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- general methodological framework of selection. In: Schaie K W, Campbell R T, Meredith W, Rawlings S C (eds.) *Methodological Issues in Aging Research*. Springer, New York, pp. 13–42
- Neugarten B L 1974 Age groups in American society and the rise of the young-old. *Annals of the American Academy of Politics and Social Sciences* **415**: 187–98
- Olshansky S J, Carnes B A, Grahn D 1998 Confronting the boundaries of human longevity. *American Scientist* **86**: 52–61
- Rowe J W, Kahn R L 1987 Human aging: Usual and successful. *Science* **237**: 143–9
- Rowe J W, Kahn R L 1997 Successful aging. *Gerontologist* **37**: 433–40
- Smith J, Baltes M M 1998 The role of gender in very old age: Profiles of functioning and everyday life patterns. *Psychology and Aging* **13**: 676–95
- Smith J, Baltes P B 1997 Profiles of psychological functioning in the old and oldest old. *Psychology and Aging* **12**: 458–72
- Soldo B J, Hurd M D, Rodgers W L, Wallace R B 1997 Asset and health dynamics among the oldest old: An overview of the AHEAD Study. *The Journals of Gerontology: Series B* **52B** (Special issue): 1–20
- Suzman R M, Willis D P, Manton K G (eds.) 1992 *The Oldest Old*. Oxford University Press, New York
- Vaupel J W, Carey J R, Christensen K, Johnson T E, Yashin A I, Holm N V, Iachine I A, Kannisto V, Khazaeli A A, Liedo P, Longo V D, Zeng Y, Manton K G, Curtsinger J W 1998 Biodemographic trajectories of longevity. *Science* **280**: 855–60
- Wachter K, Finch C E 1997 *Between Zeus and the Salmon: The Biodemography of Aging*. National Academy of Sciences, Washington, DC
- Williams R H, Wirths C G 1965 *Lives Through the Years: Styles of Life and Successful Aging*. Atherton Press, New York

J. Smith

Olfactory System

The olfactory system belongs to the chemical senses (smell, taste). We are dealing here with a sensory system whose receptive field is situated in the upper part of the nose and whose information is taken up and transmitted via a CNS protrusion, the olfactory nerves, or olfactory bulb. This sensory function essentially serves the purpose of self-preservation by enabling individuals to recognize food, assess its quality, and receive warning signals (burnt smell, poisons). The stimulus threshold is extremely low in humans, and yet humans are poor smellers compared with animals. The stimulus threshold varies considerably according to the nutritional status.

The nerve fibers of the olfactory system are spread much wider in the CNS than is the case with any other sensory system. The olfactory system exerts an essential part of its influence on subcortical centers like the limbic system. Thus, smell has a high emotional component, which accounts for its great social importance. This explains why olfactory impressions are

used to express behavior patterns in all languages. In German, for example, the expression *Ich kann Dich nicht riechen* (I cannot smell you) means 'I don't like you.'

Humans have special inherited and acquired preferences (hedonics). Thus, for example, the smell of a forest elicits a positive emotion in many people, whereas negative feelings are associated with the smell of isobutyric acid (sweat).

Because of the broad spread of the secondary and tertiary olfactory fields in the CNS, an odorant can evoke its strong conscious reaction only initially; the sense of smell must then adapt rapidly to be ready for new odorants, and we lose the perception.

Apart from the olfactory sense for self-preservation, referred to henceforth as the 'classical olfactory system,' the nose has a second chemical sense that long received little attention in humans: the vomeronasal organ or system. Its purpose lies in the perception of pheromones within the sexual sphere and thus in the propagation of the species as well as in signaling and controlling aggressions. While hormones distribute messages within the body, pheromones take over communication to the outside (Jellinek). Little is known about the neuronal pathways and connections of the vomeronasal system. An intensive and exclusively subcortical process is probably involved, which means that we are not consciously aware of the stimulation of this organ. As with the classical olfactory sense, marked hedonics also exist here that are controlled by the immunological system.

1. Anatomy of the Classical Olfactory System

The zone of smell of the classical olfactory system in the nose lies in the upper part of the nasal cavity. It covers an area of about 5 cm on either side of the nose, specifically in the region of the superior nasal conchae, the septum and the ethmoid bone (Fig. 1). This region harbors about 100 million bipolar olfactory cells in humans (220 million in dogs). The sensory epithelium also contains stem cells with the lifelong capacity for replacing olfactory cells that have died. The peripheral processes of the bipolar sensory cells rise to the mucosal surface (Fig. 2). They bear up to 1,000 hairs (cilia) on which the primary contact takes place between aromatic molecules and receptors. The hairs differ in length among the various organisms. The longer the hairs, the more points of contact for the aromatic molecules. Organisms with long sensory hairs are therefore described as macrosomatic, those with short ones as microsomatic. The hairs must be moistened constantly so as not to be destroyed by desiccation. The olfactory zone thus has special mucous glands which, in contrast to other glands in the nose, do not form proteolytic enzymes. Odorants would otherwise be broken down into substances with a different smell prior to contact with the sensory cells.

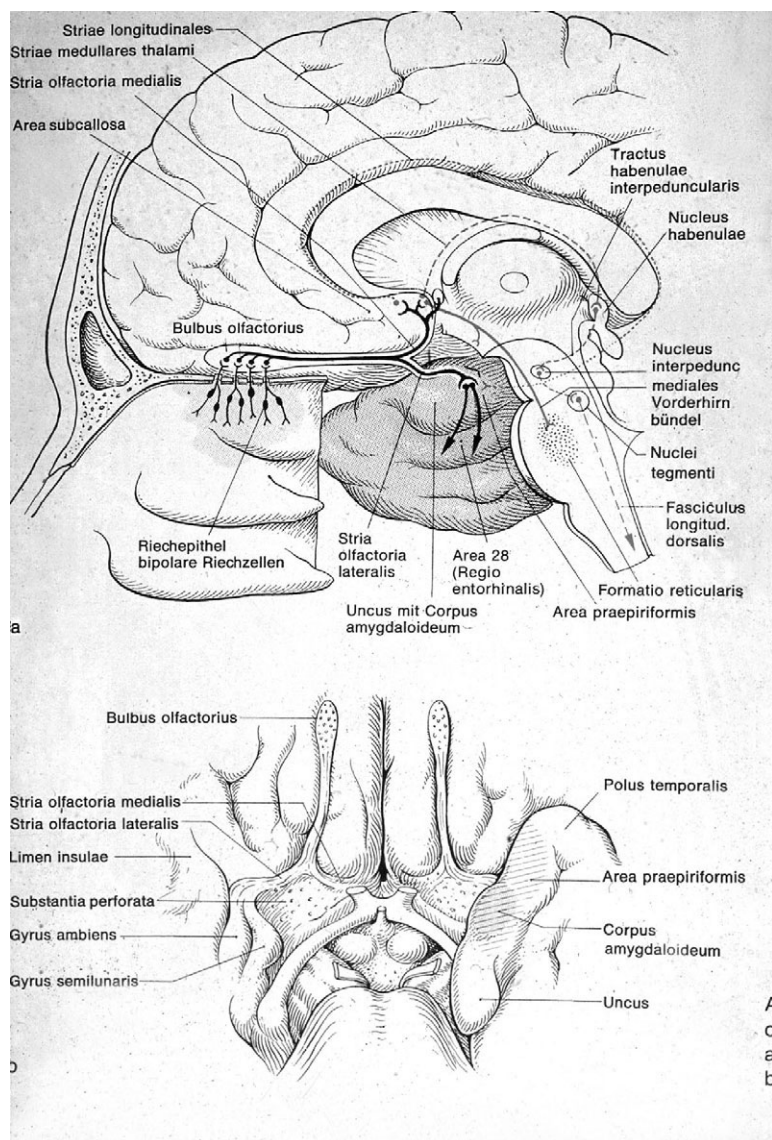


Figure 1
Anatomy of the nose with the olfactory zone

The aromatic molecules dock at special receptor proteins situated on the hairs. These proteins activate signal proteins (G proteins) which in turn trigger a cascade that sends an electric signal (action potential) along the central process of the cell to the bulb of the olfactory nerve (Reed 1992). This bulb contains cell accumulations (granules), each granule corresponding to a specific receptor molecule (Reed 1992). The expression of the specific olfactory receptor proteins is genetically determined (Buck and Axel 1991), one gene encoding each receptor molecule. Altogether, we possess about 1,000 different olfactory receptors.

Approximately 1 percent of our genes are used here, which corresponds to the largest family of genes found in humans. This underscores the profound importance of the sense of smell in man (Axel 1995).

There are about 30,000 odorants. Humans can recognize about 3,000 of these but only differentiate 300. We have a poor memory for smells, a much poorer olfactory than visual memory. Thus, we can only remember about 20 odorants.

Odorants must be volatile and lipid-soluble, otherwise they cannot be perceived. However, perception does not take place solely in the area of the olfactory

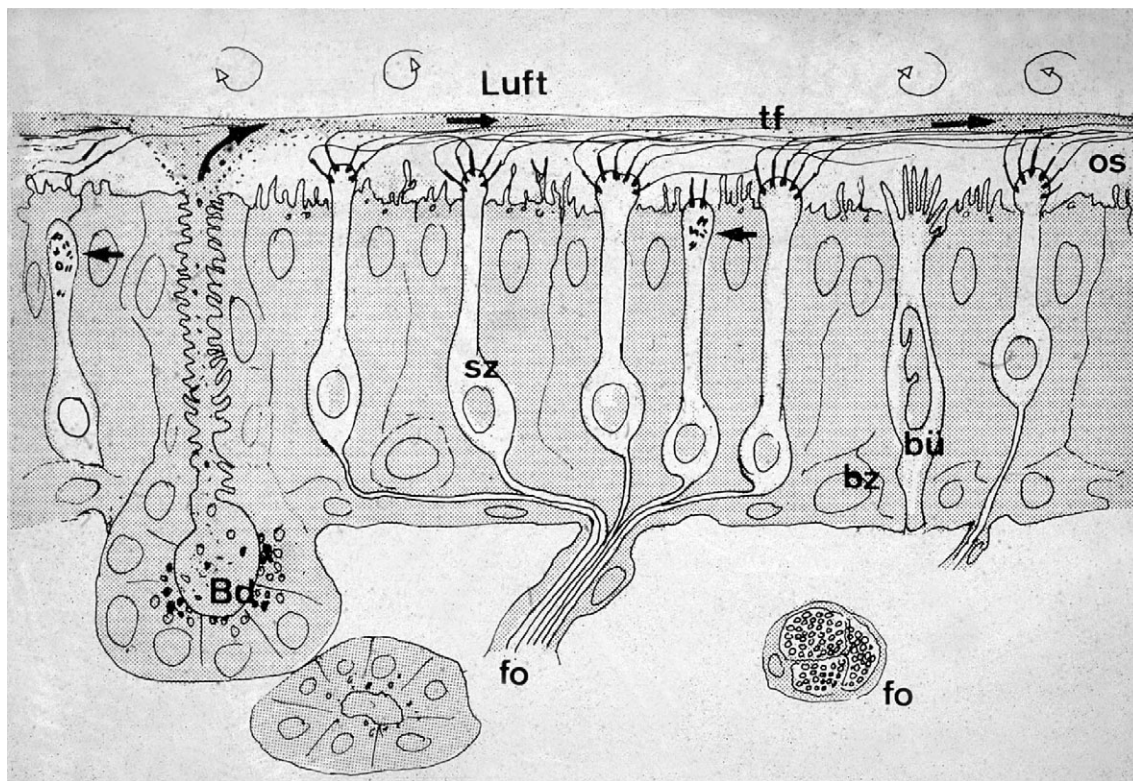


Figure 2

Detail of the olfactory mucosa with ciliated bipolar sensory cells. The cilia differ in length. (a) cilia in microsmatic organisms (for example, humans); (b) cilia in macrosmatic organisms (for example, dogs, eels, salmon)

sensory cells. Thus, it is possible to distinguish between odorants that excite the olfactory system almost exclusively, for example, coffee, cinnamon, tar, or the scent of roses, and odorants that stimulate both the olfactory system and fibers of the sensory trigeminal nerve in the nose, for example, menthol or camphor (sensation: cool) or formalin and vinegar (sensation: pungent). In addition, there are odorants that stimulate both the olfactory system and taste fibers on the base of the tongue, for example, pyridine (sensation: bitter) and chloroform (sensation: sweet).

2. Anatomy of the Vomeronasal System

The vomeronasal organ is situated in the anterior and lower mucosal areas of the nasal septum (Fig. 3). It comprises a 2–8mm pouch with a diameter of 0.2–2mm. The numerous mucous glands opening into this pouch ensure constant irrigation. At the end of the pouch there are elongated sensory cells with small mobile saccules resembling handles. Numerous blood vessels and nerve fibers are situated basal to this cell layer. The precise spread of these fibers and of the information thus transmitted to the CNS is not known.

However, stimulation of the vomeronasal organ is not perceived consciously.

The vomeronasal organ develops between the 37th and 43rd prenatal day in humans (Smith and Bhatnagar 2000). At this time, it is morphologically identical to its counterpart in animals, for which chemosensory activity has been demonstrated. Its structure changes between the 12th and 14th week. The mucosal cells develop cilia and lose contact to nerves. Thus, there are discussions as to whether the organ loses its function in humans at a very early stage, that is, in infancy. However, some findings (Monti-Bloch et al. 1998, Grosser et al. 2000) have demonstrated that the vomeronasal organ can be stimulated directly and specifically by a pheromone in adults (see below).

3. Measuring Methods

Odorants of graded concentration (e.g., 'Sniffin' sticks, butanol test (Gudziol) are inhaled to test perception within the scope of the classical olfactory system (Hummel et al. 1997). The results are based largely on subjective data. Since this leaves open the possibility

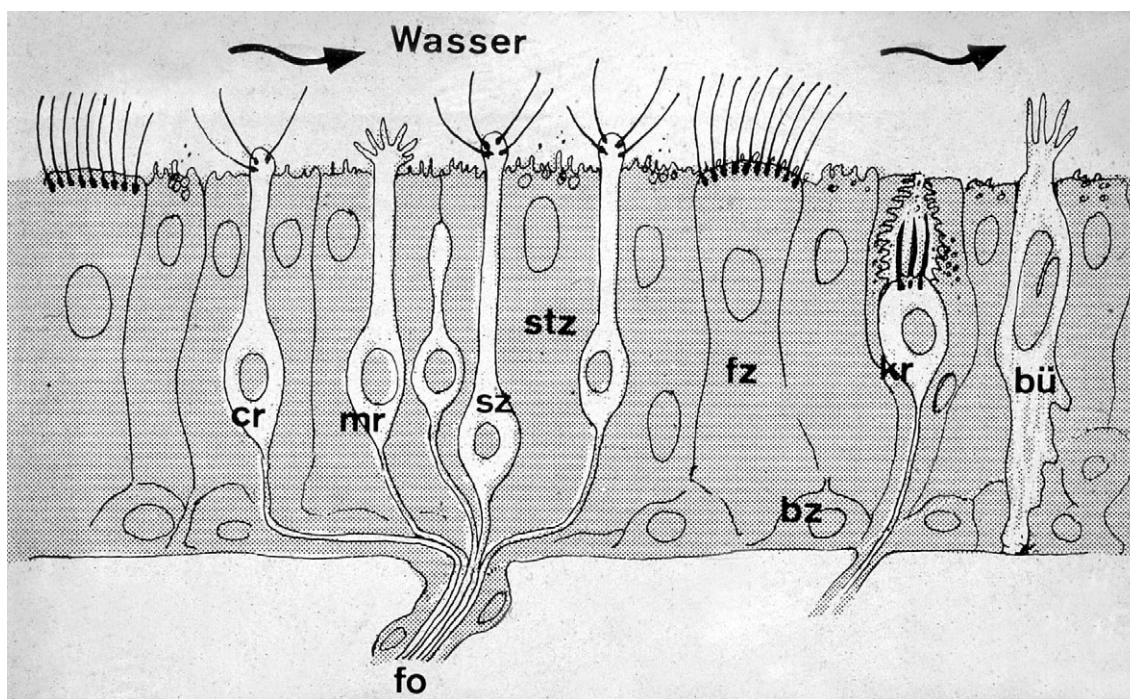


Figure 3
Anatomy of the nasal septum

of simulation and aggravation, expert opinions always require clarification by taste tests with substances that can only be smelled (e.g., peppermint solution) or by objective examination procedures. In the objective smell test, an odorant is introduced into the nose by pulsed application, and the brain waves are measured via the vertex synchronous to inhalation. The evoked test curve obtained by summation indicates the activation of the olfactory system—but not necessarily the perception of the odorant—in the cerebral cortex. Moreover, no qualitative statements can be made on the question of whether an odorant is perceived as such.

4. Physiology of the Classical Olfactory System

Very complex apparatuses were used to investigate the threshold of the classical olfactory sensation. It is $1-2 \times 10^{-14}$ mol/l in humans and 2×10^{-16} mol/l in eels. From the fact that only 10 molecules excite a receptor cell and 40 trigger a smell perception, it may be calculated that the olfactory system of the eel will be stimulated by even a thimbleful of rosewater poured into 16 times the amount of water in Lake Constance and well distributed (Jung 1994). This good olfactory sense of fish surely also explains why a salmon usually finds his home river. It probably smells its specific

odorants, and this should give us at least some idea of the impact our water pollution has on the olfactory system of fish.

Measurements have shown that the olfactory threshold changes significantly in relation to the nutritional status. Thus, the threshold is $1-2 \times 10^{-14}$ mol/l in a fasting state and rises to $3.5-5.5 \times 10^{-14}$ mol/l after a meal. The biochemical basis for this threshold variation is the sugar content in the blood. Sugar is the nutritive substance of the CNS. It makes sense for the olfactory threshold to differ in the fasting state: hungry humans and animals require a good olfactory sense for self-preservation, since they must hunt for 'prey' or use the olfactory organ for orientation (salmon fast when returning to their home river; their olfactory sense is thus optimal).

5. Physiologically-based Cooking

One of the secrets of the famous art of modern French cooking (*nouvelle cuisine*) is to maintain the fasting state and thus the good olfactory sense of the guest by serving very small portions in the individual courses. It is especially important to go easy on sweet foods and to serve dry sherry as an aperitif, for example. Sweet foods should only be consumed as a dessert. Conversely, serving a sweet aperitif, for example, port wine

or a rich appetizer can mask the taste of a poorly seasoned dish.

There are individuals with a particularly keen olfactory sense. They are usually highly paid for testing wines and other luxury items like coffee or tea or may also work as perfumers. On the other hand, there are people who cannot perceive certain odorants. There are, for example, such specific, genetically determined anosmias for isobutyric acid (sweat), hydrogen cyanide (bitter almond), and the scent of freesias. More than 80 specific anosmias have been identified thus far.

Contrary to subjective reports by women, no change has been detected in the classical olfactory sense during the menstrual cycle (Hummel et al. 1997).

In 1986 *National Geographic* magazine published an article on the sense of smell in humans. For illustration, they included six encapsulated odorants to be identified after being released by rubbing. This evolved into a gigantic global smell test with 1.5 million participants. Some of the results are physiologically significant. The test clearly demonstrated, for example, that men have a poorer sense of smell than women (something women have always said). This difference is enhanced in old age. The olfactory sense is best at the age of 20 and declines continuously with age (about 40–50 percent by the age of 80). On the other hand, the ability to smell the scent of a rose hardly decreases at all. Roses are, therefore, a suitable present for older people. Smokers consider themselves poor smellers and they are quite right.

Different odorants trigger completely different physical reactions in humans. The scent of jasmine and lemon increases alertness, while that of lavender and roses have a calming effect.

A Japanese company introduces a lemon scent into their air conditioning system in the morning to increase motivation, the scent of roses at noon to calm tempers, and different wood fragrances in the afternoon to mobilize energy reserves (PM 1/1990).

Buying behavior can also be stimulated. Adding aromatics to the air lengthens customers' shopping time by 16 percent, makes them 15 percent more willing to buy, and increases sales by 6 percent (Stöhr 1995).

There are many secretory glands in the olfactory zone of the nasal mucosa. Their primary function is to moisten and thus protect the cilia of the olfactory cells, but they also rinse out odorants. Thus, the organ of smell very quickly regains its readiness for a new stimulation. The olfactory sense adapts very quickly though to odorants that are present constantly. In other words, an odorant is no longer perceived as such after a few minutes. A dog that has taken up a trail must, therefore, run in zigzags, since he would otherwise lose the scent by adaptation of his olfactory sense. This also applies to perfume users. A person smelling a perfume will no longer perceive it after a short time if the wearer remains at a constant distance.

Hedonics are understood to be the assessment of

smell sensations. They can be positive or negative but differ from organism to organism and also among members of the same species. Thus, the smell of decay is negative for humans but positive for vultures. Europeans value the smell of pizza spices more highly than that of soybean oil. The opposite is true for Asians. Hedonics can be inherited (smell of decay) and acquired and are already passed on during gestation. Fetuses are known to react to olfactory stimuli in the mother after the 28th week of pregnancy. Thus, newborn rabbits already show a selective preference for the food their mothers preferred.

6. Physiology of the Vomeronasal System

The literature on the anatomy and physiology of the vomeronasal organ in humans is extensive and in part extremely controversial. Thus, Shoyi et al. found that the vomeronasal system has very high sensitivity to various stimulating substances, though the sensory cells in the nasal pouch do not possess distinct cilia like the olfactory cells of the classic olfactory system. In contrast, Smith and Bhatnagar (2000) already detected a transformation into ciliated cells in infancy. On the one hand, a physiological receptor function has been negated in man (Trotier et al. 2000). On the other hand, women randomized in a double-blind manner reacted specifically to the male pheromone androstadienone when applied to their vomeronasal organ in picogram quantities. Direct application of the female pheromone *pregna-4,20-diene-3,6-dione* (vomeropherin PDD) to the vomeronasal organ of men elicited a significant and dose-dependent parasympathomimetic reaction and also decreased serum LH and testosterone (Monti-Bloch et al. 1998). The threshold for pheromone detection is extremely low in animals. Hence, a male silk moth will find a female even at a distance of 10km, though not if it is sitting under a glass bell. As mentioned above, the stimulating substances of the vomeronasal system are pheromones, androstenone, and androstenol being among those found in humans. They are formed in the nasolabial groove, the axilla, the mamillae and the sexual organs. We do not perceive consciously their stimulation of the vomeronasal organ. If we think we are smelling pheromones, these are bacterial breakdown products of the respective substances, for which we also develop marked hedonics. Famous in this connection is a letter Napoleon wrote to his wife, Josephine, requesting that she no longer wash herself because he was coming home from the field.

Pheromones control not only sexual activity but also aggressive behaviors among conspecifics (Dulac 2000). Dogs mark their territory, for example. Smelling pheromones is particularly important for newborn creatures, especially while still helpless, for example, blind animals. They smell their mother's mammary glands via pheromones. Kangaroo babies are very

small creatures at birth. Guided by pheromones, they find their way unaided to the mother's pouch, where the mammary glands are situated.

Hedonics for pheromones are controlled genetically (Wedekind and Penn 2000, Wedekind and Furi 1997). They are influenced by the immune system. Thus, hedonics for the pheromones of a partner are known to be all the more positive, the greater the difference between the immunocompetence of a couple, as measured by the major histocompatibility complex. This is nature's attempt to prevent marriages between brothers and sisters. Hedonics has been found to undergo a reversal in the course of pregnancy, during which time a previously preferred partner is not very attractive. This effect is biologically understandable. The reversal only lasts as long as the pregnancy. However, women taking oral contraceptives also show a reversal of hedonics, and this circumstance harbors an implicit threat to their partnership.

7. Encyclopedia and Definition of Olfactory Disorders

Normosmia: normal sense of smell

Anosmia: total absence of the sense of smell

Dysosmia: partial impairment of the sense of smell (hyperosmia, hyposmia)

Anosmia and Dysosmia: specific, genetic: lack of receptor proteins

Respiratory: – marked deviations of the nasal septum
 – turbinate hyperplasia
 – mucosal swelling (for example, in colds)

Epithelial: – nasal polyps
 – tracheotomized patients
 – drying of the nose (ozena)
 – exogenous noxae (cadmium, chromic acid, butylene glycol, benzoic acid, hydrogen selenide (sometimes even one breath of a noxa will permanently destroy the sense of smell)
 – overgrowth of the olfactory epithelium by normal nasal mucosa

Neural: – virus infections, especially those associated with the common cold (rhinoviruses, coronaviruses, adenoviruses)
 – traumas in an anteroposterior (for example, boxing) or posteroanterior (falling on the back of the head) direction that shift the brain tangentially to the skull base, rupturing the olfactory nerve fibers at the point where they pass through it (Fig. 1)

Endocrine: – Cushing's syndrome, hypothyroidism, diabetes, B12 deficiency

Central: – traumas, tumors, influenza infection, meningitis

Parosmia: smelling a substance that is not there; The affected individual knows that the substance smelled is not there
 Cause: often nasal (partial destruction of olfactory epithelium) but also central

Pseudosmia: misinterpretation of a real olfactory impression
 Cause: psychoses

Phantosmia: olfactory hallucinations, for example, cacosmia. The affected individual does not complain about a defective sense of smell and refuses to believe he is mistaken

Cause: Central lesions
 temporal lobe tumor or abscess (as an aura in uncinata fits)
 schizophrenic psychoses

See also: Appetite Regulation; Emotion, Neural Basis of; Food Preference; Hunger and Eating, Neural Basis of; Limbic System; Memory Psychophysics; Psychophysics; Psychophysiology; Taste, Neural Basis of

Bibliography

- Axel R 1995 The molecular logic of smell. *Science America* **273**(4): 154–9
- Breitmaier E, Terpene A 1999 *Duefte, Pharmaka, Pheromone*. Teubner, Stuttgart, Leipzig, Germany
- Buck L, Axel R 1991 A novel multigene family may encode odorant receptors: A molecular basis for odor recognition. *Cell* **65**(1): 175–87
- Dulac C 2000 Sensory coding of pheromone signals in mammals. *Current Opinions in Neurobiology* **10**(4): 511–8
- Grosser B I et al. 2000 Behavioral and electrophysiological effects of androstadienone, a human pheromone. *Psycho-neuroendocrinology* **25**(3): 289–99
- Gudziol H *Butanol-Schwellentest nach Cain*. Klinikum der Friedrich-Schiller-Universität Jena, Klinik und Poliklinik für Hals-, Nasen-, Ohrenkrankheiten, Germany
- Hummel T et al. 1997 'Sniffin' sticks': Olfactory performance assessed by the combined testing of odor identification, odor discrimination and olfactory threshold. *Chemistry of Senses* **22**(1): 39–52
- Jellinek S Menschliche Pheromone: Ein Durchbruch in der Parfuemerie? *Dragoco Report* 1/99, S5–S28
- Jung H 1994 *HNO-Highlights 4Nr. 3*. MMW Verlag, Munich, Germany
- Monti-Bloch L et al. 1998 Modulation of serum testosterone and autonomic function through stimulation of the male human vomeronasal organ (VNO) with pregna-4,20-diene-3,6-dione. *Journal of Steroid Biochemistry and Molecular Biology* **65**(1–6): 237–42
- Reed R R 1992 Signaling pathways in odorant detection. *Neuron* **8**(2): 205–9

- Smith T D, Bhatnagar K P 2000 The human vomeronasal organ. Part II: Prenatal development. *Journal of Anatomy* **197**(3): 421–36
- Stöhr A 1995 Olfaktorische Stimulationen am Point of Sale. Arbeitspapier Nr. 16 der Reihe Konsum und Verhalten, Universität Paderborn
- Trotier D et al. 2000 The vomeronasal cavity in adult humans. *Chemistry of the Senses* **25**(4): 369–80
- Wedekind C, Furi S 1997 Body odour preferences in men and women: Do they aim for specific MHC combinations or simply heterozygosity? *Proceedings of the Royal Society of London Series B: Biological Sciences* **264**(1387): 1471–9
- Wedekind C, Penn D 2000 MHC genes, body odours, and odour preferences. *Nephrology Dialysis Transplantation* **15**(9): 1269–71

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Oligarchy (Iron Law)

1. Michels' Sociology of Political Leadership

Michels' classic (1959) can be read as an extended argument that continually returns in various forms to the following syllogism:

- (a) strong organization is necessary to achieve collective democratic goals,
- (b) strong organization requires delegation of popular sovereignty to an autonomous and self-perpetuating leadership cadre, and,
- (c) an autonomous and self-perpetuating leadership cadre is incompatible with true democracy.

The paradox in the syllogism is evident: organizations whose professed goals are democratic cannot themselves be democratic.

Michels' argument was strongly influenced by his friend and mentor Max Weber's perspective on bureaucracy (Weber 1978). Following Weber, Michels argued that the differentiation of an organizational elite from the rank-and-file was a product of the technical division of labor necessary in complex mass organizations. Weber's pessimistic analysis of the 'iron cage' of modern rationality was reflected in Michels' own pessimism about the dilemma faced by the party rank-and-file: the benefits of bureaucratic organization were manifold, but could only be realized by forsaking popular sovereignty. Weber also argued that the 'routinization of charisma' that led to modern bureaucratic organization was driven by the concerns of the administrative staff to secure and stabilize their position. In Michels' argument, the conservative tendency of organizational elites stems from their concern to maintain their status and livelihood.

As in Weber, Michels' argument about mass bureaucratic organization has two elements which co-exist in some degree of tension. On the one hand, the rise of bureaucracy is driven by the demand for services provided by a stunningly efficient organizational machine; on the other hand, bureaucracy is a mech-

anism of elite domination (Kitschelt 1989, pp. 69–70 distinguishes between a 'weak' theory of oligarchy based on organizational efficiency and a 'strong' theory based on elite domination). Thus, Michels moves back and forth from arguing that oligarchy is explained by the masses' adoration of and gratitude towards their leaders to arguing that it is explained by elites' ability to co-opt dissent through control over patronage and the media. The tension can be highlighted as follows: despite the leaders' subversion of the revolutionary goals and democratic aspirations of the masses, the masses remain grateful and obedient.

To explain this tension, Michels turned to another source of intellectual influence: a conservative view of the masses associated with the Italian elite theorists Vilfredo Pareto and Gaetano Mosca and the French sociologist Gustave Le Bon. Pareto and Mosca drew a sharp distinction between the elites and the masses and argued that the competence and energy of the elites made it possible for them to rule the unenterprising masses. Influenced by Le Bon's study of the irrationality of crowds, Michels argued that the masses are weakly organized and hence politically immature and even incompetent. Unable to organize themselves, the masses have a strong need for leadership. The relatively strong emphasis on psychological factors in *Political Parties*—such as the argument that the masses have 'a need to pay adoring worship' to their leaders—seems to derive from Le Bon (though we cannot forget Weber's analysis of charisma). The psychological distance between elites and masses leads the rank-and-file to behave in a deferential way towards their leaders.

While elite theory is often seen as a rejection of the Marxist analysis of class struggle—and Michels certainly used his analysis to deflate the optimism of Marxism—elements of a Marxian analysis can also be seen in *Political Parties*. At numerous points, Michels suggests that the organizational asymmetry between elites and masses is akin to a class struggle. With their monopoly over the means of production (organization), the elite is essentially able to extract surplus rents from the social movement. He analyzes the organizational differentiation of elites and masses as a process of embourgeoisement. Even (or especially) leaders of proletarian origin become culturally, educationally, and financially differentiated from their original social class and consequently lose all fraternal feeling towards the working class.

2. Parties, Social Movements, and Organizations

Michels' articulation of the iron law of oligarchy has had a broad impact on subsequent studies of political parties, social movements, and organizations. Nevertheless, the basic thrust of this subsequent literature has been to qualify and nuance Michels' portrait of the distribution of power in organizations.

One of the first important studies to follow up on