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Evolution, Structure, and Functions of Human Laughter

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Vocal communication is fundamental to human and nonhuman social interaction and is remarkably ancient and widespread across taxa (Bass, Gilland, & Baker, 2008). It is not particularly mysterious why this form of communication is so pervasive in nature—vocalizations allow animals to rapidly communicate, sometimes at great distances, as well as in coordination with one another and to potentially large audiences simultaneously. Vocal emotion production is highly conserved in mammals, meaning that selection has retained underlying brain circuitry responsible for affective vocal control, making it quite similar across many otherwise dissimilar species (Ackermann, Hage, & Ziegler, 2014; Jürgens, 2002). Humans maintain a large repertoire of vocalizations that can be studied effectively through a comparative lens, but few afford such an analysis as well as laughter. This chapter will describe human laughter from an evolutionary perspective, including discussion of its basic acoustic structure, phylogenetic origins, and social communicative functions. The study of laughter is a burgeoning research topic that provides a window into not only human vocal communication and evolution, but also the complex social cognitive niche that humans have created.

Like all biological adaptations, vocal signals follow basic principles of form and function (Owren & Rendall, 2001). An analysis of the physical properties of vocalizations can help elucidate the adaptive problems the signals are designed to solve. Some structural features are more obvious than others. For example, the loud and acute dissonance of infant crying is easy to understand as a sound that motivates adaptive caretaker action. By causing a parent to induce crying cessation, the signal enhances the fitness of both parent and offspring, driving the signaling system's evolution and design (Lummaa, Vuorisalo, Barr, & Lehtonen, 1998). If crying sounded like gentle birdsong, it would not be nearly as effective. Similarly, we can understand laughter as being a signal shaped by selection to induce positive affect for mutual benefit in senders and receivers on average, but the form-function relationship is not quite as obvious as in crying. Before we explore this issue, we will consider the specific acoustic properties of laughter, which, along with its phylogenetic history, provide clues regarding its multiple possible communicative functions.

THE ACOUSTIC STRUCTURE OF LAUGHTER

What is a laugh? Most basically, laughter is a nonverbal vocalization characterized by a specific coordination of rhythmic respiratory and laryngeal activity (Bachorowski, Smoski, & Owren, 2001; Citardi, Yanagisawa, & Estill, 1996; Luschei, Ramig, Finnegan, Bakker, & Smith, 2006; Provine, 2000; Titze, Finnegan, Laukkanen, Fuja, & Hoffman, 2008). Laughter typically occurs as a sequence of acoustic bursts, collectively known as a bout—but single laugh bursts occur with some regularity. The energy underlying laugh bouts arises from rhythmic pulsing of abdominal and intercostal muscles, forcing air through the glottis, situated in the larynx, housing the vocal folds. Initial bursts often contain the greatest energy, which then decay over time in a near-linear fashion, often affecting both loudness and perceived pitch (Titze et al., 2008). A unique feature of laughter is the rapid opening and closing of the glottis (and hence the vocal folds), resulting in oscillating bursts of energy containing tonal and nontonal (i.e., voiced and unvoiced) components. The tonal elements arise due to the brief closures of the vocal folds and subsequent vibration regimes that typically generate a fundamental frequency (f_o) associated with perceived pitch. Along with harmonic structure associated with the voice source, resonances of the vocal tract result in formant structure in laughs that determines perceived vowel sounds. Laughter generally consists of stable vowel configurations within bouts (*ha-ha-ha* rather than *ha-he-ha*) (Bachorowski, Smoski, & Owren, 2001; Provine, 2000). One cycle of closing and opening the glottis constitutes a single laugh burst, with the process often continuing for several seconds, manifesting as a structured series of complex vocal sounds. Complexity here refers to the multiple dimensions of acoustic variability we see in laughter, including not only the tonal (i.e., periodic) components such as f_o and formants, but also nontonal spectral features associated with perceived voice quality. Because of occasional high intensity moments, laugh bouts can contain chaotic nonlinear phenomena such as subharmonics (i.e., bands of energy between harmonics due to period doubling) and deterministic chaos (broadband noise) (Bachorowski, Smoski, & Owren, 2001; Fitch, Neubauer, & Herzel, 2002). These features can contribute to a variety of subjective sounds such as hoarseness, roughness, breathiness, and of course loudness.

Figure 5.1 shows the acoustic similarities between a chimpanzee play vocalization (recording courtesy of M. Davila-Ross) and an ingressive (i.e., inward airflow) laugh produced by an actor (Bill Paxton as Chet in the 1985 movie *Weird Science*). When slowed down two and a half times, this ingressive laugh sounds like a nonhuman animal, much like the spontaneous laughs tested by Bryant and Aktipis (2014). High-intensity, ingressive vocal effort often results in noisy features, such as deterministic chaos, which is evident in the example in Figure 5.1 (right column, first row). A completely ingressive laugh in humans such as the one displayed here is highly unusual in ordinary discourse. But ingressive components tied with breathing are quite common at laugh onsets and offsets. An example in Figure 5.1 shows a typical manifestation of an ingressive laugh offset (left column, third row). Laughs composed of predominantly voiced components are often perceived as being volitional (or "fake"), likely due to their apparent production by the speech system (Bryant & Aktipis, 2014). The infamous laughter of Hillary Clinton illustrates this well (right column, third row). The laugh bursts are regularly spaced, highly voiced, and contain relatively low acoustic variation across bursts, including in f_o, spectral, and duration properties. Volitional laughs functioning as backchannels (i.e., brief utterances while listening in conversation) are often low in variation both within and between bouts.

The portions of laughter linked to the closing stage of the glottal cycle are important for the sound of a laugh (e.g., f_o dynamics), but the intervals between those bursts are also crucial, and

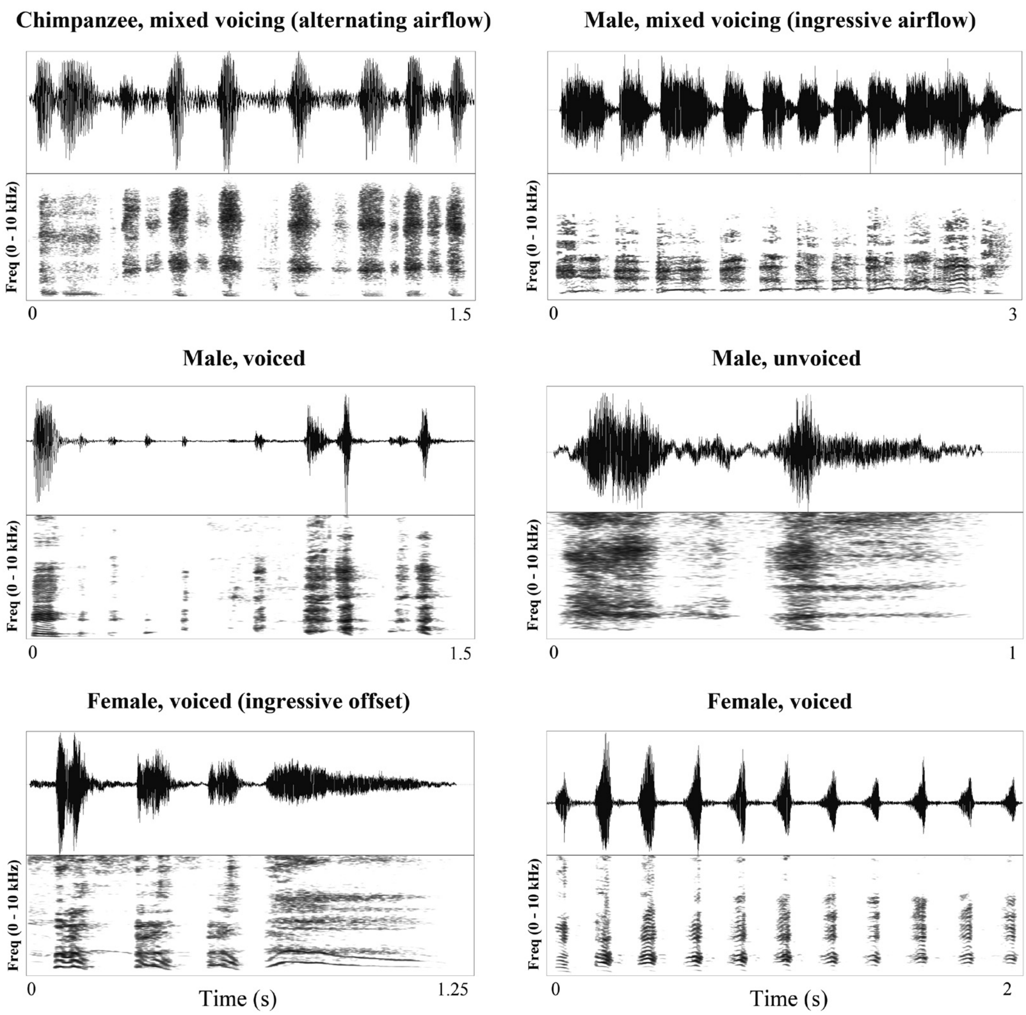

Figure 5.1 Variations in Laughter Acoustic Structure

can provide unique information regarding the nature of a laugh. One measure we developed—rate of intervoicing interval—quantifies the averaged proportion of time that a laugh spends in the open portion of the glottal stage across a laugh bout, and captures an important dimension linked to breath control. Perceptually, the measure is positively associated with judgments of laughter being spontaneous, as well as listeners confusing slowed versions of spontaneous laughter with nonhuman vocalizations (Bryant & Aktipis, 2014). Breath control is a crucial mechanistic difference between the evolutionarily conserved vocal emotion system and the human species-specific speech system. At some point during relatively recent hominin evolution, increased thoracic innervation afforded fine control over breathing dynamics that facilitated the production of long linguistic phrases with well-timed inspiratory breaks (MacLarnon & Hewitt, 1999). Consequently, vocalizations produced by the speech system contain the signature of speech-timed glottal dynamics. We will return to this issue below.

Beyond the immediate physiology of laugh bursts, researchers have described the ways that laughter production coordinates with other kinds of vocalizations, namely, speech. It appears that laughter often follows simple production rules. For example, Provine (1993) described the ways people laugh during ordinary talk, including the ways laughs are placed relative to words and sentences. Speakers punctuate sentences with laughs instead of placing them randomly within them. This rule-governed organization is due primarily to the different cortical systems underlying vocal emotion production and speech—systems that must share connections to the vocal apparatus. This fact explains phenomena such as people's inability to speak while their breathing is labored or while they are involuntarily laughing, crying, or screaming.

LAUGHTER PHYLOGENY

We can learn much about laughter by looking at evolutionarily related vocal behaviors in other primates, especially the great apes. The comparative method affords important insights into the physical forms of signals and their connections to communicative functions. Human laughter is well established as homologous to nonhuman play vocalizations (Gervais & Wilson, 2005; Panksepp & Burgdorf, 2003; Provine, 2000; Ruch & Ekman, 2001; van Hooff, 1972). Many social mammals produce vocalizations during physical play, including rats (Knutson, Burgdorf, & Panksepp, 1998), dogs (Feddersen-Petersen, 2000), chimpanzees (Davila-Ross, Allcock, Thomas, & Bard, 2011; Matsusaka, 2004), squirrel monkeys (Biben & Symmes, 1986), and other primate species (Masataka & Kohda, 1988). Play vocalizations provide an excellent example of the concept of ritualization—a process of signal evolution proposed by behavioral biologists (Krebs & Dawkins, 1984; Tinbergen, 1952). Many ritualized signals begin as cues, which can be any behavior that reliably provides some kind of predictive information to perceivers. Mutual recurrent benefits between producers and perceivers from a given pattern of predictable interaction can result in an escalation and ratcheting of signal properties and corresponding response biases (Maynard Smith & Harper, 2003). The ritualization process follows the dynamics of arms races. For example, costly signals of genetic quality in competitive mating contexts can become increasingly exaggerated in response to female resistance and choosiness.

In the case of play vocalizations, the heavy breathing associated with excessive play provides honest information about the physical state of the participants and reveals vulnerability. The continued play indicates a willingness to be vulnerable, trust in the social partner, and an investment in the action itself. Play can function in a variety of ways to prepare animals for situations they are likely to encounter as adults. For example, play fighting helps calibrate muscle systems for physical conflict (Byers & Walker, 1995), and play chasing can tune systems designed for predatory skills of hunting and killing prey (Smith, 1982). But as animals are engaged in the playful encounters—preparing for adult contexts—some of their behaviors could be potentially construed as aggressive and not playful. The exaggerated production of a by-product behavior, such as heavy breathing and panting that become ritualized into affective voicing, can reassure a co-participant during play that one's intentions are benign. The ritualized transformation of by-product vocal cues into laughter signals can contribute to increases in the frequency and intensity of play, benefitting participants over evolutionary time.

The connection between human laughter and nonhuman animal play vocalizations is most evident in acoustic analyses. Davila-Ross, Owren, and Zimmermann (2009) examined audio recordings of six ape species, including humans, producing tickle-induced vocalizations, and developed a phylogeny (i.e., an evolutionary history) of the vocal behavior based on acoustic comparisons. Their reconstructed phylogeny of laughter suggests that the last common ancestor of all extant ape species, who lived approximately 25 million years ago, likely produced a play vocalization characterized by long, noisy bursts, mostly through eggressive (i.e., outward) breath flow. Most generally, play vocalizations have evolved to be more tonal; that is, they increasingly include vocal vibration regimes (perceived as pitch), and the calls have become shorter and sometimes alternating in airflow, such as in chimpanzees and bonobos. But this class of vocalizations in humans has become incorporated into much broader communicative contexts that include verbal interaction, deeply interwoven with signaling affiliation and cooperative intentions. Of course, this includes the so-called darker side of laughter, such as taunting and ironic laughing that can be quite hostile and aggressive to particular targets. The origins of human laughter in the ritualized labored breathing of our ape ancestors help explain its unique vocal features and its affective source.

An additional factor in humans that dramatically complicates the theoretical picture for laughter is the evolution of the speech capacity that works in conjunction with vocal emotions. The dual pathway model has consequences for understanding all vocal behavior (Owren, Amoss, & Rendall, 2011). In social mammals that produce affective vocalizations, the same basic circuit underlies vocal control: a projection from the anterior cingulate, routed through the periaqueductal grey (PAG) area into laryngeal muscles (Jürgens, 2002). But one of the defining characteristics of modern humans is the ability to produce articulated speech sounds, attributable to species-specific neural projections connecting motor cortical areas to laryngeal musculature (Ackermann, Hage, & Ziegler, 2014). Having volitional control over the vocal apparatus affords the capability to mimic the repertoire of vocalizations originally produced by the emotional vocal system. As humans, we can produce "fake" cries, pain shrieks, fear screams, orgasm calls, and laughs. Volitional forms of vocalizations can be produced for deceptive and cooperative reasons, and the game-theoretic dynamics of those strategies must work in the context of evolved linguistic and emotional signaling systems. Difficulties in neuroimaging techniques have contributed to uncertainties regarding the independence of these vocal production routes, and research suggests these systems might interact in complex ways (Pisanski, Cartei, McGettigan, Raine, & Reby, 2016), further complicating the theoretical issues.

Although all vocalizations generated by the vocal emotion system have volitional counterparts, laughter is the only one that has been examined empirically for physical characteristics and perceptual correlates of different production types. Many proposed taxonomies of laughter distinguish between spontaneous (i.e., genuine/involuntary) and volitional (i.e., deliberate/voluntary) forms (e.g., Gervais & Wilson, 2005; Keltner & Bonanno, 1997). A growing body of research reveals that listeners are quite adept at distinguishing these laugh types (Brown, Sacco, & Young, 2018; Bryant & Aktipis, 2014; Lavan, Rankin, Lorking, Scott, & McGettigan, 2017; Lavan, Scott, & McGettigan, 2016; McGettigan et al., 2013; Wood, Martin, & Niedenthal, 2017), including across widely disparate cultures (Bryant et al., 2018). Moreover, neuroimaging research reveals differential activation of brain regions during both the production and perception of spontaneous and volitional laughter (Lavan et al., 2017; McGettigan et al., 2013; Szameitat et al., 2010). Because the laugh types are generated using different vocal production systems, there are predictable and documented acoustic differences, many attributable to differences in arousal during production, but also due to differential breath control in the vocal emotion versus speech systems. Spontaneous laughs typically have higher f_o, shorter burst duration, as well as fewer voiced elements, including a higher rate of intervoicing intervals (Bryant & Aktipis, 2014; Lavan, Scott, & McGettigan, 2016).

In sum, laughter is clearly evolved from ancestral ape play vocalizations, and now manifests itself as a complex signal retaining the ancestral function of signaling positive affect and cooperative intent. The evolution of volitional control over vocal behavior in conjunction with language has resulted in a diversification of laughter's functions as a strategic tool in humans' cognitive niche. We now turn to the issue of how laughter can function in social life.

SOCIAL FUNCTIONS OF LAUGHTER

Human laughter occurs most typically in the context of conversational turn-taking (Jefferson, Sacks, & Schegloff, 1987; Vettin & Todt, 2004). Despite extensive description at this level of analysis, its specific functions remain poorly understood. In social contexts, laughter is often generated by groups of people, and sometimes directed at specific individuals or other groups. The well-known sentiment, "I'm laughing *with* you, not *at* you," speaks to the important social dynamics that unfold related to laughter episodes, even within dyads. A substantive body of research in social psychology has explored the role of in-groups and out-groups in how people are affected by laughter, generally suggesting that laughter is functioning as a means to coordinate sentiment and appraisals of social situations (for a review, see Platow et al., 2005). Most treatments of laughter center on the idea of positive emotions and prosocial intent. The positive subjective feelings behind laughter are likely the product of endogenous opioid activity (Manninen et al., 2017; Wild, Rodden, Grodd, & Ruch, 2003), a process shown even to elevate pain thresholds (Dunbar et al., 2011). The proximate rewards of laughter point to an adaptive communication system, one likely functioning in social groups for the purposes of social assortment and alliance formation (Flamson & Bryant, 2013).

Signaling ongoing affiliation or cooperative intent is widely considered to be an important pragmatic function of laughter and is directly related to the affiliative function of nonhuman play vocalizations described earlier (Brown et al., 2018; Bryant et al., 2016; Bryant & Aktipis, 2014; Curran et al., 2018; Dezecache & Dunbar, 2012; Mehu & Dunbar, 2008; Morisseau et al., 2017; Owren & Bachorowski, 2003; Panksepp, 2005; Platow et al., 2005; Provine, 2016, 2000; Ruch & Ekman, 2001; Scott, Lavan, Chen, & McGettigan, 2014; Wood & Niedenthal, 2018). There are many forms of play in human behavior and most involve laughter at some level, with tickling being the classic, and likely primordial, form. In conversation, verbal play elicits laughter in a variety of contexts, including volitional laughter that can mark recognition or understanding of speakers' intentions, often with play and humor (e.g., Bryant, 2011; Jefferson, 1979). Humor and laughter are traditionally linked, but their relationship is far from simple. Provine (1993) argued that much of what people laugh at is not obviously funny, and more often than not, speakers are the first to laugh in verbal exchanges. This goes against the folk notion that people laugh primarily in response to something funny, and points to more complex signaling dynamics. The encryption theory of humor explains this nicely. According to this approach, a central reason why people generate intentional humor, whether through words, behavior, or other representations such as literature and art, is to allow social agents to assess knowledge, preferences, and beliefs indirectly (Flamson & Barrett, 2008). When humor is used as a social assortment device, laughter can function as a covert signal of shared information, affording adaptive strategies of social alignment through the mutual recognition of subtle, spontaneous signals within groups (Flamson & Bryant, 2013; Lynch, 2011; Smaldino, Flamson, & McElreath, 2018).

Research examining the darker side of laughter resonates well with a social assortment approach. Titze (1996) and others (e.g., Ruch & Proyer, 2008) have described a clinical condition (gelotophobia) in which individuals have a pathological fear of being the target of ridicule indicated specifically by laughter. Although a pathology, this hypersensitivity is an exaggeration of a phenomenon nobody wants to experience. Klages and Wirth (2014) asked people to recall personal incidents when they were the target of exclusive laughter. Relative to recalling being a part of inclusive laughter, or the activity of a typical weekday, exclusive laughter victims were more motivated to aggress, felt more social pain, had more negative moods, and experienced reduced self-evaluation. Papousek et al. (2014) examined responses to laughter as a possible social rejection cue in individuals with gelotophobia. Participants were systematically insulted through an intercom during an arithmetic task, and sometimes the insults were followed by incidental laughter (i.e., made to look accidental and not intentionally tied to the insults). When experiencing the laughter, gelotophobic individuals had marked heart rate deceleration relative to controls. Slowed heart rate is consistent with the notion that social fear can create a "freezing" response that could contribute to stopping an ongoing behavior, as opposed to the fight-or-flight response that generates heart rate acceleration and other responses preparatory for action. Overall, gelotophobes often seem to process laughter as socially relevant in ambiguous situations, revealing a hypersensitivity to the social signal. But even normal individuals have stronger and more elongated neurocognitive emotional processing of insults when they are paired with laughter (Otten, Mann, van Berkum, & Jonas, 2017).

People's disposition and social standing can affect the way they hear laughter, as well as how they produce it. For example, Oveis et al. (2016) found that individuals in a dominant social position (fraternity members versus pledges) produced more dominant sounding laughs, whereas pledges produced more submissive sounding laughs. The dominant laughter was coded as more disinhibited, including higher in pitch and faster in burst rate, both indicative of greater arousal. The difference here could be reflecting a difference in spontaneous versus volitional production, a possibility that the authors do not discuss. Submissive social actors might often refrain from producing genuine social signals, and instead feign emotional engagement deemed as more socially appropriate. Moreover, producing laughter that potentially sounds like an attempt to be dominant could have negative social repercussions. Polite laughs are one strategic option for individuals desiring social approval, as well as a means for signaling one's acceptance of their own current social position. Consistent with this idea, compared to typically developing individuals, boys at risk for antisocial behavior showed lower neural responses to laughter in the supplementary motor area, a region associated with readiness for social interaction (O'Nions et al., 2017). Moreover, boys at risk for psychopathy showed lowered activation in the anterior insula, a region connected to auditory-motor processing and integrating action tendencies with subjective affective feelings. These individuals also had a lowered motivation to colaugh. Clinical data such as these point toward the normal functioning of social-cognitive processes that crucially involve the integration of multiple social signals including laughter.

COLAUGHTER

An important but understudied aspect of laughter is the fact that most laughing occurs in the context of a group, and that people often laugh together. Research typically focuses on the role of laughter between individuals, looking at how people signal to one another, or at least that approach is implied. Theorists often either consider laughter to be some kind of reflection of an internal affective state that is then conveyed to others, or they focus on the proximate factors triggering the laughter, usually having to do with humor and what people consider to be funny. An evolutionary approach requires a functional explanation—when we are talking about expressive behavior in general, we need to think in terms of signals and cues. From this perspective, what is the evidence for colaughter being a group signal? There are many examples of group-produced signals in humans and nonhuman animals alike. Many nonhuman species collectively produce territorial advertisements, alarm calls, and signals of mateships, and humans generate group emotional signals, organized chanting and other choreographed vocal displays, as well as musical performances (Bryant, 2013; Hagen & Bryant, 2003; Hagen & Hammerstein, 2009). Are colaughing individuals inadvertently providing information regarding their social relationship to overhearers (i.e., a cue), or is the colaughter shaped by selection to signal to those outside of the group?

Although not in abundance, research has explored colaughter in a few different ways. People laugh together, and not only is this behavior associated with particular states of relationships, but listeners are sensitive to it. Smoski and Bachorowski (2003a, 2003b) examined antiphonal laughter, which they defined as laughter in response to a social partner's laughter. They looked at how this pattern of laughing occurred in developing friendships as well as between friends and strangers. Women tended to start producing antiphonal laughter in their relationships earlier than men did, and women laughed together more than men overall. Not surprisingly, friends produced antiphonal laughs more than strangers, and females produced them more in mixed-sex pairs than did males. The authors proposed that the laughter reinforced mutual positive emotions between laughers, but never suggested any kind of signaling function outside of the dyads.

More recently, Kurtz and Algoe (2017, 2015) examined the effect of "shared laughter" on personal relationships. Using both video coding for romantic couples (Kurtz & Algoe, 2015), and surveys of people online (Kurtz & Algoe, 2017), the authors reported that shared laughter (minimally defined as simply co-occurring) was associated with increased affiliative feelings and higher perceived personal similarity. Romantic couples who produced more shared laughter in recordings also reported feelings of greater support and closeness with their partners. Dezecache and Dunbar (2012) explored group laughter as a means of social grooming. They observed naturally forming conversational groups and assessed the typical conversational and laughter group size, finding that members of a social group most often laughed in groups of three or four, similar to documented conversational group sizes. By laughing in groups, individuals can essentially groom others in a way that is analogous to physical grooming exhibited by many primate species. These findings, as well as those of Smoski and Bachorowski, point to a basic function of laughter in its proximate role in relationship development. There are endogenous rewards for laughing with others, and we can signal information about our cooperative intentions and feelings of positive affect. But the acoustic design features of laughter suggest there is more to it.

Laughter appears to be well designed for intergroup communication, as it contains acoustic features traditionally associated with wide broadcast and the penetration of noisy environments. This is especially true for colaughter. Wiley (1983) described four features of vocalizations that ensure detectability and reliability: (1) alerting components; (2) conspicuousness; (3) small repertoires; and (4) redundancy. Consider the typical sound features of laughter described earlier. Laughs often begin with a loud, abrupt onset, including high frequency and loudness that can function to alert listeners. The overall sound of laughter stands out and is unique among human vocalizations, making it highly recognizable and conspicuous. Whereas a variety of sounds can constitute laughter, vocalizers generally produce limited inventories of sounds that follow some basic production rules. Common repertoires generally incorporate voiceless glottal fricatives (e.g., /h/) along with central vowels (e.g., /ə/) that together maximize airflow through the vocal tract (Stevens, 1998). Finally, laughter is repetitious with the same components being repeated on short and long timescales. Two other important features of laughter that speak to its communicative function are its contagiousness and overall loudness. One of the most effective triggers of laughter is another person's laughter (Provine, 1992), and when multiple people are laughing together, it is often significantly louder than the sound of ordinary conversation. In Figure 5.2, we see a little over 10 seconds of conversation between two female friends. Twice in this time they laugh together, and the increases in loudness during the laugh bouts relative to their talk are quite visible (and audible). Taken together, a form-function account strongly points toward a broadcast function that is different from the quiet, personal signaling that occurs in play contexts among nonhuman primates. When we laugh together, we appear to be signaling broadly to those outside the immediate communicative group.

Two recent large cross-cultural studies examined the perception of both colaughter and individually produced laughs. How well can listeners extract meaningful information about social relationships from hearing only brief isolated clips of two people laughing together? Indeed, people from all over the world, ranging from hunter-gatherers in Africa to college students across numerous industrialized countries, perform rather well on this task, with some variation—listeners everywhere could reliably identify friends versus strangers from just one-second segments of colaughter (Bryant et al., 2016). The colaughter in this study was extracted from real conversations between either established friends who knew each other on

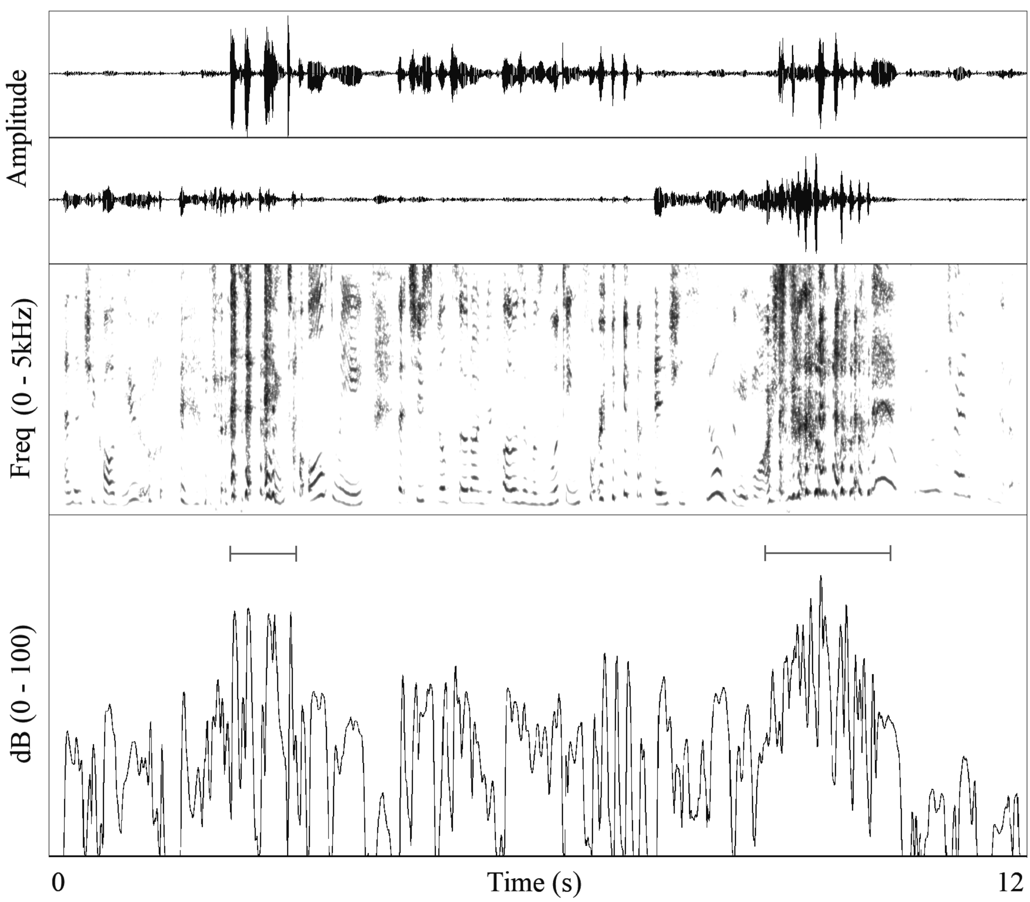

Figure 5.2 Colaughter in Conversational Context

average for about two years, to newly acquainted strangers who had just met moments prior to the recording of the conversations. One somewhat surprising finding was that people everywhere had a slight response bias to judge two women laughing together as more likely to be friends, resulting in accuracy for identifying female friends to be highest in every society. People's intuitions about female colaughter seem to hold across quite disparate societies, and as described earlier, research on antiphonal laughter found that women not only exhibit this behavior more than men, but they begin doing it earlier in their relationships.

Interestingly, listeners everywhere tended to use the same acoustic features in making their judgments. Colaughter that was faster and had irregular dynamics in pitch and loudness was often associated with friends. In a follow-up study, participants from 21 societies (many of the same study sites as the colaughter study) were able to reliably distinguish between spontaneous and volitional laughter (Bryant et al., 2018). In this study, the acoustic correlates of people's judgments were also examined, and similar acoustic features predicted judgments of laughter being spontaneous as in the previous study of colaughter between friends. What is the connection here? The most parsimonious view is that, in both cases, listeners are tracking acoustic correlates of physical arousal in the speakers. When people are in the presence of their friends, arousal is heightened. We speak with more enthusiasm and our emotions are more expressive. If, during interactions with friends, our vocal emotions are triggered more reliably, we will generate more spontaneous expressions, including spontaneous laughter. Moreover, colaughter seems to be particularly efficient in transmitting social information; better than, for example, overlapping talk (i.e., cospeech). A recent study found that listeners were able to more accurately assess whether pairs of interactants were friends or strangers using colaughter than cospeech from the same speakers that was over double in length (Bryant, Wang, & Fusaroli, 2019).

Another source of evidence for the social functions of colaughter comes from infants. Although fairly little developmental research has been done on laughter in children, a few studies have examined the social nature of laughter development. For example, work by Chapman (1973) found that 7-year-old children were much more likely to laugh in the presence of other children than by themselves. Recent work has also shown this effect in younger children, finding that 3- to 4-year-olds laugh significantly more at a cartoon when at least one other child is present, and not really much more if the number of children increases (Addyman, Fogelquist, Levakova, & Rees, 2018). Moreover, when asked about how funny they thought the videos were after watching, children's subjective ratings of funniness were associated with neither how much they laughed or smiled nor whether other children were present or not. These results show that group laughter is calibrated early and it is independent, to some degree, of external proximate triggers beyond other people laughing.

Another recent study explored infants' perception of colaughter. Using the same colaughter recordings as the large cross-cultural study described above, Vouloumanos and Bryant (2019) found that 5-month-old infants preferred to listen to streams of colaughter between friends over the same from strangers. In a second experiment, a different group of 5-month-olds observed pairings of short videos and colaughter. The videos showed two adult women acting either in an affiliative manner (i.e., silent greeting with a wave and then standing facing one another) or a non-affiliative manner (i.e., no greeting, then turning away from one another). These videos were paired with either colaughter between friends or colaughter between strangers. Infants were relatively surprised by incongruent pairs (i.e., they looked longer)—that is, affiliative interactions paired with colaughter between strangers, or non-affiliative interactions with friends' colaughter. Even in the first months of life, infants are prepared to link colaughter to social action. Such an early sensitivity suggests the action of an adaptive perceptual system.

Colaughter appears to be a reliable signal of affiliation that is readily perceived across disparate cultures and detectable by very young infants. It appears more efficient at transmitting social information than other kinds of dynamic information produced between interlocutors, such as overlapping talk. But it also appears that laughter is not well designed to provide specific group-identifying information (Lavan, Short, Wilding, & McGettigan, 2018; Ritter & Sauter, 2017), suggesting that the signaling functions are about affective intentions and potentially group alliance structure as opposed to person identification, or cultural and linguistic background. Future work here should explore the social dimensions that reliably affect colaughter behavior and examine more closely any possible coordinated dynamical features in the colaughter itself. Bryant et al. (2016) failed to find evidence that coordinated acoustic features between the individual laughs making up colaughter pairs contributed to listeners' judgments of affiliation, possibly due to the extreme brevity of the stimulus clips (~1 sec). But behavior matching during interpersonal interaction (e.g., Louwerse, Dale, Bard, & Jeuniaux, 2012) suggests coordinated multimodal features, potentially including laughter, are informative.

CONCLUSION

Human laughter constitutes a family of nonverbal social vocalizations homologous to play vocalizations in nonhuman animals. The evolution of language and articulated speech introduced a second vocal production pathway that afforded multiple interactive functions manifesting in conversational turn-taking and group contexts. Most communicative functions of laughing stem from complex social strategies of coalition formation and maintenance, including humans' universal deep motivation to develop extended social ties for successful long-term cooperative relationships. Fueled by a proximate endogenous reward system, laughter provides one of the many tools people use to signal social information, such as implicit knowledge and preferences. Recent research documents the salient social information available in temporally coincident colaughter, and the widespread ability of listeners to glean rich social information from very thin slices of colaughter stimuli. Laughter appears to function both within dyads and larger interactive groups as well as between groups. A group signaling approach explains certain ubiquitous features of laughter, most notably its loud overall sound and other features that ensure its detectability, including alerting components and conspicuous acoustic structure.

Future research should further explore the fine-grained social-pragmatic functions of laughter and how these signals occur in the context of conversation and social group dynamics. Acoustically, more work is needed to explore cultural universals and variations in laughter structure. For example, we might expect more variation in volitional laughter across languages due to the linguistic constraints on speech development, while spontaneous laughter might be relatively unaffected by that developmental process, and instead manifest itself quite similarly across disparate language and cultural groups. Laughter provides a unique window into human vocal signaling and cooperative behavior, as well as an example of how ancestral communicative behaviors become integrated with later evolving systems. The story of the evolution of laughter is central to the development of our cooperative nature and complex social lives.

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