Laughter

A SCIENTIFIC INVESTIGATION

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VIKING

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To Helen

In these Delightful Pleasant Groves (Purcell)
Irmelin (Delius)
*Khovanshschina** (Mussorgsky)
Lear (Reimann)
The Love for Three Oranges (Prokofiev)
Lucy and the Count (Deak)
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Symphony 14 (Shostakovich)
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The Tragedy of Man (Ranki)
*Die Zauberflöte** (Mozart)

FIVE

Chimpanzee Laughter, Speech Evolution, and Paleohumorology

Do we reign alone as "the only creatures that laugh," as first suggested by Aristotle over 2,000 years ago? Centuries of folk wisdom mostly agree that laughter is a uniquely human behavioral trait. But is it true? Or are we once again to be knocked from our homocentric throne? To pursue this age-old question, I sought expert advice from our closest primate relative, the chimpanzee. While tickling chimpanzees in an attempt to stimulate laughter, I made two related discoveries—why chimps can't talk, and the locomotor transformation (bipedality) necessary for the evolution of human speech. As used in this study, laughter becomes a tool to study vocal evolution.

Contrary to popular belief, our hairy cousins the chimpanzees do produce a laughlike sound, as do gorillas, orangutans, and perhaps other primates. Charles Darwin, in his classic *The Expression of Emotions in Man and Animals*, reported that "If a young chimpanzee be tickled—the armpits are particularly sensitive to tickling, as in the case of our children—a more decided chuckling or laughing sound is uttered; though the laughter is sometimes noiseless." He also notes that "Young Orangs, when tickled, likewise grin and make a chuckling sound." Dian Fossey, in her book *Gorillas in the Mist,* adds that "Tickling between [gorillas] Coco and Pucker provoked many loud play chuckles." Given these and similar reports by primate vocalization experts including Peter Marler and Jane Goodall, need we pursue the question of ape laughter further?

The answer is a decisive yes and no—in science, as elsewhere in life, things are often not so simple as they first seem. What Darwin, Fossey, and others agree upon is that chimpanzees and other great apes produce a laughlike vocalization in circumstances (i.e., being tickled, playing rough-and-tumble) in which humans reliably laugh. These are useful observations, but short on essential details. Until we recently cracked the laugh code, too little was known about the structure of human laughter to make detailed comparisons with other species (Chapter 4). We simply did not know what to look at or what measurements to make. But once armed with knowledge of human laughter, it became apparent that chimpanzee and human laughter differed in important ways.

To study chimpanzee laughter, chimpanzees were needed, and one of the best places to find them in the United States is at the Yerkes Regional Primate Research Center in Atlanta, Georgia. This institution is the home of many of the ape world's most distinguished ambassadors to humankind. For this part of the study, I teamed up with Dr. Kim Bard, then director of the nursery at Yerkes and a foster mother to many young chimpanzees who are ill, injured, or receiving inadequate maternal care from their biological mothers. Although Kim and I observed the ongoing behavior of chimps of all ages, we focused on animals of less than one year of age because they are especially playful and laugh a lot. We also chose babies because we were going to tickle them: tickling is one of the most common, reliable, and naturally occurring triggers of chimp laughter. Chimps are remarkably strong, can become aggressively boisterous

as they age, and may easily injure their human playmates. Whether tickling chimpanzees, the proverbial 500-pound gorilla, or a human playmate, it's important to have a consenting and friendly subject.

Our observations occurred within a fenced area just outside of the nursery building at Yerkes. The setting resembled a playground for a security-conscious preschool, complete with gym equipment. The tickler was Kim Bard or her assistant, Kathy Gardner. Tickling always occurred during playful interactions that ranged from light stroking, to play biting the shoulders and arms, to rolling around on the ground with an armful of exuberant young chimp. Both women were familiar to the chimps and were accepted as playmates.

When tickled by Kim or Kathy, the chimps produced a characteristic "play face" (mouth open, upper teeth covered, lower teeth exposed) and emitted a breathy pantlike sound that characterizes chimpanzee laughter.

Chimp laughter differs more from its human counterpart than is suggested by such previous descriptors as chuckling. Chimp laughter has graded variants, ranging from barely perceptible, labored breathing, to a more vigorous form in which a voiced, guttural exhalation overshadows the lower-amplitude inhalation. In cases of especially exuberant laughter, both exhalations and inhalations are voiced. The grunting sound ("ah grunting") noted by some investigators, best describes such high-amplitude chimp laughter. The few, sketchy descriptions of gorillas and orangutans suggest that they, too, make breathy, panting sounds when laughing, and exhibit a chimplike play face.

Audio recordings of chimpanzee laughter did not sound laughlike to students in two of my college classes. Almost no one hearing the tapes was able to identify the chimp sound as laughter (2 of 119), whereas almost everyone recognized adult male human laughter (117 of 119). Chimp laughter proved to be an auditory Rorschach test, triggering many associations in listeners. The most common description was "panting" (36 students)—most often believed to be that of a dog. Twelve students used other breathing-related descriptors (i.e., "asthma attack," "hyperventilation," "breathing problems,"

Figure 5.1 Play face of a young chimpanzee. The characteristic "play face" (mouth open, upper teeth covered, lower teeth exposed) accompanies pant-like chimpanzee laughter. (From Provine, 1996)

"breathing hard"). Some students noted only the animal suspected of making the sounds, including dog (10 students) or various nonhuman primates (ape, chimpanzee, monkey, or gorilla; 16 students). Other adventurous folks volunteered a variety of acts being performed during the vocalization, including "shivering" (3), "running" (2), and "masturbating" or "having sex" (5). A surprisingly large

number of students (17) attributed the chimp sounds to nonbiological, mechanical acts, most commonly "sawing" (9), but also "scraping" (2), "erasing" (3), "brushing" (2), and "sanding" (1).

Despite the students' confirmation of my impression that chimp laughter sounds like panting, it's easy to understand why many sophisticated observers since Darwin have associated the chimp vocalization with very different-sounding human laughter. Anyone who has played with chimps has been impressed with their laugh-like behavior. Consider the powerful context cues of chimp laughter—it follows tickling, it is produced during the physical contact of rough-and-tumble play, and it is accompanied by a play face that seems cheerful to most humans. And since we are, after all, each other's closest relatives, sharing 99 percent of our genes and much behavior, there is a lot of intuitive crossover. Although chimp vocalization is a homologue of human laughter and will be referred to in this book as chimp laughter, it's important to distinguish it from its human counterpart. Such distinctions are essential for our comparative and evolutionary analyses.

The most notable acoustic similarity between human and chimpanzee laughter is its rhythmic structure. Whether a chimp is "pant-pant-panting," or a person is saying "ha-ha-ha," the sonic bursts occur at regular intervals, a property apparent in the waveforms of both vocalizations. Chimps, however, have a laugh rhythm about twice as fast as that of humans. (The chimp sounds were separated—onset to onset—by about 120 milliseconds, versus about 210 milliseconds for humans.) This is because the chimpanzees vocalize during both inhalation and exhalation. If only the more strongly voiced exhalation is considered, the chimpanzee laugh rate is halved and approximates that of humans.

Contrast the scruffy-looking, relatively structureless chimp spectrum with the sharply defined "ha-ha-ha" of human laughter. The chimp spectrum lacks the clear harmonic structure typical of the human laugh spectrum. (Recall that the harmonic structure of the human laugh refers to the regularly spaced stacks of frequency-bands, each of which is a multiple of a "fundamental frequency," the bottom

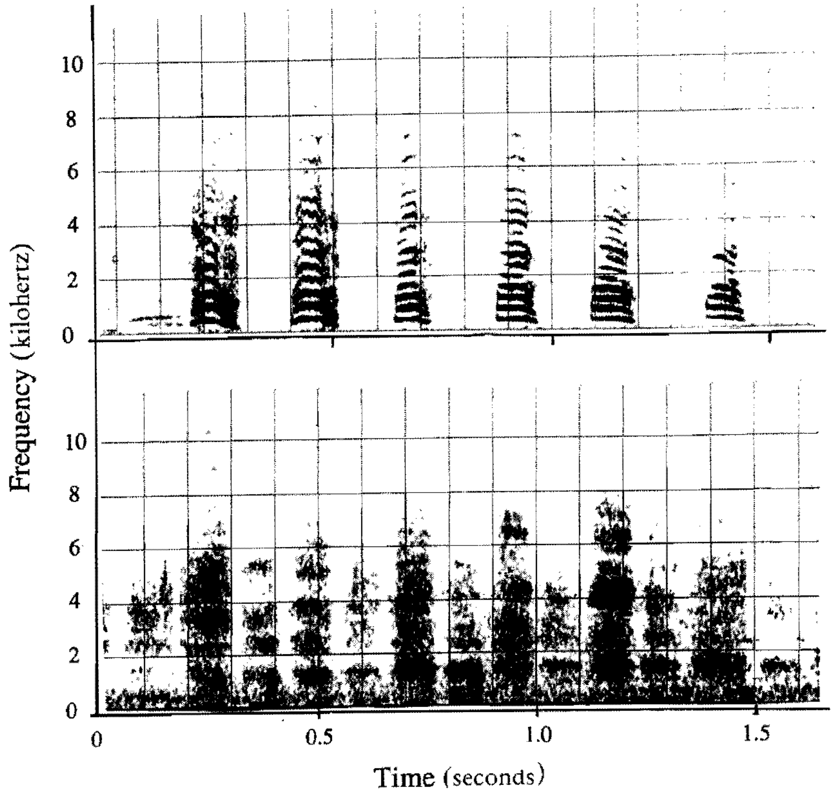

Figure **5.2** Frequency spectra of human (top) and chimpanzee (bottom) laughter. Breathy chimpanzee laughter lacks the distinct note form and strong harmonic structure (regular stacks of frequency-bands) characteristic of human laughter. (Adapted from Provine, 1996)

frequency-band of each stack.) Chimpanzee laughter also lacks the decrescendo of human laughter, the note-by-note trailing-off of loudness. Because chimpanzee laughter is panting, the volume of air available for a vocalization is renewed after each exhalation/inhalation cycle. This contrasts with purely expiratory human laughter in which the air for laugh-notes is gradually exhausted. Although chimpanzees never produce a humanlike laugh, humans can easily mimic the chimpanzee laugh.

Why Chimpanzees Can't Talk

Moving beyond acoustic analysis, we now contrast how chimpanzees and humans actually produce their own forms of laughter. A critical difference between chimpanzee and human laugh production is the relation in each species between vocalizing and breathing. The nature of this linkage explains why chimpanzees can't talk and people can. As described here, laughter, therefore, becomes a powerful neurobehavioral probe into vocal evolution

Human laughter, like speech, is produced exclusively during an outward breath—the discrete notes of laughter ("ha") are produced by chopping a single exhalation. Chimpanzee laughter, in contrast, resembles panting, with a single breathy vocalization being produced during each exhalation and inhalation. This coupling between breathing and vocalization was obvious from visual inspection and was confirmed by placing our hands on the heaving abdomens of the laughing chimps. If you want to try this demonstration and don't have a chimpanzee handy, you can, being a primate in good standing, simulate its laughter. Place your hand on your lower abdomen and pant—huff-and-puff—at a rate of four or five cycles (one exhalation and inhalation per cycle) per second. The exact rate isn't important. Note the prominent abdominal heaving associated with each pant.

Now, contrast the abdominal pulsations of chimplike panting with the smoother, tonic contraction produced by forcefully speaking the humanlike "ha-ha-ha." (Although true laughter is not a matter of speaking "ha-ha-ha," doing so works fine for this demonstration.) In this demonstration, you have experienced the very different patterns of neuromuscular activity responsible for chimp and human laughter. These differences have important implications for understanding the evolution of laughter and speech.

We humans speak as we laugh, by modulating an outward breath. If chimpanzees likewise speak as they laugh, by producing one sound per exhalation and inhalation, we have identified an important and previously unrecognized constraint on the evolution of

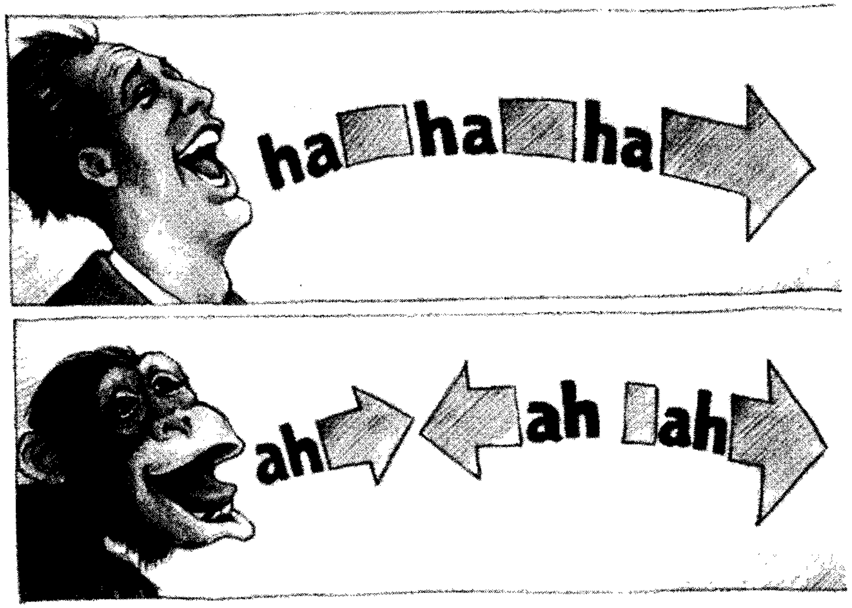

Figure 5.3 Contrast of human and chimpanzee laugh production. The sounds of human laughter, such as "ha," are produced by interrupting a single expiration (arrow). In contrast, chimpanzees produce only one laugh sound, a pant or gutteral "ah," for every expiration or inspiration (arrows). Humans laugh as they speak, by modulating an outward breath. The close coupling between breathing and vocalizing in chimpanzees may partially explain the failed attempts to teach these animals to speak English. (From Provine, 1996)

speech and language in chimpanzees and other great apes. Imagine the restrictions on your own speech if you were limited to one syllable per respiratory cycle. Chimps are captives of an inflexible neuromuscular system that is still closely tied to the essential and ancient labor of breathing. Indeed, the respiratory-vocal coupling of chimpanzees may be as limiting to the emergence of speech in the species as the structure of the tongue, larynx, and vocal tract and may be more resistant to evolutionary change. A shift in respiratory-vocal coupling would require reprogramming the neural output to muscles and the emergence of a time-sharing algorithm regulating

breathing and talking, not the more subtle structural alteration of the instrument of vocalization.

As a "thought experiment," imagine a chimp receiving a transplant of a human vocal tract and respiratory apparatus in exchange for its own. Assume that the procedure was perfectly executed and that the transplant was innervated by the chimp nervous system. Would the chimp be able to use it, learning to "play" this new mechanism to produce human speech sounds like a musician learning a second instrument? Probably not, because the new apparatus would still be controlled by the old, inflexible chimp nervous system.[1]

The woeful vocal speech competence of apes is a point of agreement in the often contentious debate about primate language. Although several researchers have reared baby chimpanzees in conditions similar to those of human children, their simian wards acquired hardly any speech. In the most successful effort, Keith Hayes and his wife, Cathy, home raised the infant chimpanzee Viki. After six years of exhaustive vocal training, Viki could manage only the marginally perceptible words "mama," "papa," "cup," and "up." The inability of chimpanzees to produce English words was once the basis of an underestimate of their general linguistic and symbolic competence. The bottleneck in the evolution of ape speech probably lies more in the domain of sound production than cognition and symbolic capacity.

Breakthroughs in human/primate communication occurred when methods were devised to circumvent the inadequate vocal apparatus of the great apes. Allan and Beatrix Gardner and Roger Fouts

[1]For a fictionalized account of such a procedure, consult *Ancient of Days* by Michael Bishop, in which Adam, a surviving member of the presumably extinct hominid group *Homo habilis*, gets surgery to alter his vocal apparatus. Benefiting from his surgically acquired speech, Adam goes on to become an eloquent and skilled player in contemporary human affairs. He even gets the girl! All that was holding back this primate was his deficient vocal apparatus and some grooming tips. Unfortunately, this science fiction treatment does not explore the problematic issue of the neural control of vocalization raised above. Neither Adam, the fictional *Homo*, nor contemporary nonhuman primates are likely to benefit so greatly from vocal touch-up surgery.

used American Sign Language (ASL) to communicate with the chimp Washoe. Francine (Penny) Patterson followed their lead and trained the gorilla Koko in ASL. David Premack worked with chimp Sarah using magnetized plastic symbols that could be strung together on a board. Sue Savage-Rumbaugh and Duane Rumbaugh trained the chimp Lana and the bonobo (pigmy chimp) Kanzi to press symbols on a large computer display or point to them on a tablet. Under the tutelage of Savage-Rumbaugh and Rumbaugh, Kanzi learned to respond to hundreds of spoken English words. (The bonobo or pigmy chimpanzee, *Pan paniscus*, is distinguished by having more humanlike vocalizations and social characteristics than the common chimpanzee *Pan troglodytes*.) Although all of these student apes developed impressive vocabularies, critics argue that they did not achieve the holy grail of "true language" with its requisite grammar and sentence structure, learning only mindless tricks. We will not engage this heated debate about ape language, focusing instead on a weak link in the chimpanzee's mechanism of vocal expression. We now explore the evolutionary events that permitted the flowering of human speech and language, and broaden the circle of considered species beyond the great apes—a line of inquiry that was prompted by the neurobehavioral probe of laughter.

Bipedalism, Laughter, and Speech Evolution

"In the beginning was the word" (John 1:1). But it is truer to say that "in the beginning was the breath," because all else in vocal communication is fashioned from it. To speak, or to produce any other vocalization, is to periodically override or modify our most basic need, breathing. Eating, drinking, and having sex collapse into insignificance if you can't catch your breath. The ability to override so vital a function as breathing in the service of sound making was a revolutionary event in neurobehavioral evolution. A second revolutionary event was the achievement of the even greater respiratory control necessary to produce speech. Evidence of this second critical transition in respiratory and vocal control comes from contrasting the laughter of chimpanzees and humans.

Among the chimpanzees, especially the more vocally facile bonobo (pigmy chimpanzee), we witness animals on the brink, but lacking that uncertain something that changes everything, that small increment that enables speech to flow forth, where before there were only simple calls and cries. The critical transitional steps to speech are difficult to envision, and may involve incremental changes that have large, nonlinear effects. The first speech sounds may have been like our first small, uncertain steps in walking, a stumbling forward, barely breaking a fall with our next, just-in-time step. Quickly, these first tentative steps gave way to bold, certain strides, leaving no trace of their genesis. The blocking, hesitancy, and repetitions of stuttering may be a consequence of this chaotic heritage, an involuntary "locking up" on the threshold of fluency, the amplified, nonlinear effect of a glitch in coordinating the complex, unwieldy neuromuscular mechanism of speech. Indeed, laughter itself may be a "stuttered" vowel sound. Although we may never discover the critical physiological event or primal moment in the evolution of speech, comparisons of chimpanzee and human laughter provide a tantalizing glimpse of what might have been.

As considered above, chimpanzee laughter is locked into the cycle of breathing, with one pantlike laugh-sound being produced per exhalation and inhalation. Chimps are unable to chop an exhalation into the discrete "ha-ha-ha"s of human laughter. What elevates this distinction in laugh-form above footnote status is that it reveals a fundamental inability of chimpanzees to modulate an exhalation, a critical condition for the production of humanlike speech. Humans laugh as they speak, by the virtuosic modulation of sounds produced by an outward breath.

Scientists have paid little attention to the neuromuscular mechanism of breath control, the respiratory engine of speech production, even in humans. By neuromuscular mechanism, I refer to the fundamental process of how neurons and muscles produce the *move-*

ments that ultimately translate into vocalizations, not the anatomical features of the vocal tract, a topic that has received more attention. The reason for the neglect of respiratory mechanism is understandable—the motor control of vocalization is not a sexy research topic. How many philosophically and psychologically oriented linguists lust after the details of thoracic anatomy or the patterning of motoneuron impulse traffic to the muscles powering and controlling breathing and speech? Yet without an anchor in the natural world of sound making, the discipline of linguistics degenerates into a theoretically driven study of synthetic issues—a battle of logicians. Speech is indeed unique in some respects, as claimed by many linguists and speech scientists, but it's no less dependent than other behavior on underlying motor mechanisms. And the analysis of these mechanisms is the key to understanding the evolution of speech.

The laugh-probe indicates that the chimpanzeelike laugh/speech mechanism with its high degree of respiratory-vocal coupling is the ancestral form. The human variant with its looser respiratory-vocal coupling evolved sometime after we branched from chimpanzees about six million years ago. Evidence of the primacy of the chimp form comes from the identification of chimplike laughter in orangutans and gorillas, apes that split off from the chimpanzee/human line several million years before chimpanzees and humans diverged.

The laugh-probe reveals no neat solution to the age-old, multifaceted enigma of speech evolution, but it does suggest promising places to look for clues. Because so much hinges on respiratory control, this literature is likely to offer novel leads. Of particular interest are the relations among the evolution of bipedalism, breathing, and speech, three events that seem, on first hearing, to be only distantly related.

I will begin with a few well-established points about the evolution of human bipedalism and speech before considering the relation between them. Humans evolved the ability to walk and run skillfully and efficiently in an upright position some time after we split off from an ancestor shared with chimpanzees. Chimpanzees and other

great apes, although not obligate quadrupeds, cannot walk efficiently or for long distances in an upright posture. The evolution of bipedality was a critical event in our species' biological and behavioral history that had consequences ranging from the freeing of hands for carrying and gesturing, to the natural selection for more stride-efficient narrower hips (less side-to-side rotation), a transition that had substantial costs to females, who had to endure more difficult birthing. The evolution of speech was another critical event in human history that occurred sometime after our branch point with chimpanzees.

I propose that *the evolution of speech and bipedal locomotion are causally related,* the basis of what I call the *Bipedal Theory* of speech evolution. (It was the "Walkie-Talkie" theory in one media account.) The common link between both acts is *breath control.* The evolution of bipedalism set the stage for the emergence of speech by freeing the thorax of the mechanical demands of quadrupedal locomotion and loosening the coupling between breathing and vocalizing.

"Running and Breathing in Mammals," a *Science* magazine article by Dennis Bramble and David Currier, spurred my interest in this topic. The authors provided comparative information about running and breathing in a variety of animals, including human joggers. They report, for example, that quadrupedal species such as horses usually synchronize their locomotor and respiratory cycles at a constant ratio of 1:1 (strides per breath). This synchronization is understandable because both locomotion and respiration use cyclic movements of the thoracic complex (sternum, ribs, and associated musculature). In addition, during quadrupedal running, the thorax is subject to powerful, repetitive impacts as the forelimbs strike the ground. Some sort of anatomical support or respiratory maneuver is necessary to strengthen the otherwise structurally weak, air-filled bag of the thorax. Humans increase the rigidity of their thoraxes by breath holding when rising from a chair without using their hands, or when lifting a heavy weight. And they may "bear down" and grunt if a task is really challenging. This act of breath holding and bearing down, which is called the Valsalva maneuver, is also used during defecation, and if you pinch your nose shut, is handy in inflating your middle ear to relieve pressure when scuba diving or landing in an aircraft.

Human runners are unique among modern mammals in having a striding bipedal gait. Our upright posture and locomotor pattern frees us of forelimb impacts and loosens, but does not abolish, the coupling between running and breathing. In contrast to the usual 1:1 ratio of quadrupeds, bipedal human runners employ a variety of phase-locked patterns (4:1, 3:1, 2:1, 1:1, 5:2, and 3:2), with 2:1 as the most common pattern. Here we have evidence of the plasticity of the human respiratory rhythm and its relation to upright bipedal gait. At this point, Bramble and Carrier's insight triggered one of my own—that bipedalism was necessary for the evolution of speech.

Bipedalism was a necessary, although probably insufficient condition for the evolution of speech in primates. Further embellishments of the vocal system were necessary, but bipedalism was a critical first step.

Further support for the bipedal theory came from a chance meeting with Ann MacLarnon, a primate spinal cord expert, at the 1996 Congress of the International Primatological Society in Madison, Wisconsin. Ann commented that my detection of respiratory limits of chimp vocalization may be related to spinal cord structure, adding that the main difference between the spinal cords of humans and other primates is that humans had more spinal cord mass in the thoracic segments controlling the neck, arms, and trunk. This is the cord region implicated above in the evolution of human respiratory control. In addition, the greater size in humans exclusively involved gray matter, the area of the spinal cord composed of neuronal cell bodies, circuits that pattern movement, and motoneurons that send nerves to the muscles. No difference was observed in white matter, the cord area composed of nerve fibers that transmit information within the nervous system.

After the meeting, I found another of Ann's contributions: her analysis of fossil remains of the Nariokotome *Homo erectus*, an ex-

tinct bipedal hominid discovered in northern Kenya. Based on inferences about the size of the hole in the fossil vertebra that sheath the spinal cord, she determined that *erectus* had a small-diameter thoracic spinal cord characteristic of nonhuman primates. Thus, the more massive human thoracic spinal cord is not a response to the challenges of upright posture or bipedal gait, an event that occurred several million years before the appearance of *erectus*. The bloom in human thoracic spinal mass was the consequence of other demands, perhaps the respiratory control of the muscles necessary for the evolution of speech. Taken together, the comparative study of primate spinal cords and the fossil record of *Homo erectus* suggest that bipedalism appeared before speech, a sequence consistent with the evolutionary scenario advanced in this chapter.

Does bipedalism signal the presence of the respiratory/locomotor/vocalization coupling necessary for speech or exceptional vocal competence? Human developmental studies offer provocative, indirect support for such a link between locomotion and vocalization. Standing alone and walking is a significant developmental milestone reached around the end of the first year of postnatal life, a birthday celebrating the acceleration of life's next great task, the development of speech and language. (The shaping of vocalization, however, starts much earlier.) Although the development of bipedal locomotion is obviously not necessary for the onset of speech (speech develops in children who never walk), it may signal the typical maturational stage when the neuromuscular mechanism for speech is in place. Children need not walk to benefit from their species' heritage of bipedality.

Does the proposed bipedalism/respiration/vocalization link hold for animals other than primates? Unfortunately, lessons to be learned from comparative analyses are limited because no other mammals either speak or routinely walk on two legs. And distantly related animals may evolve means other than bipedality to loosen respiratory constraints on vocalization.

The birds, virtuoso vocalizers and sometimes imitators of human

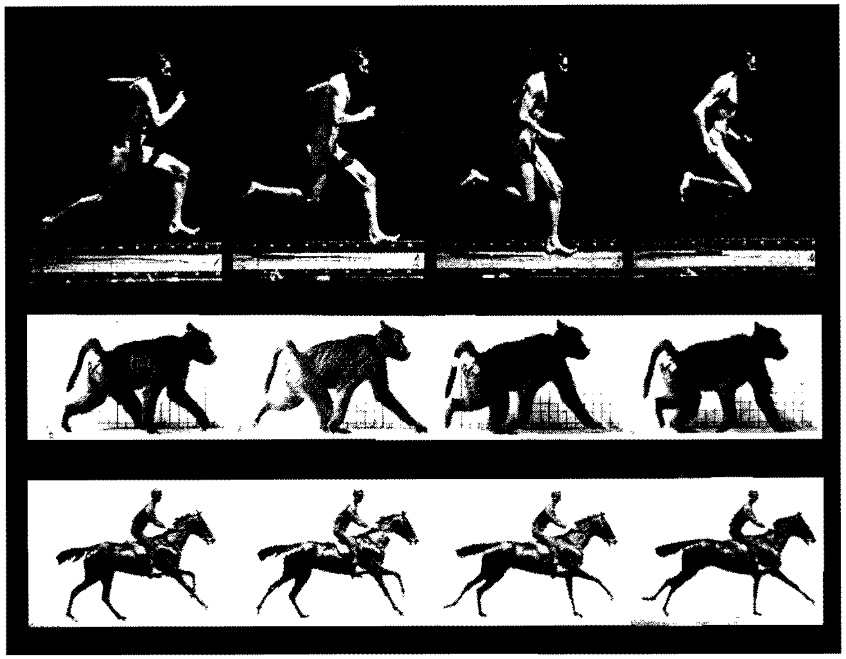

Figure 5.4 The evolution of bipedal locomotion. The emergence of bipedalism in humans' ancestors facilitated the evolution of speech by freeing the thorax of the mechanical demands of quadrupedal locomotion. Quadrupeds must synchronize their locomotor and breathing cycles to increase the rigidity of their air-filled thorax to absorb the powerful forelimb impacts during running. In contrast to the 1:1 ratio between breathing and striding in quadrupeds, bipedal human runners employ a variety of patterns, evidence of looser coupling between running and breathing. The emancipation of breathing and vocalization from locomotion was necessary for the vocal virtuosity of human speech. (Adapted from Muybridge, 1899/1957, 1901/1955)

speech, are fellow bipeds that are obviously able to redirect breathing for sound making. But birds are so specialized that they may be a unique case—the avian pectoral apparatus and forelimbs have been remarkably transformed in the service of flight, and their vocal apparatus is radically different from our own. And avian vocal competence is hardly uniform—for every mynah or songbird, there is a duck or fowl. It's significant that the African gray parrot, a bird noted for its expert mimicry of human speech and other sounds, also has

remarkable symbolic competence. In some birds, at least, vocal facility may be a step toward the emergence of language and other higher-order cognitive processing.

Whales are a fascinating class of accomplished mammalian vocalizers that circumvented the bipedal phase of vocal evolution. The respiratory apparatus of these gigantic descendants of terrestrial quadrupeds is not freed of the demands of gravity by bipedality, but by suspension in water. And whales are also capable of remarkable feats of breath holding for tens of minutes, obvious evidence of breath control, another possible behavioral marker of vocal potential. We humans, of course, can hold our breath for the less impressive, but still significant interval of one to several minutes. But breath holding by itself does not indicate vocal facility—ducks and other diving birds are not known for their song.

So what about the vocal competence of other breath-holding mammals? Hoover the seal is a remarkable case. This human-raised male harbor seal is reported to speak about a dozen English words, and even produce a rousing belly laugh. (The "words" may have been combinations of assorted vowellike sounds characteristic of seals.) Although I've not heard Hoover's laugh and could not detect discrete words on two audiotape recordings of his vocalizing, I was impressed by the speechlike quality of what I heard. (Imagine the gruff voice of an inebriated and incoherent male streetperson accosting you on the sidewalk.) Sadly, these feats of seal sound making can't be pursued because Hoover died several years ago. Perhaps another seal of vocal distinction will emerge and carry on Hoover's honorable tradition.

The present approach to the origin of speech is much nearer its beginning than its end and has gaping voids. Although the evidence relating laugh pattern, respiratory coupling, and speech competence in humans and chimpanzees is well established, other topics are less well developed. What, for example, are the specific neurobehavioral changes associated with bipedalism, and how, exactly, do they nudge the vocal apparatus toward speech production? But the bipedal hypothesis and associated data answer significant questions and may stimulate creative sleuthing for clues at the intersection of breathing, walking, talking, and laughing.

Ape Laughter and Paleohumorology

After wrestling with the origins of laughter and speech, this chapter concludes with deliberations about an issue of the here-and-now, the matter of chimp humor. What, exactly, makes chimps laugh, and does this knowledge suggest the nature of the most ancient joke? The problem is deceptively difficult. Speculation about the nonhuman psyche is one of the most treacherous and notorious pursuits in the history of psychology. Although chimpanzees are the animals most like ourselves, they differ fundamentally from us in their lack of spoken language, and lacking language, they probably lack the capacity for abstract thought necessary for most humor as we know it. To minimize the anthropomorphic biases inherent in the search for humor, our tactic will be conservative and austere, avoiding inferences about the machinations of the simian psyche. We will focus instead on the stimuli and behaviors that immediately precede laughter, the approach used previously with humans. After considering the stimulus context of infant and adult chimp laughter, the chapter will end on a more speculative note with anecdotes about ape behavior that may meet human standards for humor.

Solitary chimps, like solitary people, seldom laugh, a result consistent with laughter's role as a social signal (Chapter 3). But chimps and humans differ in the social situations in which they laugh—we humans have added something new to our still present chimplike tendencies. Adult humans laugh most during conversation. Chimps, in contrast, laugh most when tickled, during rough-and-tumble play, and during chasing games (the chimp being chased laughs most). Physical contact or threat of such contact is a common denominator of chimp laughter. Nevertheless, chimp laughter is probably less social than in humans—I have observed solitary young chimps laughing while playing with objects (balls), tickling their own feet (Can they tickle themselves?), rolling on the ground, and swinging. Roger

Fouts concurs that chimps sometimes laugh during solitary play, recalling a particular case when Moja was playing with old clothes. Chimps lack a clear equivalent to human conversational laughter in which two physically separated individuals look at each other, gesture, or vocalize before breaking up in a fit of laughter. The physicality and social context of chimp laughter resemble that of human children before the age of five or six when joking becomes prominent and intentional. Although chimps and young children engage in acts that produce laughter in others, such laughter is typically the incidental by-product of play, not its objective.

In a rare field study of the interactions between chimpanzee mothers and infants, Frans Plooij made an important discovery about the roots of laughter. Baby chimps control the behavior of their mothers, with tickle and laughter playing significant roles in a nurturant pas de deux. Compared to their human counterparts, chimp mothers rarely gaze at their babies or spontaneously engage in communication, but they do respond to their babies' actions. The chimp baby initiates mother-infant play by biting the mother, who then looks at and tickles the baby, triggering cycles of biting/tickling interplay that continue until the baby signals "too much" by "defending," fussing or crying. The baby signals the "just about right" amount of stimulation with a "play face" and laughter. In these duets, the *baby,* not the mother, initiates and regulates the interaction. Although human mothers are more proactive and attentive, laughter, smiling, and tickling retain a central role in the social interplay, with babies regulating the intensity and duration of the interaction. Laughter and smiling are means for a prespeech human baby to indicate, "I liked that, do it again," and fending away and crying are signals for "Enough!" or "Too much!"

Chimpanzee mothers rank below humans and above monkeys in attentiveness to their babies. Monkey mothers, for example, don't respond to their babies' bites like chimp mothers, but sibling and peer monkeys do. The responsiveness of these young monkey companions to biting babies may explain their effectiveness as peer "therapists" in Harry Harlow's developmental studies of baby rhesus monkeys deprived of their mothers. Whether due to ineffective play face and laughter, or to an unresponsive parent, monkey babies lack the stimulus tools necessary to capture and hold their mothers' attention in the social give-and-take typical of chimpanzee and human mothers.

Most prelaughter stimuli for chimpanzee laughter are physical, concrete, and "nonjoking." Consider stimuli for chimp laughter that may meet human standards for humor. (This criterion may not be terribly high—after all, it includes the Three Stooges, Howard Stern, and *Married with Children.*) The enterprise is hampered at the outset by the failure of chimps to signal their production or perception of humor with laughter. Although much human humor does not trigger laughter of a human audience, enough of it does to establish a pattern that can be generalized to similar, more subtle titillations that don't reach the threshold for guffaws. We are not so fortunate with the otherwise playful and laughing chimps. Without the "gold standard" of laughter to gauge the occurrence of chimpanzee humor, we must make inferences about the mental life and intentions of another species, an ill-advised pursuit. There are no systematic studies of ape humor to guide our way. The evidence is found in scattered, anecdotal reports by researchers and caregivers based on homocentric estimates of whether a given primate act meets the human criterion for "humor." Having been forewarned, let's examine some of this provocative but necessarily limited data.

Most candidates for simian humor involve cases of intentional misusing of objects and misnaming of people and things. For example, researcher Roger Fouts observed the signing chimpanzee Washoe using a toothbrush as if it was a hairbrush. Moja, another of Fouts's signing chimpanzees, called a purse a "shoe," put the purse on her foot and wore it as a shoe. Francine "Penny" Patterson observed the signing gorilla Koko treating rocks and other inedible substances as if they were foods, offering them as "food" to people.

When Koko was asked by Penny to feed a baby doll with a bottle, Koko held the bottle to the baby's eye instead of its mouth. In a misnaming incident, Koko refused to give the sign for drink (extended thumb with hand in fist position as if you are drinking from a thumb), finally providing the proper sign except that the thumb was placed in the ear instead of the mouth. In another misnaming incident, Koko spontaneously signed "bird" to a picture of a bird. But when asked later what the picture was, she signed "flower." The above cases of presumed intentional "misnaming" and "misusing" are potential jokes typical of human children of preschool age. Reports that the apes appeared to be in a playful mood, or glanced at the caregiver for evidence of the effect of their errant actions, suggests but does not establish a joking intent. Another widely noted class of misnaming involves "name calling," an act probably more amusing to human witnesses than the provoked primate signers. When upset with her caregiver, gorilla Koko referred to her as "dirty toilet." Lucy, a chimp reared by Maury and Jane Temerlin, signed "dirty cat" after a conflict with a local feline, and "dirt[illegible]ash" in regard to a disliked restraint. But are such misusing/misnaming cases errors, lies, jokes, or simply misinterpretations by caregivers?

In another possible instance of simian humor, Roger Fouts reported that while riding on his shoulders, the chimpanzee Washoe urinated on him, signing "funny" (touching her nose) and snorting, but not laughing. This incident is notable both for Washoe's reported recognition of a potentially funny event and the absence of laughter following the humorous episode. Fouts provides a second anecdote, this time suggesting an association between laughter and the act producing it. Instead of signing "You tickle Booee," the chimp Booee signed "You ——— Booee," substituting the sound of laughter ("pant-pant") for the command to tickle. In different ways, do Washoe and Booee show a primitive appreciation of the concept of "funny," the name we humans give to stimuli that make us laugh?

The sparse evidence of primate humor suggests a cognitive asymmetry whereby apes may appreciate their own self-initiated humor such as misnaming, but are bewildered by similar misnaming by others (e.g., chimp Lana), or respond to it by signing "stupid" (e.g., gorilla Koko), a response like that of human preschool children who often complain that jokes they don't "get" are "stupid" or "silly." The apes and preschoolers may lack the theory of mind necessary to infer the playful intent of others. Thus, humor may evolve in the perpetrator before the audience or victim. Here we find support for the common view of the primitiveness of the practical joke and joker.

Whatever the style of humor, alcohol primes the laugh mechanism of chimpanzees as it does in humans. Consider the report of Maurice Temerlin, who likes to share a cocktail or two with his home-reared chimpanzee "daughter" Lucy. "In some ways, Lucy is an ideal drinking companion. She is very appreciative, always making sounds of great delight when offered a drink. She never gets obnoxious, even when smashed to the brink of unconsciousness. Alcohol relaxes her and it improves her sense of humor, for she laughs, tickling herself, posturing before a mirror, making 'crazy' faces and laughing at them."

Comparative humorology is an endeavor fraught with even more problems than the controversial study of ape language. But after sharing the anecdotes of others, I am emboldened to offer my own best guess about the most ancient "joke" and the origin of the laughter it triggered. My entry into the paleohumor sweepstakes is conservative, nonlinguistic and cognitively impoverished—*feigned tickle*. Although this simple physical act may fall short of common conceptions of humor, it clearly involves "kidding," playful intent, and triggers laughter. The power of "I'm going to get you!" and its variants to evoke laughter is undeniable—young chimpanzees and humans remain suckers for this ancient and invited ruse. Unfeigned, normal tickle is an even more primal stimulus of laughter and a likely form of "protohumor," but I didn't nominate it because the response of the ticklee is more reflexive. And what was the origin of the primal laughter in these ancient ticklefests? As suggested earlier, the vocalization of laughter did not arise de novo, but originated in

the ritualized panting of rough-and-tumble and sex play, whereby the sound of labored breathing came to symbolize the playful state that produced it. The vowellike "ha-ha-ha"s that parse the outward breath in modern human laughter is one step removed from the archetypal huffing and puffing that signaled laughter and play in our ancient ancestors.