Let’s face it: most people think humor is sexy. One need not scour countless scientific journal articles to reach this conclusion. Open your favorite newspaper or magazine to the “Personals” section and you are bound to see plenty of people looking for a “good sense of humor” in a potential mate. Alternatively, do an impromptu pilot study and ask the next 10 people you meet how high humor ranks on their lists of important mate characteristics; you will likely obtain similar results.

Research has confirmed that a good sense of humor is an important human mate preference worldwide (Asia: Toro-Morn & Sprecher, 2003; Europe: Todosijevik, Snezana, & Arancic, 2003; North America: Regan & Joshi, 2002). When people are asked to rate the importance of various traits for romantic relationships, a good sense of humor is consistently at or near the top of their lists (Hansen, 1977; Hewitt, 1958; Goodwin, 1990; Smith,
Waldorf, & Trembath, 1990), sometimes outranking physical attractiveness (Sprecher & Regan, 2002; Toro-Morn & Sprecher, 2003). There is also evidence that the preference for funniness may be stronger in seeking romantic partners than in seeking platonic friends (Sprecher & Regan, 2002). Further, the preference for humor seems to increase with the duration of the relationship: we seem to value humor especially in long-term mates (Kenrick, Sadalla, Groth, & Trost, 1990).

Taken together, these findings suggest that any discussion of mating intelligence will not be complete unless the topic of humor is brought to the table. But what is humor? Is it a unitary construct or a constellation of separate components or abilities? How is humor related to intelligence, creativity, and other factors potentially related to mating intelligence and genetic fitness? Are there sex differences in humor production and appreciation that might illuminate the nature of mating intelligence? Answering these questions is no simple matter. To explore the relevance of humor to mating intelligence, one must tackle these issues and examine humor’s relationship to other psychological constructs that have been linked to mating success, such as intelligence and creativity.

Other chapters in this volume have addressed the relationship between general intelligence and mating intelligence (see Kanazawa, this volume) and the relationship between creativity and mating intelligence (see Nettle and Clegg, this volume). The terms “intelligence” and “creativity” are very broad, however. In this chapter, we argue that humor is a particular manifestation and indicator of both intelligence and creativity. A major aim of this review is to convey the complexities and subtleties of humor as played out in human mating while emphasizing the multidimensionality of the humor construct and its important links to mating intelligence. Toward this goal, we will first examine some candidate selection pressures that may have shaped the evolution of humor as a psychological adaptation. With that foundation in place, we will examine the psychometric perspective, detailing attempts to measure humor, creativity, intelligence, and their inter-relations. Finally, we will examine the evidence linking humor to mating intelligence, and suggest some future research directions.

POTENTIAL SELECTION PRESSURES FOR THE EVOLUTION OF HUMOR

Natural Selection

The central mechanism for the evolution of humor is Darwinian natural selection (Darwin, 1859), which may be defined as the differential reproduction of genes by virtue of their effects on heritable design features of
the organism. For natural selection to occur, there must be heritable variation for a given trait or behavior, and that variation must lead to differential survival and reproductive payoffs.

However, there are many different forms of natural selection at many different levels, including gene-level selection, individual-level survival selection, individual-level sexual selection, kin selection, and group selection. Evidence from archaeology, anthropology, and ethnography suggests that individual-level survival (‘natural selection proper’, in the survival-of-the-fittest sense) has played a key role in the acceleration of creative inventions and innovations. These heritable characteristics or adaptations could improve ones’ survival and inclusive fitness. This would give the individual a better chance of making a genetic contribution to subsequent generations, thereby initiating the process of genotypic change within their population (Andrews, Gangestad, & Matthews, 2002). For instance, hunting dangerous prey, a potentially fatal task, required our ancestors to creatively find ways to reduce their risk. They did so by fashioning weapons out of stones and later developing projectiles such as spears, to reduce their risks of being killed. Thanks to their ability to make something novel and useful, they reaped the benefits of their ingenuity and so did their children and kin (Berger & Trinkaus, 1995; Cattelain, 1997). The cognitive abilities for planning and remembering important ecological facts may have been extended into capacities for art, story-telling, and humor (Carroll, 1995; Gabora, 2003; McBrearty & Brooks, 2000). These marks of cleverness and progressive ingenuity likely reflect the phylogenetic development of human cognitive capacities, and represent prime examples of the impact of evolution and adaptation on our species.

So how does humor fit into this picture? One possible clue that humor evolved through natural selection is that humor is ubiquitous among Homo sapiens. All Homo sapiens have the capacity to respond to humor by laughing or smiling. There is even evidence that laughter and smiles are universally recognized and labeled as positive signals of emotional expression (Caron, 2002). Human responses to humorous stimuli (e.g., tickling) appear in infants at about 4 months of age, and their participation in humorous activities (e.g., Peek-a-boo) can be seen in infants as early as 6 months (Shultz, 1976; Sroufe & Waters, 1976). This is preceded by the occurrence of spontaneous laughter, which is one of the first vocalizations that human infants make, usually around 1 to 6 months old (MacNeilage, 1997; Sroufe & Waters, 1976; Sroufe & Wunsch, 1972). The smiles and laughter associated with pleasure have even been reported in congenitally deaf and blind children (Eibl-Eibesfeldt, 1970). This evidence has quite reasonably led many researchers to suggest that humans are genetically pre-disposed to produce and perceive humor (Caron, 2002; Provine, 2000).

However, such universals do not necessarily implicate survival-selection as an explanation. Although universality may imply that humor was
favored by selection, and suggests that an evolutionary approach to humor is appropriate, the universality of a trait gives little information about the particular selection pressures that may have favored it. Indeed, the “survival value” of a good sense of humor is not immediately obvious. Sexual selection also seems important, insofar as both sexes across cultures desire humor in prospective mates (Buss & Barnes, 1986; Feingold, 1981, 1992; Goodwin, 1990). One interesting possibility is that natural selection drives mainly the more applied or technological aspects of creativity, like advances in science and engineering, whereas sexual selection drives more ornamental or aesthetic aspects of creativity, including art, music, dance, and humor (Feist, 2001). Technical-applied creativity aims for a practical, veridical understanding of the world; it has clear survival benefits and probably emerged 2 to 3 million years ago with the origins of stone tool making. In contrast, aesthetic-ornamental creativity has no clear survival value and appears to have originated much later; indeed, some archaeologists have argued that it may be no more than 40,000 to 60,000 years old.

Social Bonding

One possible explanation for the existence of humor as a species-typical human capacity concerns its ability to promote social bonding and cohesion. This may confer an advantage on the individual humor producer or appreciator, through an implicit form of group selection. Humor’s ability to provoke delight and to influence the thoughts and emotions of the listener give the humor-producer some clear social benefits within a particular social context, even when the humor seems sort of stupid outside that context. For instance, Provine (1996, 2000) has found that the vast majority of laughter in natural settings is triggered by apparently banal remarks like “Look, it’s Andre” or “I’ll see you guys later.” Outside their immediate social context, these do not seem very witty or funny at all. However, laughing at such remarks can function “to ease social tensions, to indicate friendly intent, and to strengthen social bonds” (McGhee, 1979, p. 103). Moreover, some have argued that humor has more to do with social “good-heartedness” (Storey, 2002, p. 320) than with creative “wit” (at least in the United States, but perhaps not in Britain!). Indeed, in marital relationships, humor appears to promote intimacy, belonging, and cohesiveness, rather than hilarity (Ziv, 1988a). So whether in multi-person groups or dyads, one could argue that humor’s playfulness provides a socially binding force which, under ancestral conditions, would have promoted the individual or inclusive fitness of the person expressing it (Caron, 2002).

Although humor might function in these ways, this social-bonding view has a few problems. First, its reliance on an implicit form of group selection needs to be clarified and made more evolutionarily reputable.
Using humor to altruistically ‘promote social bonds’ within a group is not an evolutionarily stable strategy if defectors can reap the benefits of the social cohesion without paying the costs of being funny. Second, this theory cannot explain why humor sometimes fails—if it always benefited both producer and receiver, by promoting social cohesion between them, why would jokes ever fall flat? Third, this theory cannot explain the sexual attractiveness of humor, including sex differences in its production and reception, and its importance in both attracting short-term mates and in sustaining long-term relationships. Is the universal preference for humor in mates due solely to a desire for intimacy and belonging? Is there nothing sexy about humor?

**Sexual Selection**

Besides survival selection and group selection, Darwin’s theory of sexual selection (Darwin, 1871) represents another potential mechanism for the evolution of humor. Sexual selection theory proposes that, within most species, one sex (usually females) invests more in parenting, and therefore is more restricted in how many offspring they can conceive. Consequently, members of this higher-investing sex should be more selective when choosing a mate, because they must seek maximum quality in offspring to compensate for the severe limit on quantity that they face. This phenomenon of mate choice results in competition by the less-discriminate sex for the attention of the more-discriminate sex. In all mammals, including humans, this leads to males competing for female attention.

This sexual selection process is very distinct from survival selection, which is largely the competition to gain ecological resources and to avoid predators and parasites. Sexual selection theory suggests that there is a competition to mate with individuals who exhibit traits such as humor that are (in theory) metabolically expensive to produce, hard to maintain, and not easily counterfeited, because these qualities will be the most reliable indicators of genetic fitness. In recent years, Miller (1998; 2000a; 2000b; 2000c; 2001) has developed and popularized the most elaborated version of this theory. Miller suggests that sexual selection has played a much greater role than natural selection in shaping the most distinctively human aspects of our minds, including creativity and humor. He contends that creative and comedic behaviors are the results of complex psychological adaptations whose primary functions were to attract mates, yielding reproductive rather than survival benefits.

Because females are typically choosier than males (at least in short-term mating), males and females tend to use different reproductive strategies. *Intrasexual competition* is the competition for mates by driving away, intimidating, derogating, or killing one’s same-sex rivals. Because males experience much higher variance in reproductive success, they are under
much stronger selection to compete in risky, aggressive ways against their rivals. Such intrasexual competition resembles ‘survival of the fittest,’ in some respects (desperation, aggression, dominance), but its mechanisms allow for displays that are not just based on physical strength or endurance. One can become the alpha male, or “top dog” not just through brute force, but through humor—especially humorous derogation of sexual rivals (Buss, 1988). Many males will cut down a competitor by making fun of his most important sexually-selected traits, such as his allegedly inferior levels of kindness (“wife-beating psycho”), intelligence (“clodpate saphead”), physical attractiveness (“pencil-dick dwarf”), or wealth and status (“Yo, your would-be pimped-out ride is more illin’ than killin’ ”).

Such competitor-derogation parallels one of the oldest explanations for the origins of humor, the “superiority theory” (Morreall, 1987). Philosophers such as Plato, Aristotle, and Hobbes suggested that since humans are naturally competitive, humor emerged as an expression of our pleasure in being the victor. That is, we laugh because we are not the losers—at least not this time. Along these lines, Ludocivi (1933) described laughter as a symbolic baring of the teeth, and makes comparisons to other animals in which teeth-baring is a clear sign of aggressive intent. If a jest against a rival succeeds, it displays social dominance that could translate into sexual success. In hunter-gatherer societies, social dominance, control of resources, and mating success are tightly correlated. For this reason, males might use humor to display their social dominance, to deter sexual rivals, and to position themselves as desirable mates (Buss, 1994).

Females also exercise their intrasexual competition skills—they may derogate the sexually-selected traits of a female rival, such as her inferior levels of moral virtue (“skanky coke-head slut”) or physical attractiveness (“wattle-necked hippo-ass freak”). However, they aren’t likely to use the same tactics that males use, because female social status and reproductive success tends to be more influenced by social networking skill than by physical or symbolic dominance (Silk, Alberts, & Altmann, 2003). Thus humorous derogation of other females isn’t likely to be an effective means of intrasexual competition, because local males might actually favor “skanky coke-head sluts” (at least as short-term mates), and they might easily see that one’s rival does not have a “wattle-neck” or a “hippo-ass.” To promote her social status, a woman is more likely to use cooperation and kindness, rather than to display social dominance via humor. Rucas, Gurven, Kaplan, Winking, Gangestad, and Crespo (2006) argue that in tribal communities more representative of human ancestral conditions, a woman’s social status depends heavily on her desirability as a friend and peer, and having a good sense of humor does not much influence this desirability.

However, sexual selection is not restricted to intrasexual competition, where males clash on an open battlefield of wits and direct one-
upmanship. Attracting the other sex, through physical and behavioral displays, is just as important (Buss, 1998). For traits to remain sexually attractive across many generations, they must be reliable indicators of reproductive fitness. Consequently, such signals tend to be costly to produce, hard to maintain, and highly sensitive to the presence of genetic mutations. Miller (1998, 2000a, 200b, 2000c, 2001) noted that cultural displays of human creativity (including humor) satisfy these requirements. Perhaps in mate choice then, the production of humor is a valuable index of genetic fitness (Bressler, 2005), since high-quality humor cannot be easily “faked.” Indeed, Miller (1998) argued that most cultural displays (i.e., painting, poetry, architecture, etc.) are the results of male efforts to broadcast courtship displays to multiple female recipients. For example, males produce significantly more art, music, and literature than women, and the majority of this work is produced when men are between the ages of 20 and 35, at the peak age of mating effort (Miller, 1998). Some of this sex difference is surely due to historical and social differences in opportunities for being creative, and it is much more likely to reflect a sex difference in display motivation than in cognitive ability: men are not brighter than women; they are just more desperate to show off in colossally narcissistic ways that might attract sexual interest.

Some evidence suggests that Miller’s theory of sex-differentiated mating effort extends to humor production in courtship. Hay (2000) argued, based on historical sources, that humor in courtship has been much more rarely produced by females than by males. Kotthoff (2000) likewise reported evidence that males were more likely than females to produce verbal humor in informal social situations. Although quality of humor is probably a better index of genetic fitness than quantity (since quality is harder to fake, [Bressler, 2005]), the more frequent attempts by males to be funny suggest that their humor-production abilities were under stronger sexual selection.

**Summary of Selection Pressures for Humor**

In sum, several plausible mechanisms have been proposed to explain the evolutionary of humor: social bonding (group selection), intrasexual selection (humorous derogation of sexual rivals), and intersexual selection (mate choice for humor as a fitness indicator). Of particular relevance to mating intelligence are the sexual selection models, since they make the most specific empirical predictions concerning humor’s relationships to other hypothesized mental fitness indicators, such as creativity and intelligence. However, up to now, the discussion of these constructs (humor, creativity, and intelligence) has been rather vague. The rest of this chapter aims to define each construct more specifically, evaluate the psychometric
relationships between these constructs, and use this framework to com-
paratively assess the potential mechanisms for the evolution of humor.

THE PSYCHOMETRIC PERSPECTIVE

In most discussions of the evolution of humor, words such as “intelli-
gence,” “creativity,” and “creative intelligence” are frequently used. In
fact, they are often used interchangeably with “humor.” However, do
these terms really correspond to the same thing? Alternatively, does each
of these constructs reflect a distinct, unitary ability? Researchers have
spent over a century trying to measure intelligence and another half cen-
tury trying to measure creativity; only rarely have they considered the
evolutionary origins, adaptive functions, and genetic correlations between
these constructs. Our bet here is that the psychometrics of intelligence, cre-
ativity, and humor can illuminate their evolutionary history, and
vice-versa.

Creativity

What is creativity? Early Greek philosophers thought it was a mystical
inspiration from the seven muses (Rothenberg & Hausman, 1976). Freud
viewed creativity as resulting from the tension between conscious reality
and unconscious drives (Freud, 1908/1959). More recently, Greenberg
(2004) described creativity as involving “both the process and product of
unprecedented or novel perception, thoughts, or actions by which an
organism or group of organisms copes with present or potential changes in
the composition and structure of its environment” (p. 310). Though Green-
berg’s definition sounds appealingly general, it really only posits survival
payoffs for creativity (‘coping with the environment’), and it ignores
potential sexual payoffs. Likewise, there is a general consensus now that
‘creative’ things must be both novel and useful (Kaufman, in press; Mayer,
1999). Since this utility criterion is typically understood in economic, tech-
nological, or scientific terms, it frames genuine creativity as something that
must have survival payoffs—with a patentable innovation as the premier
example of a creative product. Verbal humor in courtship tends to get
overlooked as a creative activity, because its novelty need only be local
(new to the listener, rather than the patent office), and its utility need only
be reproductive (arousing to the listener, rather than contributing to eco-
nomic growth).

Researchers have tried to measure domain-general creative abilities by
assuming that divergent thinking—the ability to form unique associations
and connections—is fundamental to creative behavior. Divergent thinking
tests usually ask people to generate new ideas or uses for a particular
object, such as a brick. The most frequently used measure of creativity is the Torrance Test of Creative Thinking (1974), which is scored along the dimensions of originality, fluency, flexibility, and elaboration. Other divergent-thinking measures of creativity were developed by Guilford (1959), Getzels and Jackson (1962), and Wallach and Kogan (1965). Critics have emphasized that creativity depends not just on divergent thinking, but also on problem identification (before divergent thinking) and solution evaluation (after divergent thinking) (Plucker & Renzulli, 1999).

Experts have also extolled the need to distinguish expert-level creativity from everyday “garden variety” creativity (Kaufman & Baer, 2002; Kaufman, in press; Csikszentmihalyi, 1998). To attain greatness in any field, it takes about ten years just to reach the level of competence necessary to make a contribution (Hayes, 1989). Very few individuals have the time and resources to become an expert in multiple domains, so data on the domain specificity of genius-level creativity are limited. Though many fine art-works or epic poems represent spectacular achievements, it is in the everyday forms of human creativity, such as courtship humor, that we find the conspicuous individual differences that make psychological adaptations for creativity such relevant, reliable, and sexually attractive indicators of genetic fitness.

When we describe someone as “creative” we usually imply a rather generic predisposition towards creativity across many domains. However, being creative in one field (such as music) does not necessitate creativity in another field (such as painting). Evidence for domain-specificity comes from studies of creative performance in which a population-representative sample of participants create more than one thing (such as poems, stories, mathematical puzzles, collages and drawings), and each artifact is judged for creativity by appropriate experts (for validation of this consensual assessment technique, see Amabile, 1982). The correlations among the creativity ratings of products made by the same person in these studies have been quite low, especially when academic ability (a proxy for general intelligence) is controlled for (Baer, 1991; 1993; 1994; Conti, Coon, & Amabile, 1996; Han, 2000; Runco, 1989). Since the amount of shared variance across a wide variety of tasks is often less than 5 percent (Baer, 1993), some have argued that “creativity” is not a general factor that works across domains (Baer, 1998).

Other researchers have found that both domain-specific and domain-general processes play roles in everyday creativity. Sternberg and Lubart (1991) asked 63 university students to create various kinds of products (in domains of writing, art, advertising, and science) that could be reliably rated for their creativity. In the writing domain, they were given story titles and asked to compose a short story based on that title. In the art domain, they were asked to produce art drawings with titles such as “The Beginning of Time.” In the advertising domain, they were asked to pro-
duce verbal advertisements for a list of products. In the science domain, they were asked to solve problems such as how one might detect extraterrestrial aliens living on earth who are trying to escape detection. Participants created two products in each domain.

Sternberg and Lubart (1991) found, first, that the following resources were needed for creativity: intelligence, knowledge, motivation, appropriate thinking styles, appropriate personality traits, and the environment. Two main types of intelligence that seemed especially important for creativity were the ability to redefine problems and the ability to think insightfully. Domain-specific knowledge seems important for expert-level creativity, since without knowledge of the field, it is hard to judge which problems are the important ones to solve, and hard to judge when one has found an adequate solution. Not just the ability to think creativity but the desire to think creativity (motivation) also seemed crucial to creative production. The thinking styles most relevant to creativity seem to be the ‘legislative’ style (enjoying formulating problems and creating new ways of seeing things) and the ‘global’ thinking style (seeing the big picture and think “outside the box”). The personality traits that seemed most conducive to creativity were tolerance of ambiguity, willingness to grow, sensible risk-taking (which would now be lumped together as ‘openness’ in the Big Five system), willingness to surmount obstacles and persevere (‘conscientiousness’), and a belief in oneself (‘emotional stability’). The last component of the Sternberg and Lubart (1991) model is the environment, which sets the context for creativity and gives feedback about the quality of one’s creativity (e.g., for humor to be deemed creative, people in one’s environment need to find the joke funny). People in every culture have a sense of humor in some form, but they may differ in what they actually find funny (e.g., cross-dressing comedian Eddie Izzard may be considered hilarious in London, but baffling, surreal, and alarming in Dallas). Sternberg and Lubart (1991) suggest that a creative product or idea is the result of these many interacting processes, not all of which are cognitive abilities, and not all of which are under our control. They also found that creativity is relatively domain-specific: correlations of individuals’ creativity ratings across domains were fairly low. Lastly, they found that correlations between their measures of creativity and traditional tests of intelligence tended to be higher when the intelligence test items required innovative thinking.

In summary, creative ability can either be expressed at the expert level or the more common, everyday level. The type of humor valued in mating studies is likely to be at the everyday level of creativity—a preference for a light-hearted, amusing mate, not a professional stand-up comedian. Even though everyday creativity depends on both domain-general traits (e.g., intelligence, openness, divergent thinking) and domain-specific expertise, creativity research so far suggests that creativity is surprisingly
domain-specificity. Therefore, the ability to produce humor in a creative, witty fashion may be a unique ability, rather uncorrelated with other forms of creativity. Indeed, professional humorists seem to have developed a substantial body of humor knowledge which they employ when creating humor (Siegler, 2004). It is also important to realize that the reception of humor and creativity at the everyday level is the result of many interacting processes, some of which (e.g., listener mood and cultural background) are out of our control and may not reflect innate talent.

Intelligence

What is intelligence? Most researchers today believe that intelligence is a unitary construct (Jensen, 1998; Detterman, 2002; Gottfredson, 2002; Kyl-lonen, 2002; Petrill, 2002), a common factor underlying diverse cognitive abilities. Others emphasize lower-order factors corresponding to distinct cognitive abilities (e.g., Gardner, 1983, 1999; Sternberg, 1997, 2000). The debate is not a new one. At the turn of the 20th century, Charles Spearman (1904) argued for a general factor of human intelligence, whereas Louis Thurstone (1938) believed that the general factor was less important than the careful measurement of its components, which he thought included (a) Verbal comprehension (ability to understand spoken and written language), (b) Verbal fluency (ability to talk and write fluently), (c) Number (ability to do fast arithmetic), (d) Perceptual Speed (ability to visually recognize numbers and letters quickly), (e) Inductive reasoning (generalizing from specific cases to general principles), (f) Spatial visualization (imagining objects and their transformations), and (g) Memory (encoding and retrieving information). It is important to note here that Thurstone found a statistical distinction between verbal comprehension and verbal fluency, partially supporting his multi-dimensional model of intelligence, as well as suggesting that humor comprehension and production may involve separate processes.

The debate between Spearman and Thurstone could not be reconciled on purely theoretical grounds, but accumulating evidence supported hierarchical factor models of intelligence, with more general intelligence abilities at the top, and various ‘group factors’ (specific forms of intelligence) underneath. Two hierarchical theories that have had the most influence on modern intelligence research are the Cattell-Horn model and Carroll’s theory of cognitive abilities.

Early versions of the Cattell-Horn theory proposed that general intelligence has two major parts: fluid intelligence (gf) and crystallized intelligence (gc) (Horn & Cattell, 1966). Fluid intelligence reflects the efficient online functioning of the central nervous system (e.g., solving new abstract reasoning problems); whereas crystallized intelligence reflects
individually acquired knowledge, learned skills, and culture-specific content (e.g., composing symphonies, writing scientific papers).

The more recent model that dominates current intelligence research is Carroll’s Three-Stratum theory (Carroll, 1993). Carroll proposed this model after an extensive analysis of more than 460 data sets from the psychometric literature. In Carroll’s model, Stratum I reflects highly specialized skills (e.g., proof-reading manuscripts, understanding topographic maps, fixing bicycles), Stratum II reflects somewhat broader abilities (e.g., verbal intelligence, spatial reasoning, perceptual-motor performance), and Stratum III has only one ability, the g factor, that allegedly underlies all aspects of intellectual activity. Carroll’s model differs from the Cattell-Horn model in positing this superordinate g factor, and by assigning ‘crystallized’ abilities to lower strata.

Recently, Carroll’s model and the Horn-Cattell model have been synthesized into the Cattell-Horn-Carroll (CHC) theory (Flanagan & Harrison, 2005). Even though the CHC model still incorporates a g factor, its main emphasis is on the measurement of middle-stratum factors. The CHC theory has been influential in developing a variety of IQ tests, including the fifth edition of the Stanford-Binet (Roid, 2004), the second edition of the Kaufman Assessment Battery for Children (KABC-II; Kaufman, et al., 2005), and the third edition of the Woodcock-Johnson Cognitive Abilities Assessment (WJ III; Mather, et al., 2001).

Other contemporary researchers have emphasized the domain-specificity of intelligence. Howard Gardner (1983) introduced a ‘Multiple Intelligences’ model that included 7 distinct cognitive abilities: linguistic, logical-mathematical, spatial, musical, bodily-kinesthetic, interpersonal, and intrapersonal. Although Gardner has never demonstrated that his proposed intelligences are statistically independent, unloaded on the g factor, or irreconcilable with the Carroll hierarchical model, his model has profoundly influenced educational psychology. It also led others to propose additional possible intelligences, such as emotional intelligence, social intelligence, spiritual intelligence, existential intelligence, and now of course, mating intelligence.

Robert Sternberg (1997, 2000) also argues for looking “beyond g”. He emphasizes successful intelligence—the ability to achieve success in life by capitalizing on cognitive strengths and correcting or compensating for cognitive weaknesses, in order to adapt to, shape, and select environments, through a balance of analytical, creative, and practical abilities. According to Sternberg, analytical intelligence is required to solve problems and to judge the quality of ideas, creative intelligence is required to formulate good problems and solutions, and practical intelligence is needed to use the ideas and analysis in an effective way in one’s everyday life. As with the survival-oriented models of creativity as novelty plus utility, Sternberg’s work emphasizes practical, economic, and social forms
of success, rather than sexual attractiveness. Also, as with Gardner, Sternberg has produced little evidence that analytical, creative, and practical forms of intelligence are uncorrelated, unloaded on $g$, or anything other than mid-stratum ‘group factors’ (Brody, 2003; Gottfredson, 2003).

Regardless of these theoretical debates, almost all intelligence researchers agree that verbal intelligence is, at the very least, a distinctive ‘group factor’ or mid-stratum ability: it is highly correlated with the $g$ factor (general intelligence), but is statistically distinguishable from other group factors. It seems sensible that verbal intelligence is an important contributor to humor ability, which depends on general intelligence, and which will be correlated with many other desirable forms of cognitive ability. Thus, a good sense of humor may reveal good general intelligence, especially good verbal intelligence.

**Relationship Between Intelligence and Creativity**

What is the relationship between intelligence and creativity? Even though some researchers argue that intelligence and creativity are basically the same construct and depend upon the same cognitive processes (Weisberg, 1993), the more common view is that creativity and intelligence are overlapping, although not identical, constructs (Sternberg & O’Hara, 2000).

Several robust findings are consistent with this partial-overlap view of intelligence and creativity. First, when publicly recognizable ‘creative’ people such as successful artists, novelists, scientists, and engineers are studied, they tend to show IQs above 120 (Barron, 1963; Cox, 1926; Roe, 1952, 1972). This does not mean that people below IQ 120 are incapable of everyday-level creative behavior, but that they may be less likely to achieve expert-level creativity. Second, some evidence suggests that there is threshold effect (Barron, 1963, 1969), such that extra intelligence above IQ 120 does not much increase the likelihood of highly creative output (Sternberg, 2000). If there is an IQ 120 threshold for expert-level creativity, other personality factors such as conscientiousness, openness to experience, and emotional stability may become more important above that level. Also, in some fields such as getting elected to political leadership positions, very high intelligence and creativity may be detrimental, since they make candidates incomprehensible to the average (IQ 100) voter (Simonton, 1985).

However, a recent study challenged this threshold effect hypothesis, finding that even above IQ 120, intelligence remains highly predictive of occupational success and creative achievement (Lubinski et al., 2006). Here, creative achievement was defined much more stringently, e.g., as having achieved a tenured full professorship in a top-50 U.S. university by age 35. There may have been ceiling effects in previous creativity tests that reduced the correlation between intelligence and creativity at the upper end of the distribution.
Also, most of the support for the threshold hypothesis comes from comparisons of intelligence-creativity correlations within average-IQ versus high-IQ groups. To overcome the problem of restricted range among the high IQ groups, a recent study equated the variances of an average IQ group and a high IQ group (Sligh, Conners, & Roskos-Ewoldsen, 2005), and asked college students to complete some traditional tests of intelligence and the Finke Creative Invention Task (FCIT, Finke, 1990), which is based on the GenePlore model of creative cognition (Finke, Ward, & Smith, 1992). The FCIT requires participants to generate (the ‘Gene’ part of the model) a form (by drawing a picture) that combines three specified shapes (e.g., cone, square, set of wheels), and then interpret or explore (the ‘Plore’ part of the model) the invention as something meaningful within a particular category (e.g., transportation, toys, games). They found that crystallized intelligence displayed a threshold effect in predicting ‘creative cognition’ performance: crystallized g and creativity were more highly correlated in lower IQ individuals than in higher-IQ individuals. However, fluid intelligence showed the opposite pattern: fluid g and creativity were more highly correlated in higher-IQ individuals than in lower-IQ individuals.

Therefore, Sligh et al.’s (2005) findings suggest that the threshold effect seems to hold only for some creativity measures and some intelligence measures. This may help explain why studies find highly variable relationships between IQ and creativity, ranging from weakly positive to strongly positive (Baron & Harrington, 1981; Flescher, 1963; Getzels & Jackson, 1962; Guilford, 1967; Herr, Moore, & Hasen, 1965; Torrance, 1962, 1975; Wallach & Kogan, 1965). For instance, Anne Roe (1952, 1972) estimated the IQs of the highly creative scientists in her sample to range between 121 and 194, depending on whether the IQ test was verbal, spatial, or mathematical. Also, general intelligence may play less of a role in evolutionarily ancient domains of creativity such as art and music, than in evolutionarily novel domains such as mathematics and science (Kanazawa, this volume; McNemar, 1964). Thus, if humor is evolutionarily ancient, it may be a more reliable indicator of verbal creativity than of general intelligence. Further research is needed on this point.

Taken together, the research suggests a substantial overlap (but not identity) between intelligence and creativity. Consequently, verbal intelligence and verbal creativity may also be partially distinct. The implication for humor is that a reasonably high global IQ or even verbal IQ may be necessary, but not sufficient, for exceptional humor production ability.

Humor

Up to this point, we’ve mentioned humor several times, without describing in detail what we mean by it. Like creativity and intelligence, humor
is a complex construct that eludes a unified description or definition (Ruch, 1998). Hundreds of studies have examined the psychological nature of humor (Roekelein, 2002), but surprisingly few have conceptualized humor as an individual-differences skill or trait (Martin, 1998).

However, humor seems most relevant to mating intelligence when it is construed as a ‘trait’ in the psychometric and genetic sense—a stable, possibly heritable individual differences dimension that may be genetically correlated with other desirable traits, and which thereby might function as a fitness indicator. Also, as in other evolutionary analyses of animal signaling systems, ‘sense of humor’ is easiest to analyze when a clear distinction is made between humor production (trait display by a signaler) and humor appreciation (trait assessment by a receiver).

So far, there is vastly more work on humor appreciation than on humor production. Humor production refers to the ability to generate new instances of humor or to amuse others (Köhler & Ruch, 1996; Koppel & Sechrest, 1970). Humor production can take many forms, but most research (and our focus) has been on verbal humor, such as creating funny cartoon captions, which are then rated by judges (e.g., Derks & Hervas, 1988; Feingold & Mazzella, 1993; Kozbelt & Nishioka, in preparation; Siegler, 2004). Verbal humor is probably the most common form of humor production in natural situations, and is thus the most likely form of humor for selection to have acted upon (Bressler, 2005). Verbal humor may also show the clearest links to other known fitness indicators such as intelligence and creativity, especially when the quality of achieved humor (not just quantity of attempted humor) is taken into account.

By contrast, humor comprehension is the process of understanding or “getting” a joke, which involves requires language processing, reasoning, mental flexibility, and working memory (Shammi & Stuss, 2003), as well as problem solving (Shultz, 1972; Suls, 1972). Humor comprehension is typically assessed using multiple-choice questions where participants must correctly interpret a cartoon’s meaning (e.g., Couturier, Mansfield, & Gallagher, 1981; Kozbelt & Nishioka, in preparation; Wierzbicki & Young, 1978). Individual differences in humor comprehension may constitute an objectively assessable trait (much like reading comprehension), and may be fairly correlated with intelligence, creativity, and cultural knowledge.

Finally, humor appreciation is the experience of finding something amusing. It is typically operationalized by the intensity and duration of the “mirth response,” including smiling and laughing, or subjective funniness ratings given in response to humorous stimuli (Goldstein, 1970; Sheehy-Skeffington, 1977)—measures which cannot really be scored as correct or incorrect. Since individual differences in humor appreciation may reflect arbitrary, personality-based differences in thresholds for finding things funny, humor appreciation may not reflect an underlying skill
or ability in the way that humor production and comprehension do (Galloway, 1994; Wierzbicki & Young, 1978). On the other hand, extremely low thresholds for mirth responses are often taken as symptoms of mental illness (as when individuals with schizophrenia or mania laugh to themselves), as are extremely high thresholds (as in depression or autism). Moreover, if humor appreciation functions as part of the human mate choice system, there should be an optimal degree of responsiveness (maximum accuracy, minimal bias, and a moderate threshold) that helps receivers distinguish truly funny suitors from unfunny suitors. Indeed, an optimal humor appreciation system would comprehend many more attempts at humor than it actually finds amusing—it should ‘get’ many more jokes than it genuinely laughs at, just as a peahen can perceive many more peacock tails than she finds attractive. Thus, humor appreciation may be an important part of mate choice, just as humor production is an important part of courtship effort (Bressler, 2005; Grammar & Eibl-Eibesfeldt, 1990).

What are the psychometric relationships between humor production, comprehension, and appreciation? This question is not easy to answer, for several reasons. First, much research on individual differences in humor production, comprehension, and appreciation is plagued with methodological shortcomings, and does not meet standard psychometric criteria of reliability and validity (see critiques by Köhler & Ruch, 1996; Sheehy-Skeffington, 1977; Thorson & Powell, 1993a, 1993b). Also, few researchers have made clear distinctions between production, comprehension, and appreciation, and almost never have these traits been measured systematically in the same participants. Finally, compared to comprehension and appreciation, few investigations have examined the quality of humor production: Rockelein’s (2002) comprehensive humor bibliography of psychological research on humor, running to nearly 600 pages, includes only a few pages on humor production.

Nevertheless, some psychometric evidence suggests positive correlations between humor production, comprehension, and appreciation. Least surprisingly, comprehension seems to correlate positively with appreciation (Kozbelt & Nishioka, in preparation; Wierzbicki & Young, 1978). In a study of neuropsychiatric participants, Byrne (1956) found a positive correlation between humor comprehension (the ability to distinguish between hostile and non-hostile cartoons), and humor appreciation (actually finding hostile cartoons amusing). However, this effect held only after controlling for the confounding variable of intelligence, which likely contributes to humor comprehension but not appreciation (see below). Also, in a study of children aged 10 to 14, Masten (1986) found no correlation between comprehension and self-reported verbal funniness ratings, but did find a positive correlation between comprehension and observed
‘facial mirth response’ (smiling, laughing). Thus, while more research is needed to resolve this point, the data thus far suggest at least a mild positive association between humor appreciation and comprehension.

Evidence for a relationship between humor production and appreciation is far more tenuous. For instance, Köhler and Ruch (1996) found only very low positive correlations between humor appreciation and production, as measured by peer-rated performance criteria (rather than self-reported humor initiation). According to the researchers, this indicates that “those who rate jokes and cartoons as funny are not necessarily...able to produce many or funny punch lines; and vice versa, the wit may equally well be a person who appreciates humor or who dislikes the humor of others” (p. 18). Koppel and Sechrest (1970) found a slight positive correlation between humor appreciation and production but concluded they are largely separate constructs. Consistent with this, Kozbelt and Nishioka (in preparation) found no relationship between participants’ funniness ratings of cartoons and the rated funniness of captions created by the same participants. Masten (1986) observed no correlation between the quality of humor production and funniness ratings but she did observe a positive correlation between humor production and mirth response. Finally, Thorson and Powell (1993a, 1993b) found in a factor analysis study that self-reported humor production items loaded onto a separate factor than self-reported humor appreciation items.

Thus, there is some evidence that the association between humor production and appreciation is quite low. From a sexual signaling viewpoint, this is not surprising. If very funny individuals tend to be more intelligent and creative, they will have higher ‘mate value’ (desirability to the other sex), so they can afford to be choosier about their partners—i.e., their threshold for finding others funny will be quite high, and it will take a lot to amuse them. Thus, the very funny may seem mirthless, while those who laugh easily may have low standards, low mate value, and low humor production ability. Without understanding the distinctive functions of humor production versus appreciation, it is very hard to make sensible predictions about their likely relationship as individual-differences variables.

The strongest relationship is between humor production and humor comprehension. It makes sense that these two should be related, insofar as it would be hard to tell a funny story that was beyond one’s understanding (Attardo, 1994; Feingold, 1983). The available empirical evidence largely supports this view. For instance, Feingold and Mazzella (1993) found a positive correlation between the peer-rated quality of participants’ humor production (cartoon captioning and repartee generation) abilities and their humor comprehension (joke knowledge and joke reasoning) abilities. Kozbelt and Nishioka (in preparation) also found a positive cor-
relation between the peer-rated quality of humor production and comprehension, as measured by ability to detect “latent content” (Freud, 1905/1960) that was either matched or mismatched to a particular cartoon.

Thus, humor production, comprehension, and appreciation can be conceptually, functionally, and psychometrically distinguished. Humor comprehension is positively correlated with both production and appreciation, but appreciation and production show little association—nor should they, from a sexual-signaling viewpoint. Thus, while people do show stable individual differences in humor appreciation (e.g., Köhler & Ruch, 1996; Koppel & Sechrest, 1970), these individual differences do not necessarily represent an underlying ability (Wierzbicki & Young, 1978). Humor appreciation (mirthfulness) may instead represent a type of mate-choice threshold that tacitly incorporates one’s knowledge of one’s own mate value and likely success in a competitive mating market. The sexually desperate should laugh at almost everything; the sexually choosy should be very hard to amuse.

**Relationship Between Humor and Verbal Intelligence**

If humor production and comprehension abilities are a good reliable index of genetic fitness, then they should be positively correlated with characteristics such as intelligence, creativity, and physical attractiveness. A view of humor comprehension as incongruity-resolution or problem-solving implies a close association between humor, creativity, and intelligence (Martin, 1998). However, studies on the relationship between intelligence and humor, broadly defined, have yielded equivocal results (Galloway, 1994; Holt & Willard-Holt, 1995). Distinguishing between humor production, comprehension, and appreciation clarifies the results and reinforces the view that production and comprehension are fitness-related abilities, while humor appreciation is not.

For instance, evidence suggests a minimal relationship between humor appreciation and intelligence. Koppel and Sechrest (1970) and Landis and Ross (1933) found no significant correlations between humor appreciation and SAT scores. Byrne (1956) studied neuropsychiatric participants and found no relationship between estimated IQ and the extent to which a set of hostile cartoons were found funny. Ziv and Gadish (1990) found that gifted adolescents showed a bimodal distribution of self-reported humor appreciation: some showed high mirthfulness, while others seemed mirthless. Cunningham (1962) studied high school girls and found a significant negative correlation between IQ (as measured by the Thurstone Test of Mental Alertness) and humor appreciation (mirthfulness)—as we might expect if IQ correlates positively with mate value and choosiness. Indeed, in the few studies reporting positive associations between humor appreciation and intelligence, there are almost always
confounding factors, such as participant conscientiousness and motivation (Masten, 1986), subjectively assessing participants’ humor appreciation via interviews (Weissberg & Springer, 1961), or using unusual types of stimuli to assess humor appreciation. As an illustration of the latter, Feingold (1983) reported no correlation between IQ and humor appreciation (measured as self-reported interest in the films of Mel Brooks and Woody Allen) in “dull” (IQ < 104) participants, but a significant positive correlation in brighter (IQ > 104) participants. Here again, humor ‘appreciation’ of such films demands a certain level of humor comprehension, which should be more intelligence-related.

In contrast, positive correlations have often been found between intelligence and humor comprehension. This is not surprising: the Stanford-Binet intelligence test includes items on ‘comprehension of absurdities’ that function as a good measure of general intelligence (Ziv & Gadish, 1990). Along these lines, Feingold (1983; Feingold & Mazzella, 1991, 1993) found that verbal intelligence was positively correlated with humor and comprehension. Wierzbicki and Young (1978) observed a positive correlation between humor comprehension and IQ, estimated by the Vocabulary subtest of the WAIS, in a sample of college males. Developmental investigations (Bird, 1925; Couturier, Mansfield, & Gallagher, 1981; Masten, 1986; Owens & Hogan, 1983; Schwager, 1983) have yielded similar results. Finally, two dissertation studies (Jaffe, 1995; Schaier, 1975) found that among the elderly, humor appreciation increases with age, but humor comprehension decreases with age—effects which might be attributed to declines in fluid intelligence.

Finally, evidence concerning the correlations between intelligence and humor production ability is rather meager, largely due to the scarcity of studies on humor production. In understanding the role of humor in mating intelligence, this dearth of evidence is unfortunate, since production is the aspect of humor most relevant for testing the predictions of sexual selection theory. However, the evidence that does exist is consistent with Miller’s view. For instance, Feingold and Mazzella (1993) found a reliable positive correlation between verbal ability, measured by a multiple-choice test of word knowledge, and the quality of humor production, measured by ratings given by two judges to cartoon captions and repartee statements. Likewise, Koppel and Sechrest (1970), in a study of college fraternity brothers, found a small but reliable correlation between SAT scores and humor production ability, measured by peer ratings of newly devised cartoon captions. Finally, Masten (1986) found substantial positive correlations between both IQ and academic achievement and humor production, measured by ratings given by two judges to cartoon captions.

Since research to date has investigated only a few issues related to these constructs, much remains to be examined. However, the preliminary pattern of relationships between intelligence and three aspects of humor
(production, comprehension, and appreciation) is largely consistent with the predictions of a sexual selection account: both humor production and comprehension seem positively correlated with intelligence, and thus may represent cue to genetic fitness. In contrast, humor appreciation, which is more like a mate choice threshold than a courtship display, does not seem related to intelligence. Clearly, more research is necessary to resolve these relations, especially regarding the link between humor production and intelligence.

Relationship Between Humor and Creativity

In studying the links between intelligence and humor, at least psychometrics provides good, reliable, valid measures of intelligence. Studying the links between creativity and humor is trickier, because creativity and humor are both hard to operationalize (Humke & Schaefer, 1996; Murdock & Ganim, 1993). Most of this creativity-humor research measures creativity in quite domain-general ways, and does not clearly distinguish between humor production, comprehension, and appreciation. Ziv (1988b) noted that creativity may seem spuriously linked to humor if creativity is operationalized in rather vague ways, such as ‘divergent thinking’ (Guilford, 1959), or the ‘fluency, flexibility, originality, and elaboration of thought’ (e.g., Wallach & Kogan, 1965). Conceptually, humor production and creativity share many components (such as playfulness, risk-taking, and loose associations), as do humor comprehension and creativity (such as incongruity-resolution, and insight—Koestler, 1964; Kuhlman, 1984; Rouff, 1975). Along these lines, Murdock and Ganim’s (1993) content analysis of definitions and theories of humor suggested that humor and creativity are closely related, and that humor production is basically a subset of creativity. If this is right, then creativity should be positively correlated with both humor production and humor comprehension, just as intelligence seems to be. What, then, is the evidence regarding the psychometric relations between creativity and these aspects of humor?

As with intelligence, there is evidence for only a slight relationship between creativity and humor appreciation. Treadwell (1970), studying college students, found no relationship between self-reported humor appreciation and three paper-and-pencil tests of creative thinking: the Remote Associates Test, Gestalt transformations, and Need for Novelty scales from the Thematic Apperception Test. Schoel and Busse (1971) found no creativity difference (as assessed by two paper-and-pencil creativity tasks) between a group of ‘funny’ students (as selected by their teachers) and a control group of average students. However, the criteria for selecting humorous students included items such as “appreciates the ludicrous” (p. 34), and the authors concluded that their null result may reflect their selection criteria, which conflated humor appreciation and
humor production. Similarly, two dissertations have found no relationship between humor appreciation and creativity among first graders (Gilbert, 1977) or high school students (Townsend, 1982).

Psychometric evidence on the relationship between humor comprehension and creativity is rather scant, but several studies suggest a positive relationship. Rouff (1973, 1975) found that creativity and humor comprehension were positively correlated among undergraduates, and argued that they have a common basis in the ability to find hidden connections between apparently disparate concepts. Gilbert (1977) also found a positive relationship between humor comprehension and creativity among first graders, in contrast to a negligible correlation between humor appreciation and creativity. Moreover, “reflective” children had the greatest humor comprehension and demonstrated the most creativity.

Finally, as with humor comprehension, few studies have measured humor production in relationship to creativity, but the evidence so far suggests a positive correlation. Treadwell (1970) found positive correlations between the quality of humor production and three paper-and-pencil measures of creativity. Smith and White (1965), studying U.S. Air Force personnel, observed a positive association between wit and creativity. Townsend (1982) found quantity of humor positively predicted creative thinking in high school students. Finally, Brodzinsky and Rubien (1976) found that creativity was positively related to humor production; they also observed that men generated funnier captions than women for sexual and aggressive cartoons, but not for neutral stimuli. The scarcity of studies on links between creativity and humor comprehension or production seems more symptomatic of the lack of attention paid to distinct aspects of humor than of intrinsically weak relationships between the constructs: other investigations examining the association between creativity and humor (broadly defined) have generally found positive relationships between the two. For instance, Fabrizi and Pollio (1987) found correlations between teacher and peer ratings of the humor of 11th graders and these students’ originality and elaboration scores on the Torrance Test of Creative Thinking (in contrast to null findings with 7th graders). Several investigations (Humke & Schaefer, 1996; Kovács, 1999) have found positive relationships between paper-and-pencil creativity measures and scores on Thorson and Powell’s (1993a, 199b) Multidimensional Sense of Humor Scale, though this research did not clearly distinguish the four factors of the scale (humor production, humor and coping, humor appreciation, and attitudes toward humor). Finally, Ziv (1976, 1988b) described some studies showing that humor training is effective at enhancing creativity in adolescents.

In sum, despite limited empirical evidence, creativity seems to have positive relationships with both humor comprehension and production, but not with appreciation. This pattern echoes that found between intelli-
gence and humor (Galloway, 1994). Since creativity is also at least partially related to IQ, the prospects are good for understanding intelligence, creativity, and humor in a more integrated way, as closely related fitness indicators and likely products of sexual selection.

EVIDENCE FOR HUMOR AS AN IMPORTANT COMPONENT OF MATING INTELLIGENCE

Although the available psychometric evidence seems consistent with a sexual selection understanding of the nature and functions of humor, one might object that the evidence is fairly indirect. For instance, psychometric methods of measuring intelligence, creativity, and humor often seem artificial and ecologically invalid (Babad, 1974), particularly compared to whatever role these constructs may have played in the EEA (Storey, 2002). Moreover, one might argue that there is, so far, no evidence of increased sexual attractiveness or increased reproductive success from intelligence, creativity, or humor in a natural-fertility population (e.g., hunter-gatherers who do not use contraception)—which might be the best test of Miller’s theory. Perhaps humor, intelligence, and creativity evolved via natural selection for survival benefits somehow, and people simply prefer to socialize with others who are funny, smart, and creative, rather than humorless, dull, and unimaginative. Moreover, socializing with intelligent, funny people would allow one to benefit from their superior mental traits when new adaptive problems face one’s social group. In this view, the main role of humor in survival is facilitating adaptive social bonding and problem-solving, rather than acting as a fitness indicator in sexual selection. Is there anything specifically sexual about the function (rather than content) of humor, which could resolve this issue?

One approach is to examine sex differences in humor production that could reveal a mating function, and that would not be predicted by a sex-blind social-bonding theory. Specifically, if humor functions as a fitness indicator, and if females are generally choosier than males, then males should invest more effort in humor production, and females should show more overt humor appreciation (to encourage male courtship attempts), accompanied by a more discriminating covert humor appreciation (to distinguish which men are truly amusing). Until recently, little research has focused on sex differences in this way (Galloway, 1994). However, some recent research suggests that while men and women both say they like a “good sense of humor,” they mean different things by that: men prefer women who appreciate their humor, while women prefer men who make them laugh (Bressler, Martin, & Balshine, 2006). This is consistent with Provine’s (2000) analysis of over 3,000 singles ads, in which women were more likely to offer good humor appreciation, whereas men were more
likely to offer good humor production ability. Furthermore, Bressler and Balshine (2006) found that women rated humorous men as better potential partners, and as more friendly, fun, and popular. Women did not show any such preference for humorous women as potential friends. Additionally, a man’s view of other men’s or women’s personality attributes was uninfluenced by how funny such others were.

This is consistent with the sex differences in humor production discussed earlier (Hay, 2000; Kotthoff, 2000), and with some experimental studies suggesting sex differences in humor appreciation. If overt humor appreciation is indicated by laughter, then females demonstrate significantly more such appreciation than males (Chapell, Batten, Brown, Gonzalez, Herquet, Massar, & Pedroche, 2002; McAdams, Jackson, & Kirshnit, 1984). Further, this sex difference seems to begin in early childhood (Chapman & Foot, 1976). This sex difference in humor appreciation seems to reflect real-world differences in sexual choosiness: Grammer and Eibl-Eibesfeldt (1990) found that synchronized laughter during spontaneous male/female conversations predicted mutual initial attraction—but the amount of laughter the woman produced was most predictive of mutual interest in actually dating. Thus, both sexes treat the woman’s laughter as an index of humor appreciation and mate choice.

Further evidence for such sex differences comes from recent fMRI research examining the brain’s response to humorous cartoons (Azim, Mobbs, Booil, Menon, & Reiss, 2005). In this study, participants viewed a series of cartoons, pressed a button if they found each cartoon funny, and then rated the humor value of each cartoon. Members of both sexes found about 80 percent of the cartoons funny and showed no reliable difference in funniness ratings or response time. However, women showed more activation in left prefrontal cortex than men (suggesting deeper verbal analysis of the cartoons), and in the nucleus accumbens (the brain’s reward center, suggesting that they derived more pleasure from the humor). Finally, women were faster to rate low-humor cartoons as unfunny. Such results suggest that women may process humor more deeply, derive more pleasure from successful humor, and reject unsuccessful humor more quickly—signs that their humor appreciation may be more discriminating than that of men. Thus, males show higher mating intelligence in the sense of humor production ability, but females may show higher mating intelligence in the sense of humor appreciation ability—as the fitness indicator theory of humor would suggest.

Finally, some of the most provocative evidence for humor as a fitness indicator comes from research on shifts in women’s mate preferences across the menstrual cycle (Haselton & Miller, 2006; Miller, 2003). The logic here is that human females have concealed ovulation that allows only a brief window of time when fertilization can occur. While mating that brings material benefits (food, protection, paternal investment) would
have benefits that extend throughout the cycle, traits that are good gene indicators (e.g., creativity or humor, as hypothesized by Miller) should be more valued just before ovulation, when fertilization is most likely to occur (Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004). Only at peak fertility can a male mate’s good genes be passed on to offspring, so at peak fertility women should women pay attention to “good genes” indicators. If creativity and humor are good gene indicators, they should become more attractive to women during peak fertility, just before ovulation. Women using hormonal contraception such as the Pill (which suppresses ovulation) do not experience the associated hormonal or psychological changes, and so should not show a mid-cycle preference shift.

From this argument Haselton and Miller (2006) made some predictions about women’s mating preferences. First, higher fertility should lead women to favor male creativity more highly relative to male wealth—but only for short-term mating preferences. Preferences for long-term partners (who should stick around for many ovulatory cycles) should not be so dependent on immediate fertility fluctuations, so should have little effect on the desirability for creativity (good genes) versus wealth (good dad/provider). To test this hypothesis, Haselton and Miller asked participants to read pairs of vignettes about potential male mates: descriptions of a creative but poor artist versus a non-creative but rich artist and a creative but poor businessman versus a non-creative but rich businessman. The vignettes explicitly portrayed the creativity as a natural (and presumably heritable) trait, whereas the wealth was portrayed as due to luck (artistic fashion or a windfall inheritance). Haselton and Miller (2006) confirmed their predictions: higher fertility increased the relative desirability of poor but creative men, but only for short-term mating, not for long-term mating.

Some preliminary evidence also suggests that such ovulatory cycle effects influence female attraction to humor itself. As in the Haselton and Miller study, Miller and Caruthers (2003) had 206 female participants read vignettes about potential male mates who were described as showing different levels of humor-production ability (good, average, or bad). Women then rated a number of personality and cognitive traits for each male, and rated his attractiveness as a potential short-term and long-term mate. Three results are worth noting here. First, men described as having higher humor production ability were rated as significantly more socially sensitive, adaptable, extroverted, exciting, happy, and able to play well with kids (all $p < .01$), and as more intelligent, kind, tall, healthy, masculine, and muscular (all $p < .05$). Women seemed to be viewing humor production ability as a reliable cue of many other desirable fitness-related traits. Second, among naturally-cycling women (not using the Pill), female fertility significantly increased the short-term attractiveness of men with high humor-production ability ($r = .20$, $p = .028$, $N = 124$), but had no effect
on these men’s long-term attractiveness ($r = -0.11$, n.s., $N = 128$). There were no fertility effects on attraction to men with medium or low humor-production ability, and no cycle effects for women using hormonal contraception. Finally, among women in steady sexual relationships ($N = 105$), the rated humor-production ability of their current male partner significantly predicted their general relationship satisfaction ($r = 0.73$, $p < .001$), their expected relationship length ($r = 0.47$, $p < .001$), and their expected future likelihood of having children together ($r = 0.41$, $p < .001$). Thus, male humor production ability seems important both as a ‘good genes’ indicator in attracting women for short-term mating, and for retaining women in long-term relationships. These preliminary results are consistent with the fitness indicator view of humor, but they need replication in other labs, ideally with larger samples of naturally-cycling women, more accurate physiological measures of fertility status, and more ecologically valid ways of displaying potential male mates who differ in humor production ability.

In sum, mounting evidence supports the view that sexual selection favored the evolution of humor production ability as a fitness indicator, and humor appreciation ability as a mate choice mechanism. In particular, males and females value different aspects of humor in potential mates (females like funny males, and males like appreciative females), female and male brains respond to humor differently (females process linguistic aspects of humor more efficiently and show greater activation in reward centers), and females near peak fertility are especially attracted to males who display creativity and humor. These sex differences and cycle shifts build upon the basic psychometric distinctions between humor production, comprehension, and appreciation, which are related to each other and to intelligence and creativity in ways that are also consistent with sexual selection theory and fitness indicator theory. Since mating intelligence consists of the cognitive arsenal used to attract and retain mates, the findings so far suggest that humor, as an indicator of both creativity and intelligence, is an important part of that arsenal.

CONCLUSION

The scientific study of humor and its relationship to mating intelligence are no laughing matter. The available evidence paints a coherent but still somewhat vague picture of the relationships among sexual selection, humor, intelligence, and creativity. Far more empirical research will be needed to clarify the psychometric and functional relationships among these constructs, their role in mate attraction and intra-sexual rivalry, and their evaluation by mate choice mechanisms. Here, we propose a few directions for future research.
One clear direction is simply to clarify the basic psychometric relationships within and between the constructs of humor, creativity, and intelligence, paying closer attention to the distinctions between production, comprehension, and appreciation, and making more explicit ties to evolutionary theory. Doing so would bolster confidence in the validity of the apparent positive correlations among humor production, comprehension, intelligence, and creativity. It might also lead to discovery of positive correlations between humor appreciation ability (in the sense of accurate discrimination, not mindless hilarity), and other person-perception abilities, such as the capacities to judge intelligence, creativity, and personality traits accurately.

While some research has addressed sex differences in “sense of humor” (e.g., Bressler, 2005; Bressler & Balshine, 2006; Bressler, Martin, & Balshine, 2006; Brodzinsky & Rubien, 1976), a great deal of further work remains to be done, using more sophisticated sexual selection models that can predict specific, functional sex differences in humor production, comprehension, and appreciation. A high priority should be given to replicating the provisional results showing ovulatory cycle effects on women’s preferences for male creativity and humor production ability (Haselton & Miller, 2006; Miller & Caruthers, 2003).

Research also suggests that sex-differentiated mate preferences can be understood more clearly by distinguishing between short-term and long-term mating strategies (Buss, 2000). This distinction may be especially important in understanding mate preferences for humor (Stewart, Stinnett, & Rosenfeld, 2000). Future research should try to understand humor’s distinctive roles in initial attraction, serious courtship, relationship formation, mate retention, and deterrence of sexual rivals. Assortative mating for humor ability may be especially important to study, since it can quickly amplify the heritable genetic variation in humor ability. Assortative mating may even exist for specific types and modes of humor (Murstein, & Brust, 1985; Priest & Thein, 2003). Future research should also elucidate the conditions in which the desire for humor is expressed (short term relationship vs. long term relationship) and the reasons why the desire is expressed (good genes vs. good parents vs. social bonding) for both males and females.

Another direction for future research involves examining the natural patterns of genetic covariation between humor production ability and other fitness-related traits such as body symmetry, physical attractiveness, physical health, and mental health. For example, the fitness indicator theory of humor predicts a positive genetic (but not necessarily phenotypic) correlation between humor production ability and physical attractiveness among males. A low correlation could suggest that humor is not a very reliable good genes indicator, or that there are strong genetic or phenotypic trade-offs between growing efficient brain systems for humor production
and growing an attractive body. Several studies (Bressler, 2005; Bressler & Balshine, 2006; Bressler, Martin, & Balshine, 2006; Lundy, Tan, & Cunningham, 1998) have manipulated humor and physical attractiveness as independent variables, with interesting results. For instance, Lundy et al. (1998) manipulated both humor (using interview transcripts containing humorous self-deprecating responses) and physical attractiveness (using photographs) and found that men who expressed humor were rated as more desirable than nonhumorous individuals for a serious relationship and marriage, but only when the men were physically attractive. However, there seem to be no studies so far that examine the correlation between humor production ability and physical attractiveness in a broad population-representative sample, using double-blind ratings of humor and attractiveness (to avoid ‘halo effects’ whereby an attractive person’s humor tends to be judged more generously—see, e.g., Lundy et al., 1998). Such a halo effect might partly explain the dissociation sometimes observed between psychometric assessments of humor ability versus peer or self ratings of humorousness (e.g., Köhler & Ruch, 1996; Koppel & Sechrest, 1970).

Another possibility is that humor self-report questionnaires do not accurately capture individual differences in humor production ability in ecologically valid, socially complex settings (Babad, 1974). Of course, the standard psychometric approaches to measuring creativity and intelligence also may not be ecologically valid when applied to the mating domain. Many convergent lines of evidence, using different research methods, stimuli, and tasks, will be needed to clarify the place of humor in the overall structure of human phenotypic traits and genetic differences.

An additional complication concerns the possibility that humor production may have evolved as an ‘alternative mating strategy’—a compensatory strategy pursued by those who lack more obvious fitness indicators such as physical attractiveness or social status (Bressler, 2005). Thus, even if humor and physical attractiveness are positively correlated at the genetic level (as good genes indicators), they might be negatively correlated at the phenotypic level (given trade-offs between alternative mating strategies). If humor, creativity, and intelligence were perfectly positively correlated, there would be no need to assess them separately as fitness indicators: one trait would suffice for mate choice. If these are modestly inter-correlated, then there may be scope for mate choice to use ‘improper linear models’ (Dawes, 1979) or ‘fast and frugal heuristics’ (Gigerenzer & Todd, 1999), whereby a set of correlated variables are assessed independently then integrated using some rough-and-ready heuristic to make a judgment (in this case, about a mate’s likely genetic fitness). Only by measuring these constructs more precisely, distinguishing between production, comprehension, and appreciation, assessing their genetic and phenotypic inter-correlations, and studying the discriminatory mechanisms
adapted to judge them, will we learn whether sexual selection is indeed responsible for their evolution as distincively human forms of mating intelligence.

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