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Do pheromones influence human behavior?

信息素影响人类行为吗?

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摘要 信息素是动物进行社会交流的重要媒介, 它是否同样影响着人类的行为尚无定论. 人类所具有的高度适应性的社会行为模式、驳杂多变的外分泌物、以及部分退化的嗅觉解剖结构, 使得对人类信息素的行为效应、物质组成以至神经机制的探索充满了希望与挑战. 现有的证据提示人体的气味在多个方面表现出类似信息素的效应, 包括触发固有行为、调节内分泌水平、传递社会信息、诱发情绪起伏甚至认知变化等等. 其中, 两种类固醇物质雄甾二烯酮和雌甾四烯被视为"准人类性信息素", 二者依据接收者的性别和性取向而选择性地传递性信息、调节情绪与注意, 并对下丘脑产生特异性激活. 这些发现深化了对人类化学信号与人际交流的认识, 也为进一步的研究提供了铺垫.

关键词 信息素, 人类行为, 嗅觉, 体味, 雄甾二烯酮, 雌甾四烯

在漫长的进化过程中, 为了争夺生存和繁衍的机会, 动物不仅需要有效地探测外界环境中的危险和资源, 还需要根据种系内部其他成员的状态协调自己的行为, 如求偶或者划分领地. 媒介种系内部成员间社会信息交流最常见的载体是信息素(pheromone). 根据Karlson和Lüscher[1]的定义, 信息素指的是由个体分泌到体外, 被同物种的其他个体通过嗅觉器官察觉, 并引起后者特定反应的物质. 它也被称作外激素, 区别于生物体内部的化学信息物质——激素(hormone).

信息素的发现可以追溯到19世纪初. 当时, 法国的自然学家Jean-Henri Fabré[2]在他的实验中发现一只雌性的帝王蛾(*Saturnia pavonia*)可以吸引几十只的雄蛾. 即使把雌蛾的笼子遮盖上, 只要不是完全密封, 雄蛾仍然会飞向雌蛾. 这些现象使他相信, 这种吸引一定是化学性的, 尽管他并没有闻到雌蛾的什么味道. 事实上, 现在的研究发现, 很多对其他动物很重要的化学物质并不能引起人类的气味感知. 19世纪50年代末, 由Butenandt领导的一个德国研究小组[3]提取并确认了蚕蛾(*Bombycidae*)的信息素蚕蛾醇(bombykol)——化学成分为反-10, 顺-12-十六碳二烯醇. 他们使用30多万只雌性蚕蛾, 仅获得5.3 mg蚕蛾醇, 然而, 每只雌性蚕蛾所散发出的微量的蚕蛾醇, 却足以吸引很远距离之外的雄性蚕蛾. 这是人类首次成功识别一个信息素的化学成分.

信息素也广泛地被包括哺乳动物在内的更高等的动物所使用[4~6]. 举例来说, 雄性小鼠(*Mus musculus*)尿液中的成分甲硫基甲硫醇((methylthio) methanethiol)有吸引雌鼠的效果[7]; 未性成熟小鼠泪腺中的外分泌腺分泌肽22(exocrine-gland secreting peptide 22)能抑制成年小鼠对其的性行为[8]; 发情期的雌性仓鼠分泌的蛋白质aphrodisin可诱发适龄雄鼠的繁衍行为[9]; 公猪(*Sus scrofa domestica*)唾液中所含的雄

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烯酮(androstenone)可直接引起发情期母猪做出交配姿势[10]; 而母兔(*Leporidae*)乳汁中的2-甲基-2-丁烯醛(2-methybut-2-enal)能够启动并引导初生兔子寻找乳头的行为反应[11]. 除了繁衍和养育后代, 不同类型的信息素媒介着社会行为的众多方面, 包括踪迹信息素(trail pheromone)、领地信息素(territorial pheromone)、聚集信息素(aggregation pheromone)、分散信息素(dispersion pheromone)、驱逐信息素(repellent pheromone)、社会信息素(social pheromone)以及示警信息素(alarm pheromone)等.

生物产生的信息素物质被分泌到体外后, 需要依靠接收者的嗅觉系统进行解码和识别, 从而诱发特定行为或生理反应. 大多数的两栖类、爬行类和哺乳动物都拥有主、副两套嗅觉系统: 嗅上皮(epithelium)是主嗅觉系统的感受器官, 它将信号传导至大脑内的嗅球(olfactory bulb), 进而上传至梨状皮层(piriform cortex)、杏仁核(amygdala)、眶额皮层(orbitofrontal cortex)等区域; 而犁鼻器(vomeronasal organ)则是副嗅觉系统的感受器官, 经副嗅球(accessory olfactory bulb)中转向杏仁核、下丘脑(hypothalamus)等脑区投射[12]. 犁鼻器的嗅觉感受器(V1R和V2R)和嗅上皮的嗅觉感受器(Olfactory receptors, OR)虽然皆为G蛋白耦联受体(G protein-coupled receptors), 但它们在神经元上的表达方式以及将化学刺激传导为电神经冲动的信号传导方式上差异非常大[13], 显示两者的演化过程可能是相互独立的; 相应地, 这两个器官的感受器连接到上一级(分别对应于副嗅球和主嗅球)的模式也不尽相同[14]. 生物学家们曾一度认为犁鼻器和嗅上皮有着完全不同的任务分工, 犁鼻器负责信息素加工, 而嗅上皮负责编码一般性的气味. 但最近的行为和内分泌方面的证据显示实际情况要更为复杂也更为有趣: 依据物种的不同, 信息素和一般性的气味可以分别由犁鼻器和嗅上皮编码, 也可能同时由两者编码[7,15]. 上面举的几个例子中对信息素的编码有的发生在副嗅觉系统(如外分泌腺分泌肽22, aphrodisin), 有的则发生在主嗅觉系统(如甲硫基甲硫醇、雄烯酮).

那么, 人有信息素吗? 信息素可以影响人类的行为吗?

人类的皮脂腺和顶浆分泌腺(apocrine gland)的数量和体积都高于其他猿类[16,17], 就这一点而言, 人类是猿类中最具气味的一种了. 这些腺体释放出大量的天然物质包围着身体, 使得每个个体有了复杂的、各不相同的气味. 然而, 和大多数动物不同, 并没有证据表明人类拥有具有功能性的副嗅觉系统, 因此人类的嗅觉加工仅仅依赖于主嗅觉系统[18]. Rodriguez等人[19]在人体中发现了V1R(犁鼻器中的主要感受器)的同源基因*VIRL1*(V1r-like gene-1)的mRNA, 它在嗅黏膜中表达, 提示人类的主嗅觉系统可能部分具有其他动物中副嗅觉系统的功能. 人类以视觉, 而非嗅觉, 作为主导信息来源. 诸多在动物中"一嗅钟情"的故事, 在人类世界似乎被"一见钟情"所取代. 但值得一提的是, 人类同样有着敏锐的嗅觉能力, 可以分辨不同气味间的细微差别[20], 在视觉信息不明确的情况下, 社会性的化学线索甚至可以调制视觉社会认知[21,22].

Jacob和McClintock[23]梳理了部分关于人类信息素的实验证据, 认为它们指向4类信息素: 直效信息素(releaser pheromone)、启动信息素(primer pheromone)、通讯信息素(signaler pheromone)和调节信息素(modulator pheromone).

直效信息素的特点是引发快速而可靠的行为, 像开关一样, 一旦呈现就可以开启某种特定的反应模式. 这类信息素主要在动物中出现, 如上文提及的雄蛾被吸引, 雄烯酮引起发情期母猪做出交配姿势等. 人类社会系统以及个体的社会行为相对动物复杂许多, 这使得"开关"启动的行为模式极难辨认与确定. 目前比较清晰的证据来自于母婴互动, 母亲乳房的气味可以吸引新生儿的注意并诱发他的朝向运动[24]. 由于这些新生儿毫无后天经验, 他们对母亲乳房气味的反应被认为是天生而固有的.

启动信息素能够使接收者的内分泌水平发生缓慢而持久的改变, 甚至开启新的发育进程. 现有的关于人类启动信息素的最强的证据是"月经同步"现象(menstrual synchrony): 生活在一起的女性, 月经周期趋于同步. 研究发现, 当女性处于卵泡期后期时, 其腋下的物质缩短了闻到它的女性的月经周期, 而同样的女性处于排卵期时, 其腋下的物质却可延长闻到它的女性的月经周期[25].

Karlson和Lüscher最初关于信息素的定义, 只涵盖了直效信息素和启动信息素. 而随着哺乳动物信息素研究的展开, 越来越多的证据显示信息素作用的形式可能更为复杂和微妙. 其中包括传递释放者的性别、身份、甚至情绪状态等多种信息, 这一类信息素被命名为通讯信息素. 对人类而言, 可以从他人

的气味中分辨其性别[26]、年龄[27]，并具备分辨自我和他人体味的能力[28]，母婴间甚至可以仅凭气味互认[29]．脑成像证据显示，自我的气味不仅激活嗅觉区域，还激活加工自我相关信息的右侧额中叶区域[30]．个体释放的气味受控于人类白细胞抗原(human leucocyte antigen, HLA)[31]，并影响着择偶行为[32,33]，更倾向于找寻与自身HLA类型差异较大的个体，以优化后代的基因．然而这一点并不为个体有意识觉知，故其对人类产生的影响可能被低估了[34]．

在关于人类信息素的研究结果中，信息素的效应目前多数表现为调节接收者的情绪而非引起典型快速的行为反应，行为反应可能只是情绪变化后的结果[15]．Jacob和McClintock据此进一步拓展了信息素的范畴，把引起接收者的情绪起伏乃至认知变化的信息素称作调节信息素．焦虑状态下分泌的汗液能够消除阈下积极面部表情所产生的情绪启动效应[21]，并增强惊跳反射[35]．恐惧状态下分泌的汗液会影响闻到它的个体的情绪知觉[22]，并使其认知反应更慢但更准确[36]．厌恶或高兴状态下分泌的汗液也被发现可以使接收者的面部表情、吸气量和认知方式产生相应的变化[37,38]．虽然，反面观点认为，即便是植物的气味都有可能影响到接收者的情绪——嗅觉系统与边缘系统天然的紧密联系本身可能塑造了这样的效应．然而，体味中所传递的情绪信息并不能简单的解释成它的气味特征：被试多无法依据气味特征区分研究中所使用的嗅觉材料[39]．更有研究发现，没有明显气味的人的眼泪也可能包含信息素，并影响接收者的生理状态[40]．

上述列举的各类效应所对应的信息素物质的化学组成尚不为人知，它们为人类信息素的存在提供了线索而非明证．人体分泌物的成分和人的行为都极其复杂，确认某个或某几个物质对接收者的特异性效应无疑是科学家们所面临的重大挑战[41]．

目前，仅有两种物质被认为是人类信息素的有力候选者，它们是雄甾二烯酮(androsta-4,16,-dien-3-one)和雌甾四烯(estra-1,3,5(10),16-tetraen-3-ol)．虽然尚缺乏系统的离体和在体实验明确它们的生物活性和作用机制[41]，但这两种类固醇的来源与效应具有明显的性别特异性，故而被称作“准人类性信息素”(putative human sex pheromone)[42]．雄甾二烯酮主要存在于男性的精液和腋下的皮肤及毛发上[43]；雌甾四烯最初发现于女性的尿液中[44]．雄甾二烯酮可以提高女性交感神经兴奋性、激发正性情绪、降低负面情绪[45~48]．雌甾四烯则对男性的自主神经反应及情绪产生作用[49]．更为关键的是，这两种类固醇物质可以有效地依据接收者的性别及性取向传递性别信息，从而影响接收者的性别知觉[50]．其中，雄甾二烯酮作用于异性恋女性和同性恋男性，使他们更多的将视觉性别线索模糊的对象判断为男性；相反，雌甾四烯作用于异性恋男性，使他们倾向于将视觉性别线索模糊的对象判断为女性；对于双性恋倾向的女性而言，这两种物质则没有表现出明显的效果．在脑内，雄甾二烯酮和雌甾四烯同样以一种基于接收者性别及性取向的方式激活下丘脑——一个对于基本生理活动及繁衍行为具有重要意义脑区[51,52]．具体来说，雄甾二烯酮显著激活了异性恋女性和同性恋男性的下丘脑，而雌甾四烯恰恰相反，显著激活了异性恋男性和同性恋女性的下丘脑．

值得注意的是，实验中使用的剂量往往远超实际人体分泌物的浓度，而浓度的差异可能带来效应的变化[53]．此外，雄甾二烯酮和雌甾四烯的作用还会受到接收者的生理状态(如月经周期)[39]和情境[49,54,55]的影响．这也与部分动物实验的结果一致：一方面，信息素的合成、释放乃至对它的解码会受到体内荷尔蒙水平的调制[56~58]；另一方面，个体所处情境与过去学习经验可以改变其对信息素的敏感性以及信息素诱发的行为反应[59,60]．这一系列因素在日常行为中的复杂交互，增加了解析信息素效应的难度．

时至今日，人类释放和接收信息素的神经内分泌机制及其涉及的环路基础还是未解之谜．人的嗅上皮和嗅球如何区分编码信息素和非信息素气味，并把相关信息传递到下游脑区？不同的信息素有不同的信号通路吗？信息素的作用都是意识水平下的吗？可以有效地利用信息素的种类和剂量操控人的心理和行为吗？

一面是驳杂多变的个体分泌物，一面是高度适应性的复杂的人类行为，中间是如黑箱般的释放-接收机制，人类信息素研究还有很长的路要走，而探索的道路总是荆棘丛生又引人入胜．

参考文献

1 Karlson P, Lüscher M. Pheromones': A new term for a class of biologically active substances. Nature, 1959, 183: 55–56
2 Fabre J H. Souvenirs Entomologiques: Études Sur L'instinct et Les Mœurs des Insectes. Paris: C. Delagrave, 1891
3 Butenandt A, Beckmann R, Stamm D. On the sexattractant of silk-months. Ⅱ. Constitution and configuration of bombvkol. Hoppe Seylers Z Physiol Chem, 1961, 324: 84–87
4 Chung-Davidson Y W, Huertas M, Li W M. A review of research in fish pheromones. Chemical communication in crustaceans. In: Chemical Communication in Crustaceans. New York: Springer, 2011. 467–482
5 Woodley S K. Pheromonal communication in amphibians. J Comp Physiol A, 2010, 196: 713–727
6 Dulac C, Torello A T. Molecular detection of pheromone signals in mammals: From genes to behaviour. Nat Rev Neurosci, 2003, 4: 551–562
7 Lin D Y, Zhang S Z, Block E, et al. Encoding social signals in the mouse main olfactory bulb. Nature, 2005, 434: 470–477
8 Ferrero D M, Moeller L M, Osakada T, et al. A juvenile mouse pheromone inhibits sexual behaviour through the vomeronasal system. Nature, 2013, 502: 368–371
9 Briand L, Trotier D, Pernollet J C. Aphrodisin, an aphrodisiac lipocalin secreted in hamster vaginal secretions. Peptides, 2004, 25: 1545–1552
10 Dorries K M, Adkins-Regan E, Halpern B P. Sensitivity and behavioral responses to the pheromone androstenone are not mediated by the vomeronasal organ in domestic pigs. Brain Behav Evol, 1997, 49: 53–62
11 Schaal B, Coureaud G, Langlois D, et al. Chemical and behavioural characterization of the rabbit mammary pheromone. Nature, 2003, 424: 68–72
12 Firestein S. How the olfactory system makes sense of scents. Nature, 2001, 413: 211–218
13 Liberles S D. Mammalian pheromones. Annu Rev Physiol, 2014, 76: 151–175
14 Belluscio L, Koentges G, Axel R, et al. A map of pheromone receptor activation in the mammalian brain. Cell, 1999, 97: 209–220
15 Brennan P A, Zufall F. Pheromonal communication in vertebrates. Nature, 2006, 444: 308–315
16 Stoddart D M. The Scented Ape: The Biology and Culture of Human Odour. Cambridge: Cambridge University Press, 1990
17 Wyatt T D. Pheromones and Animal Behavior: Chemical Signals and Signatures. Cambridge: Cambridge University Press, 2014
18 Frasnelli J, Lundstrom J N, Boyle J A, et al. The vomeronasal organ is not involved in the perception of endogenous odors. Hum Brain Mapp, 2011, 32: 450–460
19 Rodriguez I, Greer C A, Mok M Y, et al. A putative pheromone receptor gene expressed in human olfactory mucosa. Nat Genet, 2000, 26: 18–19
20 Bushdid C, Magnasco M O, Vosshall L B, et al. Humans can discriminate more than 1 trillion olfactory stimuli. Science, 2014, 343: 1370–1372
21 Pause B M, Ohrt A, Prehn A, et al. Positive emotional priming of facial affect perception in females is diminished by chemosensory anxiety signals. Chem Senses, 2004, 29: 797–805
22 Zhou W, Chen D. Fear-related chemosignals modulate recognition of fear in ambiguous facial expressions. Psychol Sci, 2009, 20: 177–183
23 Jacob S, McClintock M K. Psychological state and mood effects of steroidal chemosignals in women and men. Horm Behav, 2000, 37: 57–78
24 Varendi H, Porter R H. Breast odour as the only maternal stimulus elicits crawling towards the odour source. Acta Paediatr, 2001, 90: 372–375
25 Stern K, McClintock M K. Regulation of ovulation by human pheromones. Nature, 1998, 392: 177–179
26 Russell M J. Human olfactory communication. Nature, 1976, 260: 520–522
27 Mitro S, Gordon A R, Olsson M J, et al. The smell of age: Perception and discrimination of body odors of different ages. PLoS One, 2012, 7: e38110
28 Wallace P. Individual discrimination of humans by odor. Physiol Behav, 1977, 19: 577–579
29 Kaitz M, Good A, Rokem A M, et al. Mothers' recognition of their newborns by olfactory cues. Dev Psychobiol, 1987, 20: 587–591
30 Milinski M, Croy I, Hummel T, et al. Major histocompatibility complex peptide ligands as olfactory cues in human body odour assessment. Proc Biol Sci, 2013, 280: 20122889
31 Bard J, Yamazaki K, Curran M, et al. Effect of *B2m* gene disruption on MHC-determined odortypes. Immunogenetics, 2000, 51: 514–518
32 Jacob S, McClintock M K, Zelano B, et al. Paternally inherited HLA alleles are associated with women's choice of male odor. Nat Genet, 2002, 30: 175–179

33 Ober C, Weitkamp L R, Cox N, et al. HLA and mate choice in humans. Am J Hum Genet, 1997, 61: 497–504
34 Pause B M. Processing of body odor signals by the human brain. Chemosens Percept, 2012, 5: 55–63
35 Prehn A, Ohrt A, Sojka B, et al. Chemosensory anxiety signals augment the startle reflex in humans. Neurosci Lett, 2006, 394: 127–130
36 Chen D, Katdare A, Lucas N. Chemosignals of fear enhance cognitive performance in humans. Chem Senses, 2006, 31: 415–423
37 de Groot J H, Smeets M A, Kaldewaij A, et al. Chemosignals communicate human emotions. Psychol Sci, 2012, 23: 1417–1424
38 de Groot J H, Smeets M A, Rowson M J, et al. A sniff of happiness. Psychol Sci, 2015, 26: 684–700
39 Parma V, Tirindelli R, Bisazza A, et al. Subliminally perceived odours modulate female intrasexual competition: An eye movement study. PLoS One, 2012, 7: e30645
40 Gelstein S, Yeshurun Y, Rozenkrantz L, et al. Human tears contain a chemosignal. Science, 2011, 331: 226–230
41 Wyatt T D. The search for human pheromones: The lost decades and the necessity of returning to first principles. Proc Biol Sci, 2015, 282: 20142994
42 Monti-Bloch L, Grosser B I. Effect of putative pheromones on the electrical activity of the human vomeronasal organ and olfactory epithelium. J Steroid Biochem Mol Biol, 1991, 39: 573–582
43 Gower D B, Ruparelia B A. Olfaction in humans with special reference to odorous 16-androstenes: Their occurrence, perception and possible social, psychological and sexual impact. J Endocrinol, 1993, 137: 167–187
44 Thysen B, Elliott W H, Katzman P A. Identification of estra-1,3,5(10),16-tetraen-3-ol (estratetraenol) from the urine of pregnant women (1). Steroids, 1968, 11: 73–87
45 Wyart C, Webster W W, Chen J H, et al. Smelling a single component of male sweat alters levels of cortisol in women. J Neurosci, 2007, 27: 1261–1265
46 Lundstrom J N, Olsson M J. Subthreshold amounts of social odorant affect mood, but not behavior, in heterosexual women when tested by a male, but not a female, experimenter. Biol Psychol, 2005, 70: 197–204
47 Bensafi M, Brown W M, Tsutsui T, et al. Sex-steroid derived compounds induce sex-specific effects on autonomic nervous system function in humans. Behav Neurosci, 2003, 117: 1125–1134
48 Grosser B I, Monti-Bloch L, Jennings-White C, et al. Behavioral and electrophysiological effects of androstadienone, a human pheromone. Psychoneuroendocrinology, 2000, 25: 289–299
49 Bensafi M, Brown W M, Khan R, et al. Sniffing human sex-steroid derived compounds modulates mood, memory and autonomic nervous system function in specific behavioral contexts. Behav Brain Res, 2004, 152: 11–22
50 Zhou W, Yang X, Chen K, et al. Chemosensory communication of gender through two human steroids in a sexually dimorphic manner. Curr Biol, 2014, 24: 1091–1095
51 Savic I, Berglund H, Gulyas B, et al. Smelling of odorous sex hormone-like compounds causes sex-differentiated hypothalamic activations in humans. Neuron, 2001, 31: 661–668
52 Savic I, Berglund H, Lindstrom P. Brain response to putative pheromones in homosexual men. Proc Natl Acad Sci USA, 2005, 102: 7356–7361
53 Burke S M, Veltman D J, Gerber J, et al. Heterosexual men and women both show a hypothalamic response to the chemo-signal androstadienone. PLoS One, 2012, 7: e40993
54 Jacob S, Hayreh D J, McClintock M K. Context-dependent effects of steroid chemosignals on human physiology and mood. Physiol Behav, 2001, 74: 15–27
55 Olsson M J, Lundstrom J N, Diamantopoulou S, et al. A putative female pheromone affects mood in men differently depending on social context. Eur Rev Appl Psychol, 2006, 56: 279–284
56 Cusson M, Mcneil J N. Involvement of juvenile-hormone in the regulation of pheromone release activities in a moth. Science, 1989, 243: 210–211
57 Tang J D, Charlton R E, Jurenka R A, et al. Regulation of pheromone biosynthesis by a brain hormone in 2 moth species. Proc Natl Acad Sci USA, 1989, 86: 1806–1810
58 Robinson G E. Modulation of alarm pheromone perception in the honey-bee-evidence for division-of-labor based on hormonally regulated response thresholds. J Comp Physiol A, 1987, 160: 613–619
59 Keleman K, Vrontou E, Kruttner S, et al. Dopamine neurons modulate pheromone responses in drosophila courtship learning. Nature, 2012, 489: 145–149
60 Kaur A W, Ackels T, Kuo T H, et al. Murine pheromone proteins constitute a context-dependent combinatorial code governing multiple social behaviors. Cell, 2014, 157: 676–688

Do pheromones influence human behavior?

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Social communication via airborne chemicals is ubiquitous in the animal kingdom. Such active substances were designated as "pheromones" by Karlson and Lüscher in 1959. As specified by the original definition, pheromones refer to substances that are secreted to the outside by an individual and received by a second individual of the same species, in which they release a specific reaction, for example, a definite behavior or a developmental process. Over the past fifty years, a number of pheromones with distinct functions have been identified in invertebrates as well as in mammals. In the case of mammalian pheromones, recent findings reveal that some of them are processed in the main olfactory system, contrary to the traditional belief that mammalian pheromones are exclusively encoded by the vomeronasal organ and act through the accessory olfactory system. Humans are thought as the most highly scented ape of all in terms of numbers and sizes of sebaceous and apocrine glands. The search for human pheromones, however, has met with less success. The challenges lie in several aspects: (i) Human behavior is highly complex and multifaceted; (ii) Human secretions contain an enormous number of components with changeable concentrations; and (iii) Unlike most mammals, humans do not have a functional accessory olfactory system and rely solely on the main olfactory system to process airborne chemical compounds. Nonetheless, humans possess at least one functional V1r-like gene, a counterpart of the V1r genes that express pheromone receptors in rodents. Moreover, there has been accumulating evidence indicating that human body odors exert a range of pheromone-like effects on odor recipients. These include triggering innate behavioral responses, modulating endocrine levels, signaling social information, and affecting moods and cognition, in line with the roles of releaser, primer, signaler, and modulator pheromones, respectively. In particular, two human steroids—androsta-4,16,-dien-3-one, the most prominent androstene present in male semen, in axillary hair, and on axillary skin surface, and estra-1,3,5(10),16-tetraen-3-ol, first identified in female urine, are considered "putative human sex pheromones". They have been shown to convey sexual information, modulate mood state, alter autonomic responses, and activate the hypothalamus in manners contingent on the recipient's gender and sexual orientation yet below his or her awareness. The findings to date have furthered our understandings of human chemosignaling and interpersonal communication, and have paved the way for future investigations of human pheromones. Identifying the mechanisms underlying the release and detection of human pheromones and molecularly characterizing them represent important directions for future work.

pheromone, human behavior, olfaction, body odor, androstadienone, estratetraenol

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