internal cues. In order to recognize that something is funny, we cannot focus solely on the stimulus itself but must take into account the circumstances around it. We need a person to process and interpret the stimulus and decide whether or not it is funny. By emphasizing the subjective experience of humor, we concede that it is not always possible to understand why someone finds something funny. For example, seeing a person slipping on a banana peel would be viewed by many as a funny event, but others may recoil at the view of a person falling down and would not deem the incident funny. We cannot disconnect the event itself from the cognitive processes of the person viewing the incident.

On the other hand, it is important to recognize that humor is, to some extent, objective, and there is agreement among people about what is funny and what is not. If this were not the case, comedy shows and stand-up comedians could not possibly succeed in appealing to wide audiences. These objective types of humor usually come in the form of jokes and are somewhat easier to analyze than more spontaneous, unscripted humor. Jokes are self-contained units of analysis and usually devoid of social context or external cues that might influence their evaluation for funniness. This is why jokes are frequently used in humor research as stimuli, where researchers can disband the different parts of a joke, to try to understand how the incompatible parts produce humor (Attardo, 1994; Raskin, 1984).

One simple way to characterize humor is by defining it as anything that makes an individual laugh. While still emphasizing the subjective experience of humor, this definition allows for people to respond to the same stimulus differently. One advantage of using such a simple, even simplistic, approach is that it is quite comprehensive in capturing a wide range of humorous events. The rudimentary definition is very intuitive and enables both researchers and laymen to agree on what constitutes a humorous event, without needing to apply a sophisticated definition, one that is more detached from everyday uses of humor.

Nevertheless, defining humor by its relationship with laughter has limitations. Though humor and laughter are strongly intertwined, the relationship between them is more complex, and the two are distinct concepts. While there is much overlap between humor and laughter, not everything that is considered funny makes people laugh, and not every laugh indicates the existence of humor. For example, tickling causes an involuntary laughter but there is nothing funny about the situation, and most people are irritated by it. In other cases, an individual can appreciate a joke but would not laugh out loud in response, for example, when consuming humor alone. A more complicated situation is when we recognize an attempt to tell a joke, but do not find it very funny and, therefore, do not laugh. This attempted humor does not generate laughter, though may count as humor in the view of the joke teller. Other times, people laugh when no obvious funny stimulus is present, as when they are nervous, or in some pathologies, following neurological damage, such as a stroke (Oh, Kim, Kim, Park, & Lee, 2007).

A central part of understanding humor is viewing it as a social phenomenon. Studies show that most accounts of everyday laughter arise in response to mundane comments during routine conversations, not in response to purposeful attempts to make others laugh. Provine (1993, 2000) documented pre-laugh comments that elicited laughter among listeners in regular, everyday conversations. He found out that only about 10–20 % of the comments were considered

remotely funny. Remarks such as “I’ll see you guys later” or “It was nice meeting you, too” tended to generate the most laughter. It is unclear though if such comments were perceived as humorous by the appreciators or their laughter was just an indication of social gesture. As argued before, humor is partially subjective, and the fact that for an outsider these comments were not perceived even marginally humorous does not preclude that for the people involved in those conversations, these ordinary statements were meaningful and funny. Nonetheless, it is important to acknowledge that jokes, laughter, and humor are not synonyms to each other but are distinct concepts. This is especially important because many people do perceive these concepts as the same, and most humor research focuses on analysis of jokes, or uses them as stimuli in lab experiments, as a proxy for humor.

Another key feature that helps to construe humor in its social context is the distinction between the joke teller and the appreciator, especially in the context of spontaneous humor. Many people view humor as a unified construct, not separating the producer of humor from the receiver. This dissociation is crucial since there are clear differences between the humor producer and the appreciator. The motivations to initiate humor are often very different from the impetus of those who want to enjoy humor, and being funny is much harder than just appreciating humor. Thus, when discussing humor, one must focus separately on the roles of the humor producer and the humor appreciator and their unique contributions to the existence of the humorous event. This is especially true for understanding the evolutionary roots of humor, since humor evolved within a social context, and even more so when looking at the roles men and women play in that regard.

There is little doubt that sense of humor is a multidimensional construct that includes social, developmental, emotional, cognitive, and biological aspects (Gervais & Wilson, 2005; Mobbs, Hagan, Azim, Menon, & Reiss, 2005; O’Quin & Derks, 1997). The points raised here are not intended to confuse the reader, or take an extreme view that there is no such a thing as

humor, but rather to challenge the visceral feeling most people have that humor is ostensibly easy to conceptualize and define. Nonetheless, we should also not lose sight of the larger picture, that is, that no matter how evasive the definition of humor is, it plays a large role in people's lives. As Martin (2007, p. 3) concluded: "being able to enjoy humor and express it through laughter seems to be an essential part of what it means to be human."

Evolutionary Roots of Humor

There is no consensus among researchers regarding the ultimate function of humor, but most evolutionary theories can be explained by the processes of natural selection and sexual selection. Natural selection explanations center on how humor can help individuals to survive. Humor could potentially contribute to one's health, prolong life, or help avoid dangerous situations that could reduce survivorship, either directly or indirectly. Explanations focusing on sexual selection theory emphasize the importance that humor plays in finding a mate and how it can enhance the chances of reproducing successfully.

How Do We Know That Humor Has an Evolutionary Basis?

Humor is a universal phenomenon, enjoyed daily by people of all ages, in both tribal and industrialized societies, though the exact uses and experiences vary (Apte, 1985; Davies, 1998; Martin, 2007; Weisfeld, 1993). Basic mechanisms such as surprise and incongruity in non-serious social interactions are universal in eliciting humor and producing physiological responses of mirth (Gervais & Wilson, 2005). In addition to the universality of humor, smiling and laughter have been documented not only in all human societies but also in other species, especially apes and primates (Gamble, 2001;

Preuschoft & Van-Hooff, 1997). In primates, there are two distinct facial expressions that are presumed to be homologous to human smiles and laughter. The silent bared teeth display is equivalent to the human smile and appears as a sign of submissive appeasement that leads to an inhibition of aggression in the receiver, while the relaxed open mouth display, homologous to human laughter, appears in social play as a sign of enjoyment. While these two displays are quite distinct in apes and emerge only in specific situations, they appear to converge in humans. Humans smile and laugh interchangeably in response to the same stimuli, and the smile or laughter might reflect the magnitude of joy and not the nature of the interaction as with other apes. Research suggests that laughter might have emerged deep in our evolutionary history, even as far back as rats (Panksepp, 2007; Panksepp & Burgdorf, 2003). Rats seek to be tickled by pursuing the tickling stimuli (usually a hand), which suggest they enjoy it, and tickling them produces high-frequency chirping sound, which some view as an antecedent to primitive laughter.

Support for the view that humor is well rooted in our evolutionary history comes from the fact that smile and laughter develop about the same time, early and spontaneously, in every culture in the world (Bergen, 1998; McGhee, 1979). Babies who are just born smile reflexively and start laughing vocally at about 2–4 months of age. As with many other basic facial expressions, smiles and laughs develop before language and have stereotypical expression and sounds (Ekman, 1993; Provine, 2000). People in virtually every culture in the world recognize a genuine smile (the Duchenne smile, named after the French neurologist Duchenne de Boulogne) and laughter presented to them from other cultures and attribute the correct emotion of mirth to them (Keltner & Ekman, 1994). Even babies who are born blind or deaf smile and laugh involuntarily, not needing to see or hear others around them, lending support to the notion that smile and laughter are not restricted by culture (Freedman, 1964).

Evolutionary Mechanisms That Could Explain Humor

The various evolutionary theories offered over the years to explain the adaptive function of humor vary in scope and illuminate different aspects of humor and laughter. The first of these theories was proposed by Charles Darwin himself, in his seminal work, *The Expression of the Emotions in Man and Animals* (Darwin, 1872). Darwin contemplates what function humor and laughter may confer, among other emotions and behaviors. Darwin considered humor to be “tickling of the mind,” a stimulus in the brain that produces laughter and brings joy or happiness. Laughter, in his view, occurs when an unexpected idea or a surprising event transpires, but only while the mind is in a “pleasurable condition.” Because the incongruity needs a resolution, there is a pressure of nervous energy building up in the body that needs to be discharged. Laughter serves as the medium that frees all the superfluous energy from the body. This explanation is a variant of one of the classical theories of humor, the incongruity-resolution theory (Beattie, 1778; Koestler, 1964).

Play and Humor

Researchers noted that much laughter occurs during social play, especially among children (Bergen, 1998). This connection led to the hypothesis that humor evolved from social play (Preuschoft & Van-Hooff, 1997; Van-Hooff & Preuschoft, 2003; Vettin & Todt, 2005). Children all over the world laugh the most during play, and similar to other primates, it largely arises during chase and fleeing games or wrestling with each other (McGhee, 1979). In many primates, rates of affinity among chimpanzees and other primates increase following relaxed open mouth display (the equivalent to human laughter), a display that is observed primarily during such play (Preuschoft & Van-Hooff, 1997).

Play might serve as a safe environment to rehearse and develop the physical and social skills children will need as adults, such as social

bonding and cooperation, that will later contribute to their survival. The laughter that accompanies such play signals to the participants that the activity is playful, without serious ramifications (McGhee, 1979). Moreover, humor may serve another function that scuffling has among children and other primates, a ritual or symbolic fighting that has a winner or loser without seriously hurting any of the participants (Pinker, 1997). Children and primates practice play wrestling among themselves, and the tickling and laughter involved indicate that it is “just for fun.” As adults, instead of getting involved in a physical fight, people can use humor as a refined tool to undermine superior authorities, a way to gain status or put down others, and a weapon that carries no physical risk for the individual. Laughter, therefore, indicates for both children and adults that the aggression is not real, and by using humor effectively, people can poke fun at others without putting themselves in harm’s way.

Social Function

Prima facie, humor does not seem to provide obvious survival benefits. Nonetheless, many evolutionary explanations for humor focus on the possibility that humor can contribute to one’s survivorship, either directly or indirectly, especially within the social domain. Humor serves many social functions, such as helping break down interpersonal barriers or as an ice-breaker in awkward situations or among strangers (Martin, 2007). As discussed earlier, people are much more likely to laugh when they are surrounded by others, which led researchers to hypothesize that humor evolved to facilitate bonding in social groups, as a way to promote cooperation, mitigate conflicts, or help identify in-group members (Flamson & Barrett, 2008; Gervais & Wilson, 2005). Cooperation is one of the most important features that makes humans so successful as a species. Our hominid ancestors learned that acting alone in harsh environments was too costly and risky, and cooperation among group members became increasingly important for survivorship. To facilitate such cooperation, there must be some social

mechanism that could coordinate the actions of everyone involved. Humor and laughter can serve such a function by inducing a playful mind-set that is shared by all members in the group at a given time (Gervais & Wilson, 2005). Laughter is contagious, and when everyone in the group laughs and shares the same feeling, it is easier to work together and reach the group's goals. Additionally, it might confer a benefit to the group as a whole, giving it a competitive advantage over other, less mirthful groups, though this view of group selection is less sustainable and poses serious challenges to standard evolutionary thought (Williams, 1966).

Circuit Breaker

Humor can also aid in easing the tension before a dangerous situation has the potential to deteriorate further. One evolutionary hypothesis posits that humor evolved to serve as a disabling mechanism, operating like a circuit breaker or a safety valve (Chafe, 1987). When people laugh, they are immediately distracted from anything else, and hence, laughter prevents them from doing things that are counterproductive, damaging, or even disastrous. In this view, humor is an adaptive mechanism whose function is diversion, forcing people to stop and think, and consider their actions before they do something that might be dangerous to them. Physiologically, when people laugh, their muscle tension decreases, and they are incapable of doing anything for a short time, thus disabling them from any effective action. Humor then helps to shift the focus from the external situation inward and causes one to evaluate the situation more thoroughly.

False Alarm

The distraction that laughter evokes not only could save people from trouble and from taking things too seriously, but it also sends this message to others. It alerts the surrounding people that what is happening has only trivial consequences, and there is no real threat to them in the current situation. Humor usually involves two ideas that seem incompatible with each other until the end, when the incongruity between them is resolved, and it all makes sense.

This ambiguous situation may lead someone to contemplate a serious action when it might lead to dire consequences. For example, someone might hear a strange noise at night and suspect that there is a burglar inside the house. He/She becomes vigilant and is ready to use a weapon. However, upon further inspection he/she discovers that the house cat is to blame for the noise and starts laughing. Laughter acts as a false alarm indicator that signals that nobody needs to take the situation seriously, nor allocate valuable resources and energy to it, preventing the situation from further escalating (Ramachandran, 1998).

Debugging Mechanism

From a psychological point of view, assessing an ambiguous situation correctly enables the individual to avoid wasting limited cognitive resources that could have been invested elsewhere. The brain is bombarded with information and needs not allocate resources to process insignificant events. It has been suggested that humor acts as a debugging mechanism that assists in removing erroneous ideas or information that somehow crept into one's mind and hinders its function (Hurley, Dennett, & Adams, 2011). Since our brain has limited resources, evolution should favor an efficient mechanism that would facilitate removing unnecessary and mistaken information, before it can cause any damage, and direct the brain resources to more fruitful needs. This is best illustrated with jokes, the basic form of humor. Jokes start with a setup that introduces a certain idea that leads people to believe one thing, and then the punch line alters that perception, forcing them to reinterpret that idea and realize that what they thought was actually wrong. The reward system that motivates people to conduct such debugging is manifested by the emotion of mirth, the good feeling that we get after a laugh. This is a comprehensive and nuanced theory, but most of the evidence supporting it comes from the analyses of jokes, a form of humor that is subjective and does not fully account for all humor expressions, and little other evidence supports it (for a full

review of the theory, see Greengross & Mankoff, 2012).

It is important to note that no matter what were the evolutionary forces that help shaped humor, the modern environment overstimulates our desire to consume humor, the same way eating sugary donuts overexcites our basic need for high-calorie and high-fat food that was rare in our ancestral environment (Hurley et al., 2011). This is often referred to as supernormal stimuli, the propensity to overcome something that we are evolutionarily predisposed to desire; something that was rare when we lived as hunter gatherers, but in the current environment is in abundance (Barrett, 2010). Humor might have evolved to solve a specific adaptive problem, but because the reward system is so strong, we might seek many other unrelated humor stimuli that can satisfy our desire for a good laugh, apart from its original purpose. The entertainment business capitalizes on such supernormal humor stimuli, by creating sitcoms, movies, and comedy shows that can tickle our need for endless laughs.

Sexual Selection Theory and Humor

There is no doubt that the evolutionary theories reviewed here embody some hidden truth about the forces that helped shaped humor and how it is used. However, they also have a few shortcomings. Theories focusing on the social aspect of humor center on specific situations where humor bestows some fitness benefits. For example, humor can be useful to identify in-group members or prevent us from rushing into actions that might harm us. But the circumstances in which these occurrences present themselves in daily life are rather rare. It is not clear how and why such a complex adaptation as humor would have evolved to specifically address these unique and unusual circumstances. It is also not apparent why humor and laughter should be selected as the mechanisms which enable individuals to deal with such problems. Obviously, understanding jokes depends, in part, on recognizing cultural specific knowledge and norms. But this understanding by itself is not

evidence that humor evolved to serve as the means to help identify group members from strangers. Many other social attributes, cultural systems, and forms of communication such as gossip, songs, stories, or religion can achieve the same goal (Dunbar, 1998; Sosis, 2003). Humor is a social activity, but that alone does not suggest that any social use of humor is evolutionary based.

As noted above, situations where humor can help individuals avoid pitfalls, ease tensions, or prevent an ambiguous situation from escalating are quite rare. Moreover, these are usually serious circumstances, with possible dire consequences for the parties involved. But most humor uses are among friends, in a relaxed atmosphere, when our mind, as Darwin put it, is in a “pleasurable condition.” Also, people actively seek to laugh wherever they go and do not just wait for the right (and serious) situation to arise. Oftentimes, as the history of comedy from ancient Greek and Shakespearean comedy through vaudeville shows and modern stand-up comedy demonstrates, people are quite willing to pay for a good laugh. So it seems obvious that humor plays a much larger role in the life of people than what some of the social theories suggest.

Many evolutionary theories focusing on the survival benefits of humor overlook the large individual differences in humor use and experiences. Individuals vary largely in their ability to make others laugh, their humor styles, their enjoyment of sexual and aggressive forms of humor, their motivations for using humor, how funny they think they are, and virtually every aspect of humor consumption and appreciation (Greengross & Miller, 2008, 2011; Hay, 2000; Lampert & Ervin-Tripp, 1998; Martin, Puhlik-Doris, Larsen, Gray, & Weir, 2003; Mickes, Walker, Parris, Mankoff, & Christenfeld, 2011; Thomas & Esses, 2004). Most evolutionary theories fail to recognize this diversity of humor uses and incorporate it into their theories or to explain how this variation translates into an adaptive advantage. Humor production is especially variable, as is the ability to discriminate between high- and low-quality humor (Greengross & Miller, 2011).

Theories that focus on the survival benefits of humor, that humor is good for our health, or that humor contributes to social bonding, assume that there is little variability in the ability to create humor or the funniness of the jokes. For these theories, humor itself is the focal analysis and not the individuals who produce and appreciate it. According to these theories, there is something in the quality of humor that benefits the people using it, regardless of who they are. Virtually all people get the same advantages by using humor. But knowing that a joke is funny means that there are also other jokes, which are not particularly funny. People can distinguish between good jokes and bad ones and only laugh at the jokes that they find funny (Miller, 2000a). The ability to differentiate between the two is crucial for the existence of good humor. There is a need for a theory that centers on individual differences, one that will focus on the relationship between the producer of humor and the appreciator. We need to explain why so many people vigorously pursue humor and why people with a great sense of humor are highly desired in social interactions and as mates. What does production of high-quality humor tell us about the person, and what are the benefits of portraying a great sense of humor?

Sexual selection theory offers one of the best explanations for humor's origins, functions, correlates, and social attractiveness (Darwin, 1871; Miller, 2000a). Different evolutionary life histories for males and females helped shape their mate preferences and behaviors and resulted in some disparities in the way they enjoy and use humor today. These differences arise from asymmetry in their reproductive costs and the amount of time and energy devoted to parental investment (Buss, 2003). In humans, as with most other mammals, women bear the heavier costs of reproduction, such as pregnancy and child rearing, while having a shorter reproductive span. This leads women to become choosier in selecting a mate, since the consequences of selecting the wrong partner could be much more costly (e.g., raising a child alone). Thus, women should be more attentive to cues that indicate high mate value, while men would try to signal that they are high-quality mates.

Sometimes, mate quality can be directly observed, as in the cases of masculinity in men, youth in women, and symmetry in the face and the body of both sexes—all direct indicators of reproductive value and health (Buss, 2003; Thornhill & Gangestad, 2008). Other times, assessing mate quality of another individual cannot be attained directly and has to rely on advertisement (Miller, 2000b). Mate quality is advertised by ornaments that are correlated with other traits which contribute directly to fitness. The trait being advertised has to bear some reproductive advantage for the individual; otherwise, it will not be attractive, and the advertisement also must be an honest fitness indicator, or else it will be easy to fake by other individuals. One well-known example is the peacock's tail. Peacocks possess an extraverted tail, a very heavy and colorful ornament, one that requires much energy to develop and support. The bright tail is also very visible and easy to spot by predators. It seems apparent that a shorter and lighter tail would be better for survivorship. However, peacocks with the bigger and more colorful tails, ones that are more symmetrical and costly, are actually more attractive to peahens (Zahavi, 1975; Zahavi & Zahavi, 1997). Why would the peahen select mates that seemingly reduce their survivorship chances? Why would peacocks handicap themselves by wasting valuable resources to grow and maintain a beautiful tail, one that puts them at risk? The answer is that an extravagant and costly tail is a true indicator of fitness, an advertisement for underlying genetic quality (low mutation load), a trait that cannot be observed directly by the peahens. Peacocks that are less fit do not have enough resources to allocate for the growth and maintenance of such a beautiful and burdensome tail and cannot fake such a tail. The high-quality peacocks that can afford to grow an attractive tail are advertising their mate quality by showing off that they have the resources to sustain a large, heavy tail and still survive.

Advertisement of underlying genetic quality is not confined to physical characteristics alone. According to the theory of mental fitness indicators (Miller, 2000a, 2000b, 2007), many human capacities such as language, art, music,

sports, altruism, moral virtues, and humor also evolved through mutual mate choice to advertise mate quality. These traits evolved to serve as indirect signals for individual genetic quality because they are honest, hard to fake indicators. One way these traits transfer into fitness is by being true indicators of intelligence, a trait that offers clear fitness benefits and is also highly desired when choosing a mate. Humor is hypothesized to be one such fitness indicator. Because women are choosier than men, we should expect men to use humor more often and more creatively to signal their mate quality and attract women, while women should be more sensitive to men producing high-quality humor when choosing a mate.

In the next parts, I will examine the evidence for humor production ability as a sexually selected trait and other predictions stemming from sexual selection theory and the fitness indicator theory.

Sex Differences in Humor Preferences

Sense of humor is regarded as one of the most socially desired traits. Individuals with a good sense of humor are perceived as friendlier, more interesting, pleasant, emotionally stable, fun to be around, socially adept, intelligent, and creative (Cann & Calhoun, 2001; Kaufman, Kozbelt, Bromley, Geher, & Miller, 2008; Martin, 2014; O'Quin & Derks, 1997). Moreover, a good sense of humor is consistently ranked as one of the most desirable traits in a potential mate, especially for women (Buss, 1988; Daniel, O'Brien, McCabe, & Quinter, 1985; Goodwin, 1990; Hansen, 1977; Sprecher & Regan, 2002; Todosijević, Ljubinković, & Arančić, 2003; Toro-Morn & Sprecher, 2003).

If humor is the product of sexual selection and a mental fitness indicator, it should be a sexually dimorphic trait, with some predicted differences in the way it is used and perceived. Because women are choosier, they should place greater importance on humor when selecting a mate and

be more sensitive to men who portray a great sense of humor. Men, on the other hand, should care less about women's humor ability and should not rank it as high in their mate preferences as women. They should, however, be more attentive to cues showing that women appreciate their sense of humor.

A meta-analysis conducted on seven samples with a total of 4,000 subjects found that women considered humor to be a more important trait in a mate than men (Feingold, 1992). Though effect sizes were relatively small (ranging from 0 to 0.55, unweighted $d = 0.22$, weighted $d = 0.14$) (Cohen, 1988), no single study showed that men emphasize humor more than women in selecting a mate. In a cross-national study, more than 200,000 participants were asked to rank their preferred traits in a desired partner from a list of 23 traits (Lippa, 2007). Humor was ranked first among women, while men placed it third, with a sex difference of $d = 0.22$.

These studies indicate that humor is an important trait when choosing a mate and more so for women. However, it is important to note that in many studies humor is vaguely defined, if at all, which leaves the subjects to interpret humor as they perceive it. For example, Buss (1988) found that among undergraduate students, both males and females reported that displaying a good sense of humor was the most effective act to attract mates. Yet, displaying a good sense of humor can indicate that the person laughs often, or it can mean that the person is telling funny jokes. We cannot tell from the study design and results how the subjects construe the term "display" or if men and women had different definitions in mind. As we saw earlier, though intuitively understood, sense of humor can mean different things to different people. In addition to the ambiguity of the term "humor," the relationship in which subjects are asked to state their humor preferences varies depending on the study, or it is not always stated clearly. Subjects on various studies were asked to state their humor preferences for anything from a date to a long-term relationship. In some cases, subjects were asked about a generic partner or mate,

leaving the kind of a relationship open to interpretation. Most sex differences in sexually selected traits are pronounced for short-term mating or during courtship, while for long-term relationships both sexes tend to be equally choosy (Buss, 2003; Buss & Schmitt, 1993; Miller, 2000a). For a long-term relationship, sex differences such as mate preference tend to converge on similar tastes. Thus, not mentioning what kind of a relationship the humor mate preferences refer to may be confounding the overall effects.

A good way to unmask the true sex differences in humor preferences is to look at the actual behaviors of men and women. One common method is by looking at personal ads on dating sites and newspapers. This is a more ecologically valid study since single people state their true preferences for a mate, and they have little incentive to lie. In one study that analyzed more than 500 personal ads from a singles' magazine, Smith, Waldorf, and Trembath (1990) categorized 28 common descriptors of dating preferences found in the ads. The results showed that women sought a humorous mate twice as often as men did. Women desired a guy with a good sense of humor in 41.1 % of the ads (the second most desired trait), while men indicated their preferences for a humorous partner only 20.8 % of the time (seventh overall). While it is not clear from the study what exactly accounted for a humorous preference, or how it was coded, it is quite clear that whatever the definition was, women's preference for a humorous partner was stronger than that of men. In a similar study, Provine (2000) analyzed 3,745 personal ads published on the same day by heterosexual men and women in eight different newspapers. Overall, about one-eighth of the ads included humor-related references such as "funny," "witty," and "humorous," and women were more likely to mention humor-related words, roughly 62 % more than men did.

Studies that have looked at real personal ads lend further support to the notion that humor is a sexually selected trait sought out more by women. However, it is not always easy to interpret what people mean when they say they want a

humorous partner. For example, in Provine's study, ads were separated into two groups: people who seek someone with a sense of humor and people who offer humor in their ads. A seeker was defined as someone who looks for a date that loves to laugh or that is "funny," and conversely, an offerer of humor was defined as a person who laughs a lot, appreciates good humor, or has a good sense of humor of his or her own. The problem with these definitions is that humor appreciation and humor production ability are mixed in both categories. In order to test the sexual selection theory, we need to separate the appreciators from the producers.

One study clearly separated people who are seeking humor production and those who are offering their humor production ability (Wilbur & Campbell, 2011). In the study, almost 500 college students were asked to imagine trying to get to know a potential romantic partner and rated the likelihood of using certain humor strategies in attracting this mate. The results showed that men reported a desire to use humor production statements such as "I would make a lot of jokes" or "I would try to make him/her laugh" significantly more than women. In contrast, women were more likely than men to prefer statements where they act as evaluators, such as "I would tell him/her that he/she is funny" and "I would laugh at his/her jokes." In a subsequent study, the same researchers examined real Internet dating ads of 266 people (half men, half women) from a dating site in Canada. They looked at how often people proclaimed to be funny or actually tried to be funny and how often they requested a partner with a good humor production ability. Consistent with sexual selection and mental fitness indicator predictions, men were much more inclined to offer their humor production ability, claiming that they had a great sense of humor and they could make their potential date laugh. Women, on the other hand, were significantly more likely than men to state that they want a mate that offered humor production.

A few other experiments have also looked at sex differences in humor appreciation and production ability and came to the same

conclusions. In one study, 210 students of both sexes were presented with a series of photographs of people of the opposite sex, two at a time (Bressler & Balshine, 2006). Each photograph was accompanied by a series of statements, fake depictions of the individual which were either funny or not. Only women viewing pictures of men chose the humorous men as a desirable partner more often than what was expected by chance alone. Men, on the other hand, did not show a preference for a humorous partner. In another study, Bressler, Martin, and Balshine (2006) specifically tested whether women prefer men who display a good sense of humor, and men prefer women who appreciate their humor. Seventy-five women and 55 men from a student sample read fictitious descriptions of two individuals of the opposite sex. One individual produced humor that the subject enjoyed but was not appreciative of the subject's own humor. The second individual was very receptive of the subject's own humor, but the subject did not appreciate his or her humor. Participants then had to choose which individual they would prefer as a partner for various relationship types. The results revealed that although both men and women valued a good sense of humor in their respective partners, women showed a preference for a man with great humor production ability over a man that appreciated their humor production, while men preferred a woman that would appreciate their humor over a woman that would make them laugh. Women showed their preference for a humor producer for all relationship types (dating, one-night stand, short- and long-term relationships, and friendship). Men especially valued women who laughed at their jokes for a date. Only for a friendship did men show a preference for a humor producer over an appreciator. These results support the notion that when men and women talk about wanting a partner with a great sense of humor, they mean vastly different things. Men want a humor appreciator, while women want someone that will make them laugh.

Another study examined the effects of self-deprecating humor and physical attractiveness on opposite sex romantic preferences for various

types of relationships (Lundy, Tan, & Cunningham, 1998). Fifty-four males and 58 female students were shown a photograph and a fake interview transcript from a person of the opposite sex. The person was either attractive or not, and his or her answers were either humorous or not. The subjects were then asked to rate their desire to meet this person again for anything from a date to a long-term relationship. Not surprisingly, men showed a stronger preference for dating an attractive woman, but using humor did little to increase their desire to meet her again. In fact, the data suggest that humorous women decreased their desirability as mates, regardless of how attractive they were. For women, the use of humor by an attractive man increased his desirability as a mate, for both short- and long-term relationships, but had no effect on his desirability if he was less attractive.

In sum, the cumulative research that comprises actual and imaginary choices people make when choosing a mate, including analyses of real personal ads, lends support to the hypothesis that humor is used as a mental fitness indicator, and is a sexually dimorphic trait. Men show proclivity to advertise their humor ability, and try to put more effort into producing high-quality humor, while women recognize that humor creativity is important, and seek men who offer it. Evidence from mock ads also showed that men who used humor in their ads were more likely to be successful in finding a date, but it made no difference for women using humor, as men do not particularly care if a woman is funny (though they would like her to laugh at their jokes). The emphasis that both sexes put on the humor production abilities of men, and the reverse role it plays in mate choice, is a recognition of the significance of humor creation in signaling mate quality and the fact women are choosier than men.

Humor Production Ability

In the previous part, I reviewed the literature on sex differences in humor preferences. The amassing evidence supports the view that men

try to advertise their humor production abilities while women evaluate it, providing support for humor acting as a mental fitness indicator, a product of sexual selection. In this part, I will review the evidence for sex differences in humor production ability and its effects on mating success, mating strategies, and relationship to intelligence. Women's choosiness fosters competition among men for being selected as mates. If humor is a good indicator of mate quality, women should have a penchant for finding a humorous partner, while the strong intra-sexual selection among men should result in higher humor production abilities.

The topic of sex differences in humor production abilities is often reduced to stereotypical assertions such as "Women are not funny" (e.g., Hitchens, 2007). As we saw earlier, humor is a multidimensional concept, with many definitions and multiple ways of expression. It is impossible to substantiate broad claims about such a complex phenomenon as humor. In fact, in many aspects, men and women share similar experiences in regard to humor (Martin, 2014). Moreover, the differences that we do find are generalizations, based on averages of large samples, and do not necessarily reflect an individual ability. The research presented here will focus on a very specific aspect of humor, and its relationship to mating, and should therefore not be assumed to represent the types and magnitudes of other humor-related sex differences.

Conversational Humor

There are several ways in which humor production ability could be assessed. If a great sense of humor is defined as one that makes other people smile or laugh, then by studying conversational laughter, we can compare individuals who initiate humor to those who appreciate it. If humor is a mental fitness indicator, men should be the main initiators, while women are expected to laugh more, and especially in the presence of, or in response to men. Provine (1993) studied conversational laughter by analyzing 1,200 episodes of dyadic interactions from natural conversations in shopping malls, city sidewalks,

and a university campus. Of the four possible interactions between a speaker and audience (male–male, female–female, male–female, and female–male), the male–female interaction, where the man was the speaker, produced the highest audience laughter, about 71 % of the time. When females were the speakers and males were the appreciators, men laughed only 39 % of the time. (The least amount of laughter occurred when two females talked.) In a similar study, researchers observed 212 people of various group sizes, in bars and restaurants, and documented the frequency of smiles and laughter expressed (Mehu & Dunbar, 2008). While the overall rates of smiles and laughter were similar between men and women, women laughed significantly more in mixed group interactions, especially if they were young (and more likely to be single). In contrast, the amount of laughter displayed by men did not vary, and they laughed the same amount in both mixed- and same-sex groups. Age had no effect on the frequency of laughter produced by the men. Other researchers that observed natural dyadic interactions of men and women in restaurants, shopping malls, and university campuses also reached similar results (Adams & Kirkevold, 1978; Chapell et al., 2002; Smoski & Bachorowski, 2003).

Another study that analyzed conversations of mixed-sex groups found that men were more likely than women to tell jokes, and they were also more successful in doing so, as evident by the amount of laughter manifested (Robinson & Smith-Lovin, 2001). Men also reported using more humor than women (Myers, Ropog, & Rodgers, 1997), and when asked to describe someone with an outstanding sense of humor, or to name which sex is funnier, both men and women were much more likely to choose a man (Crawford & Gressley, 1991; Nevo, Nevo, & Yin, 2001). Both men and women are also more likely to attribute humorous punch lines to men, when introduced with a cartoon in which its author's identity is obscured (Mickes et al., 2011). In addition, women believe that men's pickup lines containing humor are much more likely to be successful, compared to men's opinions of women's pickup lines (Cooper,

O'Donnell, Caryl, Morrison, & Bale, 2007). In complement to these results, a meta-analysis of sex differences in smiling that included 162 studies with over a 100,000 subjects found a tendency for women and adolescent girls to smile more than men and adolescent boys, with an average effect size of $d = 0.41$ (LaFrance, Hecht, & Paluck, 2003).

In other studies, Grammer (1990) and Grammer and Eibl-Eibesfeldt (1990) investigated whether conversational laughter indicates physical attraction. The researchers randomly matched pairs of men and women that were strangers to each other and measured the amount of laughter produced in the interaction between them. Consistent with other studies, women laughed more than men, and in addition, the amount of laughter by the woman predicted both her and the man's interests in dating each other. In contrast, men's laughter did not evoke such interest in dating in either of the pair. Li et al. (2009) also found that humor conveyed romantic interest in others. In this study, subjects who watched mock one-on-one dating sessions perceived the man to be more attracted to his date when he initiated humor, compared to when he did not. Also, the woman was perceived as more attracted to the man when she appreciated his humor, than when she did not. Thus, humor production either can enhance the attractiveness of a man or can be seen as an indicator of an already existing attraction, and complementarily, women appreciating humor indicates attraction to the men. Similarly, Penton-Voak and Chang (2008) found that smiling increased the attractiveness of women, but not men, as rated by both sexes.

Another study looked at the effect of a smiling woman on men's courtship behavior (Guéguen, 2008). On 100 different occasions, an average-looking woman made eye contact with a man who was sitting alone at a bar and either smiled at him or did not. The results showed that men who were smiled at were more than five times more likely to approach the woman and start a conversation with her, compared to when the woman did not smile at them (11 vs. 2 times). Even if the men did not approach the woman, the men who got a smile glanced at the woman for an

average of 5 s longer, compared to when she did not smile at them (7 vs. 2 s). Mehu, Little, and Dunbar (2008) also found that a woman's smile increased her attractiveness in the eyes of both men and women, while male smiles had no such effect on either sex.

The data from conversational humor studies support the notion that humor is a sexually dimorphic trait. Men initiate humor more than women, especially when interacting with women. Women, on the other hand, laugh more than men, and particularly in response to male speakers. Men's production of humor increases their attractiveness as mates in women's view, while women's smiles and laughter both signal romantic interest and enhance their attractiveness.

Studying interactions between men and women is important because the focus is on humor's most important product: laughter. However, not all humor production induces laughter in others, and people smile and laugh for various other reasons. For example, Provine (2000) found that most laughter occurs in response to mundane comments, and the speakers themselves laughed more than their audiences. Though the evidence does support the idea that humor production ability and humor appreciation are sexually selected traits, indirect measures of humor production have their shortcomings, and more direct and reliable appraisals of humor creativity are needed.

Humor Creation Ability

Relatively few studies have looked at how men and women differ in their humor creation ability, perhaps because most humor research focuses on humor appreciation, which is easier to study with jokes and cartoons. Studying humor creativity poses a challenge for researchers, but nevertheless, there have been several attempts to study the subject and specifically, sex differences in humor production ability.

One simple way to evaluate humor production is by asking people how funny they think they are. Some evidence suggests there is a modest correlation between self-rated wittiness and other more objective measures of humor ability

(Feingold & Mazzella, 1993), but overall, self-reports are not considered a reliable way to assess humor creativity. One problem with this method is that we are measuring biased perceptions individuals have about their own humor ability rather than true humor production. Most people rate themselves above average in humor ability, a statistical impossibility, and while both sexes tend to think that men are funnier than women, men overestimate their abilities more than women (Crawford & Gressley, 1991; Mickes et al., 2011; Myers et al., 1997). A more reliable alternative is to ask friends, family members, or teachers to evaluate the humor production of an individual (Bergen, 1998). This indirect method has some merit, but is usually more time-consuming and costly and hence, not very practical. Another alternative is to give subjects the beginning of a joke, and ask them to complete the punch line, either from a list of possible punch lines or from their own imaginations (Feingold, 1983). The problem with this approach is that it utilizes “canned” jokes that are not a good representation of spontaneous, everyday humor and are also too restrictive. It also is not a very reliable measure of humor creativity, which makes the whole approach less appealing.

A more objective method to assess spontaneous humor creativity is by presenting subjects with a cartoon that has no caption, and ask them to write witty captions for it, that will later be evaluated by independent judges for funniness (Brodzinsky & Rubien, 1976; Feingold & Mazzella, 1993; Turner, 1980). Several studies have utilized the captionless cartoons approach to study sex differences in humor production. In these studies, researchers either remove captions from existing cartoons or use cartoons and pictures with no captions. (In recent years, researchers have been using cartoons from *The New Yorker* magazine, which runs a weekly competition that introduces a specially drawn cartoon without a caption and asks readers to send them funny captions.) In one study, 200 men and 200 women from a student sample were asked to write as many funny captions as they could think of for three such cartoons in

10 min (Greengross & Miller, 2011). Later, six independent judges (four women, two men), blind to the sex or any other characteristic of the subjects, rated the funniness of the captions. The judges’ sex did not have an effect on the ratings, and the overall ratings yielded high reliability scores. The results showed that on average, the men’s captions were rated as funnier than the women’s, with medium effect sizes (average $d = 0.40$). Men also produced slightly more captions than the women.

In another similar study, albeit with a smaller sample, 32 students (16 men, 16 women) wrote captions for captionless cartoons, which were rated by 81 independent judges (34 men, 47 women) (Mickes et al., 2011). The results showed that on average, men’s scores were higher than women’s on the humor production task, regardless of the judge’s sex, with an effect size of $d = 0.24$. Another study that asked subjects to write both funny descriptions of people, based on photographs, and funny answers to generic questions such as “What do you think the world will be like in a hundred years?” reached the same conclusions with an average effect size of $d = 0.40$ (Howrigan & MacDonald, 2008). Brodzinsky and Rubien (1976) used cartoons from contemporary books and magazines with their captions removed to evaluate humor production ability. Four of the cartoons were overtly sexual in nature, four were aggressive, and four were neutral. Six independent judges (three men, three women) scored the cartoons for funniness. The results showed that males generated funnier captions than females for sexual and aggressive cartoons, but there were no sex differences for the neutral cartoons. The results might be impacted by women’s tendency not to enjoy sexual and aggressive humor, which might impede their ability to produce funny captions for such cartoons (Lampert & Ervin-Tripp, 1998). In another study, Edwards and Martin (2010) reported no significant sex differences in humor production ability, using captionless cartoons as their measure of humor creativity. However, the lack of significant results might be attributed to low statistical power, and calculations of effect

size based on their data reveal that men scored higher than women on the task, with $d = 0.24$, which is in accordance with other studies.

In sum, the evidence shows that both men and women believe men to have higher humor production abilities compared to women, and objective judgments of humor creativity affirm that this perception is correct and men are better than women at producing humor. These differences are small to medium, but consistent and robust. It is important to remember that these differences reflect averages, and both men and women vary in their humor production abilities. Indeed, if humor is a mental fitness indicator, we should expect variability in the ability to make others laugh. If all humor attempts were equally successful, humor would not be a good and reliable signal of mate quality.

Moreover, production and appreciation of humor are based on similar mental capacities and mutual mate choice—the result of coevolution between males and females. In order to produce high-quality humor, one must understand how humor works and be capable of anticipating how it will be perceived (Miller, 2000a). Hence, trying to create high-quality humor enables the individual to discriminate between good and bad humor ability, which jokes work and which do not, and what is funny and what falls flat. That expectation, therefore, is the key for both producing and appreciating humor, since without expectations that could be violated, there would be no evolutionary pressure to produce better and funnier humor, and sexual selection would stall. Thus, while we should expect men to produce, on average, higher quality humor than women, the differences should not be too large, and that is precisely what the data show.

Furthermore, it is imperative to remember that though females are the choosier sex, it does not mean they cannot or should not produce high-quality humor. As discussed earlier, most sex differences in sexually selected traits are more prominent in short-term mating, while for long-term relationships, mate preferences and choices tend to be similar for both sexes (Buss, 2003; Buss & Schmitt, 1993; Miller, 2000a). Because

of the disparity in parental investment and reproduction costs, men are more motivated to have short-term sexual relationships and thus are more motivated to flaunt their humor ability when interested in a short-term partner or at the early stages of courting when it is still unclear whether there is even the possibility for a long-term relationship.

Production of Humor and Mating Success

So far, we have reviewed research that shows humor to be a sexually dimorphic trait. Humor is preferred more by women, while men try to signal their quality by producing high-quality humor. Men are also the predominant initiators of humor, while women are the main appreciators who tend to smile and laugh more in general, but especially in response to male speakers. But for humor to serve as a mental fitness indicator, it has to translate into mating success. Does humor affect romantic choices? Do women actually choose men with a great sense of humor as dates? Several studies have attempted to answer these questions.

In one study mentioned earlier, researchers created fictitious online dating ads that contained a “one-liner” joke at the start of the ad (Wilbur & Campbell, 2011). One hundred and fourteen college participants (73 women, 41 men) were then asked to evaluate the humor in the ad and to state their romantic interest in that person. The “romantic interest” variable was assessed by computing an average score of the participants’ interest in either getting to know the person better, having a long-term relationship with the individual or possibly seeing themselves marrying that person. The results showed that for women’s ads, adding humor did little to attract the romantic interest of men. On the other hand, judging a man’s ad to be humorous significantly increased the romantic interests of the women evaluating it.

In a more direct test of the influence of humor production on mating success, Greengross and Miller (2011) looked at how good humor production ability translates into mating success. This

study, discussed earlier, evaluated humor creativity using the captionless cartoon task. Mating success was measured by the Sociosexual Orientation Inventory (Simpson & Gangestad, 1991), a self-report questionnaire that includes questions pertaining to actual sexual behaviors, such as age at first intercourse, lifetime number of sex partners, and acts of intercourse in the past month. The results showed that subjects who scored higher on the humor production task enjoyed greater mating success (started having sex earlier, had a higher number of sexual partners, and had more sex in general), compared to the less funny individuals. Interestingly, these results were true for both men and women, but since their actual humor abilities differ, men's humor is presumably more effective in attracting mates. This is because the motivations for men and women to use humor differ. As discussed earlier, women know that their ability to make men laugh does little to attract men, while men recognize the value of humor in alluring women. The asymmetry in the benefits of humor production ability that each sex gains could be the driving force behind men's attempts to make women laugh. It might also explain why men think they are funnier than women, regardless of their true humor ability. Overestimating one's humor abilities has its advantages for men. A man is better off thinking he can make a woman laugh, even if he often fails to do so, than not to think he is funny and therefore not make an attempt. The risk of not even trying to make women laugh may result in losing a mating opportunity. This type of cognitive bias is often referred to as a false-positive error, and is quite common for many evolutionary-based attributes. For example, men tend to overestimate women's sexual availability because it is better for men to be refused than to lose a chance at mating (Haselton & Buss, 2000).

Another study, in a more valid ecological setting, tested whether men's sense of humor helps increase their mating success. On 60 different occasions, three men sat at an outdoor table near a bar next to a young woman sitting alone. One of the three men then started telling jokes, while the two others laughed (Guéguen, 2010).

An observer noted whether the woman listened to the jokes and laughed. Half of the time, the two appreciators left, and the joke teller approached the woman, asking for her phone number. In another condition, one of the men that laughed at the jokes, but was not the joke teller, asked for her phone number after two of his friends left (in both cases it was the same confederate). The results showed that women were three times more likely to give their phone number to the man who told jokes, compared to the man who appreciated the jokes (42.9–15.4 %). The joke teller was also considered more attractive, intelligent, funny, sociable, and a more desirable mate for a long-term relationship, compared to the appreciator (with medium to large effect sizes).

One other study set out to test whether humor was a mental fitness indicator among married couples (Weisfeld et al., 2011). More than 3,000 couples in five countries answered questions regarding the importance of humor in their marriages. The results showed that, overall, both husbands and wives were happier with a humorous partner, but spousal humorousness was more important for the marital satisfaction of the wives than the husbands in all five cultures, though only three were statistically significant. In four countries (USA, UK, China, and Turkey), both husbands and wives thought that the husband produced more humor. Only in Russia the results were reversed, though frequency of humor production was the lowest there, and the women outnumbered the men, which might indicate a more intense competition for husbands.

In sum, studies confirm that humorous people, especially men, attract more mates, enjoy better mating success as measured by actual sexual behavior, and are more satisfied in their relationships. Women, on the other hand, seek mates with great humor production ability, and high levels of humor creativity enhance their interest and attraction to men. It is worth noting that these findings are somewhat at odds with another evolutionary theory, which posits that humor evolved to pique our interest in others (Li et al., 2009). According to the interest indicator theory, any individual interested in a

relationship, regardless of sex, could equally initiate humor, have the same capacity to produce humor, and should reap the benefits of great humor production ability. However, as the data reviewed here shows, humor is sexually dimorphic when it comes to mating. Men produce better humor on average, and women are attracted to men with great humor abilities. In contrast, men have little interest in a woman with high humor ability, and they are more interested in her laughing at their humor. Furthermore, according to the interest indicator model, humor production and humor appreciation are the result of physical attraction, and humor creativity should not enhance the attractiveness of the producer. While it is generally true that being attracted to someone could increase his or her perceived humor ability, research shows that the opposite is also true, independent of the initial attraction the couple might have to each other. Moreover, high-quality humor increases the attractiveness of men, but not of women, producing high-quality humor, thus lending further support to humor being a sexually selected trait.

Extreme Humor Ability

There are large individual differences in the ability to make others laugh. If humor is a sexually selected trait, one might expect not only to find sex differences in humor production ability among ordinary people but also that these differences would be manifested at the highest level of humor creativity with professional humorists. One such group of humorist is professional stand-up comedians. Comedians' great humor ability is evident not only by their occupation but also by independent tests of humor creativity. One study used the captionless cartoon task discussed earlier to assess comedians' humor production ability and compare it to a student sample. The results showed large differences in favor of the comedians, with an average effect size of $d = 1.60$ (Greengross, Martin, & Miller, 2012b). While professional comedians do not necessarily represent everyday uses of humor, studying sex differences at the extreme level of humor ability could shed light on everyday uses of humor, just as the study of

homicide can help illuminate general patterns of violence (Daly & Wilson, 1988).

To estimate which sex is a better producer of humor among professional humorists, we can look at the number of men and women in such professions. If men have better humor production abilities, then they should be overrepresented in those jobs. Though no official registry of comedians exists, all indications are that there are more male stand-up comedians. In one study of professional stand-up comedians, of the 31 comedians in the study, only three were women (Greengross, Martin, & Miller, 2012a; Greengross et al., 2012b; Greengross & Miller, 2009). Also, on the list of the 100 greatest stand-up comedians published by Comedy Central, only nine were women (<http://www.listology.com/list/comedy-central-100-greatest-standups-all-time>). In another study on professional cartoonists, researchers looked at sex differences in cartoonists' styles (Samson & Huber, 2007). The researchers made a comprehensive effort to include as many female cartoonists as possible, searching magazines, books, journals, special volumes, Internet databases, and personal contacts. In the end, they were able to find a total of 1,519 cartoonists from 61 countries. Of them, only 9 % were women.

The data on comedians and cartoonists suggest that there are far more men at the highest level of humor production than women. While there might be some societal barriers and stereotypes that prevent women from getting into or succeeding in those professions, the overwhelming disproportional representation of men and women suggests that at least some of the differences are due to men's superior humor ability at the extremely high end. Another factor that might influence the scarcity of women in such professions is lower motivation to pursue such careers. Stand-up comedy, for example, is a very demanding job, with little job security and strong competition. Women might be less inclined to desire such high-risk jobs, while men's ambition for high status would drive them to seek what is considered to be a highly sought-after profession. In the view of sexual selection theory, high status is favored by

women when choosing a mate, because it gives them access to resources which are valuable for survival, food, and health and can help raise future offspring (Buss, 2003). Thus, men's pursuit of high status and women's desire for such men as mates could motivate more men to look for a career in stand-up comedy, while for women, being a professional comedian may not enhance their mate value by much (Buss, 2003). It is worth noting that humor itself can increase mate desirability just because it is associated with another, sexually dimorphic trait such as status. Funny individuals with higher status are considered more attractive than lower status individuals, especially when using self-deprecating humor that can be seen as a form of handicap, similar to the peacock's tail (Greengross & Miller, 2008).

Humor Production as an Indicator of Intelligence

One possible mechanism in which humor could serve as a sexually selected mental fitness indicator and transfer into mating success is by signaling intelligence (Miller, 2000a). Intelligence itself is highly desirable in a potential mate, and it is correlated with fitness-related traits such as physical health (Deary, 2005), longevity (Gottfredson & Deary, 2004), physical attractiveness (Langlois et al., 2000), body symmetry (an indicator of developmental stability) (Banks, Batchelor, & McDaniel, 2010; Prokosch, Yeo, & Miller, 2005), and even semen quality (Arden, Gottfredson, Miller, & Pierce, 2008)—all associated with fitness.

Studies show a close relationship between humor production ability and intelligence. Greengross and Miller (2009) calculated the correlations between humor production and two intelligence tests, a vocabulary test and an abstract reasoning test, the Raven's Advanced Progressive Matrices (RAPM). Given that the humor production task was to make verbal jokes, it was not surprising that this humor ability yielded a stronger correlation with the verbal test than the abstract reasoning test ($r = 0.39$ and

$r = 0.27$, respectively). Also, the correlation between humor production and the verbal test was stronger for men ($r = 0.42$ compared to $r = 0.30$ for women), suggesting that verbal intelligence more strongly predicts capacity for verbal humor in men than in women. In addition, a mediation model showed that humor ability strongly mediates the positive effect of intelligence on mating success, for both sexes. The results support the view that humor is a manifestation of intelligence and that humor can translate either directly or through intelligence to mating success.

In another study that investigated the relationship between humor and intelligence, Wilbur and Campbell (2011) found that in real personal dating ads and for both sexes, those who offered their humor production abilities and those who sought partners who were funny also offered and requested intelligence, respectively, implying that the two attributes are intertwined. Moreover, when evaluating fake ads that either contained humor or not, women's judgments of men's humor were strongly correlated with how intelligent and warm they perceived the men to be. No such association was found among men evaluating women's ads, suggesting that the connection between humor and intelligence is more important for women's mate choices.

Also, professional stand-up comedians consistently score higher than the average population in verbal intelligence. One study found that the IQ scores of 55 professional male comedians, estimated based on the verbal portion of the Wechsler Adult Intelligence Scale, range between 115 and 160, with an average of 138, well above the average of 100 in the general population (Janus, 1975). In a follow-up study with 14 female comedians, the range of IQ was 112–144 with an average of 126 (Janus, Bess, & Janus, 1978). In a more recent study, vocabulary scores of 31 professional comedians were compared to those of students, and the results showed comedians to have much better verbal intelligence, which is highly correlated with general intelligence (Carless, 2000), with a large effect size of $d = 1.34$ (Greengross et al., 2012b). Though comedians are expected to score high

on verbal intelligence, as their profession requires a display of superior verbal skills, the difference from the general population is substantial.

It is interesting to note that despite the apparent correlation between humor production and intelligence, results are somewhat inconsistent. For example, Howrigan and MacDonald (2008) found an overall correlation of $r = 0.29$ between humor creativity and general intelligence as measured by the RAPM, but women's correlation was stronger compared to that of the men ($r = 0.33$ to $r = 0.15$). However, the measured intelligence of abstract reasoning may be less relevant for displaying verbal humor abilities, compared to other types of intelligence such as verbal intelligence.

A few studies have found that perceptions of an individual's intelligence are not always aligned with the perceptions of that person's humor ability. In one study, humorous individuals were rated as less intellectual than the non-humorous individuals (Lundy et al., 1998), and in another study described earlier (Bressler & Balshine, 2006), humorous people were perceived as less intelligent, though women did prefer them as mates, and rated them as more fun, friendly, and popular. The discrepancy between the existence of a correlation between humor and intelligence and the perception that they are not correlated might be attributed to the student samples used in the latter studies. College students tend to equate intelligence with being educated, a concept that is not equivalent to general intelligence as measured by standardized tests. Also, the humor ascribed to the humorous people who were evaluated by the students was immature and not sophisticated in nature. However, the fact that women actually found men more attractive for mating despite using this childish humor lends stronger support to the importance of humor creativity in mate choice.

Heritability of Sense of Humor

Evolution is all about reproduction and passing the genes from one generation to another. In order for humor to be a sexually selected trait,

it needs to have a heritable component to it. Humor production ability could be inherited either directly or indirectly through the mediated effect of another desirable trait that is correlated with humor. One such trait could be intelligence. As we saw earlier, there is a correlation between humor production ability and intelligence, and there is growing evidence that general intelligence is heritable (Plomin & Spinath, 2004; Rushton, Bons, Vernon, & Čvorović, 2007).

Only a few studies have looked at the heritability of humor, and each focused on a different aspect of humor. Unfortunately, none of the studies to date have tested whether humor production ability is heritable. Most research on the subject compared monozygous (MZ, identical) twins to dizygous (DZ, fraternal) twins. If humor is indeed inheritable, we should expect MZ twins to be more similar to each other compared to the DZ twins.

In one study, researchers compared how similar appreciation of cartoons was among MZ and DZ twins (Cherkas, Hockberg, MacGregor, Snieder, & Spector, 2000). One hundred and twenty-seven pairs of female British twins (71 MZ and 56 DZ, ages 20–75) were asked to rate the funniness of five “The Far Side” cartoons. The researchers found that shared environment, but not genetic factors, contributed to similarities in humor appreciation. In contrast, several other studies, which used different measures of humor, did find humor to have a genetic component to it. In one study of adults, 300 MZ twins and 156 DZ twins from Canada and the USA completed the Humor Styles Questionnaire, a questionnaire that measures four daily uses of humor (Martin et al., 2003). The results showed that the two positive humor styles, humor that is used to put others at ease through telling jokes and having a humorous outlook of life, had strong genetic contributions to individual differences and are attributed to nonshared environmental factors (Vernon, Martin, Schermer, & Mackie, 2008). On the other hand, the negative humor styles, styles that are used to ridicule others or make oneself the butt of the joke, were largely a product of shared and nonshared environment and not due

to genetic factors. Another study of almost 2,000 twins in the UK that used the same questionnaire found that individual differences in all four styles were due to genetic and nonshared environment factors (Vernon, Martin, Schermer, Cherkas, & Spector, 2008). Other studies which examined adolescent twin children, or compared adoptive and nonadaptive children to their parents, also found that genetic factors significantly contributed to individual differences in sense of humor, as measured by a standard humor questionnaire focusing on interpersonal and daily uses of humor (Manke, 1998). In sum, despite the somewhat mixed evidence, the data suggest that at least some aspects of humor are heritable.

Conclusion

Humor and laughter are powerful displays enjoyed daily by people all over the world. There are many mysteries yet to be unlocked regarding the origin and uses of humor, but it is clear that humor has strong evolutionary roots. The data presented here support the view that humor is sexual selected and a fitness indicator. Differences in humor production ability and humor appreciation do not seem to be random, and knowing that someone has a great sense of humor tells us something about that person, far beyond his or her humor ability. Evidence suggests that humor is a sexually dimorphic trait, and humor production is an overt manifestation of intelligence that increases mate value, especially in men. Humor could have evolved as part of mutual, sex-specific selection, where men's and women's humor production, uses, preferences, motivations, perceptions, and influences vary. Women seek mates with a sense of humor and place greater importance on finding a mate with a sense of humor, a trait that is highly attractive for them. Men, on the other hand, try to produce high-quality humor to attract women, while women's humor creativity does little to attract men. Women's laughter signals their romantic interest in a man, while men's laughter does not.

Humor serves many other functions in our daily lives, and while the data does support the view that humor production is a sexually selected trait, it does not necessarily exclude other explanations, evolutionary or not, for humor's origin, function, and uses. Humor offers a strong reward system, and supernormal stimuli tickle our desire for a good laugh all the time. Other complementary explanations could be in place, and future studies will help fill some of the gaps in empirical data on the subject.

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