REVIEW SUMMARY

NEUROSCIENCE

Poor human olfaction is a 19th-century myth

John P. McGann*

BACKGROUND: It is widely believed that the human sense of smell is inferior to that of other mammals, especially rodents and dogs. This Review traces the scientific history of this idea to 19th-century neuroanatomist Paul Broca. He classified humans as "nonsmellers" not owing to any sensory testing but because he believed that the evolutionary enlargement of the human frontal lobe gave human beings free will at the expense of the olfactory system. He especially emphasized the small size of the human brain's olfactory bulb relative to the size of the brain overall, and noted that other mammals have olfactory bulbs that are proportionately much larger. Broca's claim that humans have an impoverished olfactory system (later labeled "microsmaty," or tiny smell) influenced Sigmund Freud, who argued that olfactory atrophy rendered humans susceptible to mental illness. Humans' supposed microsmaty led to the scientific neglect of the human olfactory system for much of the 20th century, and even today many biologists, anthropologists, and psychologists persist in the erroneous belief that humans have a poor sense of smell. Genetic and neurobiological data that reveal features unique to the human olfactory system are regularly misinterpreted to underlie the putative microsmaty, and the impact of human olfactory dysfunction is underappreciated in medical practice.

ADVANCES: Although the human olfactory system has turned out to have some biological differences from that of other mammalian species, it is generally similar in its neurobiology and sensory capabilities. The human olfactory system has fewer functional olfactory receptor genes than rodents, for instance, but the human brain has more complex olfactory bulbs and orbitofrontal cortices with which to interpret information from the roughly 400 receptor types that are expressed. The olfactory bulb is proportionately smaller in humans than in rodents, but is comparable in the number of neurons it contains and is actually much larger in absolute terms. Thus, although the rest of the brain became larger as humans evolved, the olfactory bulb did not become smaller. When olfactory performance is compared experimentally between humans and other animals, a key insight has been that the results are strongly influenced by the selection of odors tested, presumably because different odor receptors are expressed in each species. When an appropriate range of odors is tested, humans outperform laboratory rodents and dogs in detecting some odors while being less sensitive to other odors. Like other mammals, humans can distinguish among an incredible number of odors and can even follow outdoor scent trails. Human behaviors and affective states are also strongly influenced by the olfactory environment, which can evoke strong emotional and behavioral reactions as well as prompting distinct memories. Odor-mediated communication between individuals, once thought to be limited to "lower animals," is now understood to carry information about familial relationships, stress and anxiety levels, and reproductive status in humans as well, although this information is not always consciously accessible.

OUTLOOK: The human olfactory system is increasingly understood to be highly dynamic. Olfactory sensitivity and discrimination abilities can be changed by experiences like environmental odor exposure or even just learning to associate odors with other stimuli in the laboratory. The neurobiological underpinnings of this plasticity, including "bottom-up" factors like regulation of peripheral odor receptors and "top-down" factors like the sensory consequences of emotional and cognitive states, are just beginning to be understood. The role of olfactory communication in shaping social interactions is also actively being explored, including the social spread of emotion through olfactory cues. Finally, impaired olfaction can be a leading indicator of certain neurodegenerative diseases, notably Parkinson's disease and Alzheimer's disease. New experimentation will be required to understand how olfactory sequelae might also reflect problems elsewhere in the nervous system, including mental disorders with sensory symptomatology. The idea that human smell is impoverished compared to other mammals is a 19th-century myth. ■

The human and rodent olfactory systems exploring the sensory world together.

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REVIEW

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Poor human olfaction is a 19th-century myth

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It is commonly believed that humans have a poor sense of smell compared to other mammalian species. However, this idea derives not from empirical studies of human olfaction but from a famous 19th-century anatomist's hypothesis that the evolution of human free will required a reduction in the proportional size of the brain's olfactory bulb. The human olfactory bulb is actually quite large in absolute terms and contains a similar number of neurons to that of other mammals. Moreover, humans have excellent olfactory abilities. We can detect and discriminate an extraordinary range of odors, we are more sensitive than rodents and dogs for some odors, we are capable of tracking odor trails, and our behavioral and affective states are influenced by our sense of smell.

The olfactory bulb is a phylogenetically conserved brain structure that receives direct synaptic input from sensory neurons in the olfactory epithelium in the nasal passages and communicates that information to the rest of the brain. Its distinctive anatomical appearance and glomerular organization have attracted scientific investigation since the 19th century (*1*–*4*), leading to 150 years of research on the bulb's circuitry and cellular neurophysiology. However, almost since these beginnings, the neuroanatomy of the olfactory bulb has inspired misunderstandings and incorrect conclusions about olfactory function in humans compared to other mammals.

The olfactory bulbs are bilaterally symmetrical ovoid structures located near the front of the brain. Olfactory sensory neuron axons enter from the olfactory nerve at the front of each bulb, and the bulbs connect to the rest of the brain through the comparatively thin olfactory tract at the rear. The seemingly limited attachment between the bulb and the rest of the brain is a distinctive anatomical feature found across mammalian species and has inspired the occasional misapprehension that the olfactory bulb is not part of the brain at all. In humans and other primates with large frontal lobes, the olfactory bulbs are flattened and positioned underneath the frontal lobe (Fig. 1, A and B), but in rodents and other mammals, the bulbs are proportionately larger and positioned prominently at the very front of the brain (Fig. 1C). This anatomical difference in bulb structure and position has been the source of a myth—that humans are "microsmatic" animals with tiny olfactory bulbs and a very poor sense of smell compared to other animals.

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Broca, religion, and the myth of "microsmatic" humans

Strangely, the idea that humans have tiny olfactory bulbs and a poor sense of smell is derived in part from the religious politics of 19th-century France. The Catholic Church in France actively fought secularization, including the denunciation of the Paris Faculty of Medicine for teaching "atheism and materialism." One of the physicians publicly singled out by bishops in the French Senate (*5*) was prominent neuroanatomist and anthropologist Paul Broca. This conflict manifested even in the day-to-day administration of Broca's academic institution and jeopardized the operation of his laboratory. Because of this socio-historical milieu, Broca sometimes interpreted his anatomical data to provide empirical support of his reductionist views.

As a comparative anatomist, Broca noted the relatively small size of the frontal lobes in other mammals and their corresponding lack of language and complex cognition, and as a brain surgeon, he noted the consequences of frontal lobe damage on human speech and thought. This led him to conclude that rather than having the disembodied soul espoused by his religious contemporaries, the "enlightened intelligence" that uniquely defined humanity could be physically located in the frontal lobes of the human cerebral cortex (*3*). When he observed that humans had relatively small olfactory bulbs and did not exhibit odor-compelled behavior to the same degree as other mammals, he concluded that the smaller relative volume of the olfactory bulb corresponded to the instantiation of free will in the frontal lobe [see note (*3*)]. Through a chain of misunderstandings and exaggerations beginning with Broca himself, this conclusion warped into the modern misapprehension that humans have a poor sense of smell.

In his 1879 work, Broca divided mammals into two categories: *osmatique* (osmatic) animals, which used olfaction as their principal sense and driver of behavior, and *anosmatiques* (nonosmatic), the small minority of species that did not. He noted that the nonosmatics could be subdivided into two categories: aquatic animals like cetaceans (e.g., whales and dolphins), which lacked basic olfactory structures, and primates including humans, because they had comparatively large frontal lobes and their behaviors were not compelled by olfactory stimuli. The initial categorization of humans as "anosmatic" was thus not principally about our olfactory abilities but about our ability to consciously choose our response to the olfactory stimuli we encountered. This fraught olfactory categorization was amended by Sir William Turner in 1890, who relabeled Broca's osmatic mammals as "macrosmatic" and subdivided Broca's anosmatics into "microsmatic" mammals "in which the olfactory apparatus is relatively feeble" (including "Apes and Man") and "anosmatic" mammals "where the organs of smell are entirely absent" (*6*). Turner does not appear to have considered that Broca's initial categorization of primates as anosmatic was not based on any study of sensory abilities.

By the time of Herrick's 1924 *Neurological Foundations of Animal Behavior* (*7*), the olfactory organs of humans were viewed as "greatly reduced, almost vestigial," coupled with the idea that "the enormously larger apparatus of most other mammals gives them powers far beyond our comprehension." This view may have contributed to the medical and scientific neglect of the human rhinencephalon, such as the claim by one neuroanatomy text that it "probably has not contributed greatly to the evolution of the human brain and will, therefore, not be considered further" (*8*). Even olfactory experts sometimes tied themselves in knots to comply with the expectation of human olfactory limitations. For instance, Sir Victor Negus reported that the area of the olfactory epithelium in the human was larger than that of the rabbit but nonetheless opened his book with the words, "The human mind is an inadequate agent with which to study olfaction, for the reason that in Man the sense of smell is relatively feeble and not of great significance" (*9*).

The derogation of human olfaction extended into 19th-century psychology and philosophy as well. Sigmund Freud was very familiar with Broca's work (his first book was about aphasia) (*10*) and believed that smell is "usually atrophied" in humans (*11*). Paralleling Broca's opposition of free will and olfactory ability, Freud posited that smell evoked instinctive sexual behavior in other animals but that in humans, the putative loss of smell caused sexual repression and enabled mental disorders, particularly if one "took pleasure in smell" (*12*). In his theory of psychosexual development, Freud described the anal and oral stages of early childhood, which centered on smell, taste, and touch, as "harking back to early animal forms of life" (*13*). Freud and Broca thus provided a pseudoscientific gloss on the idea that smell operates in opposition to a disembodied rationality that makes humans civilized and distinct from other mammals (*14*).

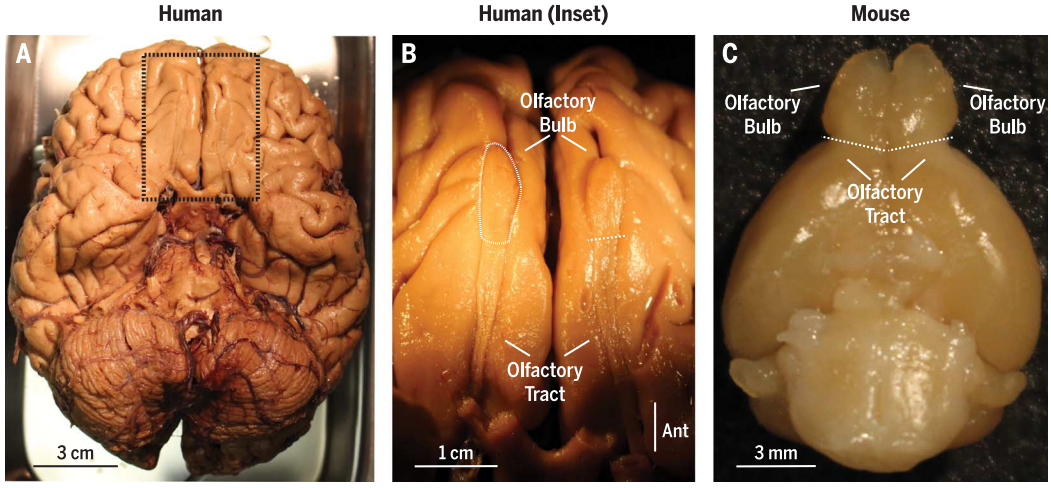

Fig. 1. Gross anatomy of the olfactory bulbs of human and mouse. (**A**) Ventral aspect of human brain, with meninges removed from the cortex. Area indicated by dotted rectangle is enlarged in (B). (**B**) View of left and right olfactory bulbs and olfactory tracts from (A). (**C**) Ventral aspect of mouse brain, with olfactory bulbs visible at the top. Up is anterior in all three panels. Dashed lines denote the approximate border between bulb and tract.

The categorization of humans and other primates as microsmatic animals with an impoverished sense of smell has survived to the present day. Not only is it the default belief for nonspecialists whose work touches on the chemical senses, but it even continues to mislead olfactory scientists. For instance, humans have approximately 1000 odor receptor genes, but "only" about 390 of these genes code for receptor proteins, whereas the remainder are noncoding pseudogenes (*15*, *16*). Because this is both a smaller fraction of functional genes and smaller absolute number of functional genes than the 1100 coding genes and 200 pseudogenes in the mouse (*17*), these numbers were immediately interpreted as a "correlate" of the comparatively limited olfactory ability in primates (*18*), although no actual sensory testing was performed. This finding has been used to claim that human olfaction is under less selection pressure than in other mammals (*19*), ostensibly because of the evolution of color vision (*20*). However, follow-up work from a broader range of species found no support for a sudden loss of functional odor receptor genes in conjunction with trichromacy (*21*). Critically, new evidence shows that 60% of human olfactory receptor "pseudogenes" are actually transcribed into mRNA in the human olfactory epithelium (*22*), and work in model organisms suggests that some olfactory receptor pseudogenes may actually result in functional receptors (*23*). Should these noncoding RNAs or unexpectedly coding RNAs turn out to be a powerful regulatory network unique to primates (say, for matching olfactory receptor gene expression to the environment) (*24*, *25*), would we then conclude that it is the basis for superior olfactory function in primates? If not, then we must be wary of confirmation bias whenever we find data "consistent with" a weak olfactory sense in humans.

Some prominent scholars pushed back against the presumption of human microsmaty. Hendrik Zwaardemaker argued in 1898 that even though human behaviors were ostensibly less driven by smell than in "osmatique" mammals, humans nonetheless "live in a world of odor like the world of sight and sound," where smells produce vague perceptions but powerful emotions (*26*, *27*). Philosopher Friedrich Nietzsche emphasized smell, embracing its perceived carnality, and used it as a recurring metaphor in reaction to Kant and Hegel's writings downplaying its importance (*14*). As evidence accumulated through the 20th century, a series of articles have converged on the conclusion that the human olfactory system is highly capable and plays an important role in interpersonal communication (*28*–*32*).

Olfactory bulb: One size fits all?

The relative size of the olfactory bulb compared to the rest of the brain is very small in primates like humans (Fig. 1), composing about 0.01% of the human brain by volume (*33*) compared to 2% of the mouse brain (*34*, *35*). However, the absolute size of the human olfactory bulb is fairly large, much bigger than the mouse and rat olfactory bulbs (Fig. 2). Whether the bulb should be viewed in relative or absolute terms is thus a natural question (*36*).

Comprehensive studies of brain morphology across species have long noted that the size of any given brain region is proportional to the size of the brain overall (*35*, *37*). Overall brain size can explain more than 96% of the variance in the size of individual brain regions across mammals (*38*). However, this rule has one glaring exception: the size of the olfactory bulb. Bulb size is independent of the size of most other brain regions and accounts for almost all of the remaining variance (*38*). Modern evolutionary theorists now consider this exception to be one of the three principles of brain scaling: (i) high intercorrelation of structure volumes, (ii) distinct allometric scaling for each structure, and (iii) relative independence of the olfactory-limbic system from the rest of the brain (*39*). Consequently, the near ubiquitous consideration of the olfactory bulb in proportion to the rest of the brain (*40*) is likely to be misplaced.

Absent good reason to consider the bulb in proportion to other structures, it seems better to examine its absolute volume. The volume of the olfactory bulb can be highly variable as a function of age and experience (*41*, *42*). In adult humans, the volume of the olfactory bulbs is typically about 60 mm^3 (*33*). The bulbs have been observed to shrink by about 25% over time in hyposmic patients (*43*) and to be 20% smaller in subjects who experienced childhood maltreatment (*44*). In the rat, the olfactory bulb doubles in volume between 3 months and 18 months of age (peaking at around 27 mm^3) as the animal itself becomes physically larger throughout adulthood (*45*), but this is unlikely to be accompanied by a corresponding increase in olfactory abilities. In the mouse, the adult bulb volume ranges from 3 to 10 mm^3 across strain and study (*46*, *47*). Across mammalian species, the relative volume of the olfactory bulb is negatively correlated with overall brain size (*48*). Despite these pronounced differences in volume, there is little support for the notion that physically larger olfactory bulbs predict better olfactory function, regardless of whether bulb size is considered in absolute or relative terms (*36*).

If relative bulb volume and absolute bulb volume are not very useful metrics, a better option may be to compare the number of neurons in

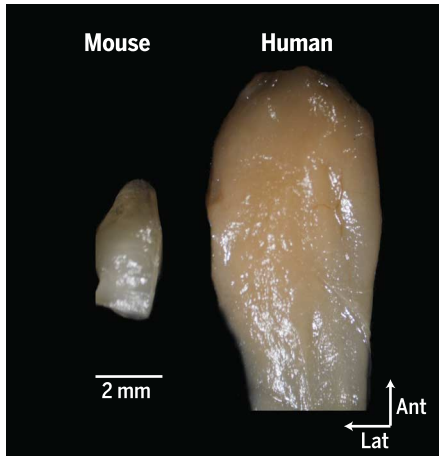

Fig. 2. Comparison of the mouse and human olfactory bulb. View is of the ventral aspect of the left olfactory bulb. Both bulbs are at the same scale.

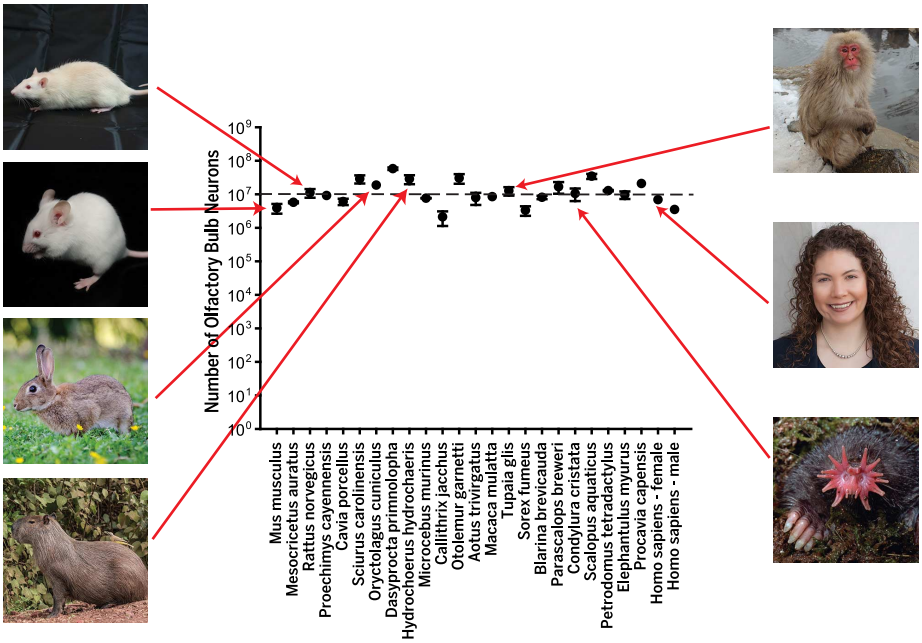

Fig. 3. Comparison of olfactory bulb neuronal numbers across mammalian species. The number of putative neurons per olfactory bulb for each species, as measured by isotropic fractionation. Numbers are drawn from Ribeiro *et al*. (*48*) and Oliveira-Pinto *et al*. (*50*).

each olfactory bulb. Early development aside, bulb volume and number of neurons can be surprisingly independent of each other. For instance, the number of mitral cells in the rat olfactory bulb remains essentially unchanged throughout adulthood, despite the bulb doubling in volume, with the existing mitral cells simply enlarging their dendritic fields (*45*). It is unclear whether these larger dendrites reflect an increase in synaptic connectivity, a change in the number of nonmitral neurons or nonneuronal cells, or simply a decreased neuronal density.

Isotropic fractionation permits the bulk measurement of neurons across structures and species (*49*). A previous review compiled the number of olfactory bulb neurons across mammalian species across fractionation studies and revisited the issue of proportionality between the number of neurons and overall brain size (*48*). The graph in Fig. 3 has expanded that data set to include more recent data measuring the human olfactory bulbs (*50*). In light of the arguments above, it is even more interesting that the absolute number of olfactory bulb neurons across these species is always within an order of magnitude of 10 million neurons. To put that in perspective, there is only a 28-fold range of olfactory bulb neuronal number in this diverse group of mammals (5.8×10^7 for the agouti versus 0.2×10^7 for the marmoset) despite a 5800-fold range in body weight (15 g for the mouse versus 73 kg for the man) and a vast range of olfactory behaviors. Alternatively, the ordering of our common experimental subjects in order of increasing numbers of olfactory bulb neurons would be: human male, mouse, hamster, guinea pig, human female, macaque monkey, rat. This ranking would likely be totally unexpected for those used to thinking of the bulb in strictly relative terms. A similar ranking might be noted for the absolute size of the olfactory epithelium in the nose, in which humans (5.0 cm^2) fall between mice (1.4 cm^2) and rats (6.9 cm^2) in modern measurements (*51*, *52*).

Why does the olfactory bulb have a roughly consistent number of neurons across species? Historically, the correlation between brain size and organism size has been interpreted to reflect the inherently larger information processing needs of larger animals—more muscle fibers to coordinate, more somatosensory input to interpret, and so forth. However, because the size of the organism does not determine the odors in its environment or its need to detect olfactory stimuli, this logic seems not to apply to olfaction.

Human olfactory structures are different from those of other mammals

Despite the grossly similar number of neurons in the olfactory bulb, the human olfactory system does have notable differences from those of other mammals. Each glomerulus in the olfactory bulb receives input from a subpopulation of sensory neurons that all express the same odor receptor, creating a glomerular map that represents odor identity (*53*). The human olfactory bulb is organized into an average of 5600 glomeruli, many more than the mouse (~1800) or rat (~2400) (*54*). This combination of a larger number of glomeruli and a smaller number of functional odor receptor genes in humans means that humans may have about 16 olfactory bulb glomeruli processing information from each odor receptor type compared to about 2 in the rodent (*54*).

Humans lack the "accessory" olfactory system (AOS), a set of parallel structures including the vomeronasal organ and accessory olfactory bulb found in many other animals. The AOS was once believed to be specialized for pheromone detection, but it is now understood to be a general-purpose system for detecting low-volatility odorants in liquid phase. Odor-based communication between conspecifics can work through both the main and accessory olfactory systems and occurs in species with and without an AOS (*55*, *56*), including humans (see below).

Another notable difference between the human olfactory system and that of other mammals is a lack of adult neurogenesis. Early reports notwithstanding (*57*), analysis of carbon-14 in neuronal DNA clearly indicates that neurogenesis is absent in the adult human olfactory bulb despite being prominent in hippocampus and striatum (*58*, *59*). This contrasts with rodents, where adult-born neurons play an ongoing role in olfactory bulb function throughout the animal's life (*60*), and even with other primates (*61*). This difference has been interpreted as consistent with the supposedly rudimentary development of the human olfactory system and our putatively limited reliance on olfaction (*58*). However, despite the lack of adult neurogenesis, the human olfactory system seems capable of much of the functional plasticity underpinned by neurogenesis in rodents (*62*).

Perhaps the most important difference between human olfactory processing and that of other animals is that (echoing Broca) humans possess much more elaborate cortical regions for interpreting olfactory inputs. This is especially true of the orbitofrontal cortex, which is much larger and more intricate in humans than in rodents, and which makes extensive connections to other neocortical regions (*63*, *64*). These differences may enable the system to integrate odors into contextual or semantic networks (*65*–*67*), or to undergo plasticity to maintain function after peripheral damage (*68*), or to incorporate learned information (*69*, *70*).

Human olfaction is excellent and impactful

Historical and anatomical expectations aside, is the human olfactory sense actually impoverished? No, the human olfactory system is excellent, although it depends on the criteria employed. For instance, dogs may be better than humans at discriminating the urines on a fire hydrant and humans may be better than dogs at discriminating the odors of fine wine, but few such comparisons have actual experimental support. When properly tested, the primate olfactory system is highly sensitive to many odors and can exert strong influences on behavior, physiology, and emotions (*29*, *71*–*73*).

Humans with intact olfactory systems can detect virtually all volatile chemicals larger than an atom or two, to the point that it has been a matter of scientific interest to document the few odorants that some people cannot smell (i.e., specific anosmias) (*74*). A prominent recent study calculated that we could also tell virtually all odors apart, with an estimated ability to discriminate more than 1 trillion potential compounds (*75*). Although this exact number is highly sensitive

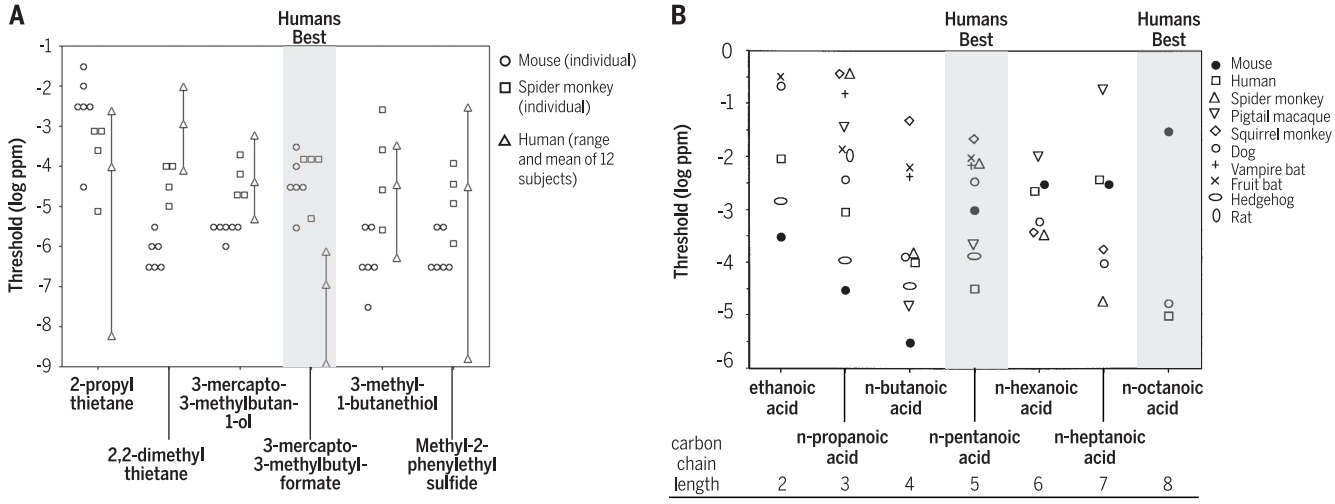

Fig. 4. Comparison of human olfactory thresholds across species and odorants. Comparison of detection thresholds (expressed as vapor-phase dilutions in log parts per million) across species, where more negative threshold values indicate lower thresholds and thus greater olfactory sensitivity. Shading indicates odors for which humans outperformed all other species tested. (**A**) Detection thresholds for human subjects (triangles), spider monkeys (squares), and mice (circles) to each of six different thresholds as measured in the Laska laboratory as part of the same experiment. Data shown are from five individual mice and spider monkeys; the triangles show the range and mean of thresholds from 12 individual subjects. All 12 humans outperformed all mice and monkeys tested for the odorant 3-mercapto-3-methylbutyl-formate and outperformed all mice for 2-propyl thietane. [Adapted from Sarrafchi *et al*. (*78*) and used by permission] (**B**) Pooled olfactory threshold values across species and laboratories for aliphatic carboxylic acids. Humans are more sensitive to *n*-pentanoic acid and *n*-octanoic acid than all other species tested. [Adapted from Can Güven and Laska (*77*) and used by permission]

to the assumptions made (*76*), it is clear that the human olfactory system is excellent at odor discrimination, far better even than the putative 10,000 odors claimed by folk wisdom and poorly sourced introductory psychology textbooks.

One key insight in comparing the olfactory system of primates and other animals has been that different species have different sensitivities to different odorants. This is presumably due to genetic variations in odor receptor complement (*77*), and may reflect differences in sensory environment or ecological niche. Cross-species comparisons thus need to employ a variety of test odorants. A recent experiment tested olfactory thresholds for six sulfur-containing odors in mice, spider monkeys, and humans (*78*). Relative olfactory sensitivity varied with odorant (Fig. 4A): Humans were three orders of magnitude more sensitive than mice or monkeys to 3-mercapto-3-methylbuytl-formate, with all 12 human subjects outperforming all of the individual animals, yet all 12 humans were worse than all of the mice (and comparable to the spider monkeys) on 3-mercapto-3-methylbutan-3-ol. Overall, the humans were most sensitive to two of the six odorants, whereas the mice were most sensitive to four of the odorants. This finding complements older literature showing that humans are comparably sensitive to dogs and rabbits for the smell of amyl acetate, the main odorant in banana (*31*, *32*), and more sensitive than mice to *trans*-4,5-epoxy-(E)-2-decenal, a component of human blood odor (*79*). A recent review of published detection thresholds for carboxylic acid odors across nine mammalian species found that humans were most sensitive to two of the six odors for which comparable data could be found (Fig. 4B). Interestingly, in Lord Adrian's seminal electrophysiological recordings of single neurons in the rabbit olfactory bulb, he noted that the threshold odorant concentrations required to evoke neural activity were quite similar to the concentrations required for the experimenters themselves to detect the odor (*80*). Similar results exist for primates besides humans (*71*, *72*).

Human behavior is strongly influenced by olfaction. Environmental odors can prime specific memories and emotions, influence autonomic nervous system activation, shape perceptions of stress and affect, and prompt approach and avoidance behavior (*81*–*83*). Humans can follow outdoor scent trails and even exhibit dog-like casting behavior when trails change direction (*84*). The human olfactory system also plays a major, sometimes unconscious, role in communication between individuals. Each person produces a distinct odor that reflects not only dietary and environmental factors but also interacts with the immune system's "self/non-self" histocompatibility markers to incorporate genetic information that permits the discrimination of kin from non-kin (*85*, *86*). The contents of this "body odor cocktail" are interpreted in parallel with environmental odors in the brain and can drive mate and food choice, as well as communicating information about anxiety and aggression in other people (*87*–*90*). We even appear to unconsciously smell our hands after shaking hands with strangers (*91*), suggesting an unexpected olfactory component to this common social interaction. Although many of these olfactory experiences do not recruit attentional resources, they can be exceptionally salient in traumatic circumstances (*92*). When such circumstances result in posttraumatic stress disorder, olfactory hallucinations frequently become part of the symptomology (*93*).

Olfactory abilities vary with factors like age, sex, and developmental stage (*94*–*97*), which may underlie differences in perception and olfactory communications. Olfaction is also modified by individual experiences, such as altered odor perception after odor-cued aversive conditioning (*62*, *98*, *99*). Moreover, the signals from the human olfactory system are being interpreted by a powerful brain in terms of context, expectation, and prior learning (*73*, *100*). Our sense of smell is much more important than we think.

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Poor human olfaction is a 19th-century myth

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Humans have a good sense of smell
In comparison to that of other animals, the human sense of smell is widely considered to be weak and underdeveloped. This is, however, an unproven hypothesis. In a Review, McGann traces the origins of this false belief back to comparative 19th-century neuroanatomical studies by Broca. A modern look at the human olfactory bulb shows that it is rather large compared with those of rats and mice, which are presumed to possess a superior sense of smell. In fact, the number of olfactory bulb neurons across 24 mammalian species is comparatively similar, with humans in the middle of the pack, and our sense of smell is similar to that of other mammals.

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