Beyond a Joke: From Animal Laughter to Human Joy?

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be consistently associated with specific DNA sequence motifs (*17*).

These comparisons suggest a number of potentially useful studies. Although technically challenging, it may prove fruitful to examine regional variation in chromatin accessibility in mammalian meiotic cells. How does this affect the action of recombination-related proteins such as Spo11? In addition to Spo11, at least 11 other proteins are involved in the initiation of double-strand breaks and recombination in yeast (*21*), and many of the responsible genes have orthologs in humans (such as, *RAD50*, *RAD51*, and *MRE11*). Comparisons of these genes in humans and chimpanzees could reveal differences that affect recombination patterns. In yeast, recombination hotspots can be eliminated by the insertion of the Ty transposable element, which suppresses recombination in nearby sequences (*22*). Thousands of *Alu* and *LINE1* mobile elements have been differentially inserted in humans and chimpanzees since their divergence 5 million to 6 million years ago (*23*). Could these elements act in a fashion similar to yeast Ty, contributing to the rapid divergent evolution of recombination hotspots in humans and chimpanzees?

Studies such as that by Winckler *et al.* demonstrate the value of comparative genomic analysis for understanding basic biological processes such as recombination, and for potentially improving the design of genetic association studies. Their work also demonstrates the utility of analyses of within-species diversity and underscores the need for DNA sequence information from large samples of humans and other species. As this information accumulates, our understanding of biology, as well as our ability to design well-conceived gene-mapping studies, will continue to evolve and improve.

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PSYCHOLOGY

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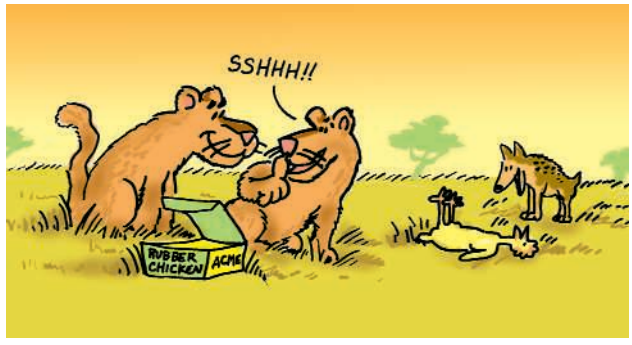
In the beginning was the word…but was the word funny? Research suggests that the capacity for human laughter preceded the capacity for speech during evolution of the brain. Indeed, neural circuits for laughter exist in very ancient regions of the brain (*1*), and ancestral forms of play and laughter existed in other animals eons before we humans came along with our *hahahas* and verbal repartee. Recent studies in rats, dogs, and chimps (*2*, *3*) are providing evidence that laughter and joy may not be uniquely human traits.

The capacity to laugh emerges early in child development, and perhaps in mammalian brain-mind evolution as well. Indeed, young children, whose semantic sense of humor is marginal, laugh and shriek abundantly in the midst of their other rough-and-tumble activities. If one looks carefully, laughter is especially evident during chasing, with the chasee typically laughing more than the chaser. As every aspiring comedian knows, success is only achieved if receivers exhibit more laughter than transmitters. The same behavior patterns are evident in the "play panting" of young chimps as they mischievously chase, mouth, and tickle each other (*2*).



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Laughter seems to hark back to the ancestral emotional recesses of our animalian past (*3*, *4*). We know that many other mammals exhibit play sounds, including tickle-induced panting, which resembles human laughter (*2*, *4*, *5*), even though these utterances are not as loud and persistent as our sonographically complex human chuckles (*6*). However, it is the discovery of "laughing rats" that could offer a workable model with which to systemically analyze the neurobiological antecedents of human joy (*3*). When rats play, their rambunctious shenanigans are accompanied by a cacophony of 50-kHz chirps that reflect positive emotional feelings (*7*). Sonographic analysis suggests that some chirps, like human laughs, are more joyous than others.

Could sounds emitted by animals during play be an ancestral form of human laughter? We have shown that if rats are tickled in a playful way, they readily emit these 50-kHz chirps (*3*, *8*). The rats we tickled became socially bonded to us and were rapidly conditioned to seek tickles. They preferred spending time with other animals that chirped a lot rather than with those that did not (*3*). Indeed, chirping in rats could be provoked by neurochemically "tickling" dopamine reward circuits in the brain (*9*), which also light up during human mirth (*10*). Perhaps laughter will provide a new measure for analyzing natural reward/desire circuits in the brain, which are also activated during drug craving (*7*, *11*).

Deciphering the neural circuitry of play-

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ful chirping in rats is an important goal of future research. Such knowledge may help to reveal how joking and horsing around emerged in our expansive higher brain regions. Although no one has investigated the possibility of rat humor, if it exists, it is likely to be heavily laced with slapstick. Even if adult rodents have no well-developed cognitive sense of humor, young rats have a marvelous sense of fun. We have already bred rats that exhibit excess playful chirping (*12*), and thereby hope to track down some of the genes for joy. Perhaps we will even stumble on new molecules to alleviate depression as well as some excessive-exuberance disorders (*13*, *14*).

Research on rough-housing play in mammals, both sapient and otherwise, clearly indicates that the sources of play and laughter in the brain are instinctual and subcortical (*1*, *3*, *8*). Although our species-typical capacities for verbal joking surely reflect highly refined cortico-cognitive skills (*15*), those incoming words must somehow tickle the ancient playful circuits of our minds for joy to occur. As we learn "to rib" each other with words, as opposed to just rough-and-tumble horse-play, we may be developing new synaptic connections to joyous neural zones that reside far below our cerebral crowns. It has long been intimated that laughter has many health benefits as well (*16*).

Human laughter, however, has a dark and dominant side. According to the philosopher Thomas Hobbes, "Laughter is nothing else but a sudden glory arising from some sudden conception of some eminency in ourselves." Experts compiling the DSM-V psychiatric guidelines may wish to consider how excessive gloating laughter contributes to "eminent-domain" disorders worthy of more precise psychiatric diagnosis. New treatments for such disorders might include strengthening the capacity for internal silent laughter (*17*), one of the few remaining mental capacities that may be uniquely human.

Many still believe that emotional feelings, from joy to grief, are special capacities of the human brain, but as Darwin taught, it just ain't so (*18*). The recognition of emotional feelings in our fellow animals should no longer be reflexively deemed an anthropomorphic sin (*4*, *8*). Perhaps it is time for neuroscience to accept that animals are capable of many emotional feelings (*8*, *19*) (despite the consternation that may cause for investigators who treasure the study of fear behaviors more than joy).

We find ourselves at the tall-tale end of an intellectual era when the animal mind was deemed nonexistent or impenetrable. Gentle Darwin was prescient when he coaxed us to see our own emotional nature as continuous with that of our fellow animals (*18*). By studying the many emotional "instinctual" behaviors and related learning capacities of other animals, we may develop excellent ways to fathom the neuroemotional foundations of human consciousness. Weighty data are tipping the scales of evidence in favor of ever more subtle affective conceptions of animal minds, *H. sapiens* included (*8*). Although our emotional systems are neither uniquely nor intelligently designed, it is a blessing that we can finally understand their affective nature (*19*). As William Blake incomparably declared in *Auguries of Innocence* (1863):

> It is right it should be so;
> Man was made for joy and woe;
> And, when this we rightly know
> Through the world we safely go.
> Joy and woe are woven fine
> A clothing for the soul divine;
> Under every grief and pine
> Runs a joy with silken twine.

If the mental lives of other animals are also created from the neural threads of joy and woe (not to mention many other feelings), we may need to openly consider the nature of their affective brains in order to understand our own. This brings special responsibilities for the scientifically sapient savants among us (*20*, *21*). Although some still regard laughter as a uniquely human trait, honed in the Pleistocene, the joke's on them.

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MATERIALS SCIENCE

Playing Nature's Game with Artificial Muscles

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Feel the pumping of your heart or leap to witness the wonder of some of nature's muscles. Skeletal muscles self-repair, provide billions of work cycles involving contractions of more than 20%, increase strength and change stiffness in response to need, generate stresses of ~0.35 MPa, contract at 50% per second, and can even transform to fuel for the starved body (*1*). They convert the energy of a safe, energetic fuel (adenosine triphosphate) to mechanical energy with higher maximum efficiency (~40%) than that achieved by a typical car engine (*1*).

Artificial muscles offering even higher performance are being sought for artificial and damaged hearts, artificial limbs, humanoid robots, and bird- or insect-like air vehicles that fly by flapping wings. How well do such artificial muscles compare with natural muscle, and what are the prospects for future advances? This Perspective focuses on artificial muscles that generate large strains (fractional changes of muscle length) of about 20%, rather than high force, high response rate, and/or high output power at low strain. Instead of mimicking nature by creating large macroscopic strains by the combined effects of trillions of molecular actuators, the artificial muscles use material deformations.

Electronically conducting polymers such as polyaniline and polypyrrole provide one type of high-strain actuator. In what is basically a battery, these muscles actuate by using dimensional changes produced by electrochemically inserting solvated dopant ions into a conducting-polymer electrode. Although first described almost two

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