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THE EVOLUTION AND FUNCTIONS OF LAUGHTER AND HUMOR: A SYNTHETIC APPROACH

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ABSTRACT

A number of recent hypotheses have attempted to explain the ultimate evolutionary origins of laughter and humor. However, most of these have lacked breadth in their evolutionary frameworks while neglecting the empirical existence of two distinct types of laughter—Duchenne and non-Duchenne—and the implications of this distinction for the evolution of laughter as a signal. Most of these hypotheses have also been proposed in relative isolation of each other and remain disjointed from the relevant empirical literature. Here we attempt to remedy these shortcomings through a synthesis of previous laughter and humor research followed by (i) a reevaluation of this research in light of theory and data from several relevant disciplines, and (ii) the proposal of a synthetic evolutionary framework that takes into account phylogeny and history as well as proximate mechanisms and adaptive significance. We consider laughter to have been a preadaptation that was gradually elaborated and co-opted through both biological and cultural evolution. We hypothesize that Duchenne laughter became fully ritualized in early hominids between 4 and 2 mya as a medium for playful emotional contagion. This mechanism would have coupled the emotions of small hominid groups and promoted resource-building

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social play during the fleeting periods of safety and satiation that characterized early bipedal life. We further postulate that a generalized class of nonserious social incongruity would have been a reliable indicator of such safe times and thereby came to be a potent distal elicitor of laughter and playful emotion. This class of stimuli had its origins in primate social play and was the foundation for formal human humor. Within this framework, Duchenne laughter and protohumor were well established in the hominid biobehavioral repertoire when more cognitively sophisticated traits evolved in the hominid line between 2 mya and the present. The prior existence of laughter and humor allowed them to be co-opted for numerous novel functions, and it is from this process that non-Duchenne laughter and the "dark side" of laughter emerged. This perspective organizes the diversified forms and functions that characterize laughter and humor today and clarifies when and how laughter and humor evolved during the course of human evolution.

*He who approaches laughter upon science bent
will find it no laughing matter.*

(McComas 1923)

INTRODUCTION

LAUGHTER AND HUMOR were accorded high evolutionary significance by Darwin (1872) and have received increasing attention from biologists and psychologists during the last 30 years. This attention has resulted in myriad empirical advances and has left laughter and humor well characterized on multiple proximate levels (see Provine 2000; Vaid 2002; Bachorowski and Owren 2003; van Hooff and Preuschoft 2003; Wild, Rodden et al. 2003). Laudably, this research has spawned a number of hypotheses attempting to explain the ultimate evolutionary origins of laughter and humor (e.g., Eibl-Eibesfeldt 1989; Weisfeld 1994; Pinker 1997; Ramachandran 1998; Harris 1999; Miller 2000; Provine 2000; Owren and Bachorowski 2001; Caron 2002; Howe 2002; Jung 2003; Storey 2003). Nevertheless, the scientific study of laughter and humor is still in its infancy relative to other comparable subjects in emotions and communication research.

Many empirical questions about laughter and humor remain unanswered or neglected. For example, most researchers (e.g., Provine 2000; Owren and Bachorowski 2003; Vettin and Todt 2004) have failed to make the important distinction between Duchenne (stimulus-driven and emotionally valenced) and non-Duchenne (self-generated and emotionless) laughter (Keltner and Bonanno 1997; see also Wild, Rodden et al. 2003). While laughter has recently been found to occur most frequently during casual conversation and not following deliberate humor (Provine

1993; LaGreca et al. 1996; Vettin and Todt 2004), researchers have yet to question whether such conversational laughter is different in kind from that following humor. This oversight might well be the root cause of the widespread confusion concerning the diversity of forms and functions that characterizes laughter today (Keltner and Bonanno 1997).

As regards theory, the results of empirical findings of laughter and humor research remain disjointed and only partially accounted for by any one framework. In most cases, such hypotheses are not mutually exclusive but potentially complementary, yet a synthesis remains unrealized. As a result, theoretical limitations abound. Most hypotheses were not informed by crucial data in the first place and so leave no room for their integration. The role of emotion in laughter and humor processes is an issue that has often been overlooked (e.g., Ramachandran 1998; Jung 2003). Another, as mentioned, has been the neglect of a potential multiplicity of laughter kinds (e.g., Provine 2000; Owren and Bachorowski 2001, 2003). A different type of shortcoming has been the utilization of impoverished evolutionary frameworks. Some researchers (e.g., Owren and Bachorowski 2001) have neglected the multilevel nature of evolution, while others (e.g., Weisfeld 1994) have failed to specify the evolutionary mechanisms by which a novel trait emerges in the context of already existing traits. A related source of problems follows from the conflation of current utility with historical genesis (Gould and Vrba 1982). The adaptive functions that have been proposed for laughter and humor range widely and are often contradictory (Keltner and Bonanno 1997), yet many functions might be more properly char-

acterized as effects, or the functions of a trait that are different from those for which the trait was originally selected (Gould and Vrba 1982). Laughter and humor may well have evolved for one function while being later co-opted for others.

Laughter and humor researchers have largely failed to interact with outside research programs, depriving both of potential insights. Such programs include social neuroscience (e.g., Rizzolatti and Craighero 2004), concerned recently with the neural bases of gesture and expression initiation and perception; positive psychology (e.g., Seligman and Csikszentmihalyi 2000), which emphasizes the sources and facilitation of human well-being and not merely the mitigation of dysfunction; evolutionary psychology (e.g., Cosmides and Tooby 2000), which provides a theoretical toolbox for analyzing the evolution of human behavior and emotion; and multilevel selection theory (e.g., Wilson and Sober 1994), which maintains that natural selection can operate at multiple levels of the biological hierarchy. Laughter and humor have also been omitted from most general accounts of human evolution, taking a backseat to evolutionary divas like bipedalism, encephalization, language, and culture.

Thus a scientific understanding of laughter and humor has been hindered not only by empirical neglect and theoretical incompleteness but also by isolation from other relevant fields. Yet many plausible, supported, and even compelling ideas have been put forward and are integrated later in this review, and it is not our aim to deconstruct arguments or undermine past research. Our aim is instead to construct, to bridge those existing islands through a synthesis of previous research and theorizing in an attempt to integrate multiple perspectives and broaden our understanding of laughter phenomena. Methodologically, we utilize a balanced evolutionary perspective and multiple levels of analysis, while explicitly incorporating recent research from several previously disjointed scientific disciplines that lend insight to the synthesis at hand. In doing so, we present an inherently interdisciplinary evolutionary hypothesis that accounts for the myriad types and functions of laughter and humor as we

observe them today. While far from the final word, this is an effort to provide a first approximation of a comprehensive evolutionary framework within which future laughter and humor research and theorizing can be conducted.

We begin by reviewing the relevant empirical data on laughter and humor, from which we distill a number of key points. We next review relevant theory and data from work on mirror neurons, positive emotions, animal play, evolutionary psychology, and multilevel selection theory. This serves as the foundation for a two-part argument about the evolutionary trajectory traveled by laughter and humor over the last 7 million years. The first part details the evolutionary elaboration of human laughter and humor from ape antecedents between 4 and 2 mya. In the second part, we argue that laughter and humor were co-opted post-2 mya by a battery of evolving hominid traits, such as volitional oral-facial muscle control and language, resulting in the myriad forms and functions of laughter found today. Predictions and future directions are discussed last.

AN EMPIRICAL CHARACTERIZATION OF LAUGHTER AND HUMOR BIOLOGICAL FOUNDATIONS

Laughter is a universal human behavior found in all cultures and virtually all individuals the world over (Apte 1985; Lefcourt 2000; Provine 2000). Developmentally, laughter is one of the first social vocalizations emitted by human infants (Deacon 1997) and emerges spontaneously at anywhere between two and six months of age (Darwin 1872; McComas 1923; Sroufe and Waters 1976; Fogel et al. 1997; Scheiner et al. 2002). Even congenitally deaf and blind children have been reported to laugh despite never having perceived and learned from the laughter of others (Provine 2000). Although recent research has revealed a great deal of acoustic variation in the form of laughter (Bachorowski and Owren 2001; Bachorowski and Smoski 2001; Kipper and Todt 2001; Vettin and Todt 2004), few deny that laughter is distinctive and universally recognizable (Edmonson 1983; Eibl-Eibesfeldt 1989; Deacon

1997; Provine 2000; Kipper and Todt 2001; van Hooff and Preuschoft 2003). Experiments have shown that a wide range of repetition intervals are unambiguously perceived as laughter (Kipper and Todt 2001; Vettin and Todt 2004). Laughter thus has a characteristic, stereotyped form (Grammer and Eibl-Eibesfeldt 1990; Provine 1991) and can even be considered a ritualized, species-specific, fixed-action pattern (Grammer and Eibl-Eibesfeldt 1990). Taken together, these facts suggest that every normal human being is strongly genetically predisposed to develop the ability to produce and perceive laughter (Darwin 1872; McGhee 1979; Weisfeld 1994; Provine 2000; Caron 2002).

Comparative and phylogenetic analyses provide additional support for considering laughter an evolved instinct. Within the context of social play, numerous primate species exhibit a phylogenetically conserved facial expression, the relaxed open-mouth or "play" face (Preuschoft and van Hooff 1997). In the great apes, particularly *Pan*, this face is often accompanied by a pant-like vocalization during tickling and chasing (Darwin 1872; Fry 1994; Provine 2000; Gamble 2001; Caron 2002). Such "play panting" is instrumental in facilitating continued playful interaction (Flack et al. 2004; Matsusaka 2004) and is more salient to chimpanzees than is the concomitant facial expression (Parr 2004). It has been convincingly argued that human laughter is homologous to this great ape play pant correlate of the primate play display (van Hooff 1972; Provine 2000; van Hooff and Preuschoft 2003; Matsusaka 2004). The evidence therefore suggests that a rudimentary precursor to human laughter has distant evolutionary origins in the common primate ancestor of humans and the other great apes at least 6.5 mya (Fry 1994).

The evolved basis of laughter is further highlighted by the cross-cultural and cross-species similarities in the stimuli that elicit Duchenne laughter. Formal humor is of course the most familiar laughter stimulus, and theorists have debated its nature for at least 2,000 years (Provine 2000). More research has been devoted to adult humor than to any other type of laughter stimulus (Provine 1996), and what emerges from the liter-

ature is something of a consensus that incongruity and unexpectedness underlie almost all instances of formal laughter-evoking humor. This is insofar as the perceived inconsistency between one's current and past experiences involves both a nonserious or playful frame and an alternate type of intelligibility, that is, a meaningful interpretation of some stimulus or event that is different from that which was initially assumed (Shultz 1976; McGhee 1977, 1979; Apte 1985; Weisfeld 1994; Ramachandran 1998; Lefcourt 2000; Gamble 2001). These prerequisites provide the basis for a remarkably wide range of humor-related laughter stimuli, such as jokes, puns, and slap-stick mishaps.

Although adult humor has received a disproportionate amount of attention relative to other laughter phenomena (e.g., infant laughter, tickling, and rough-and-tumble play), there is an undeniable relationship—a continuity of form, structure and context—that connects all Duchenne laughter-inducing stimuli (Provine 2000). Human infants spontaneously laugh when they perceive unexpected stimuli in nonserious contexts (McGhee 1976; Sroufe and Waters 1976), for instance the peek-a-boo faces of their mothers, specifically if those stimuli are novel relative to the infants' developing mental schema. The same stimuli that elicit laughter in infants can evoke crying if the situation is not perceived as safe or if the incongruity is too intense (Sroufe and Waters 1976). Tickling likewise involves the unpredictable stimulation of vulnerable areas of the body by another person (as we are unable to tickle ourselves; Weisfeld 1994; Harris 1999; Provine 2000), and must come across as unthreatening and playful or else actual attack or aggression is perceived (Provine 2000). Tickling in conjunction with mock aggression and chasing is the prime elicitor of ape laughter (Fry 1994; Provine 2000; Gamble 2001) as well as laughter in human infants (Sroufe and Waters 1976) and children (Harris 1999; Provine 2000). Social contexts facilitate laughter (Devereux and Ginsburg 2001), and laughter is 30-times more likely to occur in a social context than when alone (Provine and Fischer 1989). It has even been argued that

laughter requires another person to stimulate it (Howe 2002; Jung 2003).

There is thus an intuitive family resemblance among the different proximate causes of Duchenne laughter, such that they can be characterized as sharing a single form or structure: a sudden unexpected change in events that is perceived to be at once not serious and in a social context—that is, *nonserious social incongruity*. We will hereafter use this phrase to refer to the essential and at root singular stimulus that elicits Duchenne laughter in apes and humans. Our use of the term is not meant to constitute a formal definition of humor or of laughter stimuli, but is instead meant to serve two functions: (1) to simplify the discussion by meaningfully categorizing the stimuli of Duchenne laughter without becoming swamped by the philosophical quagmire of what is “humor;” and (2) to give this referential term some descriptive power. In regards to the first point, we still use forms of the term “humor;” especially where this was the term used by researchers or theorists in their original studies. “Humor” is generally used for formal attempts at eliciting laughter in adults, while “protohumor” refers to other forms of nonserious social incongruity, such as rough-and-tumble play, tickling, physical mishaps, and pleasant surprise in apes and infants. In relation to the second point, we do not mean to imply that any nonserious social incongruity is a necessary and/or sufficient cause of laughter, but we feel that the term nonetheless works to convey their evolutionary continuity.

This underlying connectedness among the proximate causes of Duchenne laughter has not gone unnoticed. Darwin (1872) likened humor to “tickling of the mind,” while McGhee (1979:103) called humor the “logical result of an extension of playful forms of behavior to the more abstract intellectual sphere of ideas.” Gamble (2001) referred to the laughter-evoking stimuli of infants as “primitive forms of humor,” while arguing that the laughter-eliciting stimuli of adult signing apes, most notably Koko the gorilla, has essentially the same incongruity-based structure as human humor (see also McGhee 1979). Provine (2000) in turn referred to tickling as “protohumor,” while Weisfeld

(1994:151) stated that “tickling is a rather simple, rudimentary form of humor.” Research has even shown a significant correlation between individuals who laugh when tickled and those who are prone to laugh at and use humor (Fridlund and Loftis 1990), suggesting indirectly that both are triggered by the same mechanism.

The claim that all elicitors of Duchenne laughter share a similar structure finds support in the suggestion that there is a “laughter-coordinating” center in the dorsal upper pons that serves as the common ground for the different types of Duchenne laughter (Wild, Rodden et al. 2003). This assertion was presaged by Provine (1996), who noted that different forms of laughter-inducing stimuli appear to access a single “laugh generator” despite the fact that they are perceived through different modalities. Taken together, the laughter of nonhuman primates, the spontaneous laughter of human infants, tickling, and formal adult humor all share what is essentially a phylogenetically and ontogenetically-conserved structure and context (Darwin 1872; McGhee 1979; Provine 2000), here referred to as nonserious social incongruity.

THE ROLE OF CULTURE AND LEARNING

Despite the evident biological foundation of laughter and humor, there is little doubt that laughter-evoking contexts and how laughter is interpreted are fundamentally influenced by cultural norms and learning. Goodson (2003) has called this “learning (cultural) overlay,” or the codetermination of human actions by biology and culture (see Maryanski et al. 1997), and noted how it can confound analyses of the evolutionary foundations of behavior, including laughter. Burling (1993) has also argued that no human behavior is impervious to learning and that the human “gesture-call system,” of which laughter is a component, is no exception. The impact of learning on human laughter and humor is perhaps best illustrated by the cultural variation that exists not in the structure or “theme” (Ekman 1999) of the elicitors of laughter but in the subject matter that fulfills such structure (Apte 1985; Lefcourt

2000). These specifics can vary from toilet- and sex-based humor to political humor and span a wide spectrum of cultural institutions and customs. The contexts, frequency, and intensity of laughter are also variable in different cultures, which indicates that laughter can be inhibited and elicited in accordance with display rules and varying norms and customs (Apte 1985; Weisfeld 1994).

The role of learning in laughter production is also apparent in the ways that laughter typically occurs in everyday life. Contrary to the idea that laughter is always a reaction to nonserious social incongruity, studies have shown that the speaker in a conversational interaction produces up to 46% more laughter than his or her listeners (Provine 1993; La-Greca et al. 1996; Vettin and Todt 2004). Such laughter appears spontaneous and functions to smooth interactions and promote positive feelings between interlocutors (Provine 1996; Vettin and Todt 2004). Similar laughter can be expressed simply in response to an awareness of stress (i.e., nervous laughter) and is employed to signal that anxiety is being experienced (Keltner and Bonanno 1997). The prevalence of conversational laughter among strangers suggests that norms (or nervousness) play a role in leading people to utilize such laughter to avoid misunderstandings or to facilitate friendliness (Devereux and Ginsberg 2001; Vettin and Todt 2004). These instances of laughter are all arguably examples of strategic non-Duchenne laughter, which is in effect a learned facsimile of Duchenne laughter, and is thus different in kind from it. As Provine (1993) has noted, such conversational laughter is characterized by a “punctuation effect,” where laughter never interrupts speech but is used instead to “punctuate” statements. This phenomenon is best explained by positing that such conversational laughter is being used strategically like speech as a metacommunicative marker, as opposed to being “uncontrollable” like Duchenne laughter. An exception to this, where non-Duchenne laughter does co-occur with speech, is the learned hybrid of laughter and speech dubbed “laugh-speak” that is utilized by talk show hosts and salespeople to influence the attitudes and behaviors of others (Provine 1996).

Neuropsychological studies support the position that laughter can sometimes be controlled by learning despite having ancient phylogenetic roots, as researchers have revealed the existence of two partially dissociable neural pathways underlying two different types of laughter (for a review, see Wild, Rodden et al. 2003). One is emotionally-driven and involuntary, arising in subcortical, limbic, and brainstem areas and culminating in a “laughter-coordinating” center in the dorsal upper pons; the other is a voluntary motor pattern that originates in frontal premotor areas and directly influences the motor cortex. The most salient evidence for this dissociation comes from two types of facial paralysis: emotional facial paresis, in which subjects have no spontaneous laughter response to humorous stimulation yet can volitionally mimic laughter on command; and volitional facial paresis, in which subjects have an intact automatic laughter response to nonserious social incongruity yet cannot consciously mimic such laughter (Wild, Rodden et al. 2003). These findings have been supported by brain imaging data showing that spontaneous stimulus-induced laughter and volitional laughter do indeed arise from separate neural systems (Iwase et al. 2002). The existence of two types of laughter, one involuntarily elicited and one consciously controlled, is paralleled by the existence of two separate pathways for spontaneous and volitional facial expressions (Gazzaniga and Smylie 1990; Maryanski et al. 1997) and by the observed behavioral and functional difference between Duchenne and non-Duchenne laughter (Keltner and Bonanno 1997).

While neuropsychological studies reveal two types of laughter, one spontaneous and one volitional, some laughter that appears spontaneous (i.e., occurring in the flow of conversation) is in fact not. We agree with Keltner and Bonanno (1997) and Wild, Rodden et al. (2003) that there are two types of laughter and suggest that spontaneous non-Duchenne laughter is simply volitional laughter that has achieved a degree of automaticity, and so appears spontaneous. Duchenne and non-Duchenne laughter should not be distinguished in terms of spontaneity but instead in terms of antecedent stimuli, emotional va-

lence, or physical characteristics. Vettin and Todt (2004) recently discovered that the physical characteristics of conversational (non-Duchenne) and humor-driven (Duchenne) laughter differ insofar as conversational laughter consists of fewer elements and has a lower average fundamental frequency. The simpler physical characteristics of non-Duchenne laughter might be indicative of the limited ability of people to volitionally utilize laughter. The automaticity of this non-Duchenne laughter is further suggested by Vettin and Todt's (2004) claim that people underreport the frequency of their conversational laughter because they are not aware of how often they utilize it. Non-Duchenne laughter here is akin to other learned complex motor acts that become awkward and unnatural the more we think about them but that we can nonetheless become quite adept at through practice and the conditioning of unconscious motor programs.

McComas (1923:50) was one of the first theorists to acknowledge that laughter can be subjected to learning and utilized for multiple ends. He said, Certainly the pleasures which grow out of the sensations, activities and instincts cannot account for all forms of laughter. They have no part in the laughter of derision, for example, or the laughter of embarrassment. Such laughter is an artifice. It is allied to language. It is not a natural outcome of a pleasurable experience. It is rather a means of conveying an idea, a form of statement.

After drawing this distinction, however, McComas (1923:50) noted that "it is not easy to say where spontaneous laughter ends and controlled laughter begins." This sentiment is reflected in our characterization of spontaneous non-Duchenne (or conversational) laughter, and leads us to insert here an important caveat. Terms such as "spontaneous," "automatic," "involuntary," and "nonconscious" have often been used interchangeably, while "intentional," "volitional," "voluntary," and "conscious" have been used as their antonyms. "Strategic" behaviors are usually characterized by the latter set of terms. Spontaneous non-Duchenne laughter presents a problem because it exists in varying degrees across this conceptual divide, being strategic

and learned but largely beyond conscious control. Our caveat is that empirical studies of laughter have either not been looking to distinguish Duchenne from non-Duchenne (e.g., Vettin and Todt 2004), or have not yet achieved a grain fine enough to detect the difference (e.g., Provine 1993). Even a recent discussion of spontaneous and pseudo-spontaneous nonverbal behavior (Buck and VanLear 2002) ignored the potential automatization of pseudo-spontaneous nonverbal communication, consistently referring to it as "intentional." While it is beyond the scope of this paper to untangle the empirical nature of the problem, we feel that this issue will become central to future discussions of laughter and nonverbal behavior, especially as a more realistic, neurobiologically-grounded picture emerges of the interplay of genes and experience in shaping human behavior. To be as clear as possible, we will hereafter use "non-Duchenne" to refer to spontaneous conversational laughter that occurs in the absence of attempts at humor.

EMOTION, CONTAGION, AND MULTIFUNCTIONALITY

The distinction between Duchenne and non-Duchenne laughter highlights a key feature of Duchenne laughter: its inherent link with emotional experience. The emotional concomitant of Duchenne laughter has variously been called mirth or amusement (see McGhee 1979), joy (Darwin 1872; Panksepp 2000; Panksepp and Burgdorf 2003), exhilaration (Ruch 1993), or positive affect (Bachorowski and Owren 2001), while the common theme has been the decidedly positive feeling with which it coincides. Duchenne laughter appears to be intrinsically linked to the ancient brain circuit that underlies mammalian rough-and-tumble play, which is mediated at least in part by pain-reducing opioids (Panksepp 1998). This should come as no surprise since Duchenne laughter was already described as having been derived from primate play signals (van Hooff 1972; Provine 2000). The rewarding neurochemical cocktail underlying Duchenne laughter has not been fully described (Panksepp 1998), but the quick positive conditioning of infants to their

mothers and other individuals suggests its existence (Panksepp and Burgdorf 2003). Brain imaging studies have revealed that humor appreciation—Duchenne laughter’s phenomenological correlate—does involve affective reward networks in the brain (Goel and Dolan 2001; Shibata and Zhong 2001; Iwase et al. 2002; Moran et al. 2004). Behavioral studies have also found humor and laughter associated with increased positive affect and improved mood (Neuhoff and Schaefer 2002) and reduced negative affective responses to stressful events (Keltner and Bonanno 1997; Kuiper and Martin 1998; Fuhr 2002), while numerous clinical fields have reported significant health benefits derived from laughter (see Rosner 2002).

Owing to these associations, laughter has traditionally been conceptualized as a signal designed to communicate the subjective emotional state of a sender to receivers, such that the receivers cognitively decode the information of the signal and infer the original mental state of the sender (Russell et al. 2003). Within such a paradigm the meaning of laughter has typically been labeled something comparable to “this is play” or “that was play” (see van Hooff 1972; Grammer 1990), which has parallels in the “play signals” of other species (e.g., Bekoff 1995; Pellis and Pellis 1996; Kipper and Todt 2002; Panksepp and Burgdorf 2003). Recently, however, some researchers have reconceptualized animal communication and emotional communication in humans (Rendall and Owren 2002; Bachorowski and Owren 2003; Owren and Bachorowski 2003). An affect-induction approach has been proposed (Owren and Bachorowski 2003) that abandons the traditional idea that communication carries encoded information (see Hauser 1996) and instead emphasizes the emotional and behavioral impact that expressions have on those who perceive them (Krebs and Dawkins 1984; Bachorowski and Owren 2003). Laughter has been at the heart of this proposal. Laughter production is still tied to some degree of emotional arousal (Bachorowski and Owren 2003), but laughter’s function stems not from the communication of emotional states as information but instead from the accentuation or induction of positive affect in others. This

occurs either directly by laughter’s acoustic properties or indirectly through conditioned experience (Owren and Bachorowski 2003). This conception of laughter finds support in studies showing that heard “voiced” (or song-like) laughter elicits positive affect in others (in contrast to “unvoiced” or grunt-like laughter; Bachorowski and Owren 2001; see Bachorowski and Owren 2003) and from a fMRI study that found the amygdala, a key emotion and stimulus relevance area in the brain, activated by the perception of laughter (Sander and Scheich 2001).

In addition to inducing positive affect in others, Duchenne laughter is contagious (Provine 1992); heard laughter is a sufficient stimulus to elicit laughter. With this property, laughter falls within a larger category of primitive emotional contagion (Hatfield et al. 1994) or the phenomena by which the actions and emotions of interlocutors are coupled. The more general underlying tendency of interaction partners to adopt the same postures, gestures, and mannerisms has recently been dubbed the “chameleon effect” (Chartrand and Bargh 1999). These processes of biobehavioral coupling are predictive of the finding that group size has a facilitative effect on laughter responses to humor (Chapman 1983), with increases in group size increasing audience laughter levels in response to humorous material (Levy and Fenley 1979; Butcher and Whissell 1984). The contagiousness of laughter has therefore been implicated in coupling the emotions and behaviors of individuals within a group (Provine 1992; Deacon 1997). This possibly explains the finding that laughter, as a function of humor, increases cohesiveness and cooperation within goal-oriented groups (Banning 1987; Vinton 1989; Greatbatch and Clark 2003), a conclusion consistent with evidence of the cooperative value of the chameleon effect (Lakin et al. 2003) and, more generally, the spread of affect through a group (Sporer and Kelly 2004).

Laughter today functions in so many ways and contexts that its multifunctionality has been deemed “awe inspiring” (Fry 1977). Many of these putative functions remain speculative and will require additional research to be established or falsified. As already men-

tioned, Duchenne laughter has been found to increase positive affect and improve mood (Neuhoff and Schaefer 2002) and mitigate negative affective responses to stressful events (Keltner and Bonanno 1997; Kuiper and Martin 1998; Fuhr 2002), while promoting myriad other health benefits (see Rosner 2002). Laughter can similarly be used as a defense mechanism that trivializes stressful or psychologically overly demanding circumstances (Panksepp 2000). This is perhaps best recognized as nervous laughter, or a type of non-Duchenne laughter (Keltner and Bonanno 1997), and has been subsumed into a general “laughter-as-dissociation” hypothesis (Keltner and Bonanno 1997). Duchenne laughter and its associated positive affect also enable infants to maintain interactions with novel, mildly-stressful stimulation so that they can cultivate world knowledge and develop social competence (McGhee 1976; Sroufe and Waters 1976). During conversational interaction, laughter acts as a social lubricant to lighten the mood and can make listeners more receptive, as well as increase in-group feelings (Provine 1993, 2000). Laughter can likewise function to manipulate the emotions of others to the benefit of the laugher (Owren and Bachorowski 2003) and mitigate problems or social ambivalence within a group (Caron 2002), particularly by dampening friction and violent competition between individuals and establishing dominant and subordinate relationships (appeasement laughter, Fry 1977; superiority laughter, van Hooff 1972). Laughter can promote the integration of new individuals into an already-present group structure (Gamble 2001), but can also play a role in delineating in-group and out-group boundaries (laughter’s “dark side;” Panksepp 2000) by establishing “exclusionary group identities” and by being directly aggressive towards members of the out-group (Eibl-Eibesfeldt 1989; Pinker 1997). Laughter can also function to recruit playful interaction and fitness-enhancing stimulation (Weisfeldt 1994). Lastly, as discussed, the contagious nature of laughter can function to couple the emotions and coordinate behaviors of the individuals within a group (Provine 1992; Deacon 1997).

KEY EMPIRICAL POINTS

A number of key propositions can be distilled from the above discussion that provide the basis for our synthesis. (1) There are two distinct types of laughter, each with a partially dissociable neural pathway. Duchenne laughter is stimulus-driven and emotionally valenced, originating (save for initial sensory analysis) in subcortical and brainstem regions. Non-Duchenne laughter is unconnected (except perhaps via facial feedback) to emotional experience and originates in prefrontal premotor and motor areas. One can learn to automatically employ non-Duchenne laughter for various functions, which manifest themselves in conversational laughter, nervous laughter, appeasement laughter, and aggressive or derisive laughter, among others. (2) Duchenne laughter is genetically predisposed to develop. Every human develops the laughter “program” and the signal constitutes a ritualized, species-specific fixed-action pattern. (3) Duchenne laughter is derived from the primate relaxed open-mouth display (“play face”) and its associated pant-like vocalization, and so has homologues in the other great apes. Rudimentary laughter evolved originally at least 6.5 mya, before the hominid line split from the other hominoids, and most likely resembled the pant-like laughter of chimpanzees. (4) The major elicitors of Duchenne laughter—safe surprise in infants, tickling and play in apes and human children, and incongruity-based conceptual humor in human adults and signing apes—all share a common structural and contextual ground (nonserious social incongruity) by which they each access a common “laugh generator” in the brainstem. This is despite their different sensory modalities and the variation in initial processing that must occur to sense or understand them. (5) Human laughter, despite its hardwired basis, is amenable to cultural overlay and learning and is thus code-termined by biology and culture. Not only do cultural norms determine the subject matter of humor and the contexts in which laughter is appropriate (laughter can be inhibited), but individuals can also learn to strategically employ non-Duchenne laughter in conversation. (6) Duchenne laughter is inherently

linked to positive emotional experience. Feelings of joy or playful mirth occur concomitantly with such laughter, and this playful neurobiological cocktail functions not only to improve positive affect and key aspects of health but also to mitigate negative affect and stressful situations. (7) Laughter, especially of the Duchenne type, has a congruent emotional effect on others and appears to be a medium for emotional contagion. Sender laughter induces or enhances positive affect in receivers while simultaneously eliciting laughter itself. In this way, laughter is contagious. (8) Laughter serves myriad functions in modern human society. These range from facilitating emotional stability and health, curtailing negative emotion and stress, and promoting socialization, to lubricating social interaction, easing tensions and competition, delineating and maintaining group identities, and coordinating the emotions and behaviors of a group. Laughter thus functions on multiple levels, from individual physiology and psychology to dyadic and group-based interactions.

INTEGRATING OTHER FIELDS

The above characterization of laughter can be further developed by integrating findings and ideas from several scientific disciplines that have hitherto remained largely isolated from laughter research. This interdisciplinary approach provides insights to the functionality and evolution of laughter and demonstrates the possibilities of integrating the biological and social sciences (Maryanski et al. 1997; Rozin et al. 1997) and even the integration of knowledge as a whole (Wilson 1998). The following discussion concentrates on Duchenne laughter, as only it was involved in the initial elaboration of laughter and humor in hominids. Non-Duchenne laughter becomes important in the later discussion of laughter and humor as co-opted preadaptations.

THE VIEW FROM SOCIAL NEUROSCIENCE

Recent research in cognitive neuroscience provides a mechanistic framework for understanding the contagiousness and affect-inducing properties of laughter, and hence the evo-

lution of laughter as a signal. While this framework has been mostly applied to the visual perception of action, it is equally relevant to vocal signals like speech (Rizzolatti and Arbib 1998; Stamenov and Gallese 2002; Watkins et al. 2003; Wilson et al. 2004) and to other aspects of auditory perception (Kohler et al. 2002; see Rizzolatti and Craighero 2004).

Studies with nonhuman primates have revealed the existence of now-famous mirror neurons, a class of visuomotor neurons that have the remarkable characteristic of being active not only during particular actions but also during the perception of those actions as performed by others (Rizzolatti et al. 2002; Rizzolatti and Craighero 2004). Mirror neurons were first discovered in monkey premotor cortices by researchers utilizing single-cell recording techniques and have been found to be involved in many actions including reaching and grasping as well as ingestive and communicative mouth actions like lip smacking (Ferrari et al. 2003).

This work has led to a search for mirror neurons, or mirror matching systems, within the human brain. Imaging technologies, like PET and fMRI, and neurophysiological technologies, such as EEG, MEG, and TMS, have been utilized to uncover a wider range of mirror matching systems in humans than single-cell recording techniques were able to reveal in monkeys (Rizzolatti et al. 2002). Human premotor areas for hands, feet, and mouth all appear to be at least partly constituted by neurons that are active during action, the mental rehearsal of that action, the observation of a similar action by others, and the imitation of that action. Importantly, the mirror system in humans responds to the perception of intransitive actions and not only object-oriented actions, as is the case in monkeys (Rizzolatti and Craighero 2004).

Even more recent brain imaging research on humans has tentatively revealed a neural network via which the perception of others' emotional expressions leads to covert behavioral synchrony and congruent emotion (or primitive emotional contagion; Hatfield et al. 1994). Although empathy has received more discussion than emotional contagion per se, the results of several studies (Carr et al. 2003;

Wild, Erb et al. 2003; Wicker et al. 2003; Leslie et al. 2004) have suggested that perceived emotional expressions are first matched to a receiver's own representations of those expressions in their premotor cortices. This activity in premotor and connected motor mirror systems leads to emotional contagion via activity in limbic regions that is congruent with the emotion corresponding to the originally perceived emotional expression. The crucial pathway is proposed to be the insular cortex (Carr et al. 2003), which potentially connects the mirror circuits to emotion centers by means of the limbic system. Generally, this process of emotional contagion through motor matching is best viewed as a covert simulation process (Goldman and Sripada 2005).

On a theoretical level, this research has led to a number of hypotheses about the function of mirror matching circuits. It is thought that mirror neurons function to facilitate an understanding of the actions of others, as they create a direct link between senders and receivers and allow the simulation of perceived actions through extant representations of those actions in the observer (Rizzolatti and Craighero 2004). The "shared manifold of intersubjectivity" hypothesis proposed by Gallese (2003) views mirror neurons as the constituent elements of a system for the empathic understanding of others. This hypothesis posits that mirror-matching systems are a basic organizational principle of the human brain and human society, creating an intersubjective social space where individuals can experience and appreciate the movements, sensations, and emotions of others.

As discussed, Duchenne laughter co-occurs with positive affect, and its perception elicits positive affect and even laughter in receivers. Laughter has even been explicitly acknowledged in discussions of primitive emotional contagion (e.g., Hatfield et al. 1994), although only in passing. These qualities make laughter highly amenable to exploration within a mirror system paradigm. Yet surprisingly, laughter has received little attention from mirror system researchers. However, laughter has been characterized as a "resonance behavior of the first type," or a behavior that is prone to be immediately repro-

duced by others because its perception directly activates neurons that generate motor movements identical to those perceived (Rizzolatti et al. 1999).

This proposal has received hitherto unrecognized support from other neuroscientific studies. A somatotopically organized area of the brain, Brodmann's Area 6, or the supplementary motor area (SMA), has been implicated in all the requisite aspects of laughter phenomena that would be predicted from a mirror system account. The SMA is active during: (i) laughter production, both in Duchenne and non-Duchenne laughter (Iwase et al. 2002); (ii) imagined or internal laughter (Shibata and Zhong 2001; Osaka et al. 2003); (iii) laughter perception, although to varying degrees (K Sander personal communication February 23, 2005; D Shibata, personal communication November 16, 2004); and (iv) humor appreciation (Iwase et al. 2002; Mobbs et al. 2003). The human SMA has been implicated in some more general accounts of mirror system activity involving the observation of grasping movements (see Rizzolatti et al. 1999), the specular (left/right reversed) imitation of hand movements (Koski et al. 2003), and facial expression observation and imitation (Carr et al. 2003; Leslie et al. 2004). In these studies, there was increased SMA activation during imitation, which parallels the results with laughter (Shibata and Zhong 2001). Most significantly, electrical stimulation of points in the SMA has been found to elicit Duchenne laughter (Fried et al. 1998). The authors noted that this same area of the SMA is associated with speech initiation and stuttering, phenomena already being discussed in terms of mirror system activity (Kalinowski and Saltuklaroglu 2003). Supporting the proposal of Carr et al. (2003), the insula and amygdala have been found to be active during laughter perception (Sander and Scheich 2001) and humor appreciation (Goel and Dolan 2001; Mobbs et al. 2003; Moran et al. 2004).

Together this evidence suggests that the perception of laughter involves a mirror circuit centralized in the SMA, whose activity feeds into limbic areas via the insula, and in so doing elicits positive affect congruent with the perceived laughter. Such a mechanism

could be considered within the established framework of a perception-action model (see Preston and de Waal 2002) and would formalize the hypothetical laughter contagion mechanisms that Provine (1996) referred to as a “laugh detector” and a “laugh generator,” although in this framework they would essentially depend on a more general and singular mirror mechanism.

Laughter and yawning have traditionally been seen as embodying the best examples of contagious behaviors in humans (Provine 2000). While this might well be the case, we think it is worth distinguishing them. The key difference is that laughter evolved in relation to a mirror system as a signal, whereas yawning did not. Laughter is unique to the great apes and uniquely elaborated in humans. While Panksepp and colleagues (e.g., Panksepp and Burgdorf 2003) have suggested that rats laugh as well, rat laughter is surely analogous and not homologous to ape laughter as the many mammalian species intermediate to rats and apes have never been documented to laugh. Yawning, in contrast, is an ancient reflex ubiquitous to vertebrates that evolved to regulate individual arousal irrespective of social contexts (Baenninger 1997). Yawning is only contagious in great apes (Anderson et al. 2004) and humans (Provine 1986) and only insofar as it interacts with novel ape cognitive abilities. The point of this contrast is the assertion that the neural bases of laughter and yawn contagion (e.g. Platek et al. 2005; Schurmann et al. 2005) should not necessarily be the same since laughter is a more complex and variable signal that evolved in relation to a mirror system and is thus much more likely to involve such a system than is yawning. The two behaviors deserve to be evaluated on their own terms and only then compared.

Regardless of the details, the most important implication of mirror system research for laughter is that the neural network involved in the production of a given action is also activated during the perception of that action in others. This idea suggests an inherent link between senders and receivers such as that already found in laughter. Significantly, it has been shown that only Duchenne laughter has the capacity to undo negative emotions and

stress (Keltner and Bonanno 1997), while only “voiced,” or fully vocalized, laughter (Bachorowski and Owren 2001), that is emotionally-driven (Keltner and Bonanno 1997), has the capacity to elicit positive affect in others. Also, Smoski and Bachorowski (2003b) showed that those laughs that are most strongly associated with the induction of positive affect are also most facilitative of antiphonal (or laughter-elicited) laughter. Grammer and Eibl-Eibesfeldt (1990) also found that only voiced laughs were correlated with an interest in seeing one’s experimental partner again, indicating the association of such laughs with positive affect. This is logical from the perspective of mirror circuits, as only the perception of Duchenne laughter would have been matched by the activation of motor patterns that influence emotion pathways.

If Gallese (2003) and colleagues are correct that there is a shared manifold, in which the same system is used to perceive and send a signal, then laughter should be viewed as a constituent part of such a manifold, and the functions of laughter should be reexamined in light of the manifold’s overarching function(s). We want to emphasize here a putative function for laughter that others have suggested—namely, coupling the emotions of group members and coordinating their actions (Provine 1992; Deacon 1997). Deacon (1997:429) referred to laughter and crying as “vehicles for coordinating the emotions of a social group” and considered them “a sort of preestablished harmony,” while Provine (1992:3) asserted that “. . . contagious laughter . . . is an example of a social coupling process that synchronizes the biological and behavioral state of a group.” The mirror-system perspective independently suggests such an inherently social function for Duchenne laughter as it benefits all involved individuals by being a medium for playful emotional contagion. The mirror-system perspective goes one step farther by providing a novel and plausible neural mechanism. In this view, mirror neurons are the proximate basis (Preston and de Waal 2002) of the shared manifold, while the resulting emotional synchrony (or social understanding) requires a complementary ultimate explanation in terms of group-based functional integration.

THE VIEW FROM POSITIVE PSYCHOLOGY
AND PLAY RESEARCH

The field of positive psychology focuses on the determinants of optimal human performance (Seligman and Csikszentmihalyi 2000) in contrast to the traditional focus in psychology on dysfunction. The work of Fredrickson (1998) is most relevant to our discussion of laughter and humor.

Utilizing an adaptationist perspective, Fredrickson formalized the Broaden-and-Build model that accounts for the form and functions of positive emotions, such as joy, interest, contentment, and love. According to Fredrickson, these positive emotions “serve to broaden an individual’s momentary thought-action repertoire, which in turn has the effect of building that individual’s physical, intellectual, and social resources” (Fredrickson 1998:300). Fredrickson additionally proposes that positive emotions function to “undo” the effects of negative emotional experience. A recent study has shown that positive emotions do indeed promote psychological resilience in the face of stress (Tugade and Fredrickson 2004). Fredrickson proposes that joy specifically fosters the urge to play, in the broadest sense of the word, and that this play builds resources while promoting social cohesion, cooperation, and even altruism.

Though not elaborated by Fredrickson (1998), research on animal and human play largely corroborates her account. It is becoming established that the social and developmental advantages of play outweigh its immediate costs (Sharpe et al. 2002; de Oliveira et al. 2003; Fagen and Fagen 2004). The most widely accepted function for play entails the facilitation of physical, cognitive, and emotional development (Byers and Walker 1995; Spinka et al. 2001), particularly in juvenile organisms (Fagen 1993). Play functions to promote synaptogenesis and muscle differentiation (Byers and Walker 1995) while training individuals to deal with unexpected physical, cognitive, and emotional stressors (Spinka et al. 2001; Donaldson et al. 2002). Social play can also decrease aggression (Drea et al. 1996), increase fairness and cooperation (Bekoff 2001), and it can be used as a tool for social assessment and for promoting the es-

tablishment and maintenance of social bonds (Pellis and Iwaniuk 2000). Social play in chimpanzees has been shown to mitigate tensions arising in potentially competitive contexts, such as just before feeding (Palagi et al. 2004). Social play in humans, in turn, has been shown to facilitate competitiveness without aggression (Grave-Ardec et al. 2003) while serving both training and social assessment functions (Fry 2005). And as discussed, social play appears to have a distinct circuit in the mammalian brain (Panksepp 1998) that is mediated, at least in part, by pain-reducing opioids (Panksepp 1998; Van den Berg et al. 2000; Guard et al. 2002). The functions of play are thus not unlike those subsumed within Fredrickson’s model of positive emotion.

Our account of laughter and humor is highly compatible with Fredrickson’s Broaden-and-Build model and the literature on play. As we have shown, Duchenne laughter is inherently tied to positive emotional experience and functions in essentially all of the ways that Fredrickson proposed: to create a playful mood that “undoes” negative emotions while promoting individual and group-level functioning. Laughter appears to function in many of the same ways as social play, particularly since laughter often follows from social play and facilitates playful interaction (Weisfeld 1994; Matsusaka 2004). Insofar as social play is functional, so too is Duchenne laughter. As Panksepp (1998:287) has argued, “it is reasonable to suppose that the sources of human laughter go back to ancient social engagement systems that first mediated mammalian playfulness.” It is noteworthy that humans play across the lifespan and to a degree not seen in other animals, such that some have even referred to humans as *Homo ludens*, or “playful man” (see Bjorklund and Pellegrini 2002). Laughter (and the joy associated with it) does indeed appear to be linked with play, not only in children but also in apes and human adults. This supports our argument that all genuine laughter-eliciting stimuli share a common evolutionary and mechanistic basis derived from social play in primates.

Fredrickson’s (1998) Broaden-and-Build model of positive emotions has the potential to formalize the functions served by Du-

chene laughter. It has been suggested that the contradictory functions that are often attributed to laughter (i.e., promoting play, and showing aggression) arise from the simple fact that Duchenne laughter is typically not distinguished from non-Duchenne laughter in discussions of laughter's functionality (Keltner and Bonanno 1997). We maintain that this is indeed the case and suggest that the functional model proposed by Fredrickson (1998) be used as a foundation for considering the functions of Duchenne laughter.

Taken together, the literature of social neuroscience and positive psychology suggests that Duchenne laughter functions to promote group cohesion and resource-building social play by spreading playful emotions. This idea is similar to the function of play panting in chimps (Flack et al. 2004; Matsusaka 2004) and to Weisfeld's (1994) account of laughter in humans, although where he emphasized the musical quality of laughter and cognitive mediation, we emphasize mirror-neuron based emotional contagion. The next point to be addressed is the nature of the stimuli (nonserious social incongruity) that elicit Duchenne laughter.

THE VIEW FROM EVOLUTIONARY PSYCHOLOGY

While the perspective provided by Fredrickson (1998) takes valuable strides towards formalizing the value inherent in positive emotions, and thus in Duchenne laughter, there is also an element that is missing. Fredrickson (1998:303) discusses how emotions evolved "because they promoted specific actions in life-threatening circumstances and thereby increased the odds of the ancestors' survival." This applies most obviously to negative emotions, which coordinate the body to act adaptively in the face of a specific stimulus, such as a fight-or-flight response when something dangerous suddenly approaches. But positive emotions do not occur in life-threatening situations, and so presumably would not have been selected to promote such specific, necessary "action-tendencies" (Fredrickson 1998). However, this ignores the nature of human laughter, which is a specific bodily response to a very specific stimulus

(i.e., nonserious social incongruity). This means that in order for laughter to be understood, one must consider the reason why it would have been adaptive for an individual to playfully influence others in the face of nonserious social incongruity. This position is made most intelligible from the perspective of evolutionary psychology (Cosmides and Tooby 1997).

Modern emotion theorists (e.g., Ekman 1999) treat emotion as a response to the perception of a specific stimulus that adaptively coordinates the physiological, experiential, and behavioral aspects of an individual in the context indicated by that stimulus. An evolutionary psychology perspective in particular (e.g., Tooby and Cosmides 1990; Cosmides and Tooby 2000) takes this insight and asks why, in adaptationist terms, a given coordinated emotional response is conjoined with a given stimulus. One guiding assumption is that the stimulus was a recurrent component of the human ancestral environment while the coordinated behavior evolved in relation to that stimulus, such that those individuals who responded appropriately to the stimulus would have had relatively increased fitness. The coordinated reaction would thus have evolved in the human environment of evolutionary adaptation (EEA) in conjunction with the ecological, social, and morphological characteristics of our ancestors. The stimulus (or class of stimuli) would have constituted a specific adaptive problem and been the selective agent driving the evolution of the emotional reaction. By this logic, one must question what function the reaction would have served our ancestors.

Duchenne laughter fits well into the general emotions framework outlined above. It is best seen as the behavioral component of a positive emotional reaction to a specific stimulus, nonserious social incongruity. Laughter's accompanying physiological response is sympathetic arousal (Fry 1994; Panksepp 1998), while the experience is "joy" (Panksepp 2003) or "exhilaration" (Ruch 1993). In this framework, the affect of joy and the behavior of Duchenne laughter occur simultaneously in response to the same stimulus. The significance of the reaction lies not in laughter occurring when we reach a certain level

of arousal, as many others have maintained (e.g., Owren and Bachorowski 2001), but in evolution having conjoined the affective and behavioral components in the face of a common stimulus. Laughter is also a signal, not just a behavioral response, a fact highlighted both by the dependence of laughter on a social context and its effect on receivers. There is a distinct difference between fighting or running and laughing; the former work to influence the individual experiencing the emotion, the latter functions to influence other individuals (Owren and Bachorowski 2003).

Why in the face of nonserious social incongruity is it adaptive for an individual to be rendered playful, and for him or her to elicit in others positive affect and playful tendencies? This question will be central to our later discussion and follows logically from the program of evolutionary psychology. However, at the outset, we wish to make clear that while we find value in this approach to emotion and to laughter and humor in particular, it does have its limitations. Evolutionary psychology has been increasingly criticized for relying too heavily on adaptationist thinking, employing unrealistic assumptions about brain modularity, and ignoring comparative evidence and the many homologues among humans and other animals (see Panksepp and Panksepp 2000; Lloyd and Feldman 2002). As we have argued, laughter and humor have obvious homologues in other great apes and derive their form from a distant primate heritage. The affective circuit underlying Duchenne laughter is also ancient, existing ubiquitously among mammals and forming the foundation for many affiliative and social play behaviors (Panksepp 1998). For this reason it would be misguided to formulate a hypothesis that recounts laughter and humor evolving *de novo*. Instead, we are interested in the process by which laughter and humor initially changed in degree (not kind) from what is found in other great apes. Phylogenetic considerations will therefore take center stage in our account despite typically being accorded secondary importance by evolutionary psychologists (e.g., Cosmides and Tooby 1997). Ancestral environmental conditions and uniquely human selective pressures will be invoked, but only to describe

why laughter and humor were elaborated in humans relative to other apes. In identifying an "adaptive problem," we are thus not following the modularity assumption that each adaptive problem was solved by the evolution of a novel piece of cognitive equipment (e.g., Cosmides and Tooby 1997). Rather we focus on the phylogenetic origins of laughter and humor and argue that an extant trait was co-opted and elaborated in the face of novel selection pressures. The mirror system perspective (Gallese 2003) suggests such an ancient and general mechanism while also being evolutionarily and neurobiologically plausible. Invoking the historical logic of evolutionary psychology we try to stay as close to the empirical facts as possible while avoiding the adaptationist excesses of mainstream evolutionary psychology (see Panksepp and Panksepp 2000).

THE VIEW FROM MULTILEVEL SELECTION THEORY

Many have argued that laughter is adaptive, but few have thought carefully about the level at which laughter is adaptive. This question has been neglected in part because of general skepticism about group selection since the 1960s, causing all adaptations to be interpreted as forms of individual or genetic self-interest. Multilevel selection has recently returned to respectability as a theoretical framework, especially in the case of human evolution, where social processes can radically alter the partitioning of phenotypic variation within and among groups (Sober and Wilson 1998; Boehm 1999; Hammerstein 2003; Richerson and Boyd 2004; Wilson 2004). Since laughter is quintessentially a social process that alters the behaviors of others in addition to the self, it is worth examining its fitness effects from a modern multilevel perspective.

To begin with a brief tutorial, consider a population that varies for a trait such as laughter and is divided into a large number of social groups. There will be variation within groups (some individuals who laugh more than others or who get others to laugh more) and also variation between groups (groups in which laughter occurs more than

in others). Suppose that laughter is selectively advantageous and evolves in the total population. This can happen in two ways. First, individuals who laugh can be more fit than individuals in the same group who do not laugh. Second, groups in which laughter occurs can be more fit than groups in which laughter does not occur. The differential contribution of groups to the total gene pool can thus be an agent of evolutionary change as surely as the differential contribution of individuals within groups. Total evolutionary change is a combination of within- and between-group selection, which can operate in the same or opposite directions.

The rejection of group selection is the claim that within-group selection is invariably stronger than between-group selection (Williams 1966). This claim may have been reasonable in the 1960s, but it is no longer credible based on theoretical and empirical advances that are reviewed elsewhere (Sober and Wilson 1998). Many evolutionary biologists routinely partition selection into within- and between-group components (often using statistical methods such as the Price equation; Frank 1995) and conclude that traits evolve by group selection despite being selectively neutral or disadvantageous within groups. It should be noted that group selection remains controversial in part because of widespread confusion about the concept of selfish genes. Genes that evolve are called selfish because they replace the genes that did not evolve—regardless of whether the selective advantage was within or between groups. The argument for selfish genes is not an argument against group selection. In the terminology of selfish gene theory, it is the concept of vehicles, not replicators, that is relevant to multilevel selection. To say that the group is the vehicle of selection is roughly equivalent to saying that the trait evolved by group selection (Dugatkin and Reeve 1994; Wilson and Sober 1994; Sober and Wilson 1998).

These ideas provide insight into the conditions under which laughter and humor were elaborated in humans. We argue that the benefits incurred through laughter and play often occur at the group level as well as at the individual level, and between-group selection could thus have played a significant

role in the elaboration of laughter and humor in humans. We also argue that both within- and between-group selection would have driven the elaboration of laughter and humor in the same direction. To support these conclusions, we argue that laughter imposes few or no within-group costs while also promoting between-group variation through contagion and within-group bond formation. These ideas will be used to evaluate one of the most recent and detailed evolutionary theories of laughter proposed by Owren and Bachorowski (2001).

A HISTORICAL ACCOUNT OF THE ELABORATION OF LAUGHTER AND HUMOR

Detailing an evolutionary scenario for a given set of traits is a bold endeavor that runs the risk of becoming an unsubstantiated “just-so story.” Nevertheless, there are a number of clues amenable to scientific evaluation that can be utilized to triangulate the time frame and contexts of the evolutionary elaboration of laughter and humor.

ESTABLISHING A TIME FRAME

The first clue comes from the phylogenetic origins of laughter and humor mentioned earlier. The laughter-like vocalization accompanying the play face in chimpanzees, gorillas, and orangutans suggests that the relaxed open-mouth display was originally elaborated in the hominoids sometime before the hominid line diverged around 6.5 mya (Fry 1994). Human laughter is moreover a highly derived form of the generalized hominoid laughter (van Hooff 1972; Provine 2000). This indicates that the major changes to laughter since its emergence from the relaxed open-mouth display occurred in the hominid line subsequent to its split from the other hominoids between 5 and 7 mya (Jurmain et al. 2000). Similar reasoning applies to humor (Gamble 2001).

A second line of evidence relates to bipedalism, which was fully developed in human ancestors (presumably the australopithecines) about 4 mya (Jurmain et al. 2000). This is of great importance because bipedalism effectively lifted the morphological constraints that allowed laughter to evolve as the

dynamic signal found in humans today (Provine 2000). Provine's Bipedal Theory (2000; see also Aiello 1996) maintains that bipedal locomotion freed the thorax of the mechanical demands of quadrupedal location and loosened the typical mammalian coupling of vocalizations with breathing. This made language possible but also allowed laughter to become ritualized in humans as a stereotyped vocalization, in contrast to the one-syllable-per-breath play panting of chimpanzees (Provine 2000). Chimpanzees cannot laugh like humans because their anatomy inherently constrains their vocal abilities; these constraints vanished in hominids when they began walking on two legs (Provine 2000).

The brain case volumes of various hominids provide additional relevant evidence, especially when combined with modern neurobiological data. This convergence is particularly relevant to the relationship of laughter to language. While some have argued that laughter evolved in tandem with or subsequent to language (e.g., Caron 2002), it is more likely that the ritualization of laughter began shortly after the hominid transition to bipedalism and considerably before the evolution of language.

Language is wholly dependent upon the high degree of encephalization found in humans (Deacon 1997). It is specifically the cortex—including frontal, prefrontal, parietal, and temporal cortices—that underlies human language abilities. Yet the requisite increases in gross brain volume in these areas that preceded (and coevolved with; Deacon 1997) the evolution of language in humans did not begin until around 2 mya, with *Homo habilis* (Deacon 1992). When these numbers are corroborated with current neurobiological findings relating to laughter and language, it becomes apparent that laughter most likely did evolve independently of language, insofar as the cortical areas elaborated in humans and necessary for language abilities are largely unnecessary for Duchenne laughter that stems from nonlanguage-driven stimuli, such as play, tickling, and visual incongruity (Deacon 1992; Wild, Rodden, et al. 2003). Such laughter originates in subcortical, limbic, and brain stem areas that are largely shared with other primates. Du-

chenne laughter does not depend on the higher cognitive centers that are uniquely elaborated in humans. Human laughter is much more akin to primate calls than to human language (Deacon 1992, 1997; Burling 1993; Provine 2000; Rendall and Owren 2002), and Deacon (1992) has proposed a model that details the gradual transition from primate-like vocalizations to language in hominids. In this model, the major neural reorganizations that resulted in modern speech abilities did not begin until around 2 mya after laughter and crying were already fully developed (Deacon 1992; see also Burling 1993). Further buttressing this idea is Fry's (2002) suggestion that one can infer the evolutionary age of behaviors from the relative evolutionary ages of the brain areas on which they depend. With Duchenne laughter originating subcortically in the brain stem and language depending on highly derived cortical structures, Fry's logic supports the proposal that laughter is evolutionarily more ancient than language.

The developmental trajectory of laughter in human infants further supports this position. One of the first infant social vocalizations, laughter develops at anywhere between two and six months of age (Scheiner et al. 2002), well before language (Deacon 1997) and even precedes the earliest syllabic imitation and experimentation (Scheiner et al. 2002). Many agree that prelinguistic laughter is an integral tool of infant social interaction and self-regulation prior to the time when language can be utilized (Darwin 1872; McComas 1923; Sroufe and Waters 1976; Deacon 1997; Panksepp and Burgdorf 2003). The proximate causes of laughter viewed phylogenetically and ontogenetically are also indicative of laughter's prelinguistic origins. It is no doubt significant that ape laughter is elicited primarily through tactile stimulation (Provine 2000; Gamble 2001), since infant laughter begins thus but progresses from increasingly visual and then auditory stimulation (Sroufe and Waters 1976) to human adult laughter that occurs primarily during symbolic communication (Provine 2000). Insofar as ontogeny does recapitulate phylogeny among closely related species, this developmental series indicates that vocalized

Duchenne laughter is more ancient than language.

Contrary to some of the prevailing evolutionary accounts (e.g., Caron 2002), Duchenne laughter was likely already ritualized when language abilities and their requisite cortical reorganization began to evolve in hominids around 2 mya. When this proposition is combined with Provine's (2000) argument that bipedalism was a necessary precondition to the ritualization of laughter in hominids, a historical window is established between approximately 4 and 2 mya during which laughter most likely evolved into the ritualized vocalization found in humans today.

If laughter was elaborated between 4 and 2 mya, then the number of variables that could have come to bear on the evolution of laughter is greatly reduced. A discussion of the initial ritualization of laughter need not take into account such factors as the volitional control of behaviors (like laughter), cultural overlay, a *Homo sapien*-level Theory of Mind, and language, since these variables would not have existed until after 2 mya. Deacon's (1992;1997) model supports this proposition. Advanced culture and technology also began no sooner than with *H. habilis*, the first species of hominid to fabricate the stone tools that are the antecedent to all other human cultural artifacts (Jurmain et al. 2000). The possession by humans of a complete Theory of Mind (Premack and Woodruff 1978), or the ability to attribute a full range of mental states (including beliefs and desires) to ourselves and to others, is almost certainly unique to the human species, which indicates that such an ability might not have evolved until as late as 40 kya (Baron-Cohen 1999). The evolutionary consequences that resulted from these variables actually interacting with laughter post-2 mya will be considered after we establish the circumstances under which Duchenne laughter was initially ritualized.

IDENTIFYING THE ADAPTIVE PROBLEM: FORM FOLLOWS FUNCTION AND THE EEA

If we tentatively accept that laughter was ritualized to human levels following the footsteps of bipedalism and preceding the evo-

lution of uniquely human cognitive capacities, then the potential adaptive problems that Duchenne laughter might have been elaborated to solve are greatly reduced. This is especially true if one considers that the form of a given adaptation tends to follow that adaptation's function (Cosmides and Tooby 1997). We have argued that the form of laughter is such that it can be considered the behavioral component of a positive emotional reaction to nonserious social incongruity, and that beyond being an overt behavior it is specifically designed through ritualization to be a medium for playful emotional contagion. Another relevant feature of laughter and play is that both are very dependent on levels of perceived seriousness and satiety (Fredrickson 1998; Biben and Champoux 1999; Gamble 2001; Sharpe et al. 2002). Duchenne laughter and play only occur when individuals are well nourished (Sharpe et al. 2002) and do not perceive any threat to their immediate being (Gamble 2001). This is implicit in the nonserious qualification that accompanies our general characterization of the Duchenne laughter stimulus. For example, differential safety levels determine whether an infant will laugh or cry at an unexpected social event (Sroufe and Waters 1976) or whether a tickler is menacing or playful (Provine 2000). Also, we are prone to laugh if someone trips and falls suddenly (social incongruity), but if we recognize the accident is serious, we rush to aid the person instead. Thus, the necessity of nonseriousness or positive emotion for laughter and playful behavior can be viewed as a design feature that constrains their potential circumstances of occurrence.

In her account of the evolutionary significance of positive emotions, Fredrickson (1998) argues that such an emotion program evolved in humans specifically in response to the "moment-to-moment fluctuations in safety and satiation" experienced by our hominid ancestors "as [they] made their way across land" (Fredrickson 1998:312) and to a problem they would have thus encountered: ". . .when and how should individuals build resources for survival?" (1998:313). Fredrickson (1998) answers that during fleeting periods of safety and satiation, when danger was

relatively low and needs were otherwise met, positive emotions broaden thought-action repertoires and build physical, cognitive, and social resources, thus promoting fitness.

The living conditions that Fredrickson (1998) describes, of fluctuating food supplies and constant dangers, are in accord with the current hypotheses of the living conditions that hominids experienced following the transition to bipedalism around 4 mya (Foley 1996, 1999). The prevailing notion is that along with the emergence of bipedalism went the transition of hominids to more open, savanna-type environments, as climate-induced habitat changes in Pliocene Africa created drier habitats and more dispersed and poorer-quality foods (Foley 1999; Owren and Bachorowski 2001). This transition entailed increased daily foraging times, distances traveled, and home range areas of hominid groups, as well as increased predator pressure and inter-group competition (Foley 1996). Together these changes led to drastic increases in time stresses for early hominid groups (Foley 1996, 1999), and most likely also in physical and psychological stresses. Increased social stresses would also have occurred, as they would have resulted both from other stressors (i.e., physical and psychological) and from the need for new types of social organization, including increased cooperation among unrelated individuals (Owren and Bachorowski 2001).

One issue not stressed by Fredrickson (1998) is the means by which early hominids could have recognized, albeit implicitly, that a given context was safe, and thus fit for the playing and exploring. Another point is that within-group variation would have undoubtedly led some individuals to recognize proper safe contexts more readily, while others carried over the lingering effects of prior negative emotions into times of safety and satiety and in effect dampened the potential for positive emotions (see Biben and Champoux 1999). When laughter and humor are placed within the context of Fredrickson's (1998) conception of the role of positive emotions for early hominids in the face of increased time and body stresses, a novel connection emerges: if positive emotions functioned during "free" time to prepare individuals for the

increased demands of bipedal life, and if such free times were fleeting and occurred unpredictably, then there would have been selection on hominid behavior for an adaptive mechanism whereby positive emotions could be quickly and effectively elicited when times were safe. Additionally, if positive emotions could be efficiently transmitted between individuals then even those who did not recognize the safety of the situation, or who had a lingering negative mood, could be recruited into playing through the elicitation of positive affect. At this point it should barely need suggesting that hominid humor and laughter could potentially have functioned in just this fashion.

To make this scenario feasible, our analysis will make explicit (1) the nature of the stimuli and signal of laughter as these would have existed and been elaborated between 4 and 2 mya, and (2) the fitness benefits that would have thereby been conferred to the sender and the receiver(s) of such a signal and to their group as well. Paramount is the relation of these considerations to the hypothesis that laughter became ritualized in hominids as a mechanism whereby individuals and groups could more readily capitalize on fleeting moments of safety and satiety in order to "broaden and build" (Fredrickson 1998) their thoughts and resources through social play.

THE ROOTS OF HUMOR

The first issue at hand is the nature of the stimuli that elicit Duchenne laughter. A number of such stimuli have been identified in this paper and elsewhere. We have argued along with Provine (2000) that tickling and social play constitute the origins of laughter stimuli as shared with nonhuman primates and served as the base from which hominid humor was elaborated. Social play among chimpanzees is most prevalent among juveniles (Fagan 1993) and has been shown to occur most frequently leading up to feeding time (Palagi et al. 2004). This suggests an instrumental role in mediating stresses to facilitate group functioning, and is supported by the finding that play often co-occurs with grooming, an activity often considered the

glue of primate societies (Dunbar 1996). Such specificity in chimpanzee social play contrasts with modern human social play, which seemingly occurs at all times and throughout the lifespan (Bjorklund and Pellegrini 2002). With play nearly ubiquitous among mammalian taxa (Spinka et al. 2001), social play and tickling would undoubtedly have been present among hominids, initially resembling chimpanzee play in context and frequency but later approaching the characteristics of play in humans. How did such a transition occur?

Drawing from Fredrickson's model (1998) we propose to bridge these interspecies differences by arguing that, following the transition to bipedalism, there would have been tremendous selective pressures on hominids for the types of broadened thoughts and developed resources that Fredrickson describes. As a result, there would have been selective pressures for positive emotion and its proximate causes, social play among them. All moments that did not explicitly preclude social play (or that satisfied requisite conditions of safety and satiety) would have become highly amenable to such play, with selection favoring those individuals who could experience positive emotions and play whenever possible. The role of protohumor in fulfilling such selective pressure is straightforward: events mirroring social play and tickling in their qualities of nonserious social incongruity would have inherently indicated that a situation was safe and conducive to positive emotion and social play. The neuroanatomical mechanism through which play and tickling elicited laughter in apes was thereby evolutionarily broadened in hominids, such that "playful" stimuli were decontextualized from the physical act of social play itself, and Duchenne laughter could be triggered by a more generalized type of nonserious social incongruity. Such a connection between stimulus and context need not have been present in the minds of perceiving hominids, but the tendency to react in such a way to a stimulus—the key to the evolution of adaptive emotions (Cosmides and Tooby 2000)—would have been selected for and preserved by the correlation in nature between nonserious social incongruity and safe situations. In short, hominids be-

came more playful through an evolutionary process that made more aspects of experience appreciable as "funny." We can recognize this today in the extent to which play permeates our social and developmental lives, earning humans the nickname "homo ludens" (Bjorklund and Pellegrini 2002).

To flesh out this idea, what we now call slapstick humor (or physical mishaps that result in no real harm) could very well have emerged from this process. Witnessing another individual unexpectedly trip or slip (from an awkward bipedal gait?), while simultaneously recognizing the nonseriousness of the mishap, often elicits laughter in humans today—observe the commercial success of *The Three Stooges* and *America's Funniest Home Videos*. Such a mishap could have become a potent elicitor of laughter in early hominids as a result of Pliocene pressures for increased social play. Ramachandran (1998) has recently proposed that in such a situation, laughter functioned as a signal to alert others that a potentially serious situation had in fact turned out to be nothing of the sort. Ramachandran (1998) has argued convincingly that such nonserious social incongruity would have been present in the hominid EEA characterized above, and it would have been a reliable indicator of the safety of situations. Due to the costs imposed on individuals who were slow to utilize safe and satiated situations, such generalized nonserious social incongruity would have been selected to be a potent distal elicitor of laughter, positive emotion, and play. The broadening of the laughter trigger thereby converted some stimuli—such as near accidents, flatulence and excretion, and sexual mischief—from potential sources of social stress to elicitors of social play and positive emotion. This interpretation is in contrast to the stimulus reward account of Weisfeld (1994), whose emphasis on "fitness enhancing stimulation" has trouble accounting for such protohumor.

THE RITUALIZATION OF LAUGHTER

The above account of the roots of humor is meant to add coherence to our account but it could turn out to be an unnecessary addendum once the humor capacities of nonhu-

man apes are fully described. Such capacities have never been systematically studied across species, and it is possible that the appreciation of humor in apes is little removed from that in humans (see Gamble 2001). In contrast, laughter as a signal is inarguably elaborated in humans, and so accounting for its ritualization is of paramount importance. In the process of ritualization, a signal changes in structure so that it is more prominent and unmistakable, and thus more readily perceptible (Eibl-Eibesfeldt 1989; Grammer and Eibl-Eibesfeldt 1990). This occurs through the simplification of a signal via the addition of rhythmic repetition, an exaggerated amplitude, and stereotypic structure. The releasing threshold of a signal is also lowered during ritualization. All of these changes took place during the evolutionary transition from ape play panting to human laughter (Grammer and Eibl-Eibesfeldt 1990).

The ritualization process of Duchenne laughter was surely intertwined with its affect-inducing properties that are now being described in humans (Provine 1992; Hatfield et al. 1994; Bachorowski and Owren 2001). Arguably the most potent stimulus in our EEA for signaling safe times, eliciting in individuals playful affect, and undoing lingering stress and negative emotional valence was the laughter of others originating from social play or "false alarms." Such laughter would have signaled the playfulness of conspecifics and, if able to tap into the emotional systems of receivers, would have elicited in them a playful state. The ritualization process simply made laughter more affective at affect induction.

The shared manifold perspective described earlier (Gallese 2003), in which the same system is used to perceive and send a signal, makes the evolutionary ritualization of laughter all the more intelligible. Insofar as laughter is contagious and can function as its own releaser, lowering its releasing threshold would have occurred with an exaggeration of the signal itself. Laughter, becoming more perceptible, would have more readily elicited laughter in receivers by virtue of the receiver's own laughter program also having been exaggerated through ritualization. Even a process as simple as laughter evolving to be max-

imally different from other signals would have rendered the mirror matching of laughter more effective (see Deacon 1997 for a description of such "disruptive evolution" as applied to laughter and crying). With senders and receivers coevolving (Buck and Ginsburg 1991), and variously being one and the same individual, exaggeration of the production mechanism would have been equivalent to exaggerating the perception mechanism.

What selection would have driven this ritualization process? Fredrickson (1998) has already argued for the adaptiveness of the emotion itself—to broaden thought-action repertoires and to build physical, psychological, and social resources, in this case through social play. Positive emotions also undo negatively valenced emotions, which dampen tendencies to play and can have detrimental effects on individuals over the long term (Fredrickson 1998; Tugade and Fredrickson 2004). Laughing—that is, sending a signal in the face of nonserious social incongruity—would have been adaptive by inducing in others a positive state, and thereby effectively recruiting them to engage in social play with the laugher. It is in the evocation of this social play via emotional contagion that the essential adaptive value of the signal of laughter (as apart from its affective concomitant) resides. Those who were more adept at becoming playful during the appropriate times while also eliciting in others a playful state would have found themselves with relatively increased within-group fitness through the benefits of social play (Byers and Walker 1995; Spinka et al. 2001). This function is not unlike that served by play panting in chimpanzees (Flack et al. 2004; Matsusaka 2004) and that proposed for laughter by Weisfeld (1994). It should be noted that in arguing for the within-group adaptiveness of laughter via the adaptiveness of social play, we are not espousing a particular function for social play beyond the facilitation of development (Byers and Walker 1995; Spinka et al. 2001) and the "broadening and building" developed by Fredrickson (1998).

The receiver side of the laughter event is highlighted by Ramachandran's model (1998) and fits ideally into the above framework with one major amendment. Whereas it

makes sense that heard laughter functioned to recruit others into playing during safe times, and that it would have been adaptive for individuals to be influenced by the laughter of others, Ramachandran (1998) ignores the emotional component of laughter. While he treats laughter as a cognitive “false alarm,” we have instead argued that laughter is a medium for emotional contagion, a mechanism for transmitting positive emotion and playfulness. In fact the concept of automatic resonance behavior (Rizzolatti et al. 1999) mediated by the shared neural bases of perception and action invokes no need for cognitive mediation. In this light, it would have been adaptive for individuals within a group to be influenced by the laughter of others as it would have allowed them to immediately capitalize on safe situations. The affect-inducing property of laughter could even have allowed the laughter of others to quickly mitigate the minor pain or stress experienced by the subject of a laughter-inducing near-mishap, especially before hominids were able to infer that they were being laughed at (see later discussion). So through both the elicited positive emotion and the emergent social play, the fitness of the hearers of laughter would have increased during periods of increased stress. While others have given the name “manipulation” (Krebs and Dawkins 1984) to an influence over conspecifics such as that which Duchenne laughter has, the evidence suggests that such a term would have to be amended with “mutually beneficial” if applied to Duchenne laughter. Of course, this does not have to hold for non-Duchenne laughter (see Owren and Bachorowski 2003).

The shared benefits incurred by both the sender and the receiver of Duchenne laughter imply that there would have been robust within-group selection driving the ritualization of laughter towards increased perceptibility, elicitation, and distinctiveness from other signals. Since produced and perceived laughter potentially depend on a common mechanism, as suggested by a mirror system perspective, ritualization of the signal would have been selected for by the fitness benefits gained by individuals who were at different times both sender and receiver.

A number of additional conclusions can be

drawn by examining these ideas from a multilevel perspective. First, the benefits of laughter that have been proposed are also often group-level benefits. They benefit the group of people unified and often defined by laughter, compared to groups in which the traits associated with laughter are absent or less prevalent. The individuals who possess the traits benefit as members of their group, but it is not obvious that they benefit more than other members or that their within-group advantage is the driving force, compared to the collective benefits. Everyone in a given group benefits from such signaling and coordination mechanisms, not just the ones who produce the signals. Bekoff's (2001) arguments about social play agree with this argument.

Second, even if the traits associated with laughter do not provide a strong within-group advantage, neither do they impose a strong within-group disadvantage. Sociobiology has been excessively concerned with the concept of strong altruism, in which individuals can benefit others only at a cost to themselves. This negative tradeoff sometimes exists (e.g., when you can save a drowning person only by jumping into a river), but many traits substantially increase the fitness of everyone in a given group—including those possessing the traits—at little or no private expense. These traits can evolve on the strength of their group-level benefits relatively unopposed by selection within groups. Rather than assuming a negative tradeoff between benefits to others and cost to self, it is useful to distinguish two potentially independent concepts: coordination and distribution (Wilson 2001). The question of whether a group functions well or poorly is a matter of how members coordinate their activities. The question of whether the traits evolve depends on how the costs and benefits of coordination are distributed among the group members. If coordination can be achieved with a relatively equal distribution of costs and benefits, then group-level adaptations can straightforwardly evolve. Many of the traits associated with laughter appear to exist in this category.

Third, laughter favors group selection in the same way that culture does. Cultural group selection is powerful because the social transmission of behaviors creates differences

among groups more easily than the genetic transmission of behaviors (Boyd and Richerson 1985). For example, it is easy to imagine everyone in a group adopting a culturally acquired behavior, which makes them very different from other groups. The only way for comparable variation among groups to arise for genetically acquired traits is for the groups to be clonal. The contagious nature of laughter makes it similar to forms of cultural transmission in its effects on behavioral uniformity within groups and differences among groups. Even a single person who laughs can change the mood and behavior of an entire group, thereby increasing between-group differences. If laughter increases the social play in a group, such a difference would increase the fitness of that group relative to others (see Bekoff 2001), thereby driving group selection.

These conclusions can be used to evaluate one of the most recent and detailed evolutionary theories of laughter by Owren and Bachorowski (2001), who propose that laughter evolved in response to the selfish exploitation of emotional signaling by cheaters. They envision a coevolutionary arms race in which: (1) cooperation was first fostered among unrelated individuals through an honest emotional signal, namely, smiling; (2) smiling was then corrupted by the evolution of cheaters who could volitionally mimic smiling and exploit the cooperation of others; and (3) laughter then evolved through an elaboration of the original smile mechanism in effect to replace smiling as a harder to fake signal for promoting cooperation. The concept of honest signaling is being used to explain a number of subjects besides laughter, such as religion (e.g., Irons 2001; Nesse 2001; Sosis 2004). In the case of laughter, however, there are a number of problems with Owren's and Bachorowski's account. First, the fact that they call it a "selfish gene" account says nothing about levels of selection, which requires a comparison of fitnesses within and among groups. Second, they assume that cooperation is always vulnerable to exploitation and cannot evolve in the absence of iron-clad hard to fake signals. This assumption is not based on a consideration of laughter per se, but is made axiomatically for all forms of co-

operation. We have already criticized this assumption and suggested that Duchenne laughter occurs in contexts where coordination can be achieved with little danger of exploitation (i.e., safe and satiated contexts). Third, their account assumes that laughter evolved late in the coevolutionary sequence, after smiling was corrupted as a signal, whereas all the evidence that we have reviewed points to the early evolution of laughter, prior to volitional control, and with different phylogenetic origins for smiling and laughter (van Hooff 1972). We do not wish to entirely reject the concept of laughter as an honest signal, but we think that Owren's and Bachorowski's account fails as a primary explanation of laughter.

Both within- and between-group selection driven by the environmental conditions of the Pliocene help to explain the elaborated condition of protohumor and Duchenne laughter in humans. Modern multilevel selection theory thus provides an excellent framework for the study of laughter. The dynamics of laughter within single groups is a complicated subject in its own right. The manner in which groups form, interact, and disperse adds another layer of complexity. Multilevel selection theory provides a way of managing this complexity by first focusing on single groups as evolutionary units and then focusing on the differential contribution of groups to total evolutionary change. Given the strong group-level advantages, the weak disadvantages within groups, and the population structure of early hominid groups, there is ample scope for laughter to have evolved on the strength of group-level, in addition to within-group, benefits.

SUBSEQUENT CO-OPTATION AND THE DIVERSIFICATION OF FUNCTIONS

With Duchenne laughter and protohumor thus established in early hominids, the form and functional value of these traits would have been present during subsequent evolutionary transitions through various species including *H. habilis*, *H. erectus*, and eventually *H. sapiens*. This means that Duchenne laughter and protohumor would have been present in the prehuman behavioral repertoire as

various advances were made in successive species, including the evolution of volitional oral-facial muscle control, the invention of material and cultural artifacts, language, the evolution of a *Homo sapien*-level Theory of Mind, and the emergence of fully modern humans and their societies, belief systems, technology, and cultural variation. We suggest that each of these evolutionary novelties interacted with the already-present laughter program resulting in the various forms of laughter that we now find and their myriad functions in different social contexts. We propose that it is from this process that non-Duchenne laughter arose. We also maintain that there is a necessary continuity between all types of laughter, as they are all derived from the primate play display, hominoid proto-laughter, and hominid Duchenne laughter.

Essential to our account is treating Duchenne laughter as a system that was co-opted by volitional motor circuits, allowing humans to use its affect-inducing properties to strategically influence others. In this sense, it was the effect of Duchenne laughter on others that was co-opted. Whereas Duchenne laughter originally evolved in the context of protohumor and functioned as a medium of joyful emotional contagion, non-Duchenne laughter came to occur in aggressive, nervous, or hierarchical contexts, functioning to signal, to appease, to manipulate, to deride, or to subvert. Such a transition is supported by the existence of two neural circuits for laughter (Wild, Rodden et al. 2003) and by the work of Deacon (1992, 1997). Duchenne laughter was also expanded by new elicitors, including language and mental state attribution. These stimuli came to elicit the full Duchenne laughter program insofar as they conformed to the structure of the already established trigger mechanism, nonserious social incongruity.

For example, humans can now voluntarily access the laughter program and utilize it for their own ends, including smoothing conversational interaction, appeasing others, inducing favorable stances in them, or downright laughing at people that are not liked. This is apparently the result of the evolution of volitional prefrontal motor circuits that have allowed humans to have a generalized kind of

willful control over oral-facial and respiratory-laryngeal motor systems (Deacon 1992). The uses to which such non-Duchenne laughter can be put stem from the established characteristics of Duchenne laughter, particularly its direct and indirect effects on others. Laughter's direct effects are the evolved affect-induction properties of the specific signal or its ability to emotionally influence pre-attuned receivers, while its indirect effects are derived from receivers' learned associations between laughter, play, and positive affect (Owren and Bachorowski 2003). In the case of aggressive laughter, this connotation implies that the laugher derives pleasure from the misfortune of another. Laughter's capacity to function metacommunicatively (Caron 2002) as a conversational sign that frames behavior with playful intention (Provine 2000) also arguably stems from the intrinsic playful and pleasurable qualities of laughter and laughter's effects on others (Owren and Bachorowski 2003). Even the convergence of smiling and laughter that can be observed in modern humans (despite the different phylogenetic origins of the two displays; van Hooff 1972; van Hooff and Preuschoft 2003) is arguably the result of learned mimicry of the two signals by these higher human cognitive abilities that creates a functional hybrid utilized during conversation.

Language is a related evolutionary development made possible by such novel prefrontal circuits (Deacon 1997). A linguistic system enables symbolic representations of the world to conceptually invoke the recognition of nonserious social incongruity. This is the formal humor we know so well, which has come to take myriad forms and have as its subject matter innumerable cultural symbols and institutions (see Apte 1985). It is again significant that language can only spontaneously trigger Duchenne laughter if the structure and context of the statement or story embodies nonserious social incongruity and the already-established laughter mechanism. This relationship between old and new explains why certain constraints are imposed on the types of statements and stories that elicit laughter—why a well-timed and precise buildup of expectation is so necessary for effective humor (Ramachandran 1998), and

why only a specific, playful, alternately intelligible type of punch line is humorous.

Humans can also now find nonserious social incongruity in the inferred subjective states of others, in the discrepancy between their intentions and their actions or between their beliefs and reality (Howe 2002; Jung 2003). Such a reading of another's mind can facilitate the strategic use of humor, as one must presumably understand what is expected by others in order to present them with the unexpected. This ability adds an additional new dynamic to laughter perception because it allows one to infer in a laughter the mental states and intentions that elicited the laughter, and as a result to attribute a new kind of situational and context-dependent meaning to the observed act of laughter (Jung 2003). Quite possibly it is from this ability that much "aggressive" laughter arises, as the hearers of such laughter can thereby recognize it as being aggressive. This ability to read another's mind allows people to recognize that they are being laughed at and are thus part of the out-group. The sender of such laughter is either intentionally laughing (non-Duchenne) to be aggressive or is simply laughing (Duchenne) at what he or she perceives to be nonserious social incongruity. Such incongruity is in this case nonserious because the aggressive laugher has no inherent concern for the well-being of the target of the laughter, and it is this lack of concern that the target can then infer. More generally, the interaction of "mind-reading" abilities with conversational laughter creates myriad opportunities for nuanced information to be conveyed as variability in laughter acoustics is correlated with different social contexts (Vettin and Todt 2004). Laughter does function to convey information under some circumstances, as opposed to simply inducing affect (see Deacon 1997; Owren and Bachorowski 2003; Vettin and Todt 2004), but arguably only insofar as conversational laughter interacts with a human-level understanding of others' intentions.

One last elaborated example should make the process of co-optation more concrete. Dunbar (1993, 1996; see also Provine and Fischer 1989) has proposed that language evolved in hominids to replace grooming as

the prime means of managing the prehuman social environment. He proposed that selective pressures for increased group size led language to evolve to manage social relationships through the sharing of social information, or gossiping. Dunbar's theory has been criticized on the grounds that language by itself could not have functioned like grooming (Power 1998) because the functional basis of grooming is the honest time commitment that it entails and the opiate release that it facilitates. Language is a cheap signal that can be used dishonestly and provides no such pleasurable stimulation (Power 1998), that is unless conveyed as humor or word play; only then can language elicit in others what is effectively a parallel emotional response to grooming. This idea is referred to as the "vocal grooming hypothesis" (Dunbar 1996; see also Vaid 2002). That humor and laughter could have been utilized thus is supported by our argument that Duchenne laughter and protohumor were fully established when human language began to emerge. This idea further suggests that language might have necessarily evolved in relation to humor and laughter, with the capacity to conceptually mimic, using symbols, the structure of protohumor.

In this scenario language and humor would no doubt have coevolved to some extent, with language and speakers becoming more adept at eliciting laughter and the laughter mechanism becoming more susceptible to conceptual triggering. But the instructive aspect of this hypothetical example is that only the original properties of Duchenne laughter would have allowed it to be evolutionarily harnessed by language. Only insofar as language was able to conform to the structure of the already established elicitor of laughter could it trigger the laughter response. Thus, Duchenne laughter was present to be co-opted by language (and by the mental abilities that language requires), but as such there needed to be some point of contact between the two systems—in this case, the potential of language to represent nonserious social incongruity, and the affective properties of laughter that constituted its functional potential and endowed it with the capacity to be utilized for vocal grooming.

There is a precedent for taking a co-optative view of emotion systems. Rozin and colleagues (e.g., Rozin et al. 1997) have detailed how the ancient mammalian food rejection system of disgust was co-opted by human cognition to play a role in cultural value systems. Previous laughter researchers have speculated along similar lines. Fry (1994:121) asserted, "... mirthful laughter is probably another of those archaic adventitious behavior complexes which has been swept up in the flowing of time and evolution and carried far beyond its original activity." Likewise, Panksepp and Burgdorf (2003:541) said "... the subtleties of human adult laughter, so abundantly expressed during cognitive delights of humor, may highlight how certain ancient emotional processes interact with refined cognitions within higher reaches of the brain-mind." Caron (2002:267) argued in turn that "as hominids became humans, laughter would have become useful as part of an increasingly more abstract language." To our knowledge, however, this is the first time that such a notion regarding laughter and humor has been incorporated within a formalized theoretical framework.

A final conceptual point needs to be kept in mind. The evolutionary scenario we have detailed exists in two parts: (1) the initial elaboration of Duchenne laughter and protohumor in hominids; and (2) the co-optation of laughter and humor for novel functions. The first argument is more tenuous, attempting to pinpoint the actual conditions under which laughter evolved and the adaptive functions that laughter originally served. Contentious is the point that laughter was originally ritualized in hominids more than 2 mya to serve as a mechanism for transmitting playful emotion among members of a group. While supported by several lines of evidence, the idea is admittedly and perhaps inevitably speculative. Yet the second argument does not depend entirely on the validity of the first. While the history and initial characteristics of Duchenne laughter are essential to treating laughter as a preadaptation, the specific circumstances under which laughter was ritualized are partially irrelevant to laughter's later elaboration. This is as long as laughter was fully and appropriately developed when the

implicated abilities began to evolve post-2 mya. Regardless of the driving forces and circumstances of Duchenne laughter's historical genesis, viewing non-Duchenne laughter as an evolutionary derivative of Duchenne laughter makes sense of the variety of forms and functions that characterize laughter today. Without such an explicit recognition of the co-existence of Duchenne and non-Duchenne laughter, and of playful, appeasing, aggressive, and dissociative functions, the claim of Keltner and Bonanno (1997) holds true: the science of laughter is, and will continue to be, swamped in contradiction and confusion.

PREDICTIONS AND FUTURE DIRECTIONS

The core objective of this paper has been to synthesize the many data and specific hypotheses of the evolution and functions of laughter and humor into a single evolutionary account that includes phylogeny and history as well as proximate mechanisms and adaptive significance. Perhaps the most immediate criticism that can be made of our evolutionary hypothesis is that it has all the makings of a "just-so story." If this were the case, we would have indeed woven a fine tale but it would be unfalsifiable and therefore not scientific. We contend that it can be falsified in a number of ways, and we derive a number of testable predictions that lend genuine scientific value to our account. In some cases these predictions diverge from or challenge directly the work of other researchers, and where this is the case we have tried to note the opposing perspectives.

The level of historical detail that we incorporated into the first part of our argument is contentious but potentially stands to be rebutted. This would be contingent upon a closer analysis by physical anthropologists of hominoids and hominid fossils reliably dated from the middle Pliocene. While we incorporated Provine's (2000) Bipedal Theory into our account, we did not discuss the specific fossil evidence of such a transition other than noting the evidence for bipedalism by 4 mya. Neither did we discuss the larynx, to which changes might have needed to occur in order for laughter to go from pant-like to "voiced."

Although laughter should not have required the same types of morphological changes as language (for instance alterations to the tongue, palate, and teeth to allow for the production of phonemes), some changes to the basicranial structure of hominid skulls would perhaps still have been needed. These changes, if in fact necessary to our account, should be observable in the fossil record. We say "if necessary" because the actual physical requirements of human laughter have not been established, and so a collaboration of anatomists, biophysicists, and paleoanthropologists is apparently in order. It should be noted, however, that even the anatomical prerequisites of speech have proven hard to infer from the fossil record (see Fitch 2000).

The neuroanatomical components of our account also include concrete propositions that stand to be falsified by future research, the most revealing of which will probably require advanced neuroimaging techniques. Our argument that the different proximate causes of Duchenne laughter all share a common form (nonserious social incongruity) leads to the prediction that the laughter following from these different stimuli (infant laughter, laughter from tickling and play, and the various distally perceived forms of humor) should share a singular mechanism on at least some level. The substrates of initial processing will no doubt differ (and indeed do; Goel and Dolan 2001), but the last stage of higher-level perception, which triggers the "laughter-coordinating" center (Wild, Rodden et al. 2003), should be singular and presumably involve incongruity detection and/or resolution (see Fry 2002). Comparatively, our hypothesis predicts that the laughter of apes (both tickle/play induced and symbolically elicited) should derive from a homologue of this cognitive "laugh generator" (Provine 2000). Following the work of van Hooff (1972), we would also predict that smiling and laughter spring from different neuroanatomical bases except insofar as they either hybridize under volitional and/or learned control or require similar motor commands. This contrasts with the work of Owren and Bachorowski (2001), which sees laughter as an elaboration of smiling and so

predicts a singular mechanism for both signals.

Our integration of a theoretical mirror mechanism predicts that the singular laughter production mechanism should also be active during the perception of laughter, specifically Duchenne laughter that induces positive affect. Such a finding would suggest the existence of "echo-neurons" to go along with the visuomotor neurons uncovered already (see Rizzolatti and Craighero 2004), although these neurons might well represent vocal tract configurations and not sound per se (see Liberman and Whalen 2000; Rizzolatti and Arbib 1998). As discussed above, we implicated an area of the SMA as the locust of the laughter motor program, but this is by no means exclusive as much more research in the area is warranted.

We predict that prefrontal and temporo-parietal areas (Saxe et al. 2004) involved in Theory of Mind tasks, such as belief attribution, should be activated during the perception of laughter that induces negative affect, specifically insofar as such negative affect follows from an interpretation that the laughter was aggressive or derisive based on context and knowledge of the laugher. We also predict that "mind-reading" abilities should not be necessarily required for the perception of all laughter inducing stimuli, since we argue that laughter was first ritualized prior to the evolution of a full human Theory of Mind (Baron-Cohen 1999). We might predict something of a "continuum of activation" in which mind-reading abilities are progressively more activated as one moves from infant laughter to tickle- and play-induced laughter to physical humor and finally to formal symbolic humor. This stands in contrast to the work of Jung (2003), which predicts that mind-reading ability is involved in all laughter.

The perception of laughter is prime for further exploration using neuroimaging techniques (Sander and Scheich 2001; Shibata and Zhong 2001). As a fascinating new direction for future research, the simultaneous imaging of multiple subjects interacting or performing the same task (see Adolphs 2003) holds promise for fleshing out the complex nature of laughter production and perception in varying contexts. Unfortunately neu-

roimaging research on the production of laughter is in many cases not feasible with current technology due to motion artifacts (Iwase et al. 2002). Measuring motor-evoked potentials (MEPs) from muscles in the mouth and tongue region (see Fadiga et al. 2002; Watkins et al. 2003) could assess the extent to which motor areas that control laughter are activated during the perception of laughter.

To take a different tack, children with autism might be investigated. Several groups of autism researchers have recently proposed that the disorder is at base an imitation deficit and that this primary inadequacy cascades into the other social and emotional deficits that have traditionally characterized autism, such as those involving emotion sharing, empathy, theory of mind, and social norms (see Williams et al. 2001; Rogers et al. 2003; Williams et al. 2004). Mirror neuron dysfunction has even been explicitly implicated as the root of autistic disorders (Williams et al. 2001). If this characterization of autism is on the right track, then one would derive from our account a number of predictions regarding laughter and humor in autistic individuals. These include: (i) few problems in detecting or laughing at tactile or visual protohumor (such as tickling, social play, peek-a-boo, and slapstick humor); (ii) reduced reaction to intention- and norm-based humor; (iii) inappropriate or inexplicable laughter because of disrupted social expectations and unusual notions of incongruity; (iv) laughter at serious social incongruities; (v) a lack of responsivity to the laughter of others and to humor based in facial expressions; and lastly (vi) a lack of effort to elicit laughter from others since such laughter would not feed back positively on an autistic child via contagion. Remarkably, a recent study on laughter and humor in autism (Reddy et al. 2002) supported every one of these predictions, and none of the study's findings were left unexplained by our account.

Laughter that occurs during everyday social interaction in response to banal comments and humorless conversation is now being studied (Provine 1993; LaGreca et al. 1996; Vettin and Todt 2004). The unstated issue is whether such laughter is similar in kind

to laughter following from humor. Although conscious control of laughter in natural social contexts has been tentatively discredited (but not systematically explored; Provine 2000; Owren and Bachorowski 2001), that does not preclude learning and automatization from playing a major role in non-Duchenne laughter. This type of laughter is probably learned through practice and the conditioning of nonconscious motor programs, and has only emerged as modern human cognitive abilities evolved post-2 mya. We have also implied that it is this type of laughter that constitutes the bulk of conversational laughter, something not discussed in the accounts of Owren and Bachorowski (2003) and Vettin and Todt (2004). Our position thus raises a number of novel questions. Is conversational (non-Duchenne) laughter typically learned? If so, what are the respective roles of conscious and unconscious processes in the utilization of such laughter? Does such laughter ever precede, coincide with, or follow from positive affect? Ontogenetically, how and when does such learned laughter develop in relation to the Duchenne laughter of infants? What determines the differential effectiveness of individuals at strategically utilizing such laughter? Does such conversational laughter occur cross-culturally, and if so does it follow similar patterns? We would predict greater cross-cultural variation in the contexts and physical characteristics of conversational as opposed to humor-driven laughter, suggesting conversational laughter is essentially a learned skill. We would similarly expect the punctuation effect (Provine 1993) to vary across cultures as it should apply most strongly to non-Duchenne conversational laughter.

We have not discussed gender differences in laughter production. The main reason for this is straightforward: researchers have consistently found no differences in the average number of laughs produced by males and females in social contexts (Martin and Kuiper 1999; Devereux and Ginsberg 2001; Bachorowski et al. 2003, as cited in Owren and Bachorowski 2003; Smoski and Bachorowski 2003a; but also see Provine 1993). The second reason is more complex. The only other consistent gender-related finding is that females tend to laugh most around males in

conversational interaction (Bachorowski et al. 2003, as cited in Owren and Bachorowski 2003; Grammer 1990; Provine 1993; Smoski and Bachorowski 2003a). However, researchers have documented this pattern without distinguishing Duchenne from non-Duchenne laughter. It is therefore quite possible that such a pattern describes only one type of laughter or that it will not hold across cultures. We would predict that this pattern will be robust across cultures if it does involve Duchenne laughter but that it will prove to be unreliable if it merely involves non-Duchenne laughter and culture-specific social norms.

These issues are of utmost importance as researchers begin the task of distinguishing classic stimulus-driven Duchenne laughter from non-Duchenne conversational laughter. It bodes well for our account that the findings of Vettin and Todt (2004), described earlier, suggest the proximate basis for the functional differences of Duchenne and non-Duchenne laughter and a means of telling them apart in future observational studies. It should be noted, however, that the facial feedback hypothesis (and its claim that mimicking an emotional expression elicits the corresponding affect; see McIntosh 1996) complicates attempts to distinguish Duchenne from non-Duchenne laughter on the basis of emotional valence alone, but it also suggests that the presence of positive affect following non-Duchenne laughter does not prove it is similar in kind to Duchenne laughter.

We have argued that Duchenne laughter is essentially a medium for emotional contagion operating through an intersubjective mirror system. Such a perspective has implications for treatments of all nonverbal behavior, language, and more generally, considerations of human social evolution. Given a mechanistic basis, like that proposed by Gallese (2003) and his colleagues, these phenomena provide an organizational principle for humans as social beings, facilitating the empathic understanding of others, the emotional coupling of group members, and the establishment of coordination among interacting individuals. The evidence indicates that an early form of the shared manifold was already present in hominoids when the hominid line diverged,

as mirror circuits were first discovered in monkeys and chimpanzees show evidence of primitive emotional contagion (Parr and Hopkins 2000). Hominid evolution therefore involved not the evolution of a mirror matching system from scratch but (among other things) the evolution of elaborated motor movements within a pre-existing system. Signals conjoined with emotional experiences are ideal examples of such elaborated movements. Humans have a highly ritualized and conventionalized nonverbal communication system (Eibl-Eibesfeldt 1989), particularly regarding expressions of positive emotions (Tomasello et al. in press), and ritualized Duchenne laughter is no exception. A question can then be posed: If emotion is essential for action (Damasio 1994), then might not shared group emotion be essential for group action, that is, for solving the problem of coordination (Wilson 2001; Spoor and Kelly 2004)? If answered in the affirmative, then laughter and other elaborated emotional expressions might well be a fountainhead of human uniqueness. Empathy through the communicatory coupling of individuals has in fact been implicated in human cooperation and altruism (Lakin et al. 2003). So while cultural institutions are thought to organize humans to the level of a "crude superorganism" (Richerson and Boyd 1999), the present argument implies that there is a much more fundamental mechanism for human organization than cultural institutions—a mechanism that predates such institutions and even language and could have been a prerequisite to the emergence of such evolutionary novelties.

Future research can explore this possibility in many ways. These include social experiments that measure the unique efficacy of humor and laughter (and other nonverbal behavior) at promoting relative group-level fitness (see Banning 1987; Vinton 1989; Greatbatch and Clark 2003), and agent-based modeling techniques, which are gaining sophistication and relevance in relation to human social evolution (see Kohler and Gummerman 2000). Perhaps most importantly, the above discussion is founded on assumptions of ape abilities. Future comparative studies of the cognitive, emotional, and expressive capabilities of other primates, particularly chim-

panzees (e.g., Parr and Hopkins 2000; Parr 2004), will shed tremendous light on such considerations of human social evolution.

The main goal of this paper has been to integrate theory and data across disciplines, thereby gaining insight while also exposing scientists on different fronts to novel research and theory. We think that laughter researchers have much to learn from and offer to social neuroscience, positive and evolutionary psychology, and multilevel selection theory. As a specialized subfield of research on non-verbal behavior and communication, the findings of laughter researchers hold relevance to all fields that concern themselves with human behavior, social interactions, social organization, and both verbal and non-verbal communication. An increasingly im-

pressive catalogue of data is emerging from studies by social psychologists with ethological dispositions, and we feel that laughter research deserves to be integrated into the larger fold as a serious topic of scientific study that must be accounted for in discussions of human behavior and evolution.

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