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Human pheromones and body scents:

Do they influence our behaviour?

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Abstract

Pheromonal communication in the animal world has been of great researchers' interest for a long time. While extraordinary discoveries in this field were made, the importance of the human sense of smell was of far lower interest. Humans are seen as poorsmellers and therefore research about human olfaction remains quite sparse compared to other animals. Nevertheless amazing achievements have been made during the past 15 years.

This diploma thesis is a collection of available data on this diversified topic and aims to be a controversial discussion on the role of putative human pheromones in our modern way of living. While the focus is definitely put on behavioural changes evoked by putative human pheromones the following article also includes other important aspects such as the possible existence of a human vomeronasal organ. If pheromones do have an influence on human behaviour there has to be a receptor organ. How are human body scents secreted and turned into odourous substances? And how can conspecifics detect those very odours and transmit them to the brain? Apart from trying to answer those questions, the most likely candidates for human pheromones are taken on account and their impact on behaviour is shown in various details. Those include the influences on the female menstrual cycle, mood changes, the role of chemosensory anxiety signals as well as pheromonal guidance of mate choice.

Zusammenfassung

Die chemosensorische Kommunikation zwischen Tieren mittels Pheromonen ist seit langem von großem wissenschaftlichem Interesse. Während das menschliche Geruchsvermögen kaum beachtet und bei weitem unterschätzt wurde, sind herausragende Entdeckungen über Pheromone bei Tieren gemacht worden. Da bei Menschen die verbale und visuelle Kommunikation gegenüber der geruchlichen zu überwiegen scheint, wurde ihr Geruchssinn bisher nur unzureichend untersucht. Dennoch kam es in den letzten 15 Jahren zu erstaunlichen Errungenschaften.

Diese Diplomarbeit fasst verfügbares Wissen über dieses weit gefächerte Thema zusammen und diskutiert die strittige Rolle menschlicher Pheromone in unserer modernen Welt. Während der Schwerpunkt auf Verhaltensänderungen durch vermeintliche Pheromone liegt, beinhaltet der folgende Artikel auch andere wichtige Aspekte, wie die mögliche Existenz eines menschlichen vomeronasalen Organs. Sollten Pheromone einen Einfluss auf das Verhalten des Menschen haben, muss es dafür ein Rezeptororgan geben. Eine weitere wichtige Frage lautet wie Körperdüfte sezerniert werden? Und wie diese von geruchlosen in geruchlich erfassbare Stoffe umgewandelt werden, die von Mitmenschen an das Gehirn weitergeleitet werden können? Abgesehen davon werden die wahrscheinlichsten Kandidaten menschlicher Pheromone vorgestellt und ihr Einfluss auf das Verhalten detailliert beleuchtet. Dies beinhaltet den weiblichen Zyklus, Stimmungsänderungen, die Rolle chemosensorischer Angstsignale und die durch Pheromone gesteuerte Partnerwahl.

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1. Introduction

Social signals spread with the individual's body odour, so called pheromones, transmit a wide range of information. While chemosensory-based communication is commonly known as a vital signaling tool in many species the importance of the human sense of smell has by far been underestimated.

1.1. Pheromone definition

The term "pheromone" derives from the Greek words "pherein" and "horman" – to transfer and to excite. Karlson and Luscher first introduced pheromones as hormone like substances that are yet very different: They are being secreted outside the body in order to serve communication between conspecifics rather than being secreted into the blood for humoral correlation.[1]
McClintock[2] postulates the existence of two pheromone classes. "Signal or releaser pheromones" have short term effects on behaviour and function as attractants and repellents while "primer pheromones" produce a more enduring impact on the receiver's physiology via the hypothalamic-pituitary-adrenal activation. Therefore, the different pheromones can be categorized in *"aggregation pheromones, alarm pheromones, epideictic pheromones, territorial pheromones, trail pheromones, information pheromones and sex pheromones".*[3-9]

1.2. Human body odour

The increasing knowledge about pheromones in many different species has led researchers to question the human world of

odours. Unfolding the hidden mysteries of smells and the way they are transmitted as well as perceived in humans means to face some critical questions. Humans don't fall instinctively into behaviours in response to an odour. And their sexual activity is not limited to the moment of ovulation as it is in most other animals. This brings up the necessity to differentiate learned associative responses from instinctive responses to putative pheromones. To work out a separating line between these two in experimentally controlled studies seems to be nearly impossible as humans are thinking individuals with the power of judgment and self-assessment. And studies in a laboratory environment might not truthfully reflect what is happening in real life as most of human behaviour seems to be highly context specific.

Human olfaction was long underestimated as humans are believed to be microsmatic (poorsmellers) while featuring highly developed powers of vision.[10] Certainly visual and verbal cues are of utter importance in human communication especially at a distance. But between closely connected individuals smells also play an important role, for example between mothers and infants and for a variety of sociosexual behaviours.

The human's main odour-producing organ is the skin with its apocrine glands. These are located all over the body surface but have a far higher concentration in some areas: the axillae, the nippels, the pubic, circumoral, genital and circumanal regions as well as eyelids and outer ear. The intensive hair growth in the axillae and the genital regions enables the odour to be spread by evaporation over a large surface. And the axillae is well situated in order

to bring the individuals body odour as close as possible to the nose of other conspecifics. The warmth of those body parts also helps the circulation of odours and produces a perfect climate for bacterial activity: Coryneform bacteria transform the odourless androstadienol and androstadienone into the odourous 5α-androstenone.[11-13]

2. Detection of human odour

Tirindelli et al.[14] summarized the fact that most mammals have a main olfactory system as well as an accessory olfactory system, the vomeronasal organ (VNO). In contrast to earlier interpretations both are actively involved in pheromonal communication. Therefore, a functional VNO is of utmost importance for communication purposes of many animals and insects.

2.1. Vomeronasal organ in humans

According to this knowledge the question derives how putative pheromones are processed in humans.

2.1.1. Morphological observations

In humans an anatomically similar structure to the VNO is situated in the anterior third of the nasal septum, approximately 1 cm dorsal to the columella and 1mm above the floor of the nose.[15] The size of these pits ranged from ~1 mm to ~2.5 mm[16] and show up as a duct-like invagination of the epithelium. "*It is surrounded by numerous exocrine glands with short ducts. The fine*

structure of these glands suggested a serous secretion. In the depth of the invagination, pseudostratified columnar epithelial cells were seen that had plump processes, kinocilia and microvilli at the apical cell membrane."[17]

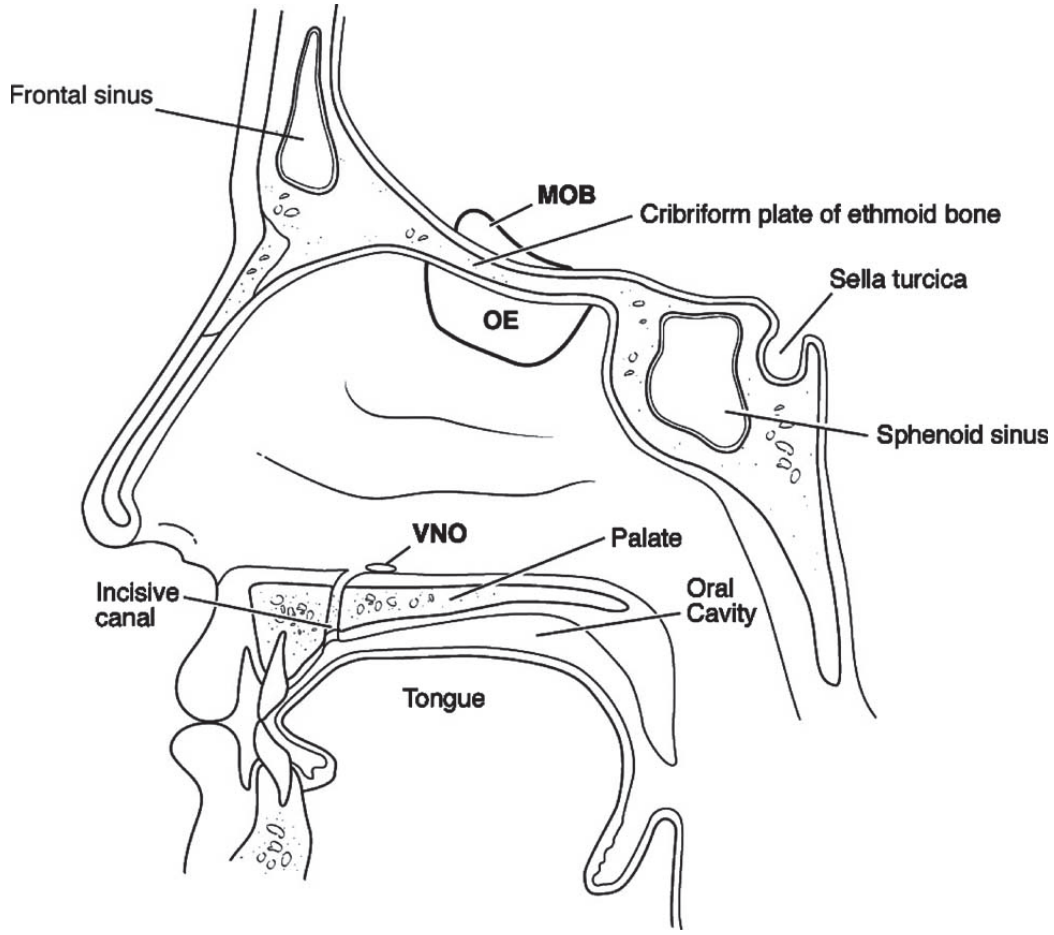

Figure 1: Schematic diagram showing the approximate location of the VNO[15]

This structure is very unique in its morphology and definitely different from the VNO found in other species. Various researchers tried to estimate the percentage of humans expressing VN pits at all. The overall results showed a huge variety depending on the method used to detect the VNO. Bhatnagar et al.[18] proved that serial histology is the only proper way to identify the VNO. Some false results may be explained as well through

misidentification of the nasopalatine duct[19] or fossa[18] for the VN pit.

Probably the most representative study in this context was conducted by Trotier at al.[16] They aimed to obtain a good estimation of the percentage of human VNO by using a really large population. Based on a very carefully conducted study setting *"13.2% of the examined individuals showed a pit on each side of the septum, 13.4% had a pit only on the left and 12.4% of the subjects had a pit only on the right side. In summary 39% of the human population have at least one well-defined vomeronasal pit".*[16] Knecht et al.[20] found similar evidences and also showed that expression of a VNO is not age or gender dependent.

2.1.2. Immunohistochemistry

However, although the vomeronasal organ is found, it is still not sure whether or not the VNO has a function in humans. Foltan and Sedy[21] for example are one of the very few researchers that postulate a functional VNO in humans. It is to say that those two researchers provide no data to support their hypothesis respectively wrongly cite articles. They present rodent data when speaking about the human VNO and do not mention research articles that suggest that the adult human VNO is non-functional.
Monti-Bloch et al. and Monti-Bloch and Grosser[22,23] showed that stimulation of the VNO with the putative human pheromone androstadienone evoked a voltage change in terms of negative potentials. This finding led the researchers to the conclusion that the VNO is functional in adults.

However, in this case, vomeronasal receptor neurons and nerve bundles as a neuronal connection with the brain should be detectable.

Olfactory marker protein (OMP) is a reliable detector for functioning olfactory neurons as it can be found in mature neurons of the olfactory epithelium[24,25] and in the functional vomeronasal organ of other species[26,27]. Takami et al.[28] were unable to find OMP in the human VNO. Trotier et al.[16] used Anti-OMP in order to detect OMP. This antibody against the olfactory marker protein failed to stain any VNO cells of humans, suggesting that chemosensory vomeronasal neurons are not present. Instead most vomeronasal epithelium cells express keratin proteins, a marker of epithelial cells that is not expressed by olfactory neurons.[16]

Vomeronasal nerve bundles do not seem to exist either, as protein S-100 (expressed in Schwann cells) could not be detected by the use of antibodies.[16,29] Recently important compounds for VNO sensory transduction such as the V1R, V2R and V3R receptors[30,31] and the ion channel TRPC2 have been identified.[32-34] The presence of TRPC2 channels is shown to be essential for a functioning VNO.[35,36] Similarly mice that are deficient in expressing V1R genes develop serious behaviour problems due to the loss of VNO function.[37] They fail to defend themselves and their offspring against intruder males and TRPC2 mutant males are vigorously hitting on other mice, disregarding their gender. Interestingly the TRPC2 gene and the vast majority of V1R, V2R, V3R genes are pseudogenized in humans.[35,38-41]
In order for messages to be sent from the vomeronasal receptor cells to the brain neurons would need to build a

connection to an accessory olfactory bulb. However, such bulb is found to be absent in humans.[29,42] This loss of VNO signaling components leads to the believe that the VNO is vestigial. Nevertheless the notion of a non functional VNO does not explicitly exclude that humans do communicate through pheromones. It might only be an evidence that humans are using a different olfactory structure than other animals do.

2.2. Development

Even though the accessory olfactory bulb is not present in adult humans it can be found in fetuses of different gestation stages (8, 18 and 26 weeks).[42-44] Afterwards however, the bulb regresses leaving a vestige behind.[42]

The VNO does not seem to have a function in later life, but it surely plays an important role for the migration of GnRH-secreting cells towards the hypothalamus. Just like in other mammals nerve fibers emerge embryonically from the developing organ to the brain[45] as specific cells can be detected in the bilateral vomeronasal organs of 8-12 weeks old fetuses.[46] This is an essential step for gonad function after puberty which totally depends on hormonal secretion. In people with Kallmann's syndrome (a genetic endocrine disorder) for example the migration does not take place which leads to no secretion of hypothalamic GnRH[47] and therefore to hypogonadism. People with Kallmann's syndrome might not even respond to putative human pheromones at all[10] and are most often anosmic.

However, after the initial step of GnRH-secreting cell migration the neuronal connections disappear and the organ regresses: No neuronal connections are found between the VNO and the brain after week 32 in gestation[16,29,42] whereas between weeks 8 and 14.5 the VNO appeared to increase in complexity.[48]

2.3. Smell detection tests

According to all the evidences listed earlier it would be quite surprising if the VNO could be stimulated by putative human pheromones such as estratetraenol, androstadienone or androstenone.

In the past couple of years several meaningful studies were conducted. The idea behind seems to be logic: If the VNO is a functional organ the perception of putative human pheromones should be altered when the VNO is manipulated. Knecht et al.[49] for example measured sensitivity towards androstenone and tried to figure out whether there was a difference in olfactory function when the VNO was occluded or not. Interestingly subjects with occluded VNO showed no difference when stimulated with androstenone. In the same study setting Knecht et al. found out that subjects without detectable VNO did not show different olfactory sensitivity towards androstenone compared to their counterparts with a VNO.

However, androstenone is not generally accepted to be a human pheromone whereas androstadienone (AND) is supposed to be the most likely candidate for such a chemosignal.[50]

Frasnelli et al.[51] therefore stimulated different subjects with androstadienone and discovered that functional occlusion of the VNO did neither alter the perception of AND nor change the patterns of brain activation anyhow.
Another approach was to test patients that suffered from severe nasal polyposis. As odours can no longer reach the olfactory cleft, those people are anosmic. However, this should not affect the function of the more distally located VNO as long as the VNO is considered as functional. When Savic et al.[52] confronted healthy subjects with estreatetraenol (EST) it typically activated the hypothalamus. Such an effect could not be observed in the patients group.
All these different evidences strongly indicate that the VNO is not a functional organ in humans but only vestigial. This knowledge does not conflict with the idea that pheromones do indeed play a role in human life but it leaves the question of which sense organ is actually capable of transmitting the olfactory information to the brain.

Just like the VNO the Grüneberg ganglion has been detected only in fetuses and regresses during gestation.[53] Therefore, the only sensory channel that would possibly allow pheromone detection seems to be the main olfactory system itself.[51,52] The finding of the V1RL1 vomeronasal receptor in human olfactory mucosa may support this hypothesis[54] as it shows that the humans accessory olfactory system has most likely been integrated into the main olfactory system.[54]

Nevertheless common odours are processed differently than putative pheromones. Common odours "*engage only the*

olfactory brain (amygdala, orbitofrontal and insular cortex)"[55] while pheromones activate the anterior hypothalamus. Yet the reception mechanism of putative pheromones and their detailed transmission to the central nervous system remain unclear. Therefore, more studies are needed to shed light on the role of the main olfactory system in human pheromone sensation.

3. Individual body odour - MHC

Pheromones are known to specify the species and sex of a being but the body scent also marks an individual member of a species with a unique coding.[56] Where does this individual body scent derive from? The major histocompatibility complex (MHC) seems to be genuinely involved. The MHC is a very diverse cluster of genes[57] that occurs on the cell surface. Its main task is the processing and presentation of antigens. Therefore, the MHC is well known for immune recognition of "self" and "non-self" and is also linked to transplantation rejection.

3.1. Avoidance of MHC-similarity in humans

Many animals like mice, birds, fish and sand lizards choose their mate for MHC dissimilarity to avoid inbreeding.[58-61] The increased genetic diversity is associated with a better immune system and consequently enhances the offspring's health and fitness advantages.

The human main histocompatibility complex, also known as the human leukocyte antigen (HLA), has been difficult to study as the human leukocyte antigen loci are highly

polymorphic with millions of unique genotype combinations.[62] Nevertheless different researchers have tried to figure out whether humans as well try to encourage heterogeneity of MHC.
In 1991 Reznikoff-Etievant et al.[63] found out that babies with significantly reduced birth weight are correlated to parents that share a rather similar MHC expression. In the same year Weckstein et al.[64] discovered that such couples also have problems to achieve pregnancy at all. And only a short while after, it was proven that recurrent spontaneous abortions are most often found when dissimilar MHC genes are missing.[65]

3.1.1. Different human populations

Conflicting results have been reported as to whether humans are actively trying to avoid homogeneity in MHC or not. It seems as if MHC related mate choice does indeed influence some human populations but not all of them.
In a study that involved 200 couples from South Amerindian tribes no evidence for avoidance of MCH similarity was found.[66] The results were comparable to those of random mating.

However, Ober et al.[67] took a look at Hutterites, a small genetically isolated group of believers nowadays located in North America. They scanned 411 couples for HLA types and found remarkably fewer HLA matches among partners than would be expected by chance alone. As well European American couples showed more MHC-dissimilarity than random spouses.[68] Such congruence cannot be explained by

demographic processes but leads to the hypothesis of disassortive mating.

3.1.2. MHC-based olfactory signaling

But how is it possible that humans unconsciously mate with MHC dissimilar partners? This brings us back to the initially proposed two functions of the MHC: immune system and individual body scent. Even if human-based research in this area is absolutely sparse, some studies lead to the belief that MHC-based olfactory signaling does take place.[69] Mice for example can recognize a human by its urine[70,71], which shows that MHC-specific odorants must exist.
It is assumed that during cellular turnover MHC gene fragments are being excreted together with body fluids.[54] This process obviously maintains the unique individual body odour.

Several different study settings were conducted between 1980 and 1997 with rather interesting discoveries about human olfaction and MHC involvement.

Schleidt and Schleidt et al.[72,73] found out that individuals were able to identify their own odour as well as the ones of their closest relatives by smelling axillary odour. They could even distinguish between the two sexes. Other experimenters showed that parents could differ between the different odours of their own children which shows that body scents allow authentical kinrecognition even among humans.[74]

Later on Wedekind et al.[70] focused his interest on putative MHC-dependent mate preferences in humans. Several male students were asked to wear the same T-Shirt for a couple of nights without using any additional odorants like soup or deodorant. Afterwards a group of female students rated the odours of these T-Shirts for pleasantness. They scored the T-Shirts of men with fewer MHC genes in common as more pleasant than the ones that were more MHC similar. This effect did not occur once the women took the contraceptive pill. In another study setting Wedekind and Fury[75] made men and women score the pleasantness of T-Shirt odours and came to the same conclusion. The unpleasantness was linked to the degree of MHC similarity between smeller and wearer as long as the women did not use oral contraceptives. The subjects also were reminded of their own partner's odour when smelling a dissimilar MHC-type which leads to the suggestion that also in real life they unconsciously go for disassortive mating.

In another sweaty T-Short experiment however, males and females were chosen from different ethnicities. Here females preferred paternally matching HLA-associated odours to those that showed fewer matches to their own.[62]

The lack of congruence in the research results shows that MHC-dependent mate choice in humans still needs deeper consideration.

Yet there is one aspect that scientists agree about: Women are far better at odour detection than men.[76-78] But this doesn't mean that men do not have a great sense of smell. One interesting aspect is that men are more attracted to

the smell of female bodies during certain times of a woman's menstrual cycle.

4. Female menstrual cycle

4.1. Synchronization of menstrual cycle

For sexual reproduction and fertilization purposes the women's body goes through periodical and physiological changes. Lead by the endocrine systems three different phases occur: the follicular phase, the ovulation and the luteal phase.
There are many interesting facts showing that the female menstrual cycle is closely linked to human body scents. For example the timing as well as the length can be modulated only by perceiving the right odours.

Such odours that come from the female vagina are referred to as copulins. They are volatile fatty acids that change their content according to the different phases of the menstrual cycle.[79-81] Copulins are known to affect mating behaviour in rhesus monkeys and are believed to have similar effects on humans.

Already in 1971 McClintock[82] showed that the menstrual cycles of young women living together tend to synchronize. Over the years different studies have proven this finding as well in close friends and/or room-mates[83-85], co-workers[86,87] and female members of bedouine families[88].

Consequently women who spend a lot of time together are shown to experience menstrual synchrony. But it does not explain whether this effect is due to similar environmental

stimuli or if it really derives from a pheromonal influence. Therefore, some studies were conducted without social contact of the subjects. Only female axillary extracts were applied to the nose of other women for a certain period. The recipients experienced a time shift of their menstrual onset according to the donor's one.[89,90] These underarm compounds either delay or accelerate the luteinizing-hormone surge of the recipient women[91] and are also able to speed up the pulsatile frequency of luteinizing hormone.[92]

4.2. Disruption of menstrual cycle

But this is not the only pheromonal influence on the menstrual cycle. Beside the synchronization Jacob et al.[93] were able to observe the exact counter effect. They collected the body odour of breastfeeding women by making them wear a pad between underarm and breast. These breastfeeding compounds then disrupted the cyclicity of nulliparous women and increased the variability of ovarian cycles. In addition to that finding sexual motivation (desire and fantasies) of non-lactating women were increased by the body odour of breastfeeding women.[94]

4.3. Influence of male body scents on female menstrual cycle

Those were only effects of female body scents but also men's pheromones lead to alteration of the ovarian cycle. Cutler et al.[95] chose women with unusual cycle length and were able to show that their cycles became more regular when they were opposed to male underarm compounds over a

certain period. And just like female axillary odour, men's underarm compounds also effected the pulsing of luteinizing hormone.[96]
Another effect of men's hormones on female bodies might be that girls who grow up in single-mother homes experience later puberty than the ones that grow up with a stepfather.[97]

4.4. Other relations between body scents and menstrual cycle

The women's menstrual cycle in relation with human pheromones plays a major role on women. Not only the timing of the menstrual cycle is being addressed by body scents, but also the female ability to smell, their mood and the perception of men's attractiveness are depending on the different phases of the menstrual cycle.

Morofushi et al.[85] found out that the synchronization of women's ovarian cycle is linked to the ability to smell androstenol. Women who have a higher detection threshold for androstenol are most likely not synchronizing their menstrual cycle with other female subjects while synchronized women can detect androstenol also at rather low quantities.

In the context of smell sensitivity another finding is highly interesting: Women's smell sensitivity towards the male pheromone androstenone varies throughout the different menstrual cycle phases. It reaches the highest peak in the moment of ovulation as long as no contraceptive pill is being used.[98] When conception is most likely women's

emotional perception of androstenone is triggered in order for it to appear more pleasant.[99,100]

More recently Watanabe et al.[101] wanted to verify the previous findings. As a marker they used the "olfactory contrast", which is defined *"as a slope of the dose-response relation and therefore provides recognition ability for the changed intensity of odorant".* According to Watanabe et al. the olfactory contrast was significantly increased during ovulation.

It is well known that attractiveness and facial symmetry are important criteria for human mate choice. Men with more symmetrical faces are supposed to be physically fitter and show less signs of depression and anxiety.[102,103] They also have more sexual partners than their asymmetrical counterparts.[104]

Several researchers dared to ask whether human body odour might be linked to mate quality in any kind of way. Rikowski and Grammer[105] measured the facial symmetry of 16 male and 19 female subjects. The women did not use oral contraceptives and were all in different phases of their menstrual cycle. The subjects were requested to wear the same T-Shirts for two nights in a row and afterwards rate photographs of the opposite sex and their according T-Shirts for attractiveness and pleasantness. One positive correlation was found: Women who were in the most fertile phase of their menstrual cycle judged the odour of symmetrical men as more pleasant as the asymmetrical ones. Gangestad and Thornhill[106] conducted a similar study. 52 women rated the odour of 41 men's T-Shirts. Women at a low fertile moment within their menstrual cycle as well as

contraceptive pill users showed no preference for any of the men's odours. But high fertility women once more rated "symmetrical-face-odour" as more pleasant.
One year later Thornhill and Gangestad[107] conducted another study even more carefully. They took a larger sample (80 men and 82 women) and made sure they controlled various factors that were not taken on account in the previous study. Again they came to the same results, therefore suggesting that "the scent of symmetry" may be an additional index for male mate quality.

Non-verbal behaviour traits might also belong to such indices. Most recently Roberts et al.[108] revealed that *"the attractiveness of male non-verbal behaviour is predicted by perceived quality of their body odour"*.

And the odour of dominant men is preferred by non-single women during ovulation. Havlicek et al.[109] asked 48 male students to fill in a questionnaire on dominance and collected axillary odour samples from them. Afterwards they questioned women for their odour preferences and tried to find correlations between odour pleasantness and male dominance. Such correlation was found for non-single women during their fertile phase but not for non-ovulatory or single women.

5. Pheromonal influences on men

Even if men do not experience a rhythmic change of their hormonal status like women they are still being affected by human body scents. Berliner et al.[110] found out that

putative pheromones change the pulsatile frequency of luteinizing hormone in men too.
Even the earlier mentioned copulins of the female vagina were shown to have an impact on men[10]: The fatty acids stimulate male androgen secretion and have a positive impact on men's rating of female photographs.

The above mentioned phenomenon of women preferring men's odour at time of ovulation is closely linked to the fact that also men find the scent of an ovulatory women more pleasant than during other phases of the menstrual cycle.[111,112] Even though the moment of ovulation is not perceived consciously by humans[10] this shows clearly that olfaction plays an unconscious role in properly timed reproduction. Chemosignals are able to trigger men's and women's need for sexual intercourse in a way that remained unnoticed for long. Nevertheless human's sexual activity is more complex and not only limited to the moment of ovulation. Therefore, it is sure that many different aspects play together in this issue.

6. Pheromonal substances of the human body

When Martha McClintock[82] in the 1970s started her researches about the influence of body scents on the female menstrual cycle it was not certain whether human pheromones do exist or not. The more recent papers cited above, show clearly that such chemosignals do indeed play a role in human's life. But what are the substances that can be seen as pheromones?

It is likely that pheromones have evolved from hormones.[113] Hormones are biochemical messengers that are being produced by special donor cells and transported via the bloodstream towards their receiver cells in order to create a highly specific effect. One particular hormone family is the sex hormones, chemically seen as sex steroids. Several derivates of those sex steroids are the most likely candidates for human pheromones and therefore it is necessary to take a closer look especially at the substances androstadienone, androstenone, estratetraenol and androstenol.

6.1. Androstadienone

One such steroid is androstadienone (4,16-androstadien-3-one), an androstene found mainly in men's axillary secretion. The concentration in female axillae is 20 times lower than the men's one.

Androstadienone detection was shown to be experience dependent.[114] When subjects are repetitively exposed to the odour of androstadienone they show an increase of sensitivity[115], a decreasing threshold as well as changes in the way they perceive the odour.[116,117] While threshold is still low the smell is pleasantly described as floral, minty and fruity[113] but with rising sensitivity it changes to urine, musky and unpleasant.[118,119] Such an increase in odour sensitivity is very exceptional as usually habituation or generalization would take place.
Jacob et al.[114] have tried to explain this phenomenon through the existence of two different odour channels. One pleasant channel with low-affinity receptors and one

unpleasant channel represented by high-affinity receptors. With increasing sensitivity the high-affinity channel is activated at thresholds far below the ones necessary for the channel with pleasant odour-qualities. That would explain why the odour quality becomes putrid.

Savic et al.[55] came up with an even broader hypothesis: They suggest the existence of a separate neuronal olfactory pathway. Also Lundström et al.[50] believed this was the only possible explanation to the fact that androstadienone elicits between 13% and 20% faster than chemically similar control odorants. This finding cannot merely be explained by learned responses or by different odour perception.
Schild and Restrepo[120] showed that the mucus transfer of chemically different odour types can lead to variable processing times. But Lundström et al. did choose chemically very similar odours. The hypothesis that less pleasant chemosignals are processed faster[121] cannot shed light on this question either as then androstadienone should elicit slower than its control substances and not faster. Therefore, Lundström et al. claim the existence of a neuronal subsystem for androstadienone as it was found in Old-world monkeys.[122]

Another plausible explanation not mentioned by Lundström et al. might be the adaptation towards environmental stimuli.[123] The odour of androstadienone might be of such high relevance for humans that it is processed faster than stimuli of less importance. Gottfried[124] emphasizes the importance of learning and experience in human olfactory perception. Olfactory-learning has a modulatory effect on our odour perception even though it is surely different from learning in other contexts.

6.2. Androstenone

A very recent research validated this suggestion. Women who already had sexual experience with one or more partners rated the smell of androstenone as more pleasant than women who had no sexual contact yet.[116]

Androstenone (5α-androst-16-en-3-one) can also be found in humans. It is a known pheromone in boars which leads females to acceptance behaviour towards males and is supposed to have important effects on human behaviour too.[125]

Just like people can increase their sensitivity towards androstadienone the same effect was proved for androstenone.[126]

6.3. Estratetraenol

Estratetraenol (1,3,5(10),16-estratetraen-3-ol) is another possible candidate for human pheromones and shows a similar structure as estrogens. It can be found in female urine. Jacob et al.[127] conducted a double-blind, repeated-measures experiment and found out that estratetraenol has an influence on men: It raises skin temperature and increases skin conductance.

6.4. Androstenol

Another steroid, androstenol (5α-16-androsten-3α-ol), is also regularly mentioned in the discussions about human pheromones. Ebster and Kirk-Smith[128] for example showed

that men's product choice can be manipulated by androstenol. They rated male magazines as better and more masculine when exposed to the putative pheromone.

This little excursus to the sex steroids of the human body shows clearly that those compounds are unlike the vast majority of odours and smells. But what makes them become so different? Future studies should try to address this very issue more deeply.

7. Physiological responses and changes in brain activity

Several studies have looked not at behavioural effects but at physiological changes of human pheromones and have come to remarkable results. Very recently Marazziti et al.[129] suggested that *"the application of male axillary extracts to women may modify the affinity of their platelet 5-HT transporter"*.
Van Toller[130] reported an increase of skin conductance when subjects were exposed to androstenone. Androstadienone and estratetraenol also increase skin conductance and they both raise skin temperature in men while lowering it in women.[127]
Wyart et al.[131] showed that androstadienone influences the endocrine state of women as it leads to an increase of cortisol levels while Berliner et al.[110] observed changes in respiratory rate and cardiac frequency.

As mentioned before pheromones and common odours activate different regions of the brain. Human pheromones activate the hypothalamus in both men and women, but there are slight differences: The centre of activation in females is

the preoptic and ventromedial hypothalamus while men's activation focuses in the paraventricular and dorsomedial part.[132] Those are areas that are associated with olfaction as well as with sexual behaviour, emotions, social skills and the ability of being focused.[133,134]

8. Sexual orientation

In contrast to the described effect more recent studies came to a different interpretation. The hypothalamic activation does not only depend on gender but mainly on the subject's sexual orientation.[135]

The sexual identity and orientation of a person is an individual pattern depending on the attraction to the opposite gender, the same gender or both sexes referred to as heterosexuality, homosexuality or bisexuality.

In most of the countries marriage to a same sex couple is still not allowed and in many places even same-sex sexual activity is forbidden/punished. Discrimination and ostracism is a constant companion for many homosexuals and some associations preach the ability to "heal their disease". But how does sexual orientation manifest itself in an individual? Some experiments in context with human pheromones are able to answer some striking questions.

When stimulated with androstadienone homosexual men showed the same brain activation as heterosexual women rather than heterosexual men[55], even though they used the same processing as heterosexual men when exposed to common odours.

As described above heterosexual women process androstadienone via the anterior hypothalamus. Lesbian women however, don't share this profile but use the main olfactory system instead.[136] Furthermore, homosexual women are processing estratetraenol just like heterosexual men.

Savic et al.[137] managed to prove later on that these findings cannot be explained by learned responses but by neurobiological discoveries. They used positron emission tomography and magnetic resonance imaging in order to show *"sex-atypical cerebral asymmetry and functional connections in homosexual subjects."*[137] In summary, homosexual men share similar brain activity with heterosexual women and homosexual women have more in common with heterosexual men.

Homosexual men and heterosexual women do not only have the same hypothalamus activity when stimulated with human pheromones. They also have a high affinity for the odour of androstenone. Pause[113] sprayed seats with androstenone and showed that heterosexual men tried to avoid those impregnated chairs, while heterosexual women and homosexual men were actively looking for them.

Most recently Adolph and Lübke et al.[138] once again put their focus on olfaction related brain processing and found out that body scents also carry information about a person being a potential partner. Homosexual and heterosexual subjects consistently showed shorter P2 (a component of brain evoked response potential) latencies when smelling the odours of their sexually preferred gender, while they showed longer P3 amplitudes for undesirable partners.

Sergeant et al.[139] made another interesting discovery. Sexual orientation does not only seem to influence olfactory perception but also human's odour production. Women rated homosexual men differently than heterosexual men. They preferred the smell of homosexuals, but did not rate them any different than unused T-Shirts.

9. Emotions and mood

Emotions and moods are great markers for a person's mind set. In general, moods are described through positive or negative scales simplified by speaking of being in a bad or a good mood. Our emotions are triggered by different stimuli or events and also depend on a person's temperament or personality.
Those triggers can be of very different nature and recent research shows that olfaction and emotion synergize with one another on the social level.

Jacob and McClintock[140] postulated that androstadienone and estratetraenol modulate people's mood state. Both steroids had positive mood effects in women while they decreased positive mood in men. Bensafi et al.[141] also tested the effect of androstadienone and estratetraenol. The subjects were put into different situational contexts that were either neutral, happy, sad or sexually arousing. Only during the sad situations androstadienone managed to keep female subjects in a positive state of mind while it rose negative feelings in men. Women also tend to be more sympathetic under the influence of androstadienone.[142] In general, this steroid is able to reduce stress and other negative feelings in female subjects.[143] Above all it

leads to more relaxed feelings[96] and has a positive influence on women's ability to be focused.[144] All these effects do not change according to the menstrual cycle phase but are independent of it.

Villemure and Bushnell[145] made another interesting discovery: Androstadienone seems to have an effect on pain perception. The researchers exposed subjects to androstadienone while inducing pain. Compared to unscented air androstadienone improved mood in women as mentioned above. This effect only occurred when pain was still absent. As soon as women received painful stimulation the perception of it was even increased in combination with the smell of androstadienone.

Chen and Haviland-Jones[146] went one step further: They hypothesized that human odours in general lessen other humans' depressive mood. This effect is not supposed to depend on the amount or pleasantness of the perceived odour but on age and gender. According to them women have a greater positive mood effect than men and the same goes for older people compared to younger people. Therefore, older women's odour reduces negative mood best.
It is questionable whether this finding is a real breakthrough in the scientific world. After a careful examination of the data given by the researchers one can understand that there is no report of increased positive mood at all but only a decreased negative mood.[147] Furthermore as a tool for mood ratings they used the DES (Differential emotional scale) which is meant to find out how often subjects go through mood changes rather than commenting their actual mood state. Participants were asked to rate their mood only two minutes after the

perceived odour, which does not make much sense according to the nature of the DES. And above all Chen and Haviland-Jones failed to compare their results to a valid placebo effect.[146]

10. Chemosensory anxiety signals

The same two researchers also found out that human can detect other people's emotions only by smelling their body scents.[148] Odour samples of fearful people activated areas in the brain that are in charge of processing anxiety signals. But once again a broader study setting would have been useful in order to verify the truthfulness of this finding. The researchers investigated only anxiety signals, leaving a placebo control and all the other social emotions totally behind.
On the other hand also Ackerl et al.[149] suggest that women have indeed the ability to receive the "scent of fear". Women's axillary odour was taken while watching either a frightening or a neutral film. Before and after this presentation the researchers took saliva cortisol samples in order to measure the hormonal reaction towards the fear. When those odours were presented to other female subjects they were able to differentiate between frightened and non-frightened odour.

Prehn et al.[150] discovered that chemosensory anxiety signals have an increasing effect on the startle reflex, suggesting that it is a part of our unconscious defensive behaviour. Also Pause et al.[151] investigated this issue. They collected sweat pads from students either waiting for an oral exam or doing sports exercise. The subjects

perceiving the anxiety odour showed an augmenting startle reflex compared to the control odour.
Two according works used neuroimaging in order to examine neural perception of human chemosensory alarm signals. Mujica-Parodi et al.[152] took sweat samples of people during their first time tandem skydive. Recipients of this anxious sweat showed a specific amygdala activation compared to non-stressed odour.
The fMRI results of Prehn-Kristensen et al.[153] verify that *"chemosensory signals of anxiety activate brain areas involved in the processing of social anxiety signals (fusiform gyrus), and structures which mediate the internal representation of the emotional state of others (insula, precuneus, cingulate cortex). In addition, the physiological adjustments to chemosensory anxiety signals include attentional control systems (dorsomedial prefrontal cortex, thalamus) and a supramodal unit, timing the different emotional processing systems (vermis, cerebellum)."*

Another study investigated the effect of stress odours on neural activity. Rubin et al.[154] collected sweat samples of subjects during a stress condition (first time skydive) and a control situation (exercise) and made them watch pictures of neutral, ambiguous or angry faces. As expected the late positive potential (a brain potential that is important for recognition memory) during the control condition was larger for threatening than for neutral or ambiguous faces. But in the stress condition the late positive potential was increased for all face expressions.
In general, it is interesting that *"the processing of almost odourless chemosensory anxiety signals requires*

enhanced neuronal energy" measured as an increased P3 amplitude.[155]

However, chemosensory anxiety and stress cues do not only influence humans' brain activity but also their behaviour. Zhou and Chen[156] found out that fearful odour changes the affective perception of women: They rated ambiguous faces as more fearful when smelling anxiety sweat samples. When the facial expressions were clearer this effect did not occur. Therefore the researchers postulate that olfaction can sharpen visual emotional perception.
A similar effect was observed for men. They rated ambiguously happy faces as less happy while smelling anxiety cues compared to the control condition.[157]

Also Pause et al.[158] took anxiety and control sweat samples. They primed subjects with sad, happy or fearful faces and made them rate neutral facial expressions afterwards. Women primed by happy faces rated neutral faces as more positive when smelling control odour, but when smelling chemosensory anxiety signals the priming effect of happy faces was clearly reduced. It was also shown that the odour of men who are in an anxious state of mind is able to escalate fear in women recipients.[159]

Chen, Katdare and Lucas[160] explored human cognitive performance in relation to fearful odours. Subjects who went through a word-association task while smelling anxiety body scents were more accurate and still not slower than those who found themselves in a neutral condition.
It is also known that people with a high personal fear show a higher risk taking behaviour when it comes to decision-making. And as fearful chemosignals and the process of

decision-making show very similar brain activation patterns Haegler et al.[161] decided to search for similar effects on risk taking behaviour between fearful odour and high trait anxiety. Male donors collected their sweat either during a high rope course (anxiety sweat) or an exercise condition (control odour). Female recipients were asked to play a computerized risk game during odour exposure. The women showed a seriously higher venturous behaviour towards the most risky choices when smelling fearful odour.

Overall it seems as if people with high social anxiety vary in their way to process fearful odours.[162] Their neural processing of social fear signals is slower than that of non-socially anxious individuals.[154]

11. Emotional tearing

However, olfactory communication of emotions is not only restricted to stress and fear but also includes other feelings. Emotional tears and sadness are another field of recent research. Emotional tearing is a behaviour that was found uniquely in humans. Gelstein et al.[163] exposed men to women's tears of sadness collected on pads. An obvious reduction of *"self-rated sexual arousal, physiological measures of arousal, levels of testosterone"* and hypothalamus activity was observed. Consequently weeping reduces women's attractiveness through the eyes of a man[164] but might also lower men's violence due to fewer testosterone levels.
Additionally Oh et al.[165] wanted to find out whether there is a correlation between smelling sad tears and human appetite. The researchers could find no change in food

intake through tearing odour but verified the reduction in testosterone levels.

12. Competition

In other animals chemosignals of competition are very often used to help those species adapt their behaviour according to the actual situation. Those signals seem to be also communicated between humans. A badminton match served as the research condition for collecting competition sweat samples. The testosterone levels of those donors were higher than the ones of the control subjects during exercise. When odour recipients were exposed to either competition chemosensory signals or control odours they showed a larger skin conductance response during the competition condition.[166]

13. Mate choice

Reproduction of animals is another behaviour that is influenced by pheromones. A large number of studies managed to confirm pheromonal effects on animals' socio-sexual behaviour and mate choice. But even though most of the recent scientists are optimistic that pheromones do exist in humans it remains questionable whether they also influence human sexual reproductive behaviour. Several studies have investigated this topic and yet the outcome is disputably discussed. The different methodologies in laboratory settings make comparisons difficult and carefully conducted double-blind, placebo-controlled, crossover studies are sparse.

13.1. Attractiveness ratings

One of those very few studies was carried out by Thorne et al.[167] who asked women to rate male vignette characters and faces for attractiveness. Women under the influence of male axillary pheromones rated men as significantly more attractive than the control subjects. Also Cutler and Genovese[168] showed that topical application of a synthesized pheromone raises sexual attractiveness in female subjects.
Even the earlier mentioned "scent of fear" seems to have an impact on female attractiveness ratings. Male sweat samples collected during a theoretical exam were rated as less pleasant than odours of sweat donors with low cortisol levels.[169]

13.2. Pheromonal influence on sexual intercourse

Several other studies investigated not only ratings of attractiveness but actual changes in social interactions evoked by pheromone exposure. They all have examined whether sexual intercourses of subjects would increase under the influence of human pheromones.
Cowley and Brooksbank[170] asked 38 men and women to wear a necklace for one night which was either prepared with odour of the opposite sex or a control odour. The following morning the subjects made statements about their sexual behaviours. Women who were exposed to androstenol reported far more interactions with men then the other groups.
Also McCoy and Pitino[171] were setting their focus on sociosexual behaviours in women. After a baseline period of 2 weeks the women's preferred perfume was infused with either a synthetic female pheromone or a control liquid.

While all subjects showed no obvious difference during baseline period, the pheromone group significantly increased its sexual intercourses, sleeping next to a partner and formal dates afterwards. Nevertheless the frequency of masturbation did not differ in any kind of way.

Cutler et al.[172] asked men to make records on 6 different sociosexual behaviours after adding up either placebo or a male pheromone to their aftershave. Once again the pheromone group showed a higher number of sexual intercourses and nights spent beside a female partner, but no difference in masturbation. All three studies show that the reported changes involve an individual of the other sex, while masturbation does not vary. Therefore, human pheromones are acting as sex attractants rather than increasing sexual motivation. More recently Friebely and Rako[173] confirmed the earlier findings once again. Their subjects (postmenopausal women) increased the amount of kissing, petting and romantic exchanges when exposed to human pheromones.

However, there is still need for more representative studies in this field as the methodology of all those researchers could have been far better. For example no assessment of the actual subjects' attractiveness was used. If the individuals in the pheromone group were more attractive than in the placebo group, it was probably easier for them to increase their sexual intercourse. Also the important personal status within the groups was not taken on account. Some subjects were singles, others in relationships or even married, which makes comparisons rather difficult. Above that the different studies made no record of other factors that might cause behavioural changes. Also a romantic weekend trip or a birthday party

could have been a plausible reason, besides the suggested pheromones. Therefore a clear analysis is difficult and maybe false interpretations have been made.

13.3. Ecological validity is needed

As described before putative human pheromones very often elicit mood effects in humans. Nevertheless it has also been shown that those mood changes only appear under certain conditions. The positive mood shift in women presented by Jacob et al.[127] for example occurred only when a male tester was present. Lundström and Olsson[174] verified this finding in a double-blind, within-group study. When women were tested by another woman no mood shifts were detectable. This result shows that pheromones need a sufficient context to follow their intention.
Lundström and Olsson[174] seem to adduce another evidence for this suggestion: They were not able to confirm women's increased attractiveness ratings when exposed to androstadienone. For their experiment Lundström and Olsson used pictures (only neck and face) of men shown to women on a computer. It might be possible that this situation was not ecologically valid enough in order to evoke a pheromonal response in female subjects. In general, it is disputable whether a laboratory environment provides a sufficient context for investigating behavioural effects of putative human pheromones.

13.4. Speed dating experiments

According to those thoughts Saxton et al.[175,176] tried to work out a study setting that would respect the normal

social circumstances as much as possible in a scientific experiment. They decided that a speed dating environment would probably meet these requirements best.
Speed dating is a form to socially introduce singles to one another. Each participant meets each person from the opposite-sex for a certain amount of time and if two individuals agree to like each other they exchange contact details. The goal is to estimate in a short amount of time whether the counterpart could be a potential partner or not. Therefore, speed dating is seen as an adequate surrounding for investigating the influence of human pheromones on mate choice.
In a first study Saxton et al.[175] selected 22 males and 25 females and topically applied either androstadienone masked with clove oil, clove oil alone or water above the women's upper lip. While participating to the speed dating, women were asked to evaluate men's attractiveness. Subjects who were infused with androstadienone rated men as significantly more attractive then the two control groups. Also the second experiment of Saxton et al.[176] used a speed-dating context for their research. In three different cycles women under the influence of androstadienone or control substances rated men's attractiveness and once again judgments of the pheromone group were more positive. This finding provides strong evidences that men's chemosignals are able to modulate women's judgments. On the other hand one cannot rule out the possibility that men behaved differently too. They may have also perceived the odour even if they were further from the odour source.

Most interestingly men's odour does not only influence female behaviour towards the opposite sex but also intrasexual competitive behaviour.[177] Women during

different phases of their menstrual cycle were asked to have a look at different male and female faces. While the researchers recorded the women's eye-movements participants were also exposed to androstadienone odour or a control substance. Those subjects who were close to the moment of possible conception were looking much oftener at female faces than at men's ones. No differences between odour or control group were found. On the other hand low fertile women exposed to androstadienone increased their competitive behaviour towards women through looking at female faces far more often. Thus the authors suggest that certain pheromones can lead to competition among humans of the same sex.

All these evidences show that chemosensory signals transmitted by olfactory receptors well influence human sexual behaviour and therefore help to choose the right partner.

13.5. Sperm chemotaxis

Obviously gametes also experience a little guided help towards fertilization. Just as rats sperm are known to express olfactory receptors[178] it was possible to show that human sperm chemotaxis does also exist[179]: Human sperm responds immediately to a chemoattractant.[180]

14. Conclusion

Olfaction is one of our five basic senses providing the ability to immerse into a unique world of sensations. This review aimed to figure out whether pheromones play a role

in human communication or not. It was shown that humans do indeed spread body odours mainly via the skin and some researchers suggest they function as chemosignals rather than pheromones. Looking at the human vomeronasal organ makes us believe that this opinion might be right: Although the presence of a VNO is generally accepted in the early life of a fetus, it degenerates during gestation, leaving many neurochemical and neuroanatomical evidences for a non-functioning vomeronasal organ behind. Yet the notion of a vestigial VNO is no proof for the absence of pheromones in human life. It is most likely that pheromones can be transmitted via the main olfactory system. However, the way how human pheromones are mediated is mainly unknown and further investigation is needed in order to identify related pathways including receptors and ligands.

Another important aspect is that common odours and pheromones are processed differently and also activate different brain areas. Pheromones are supposed to trigger social responses and the fact that hypothalamic activation depends on sexual orientation very well meets this criterion. Even though several studies have demonstrated strong evidences for androstadienone and estratetraenol to be pheromonal substances no compound has been undisputedly accepted so far.

Many different behavioural responses have been detected by now. Among the first reports was the synchronization of the menstrual cycle in women that live together. Also humans' ability to recognize sexual orientation, gender and kin was a big discovery and finally detection of genetic MHC-differences only via chemosignals seems to be proof enough. While pheromones have been shown to evoke mood shifts, recent research efforts were put on the effects of chemosensory anxiety and sadness signals.

It is highly visible that many intersexual behavioural effects only exist due to pheromonal communication. Most of it seems to come down to sociosexual and mating behaviour. All these present data demonstrate that human pheromones do indeed exist. Nevertheless it remains unclear to which extend pheromones impact our course of action as human behaviour is very complex and led by many different cues.

The knowledge of human chemosensory communication raises further questions. How does our modern striving for inodourousness and cleanliness cope with the outcomes of all these cited studies? Are we not disseizing ourselves from a natural way to communicate by trying to erase those traces of communication from our bodies? And how do industrial perfumes interfere with these elemental behavioural cues? So far nobody can explicitly answer those questions. But interestingly it could be shown that the artificial fragrances do still have positive effects. Capparuccini et al.[181] figured out that the use of perfumes is *"potentially involved in mate choice and may elicit strong hedonic responses that can dominate visual signs, with a cross-modal interaction".* Those fragrances do not only mask our body odour but are instinctively chosen by the individual to well interact with the personal odour. The mix of a subject's body scent with the preferred perfume is rated as more pleasant than the mix of this body odour with a randomly chosen fragrance.[182] Additionally the self-confidence and self-perceived attractiveness of men are enhanced by the use of fragrances with antimicrobial agents which makes them appear more attractive to women.[183] This interference between personal body pheromones and industrial perfumes is another possible field for further examination on human pheromones.

15. References

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16. Figures

Figure 1: Schematic diagram showing the approximate location of the human vomeronasal organ at the base of the nasal septum

Abbreviations: MOB, main olfactory bulb
OE, olfactory epithelium

according to M. Halpern, A. Martínez-Marcos, *Progress in Neurobiology* **2003**, *245*

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