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# Emotional contagion in humans: study of the transmission of positive emotions through endogenous and exogenous odors carried by the body

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## **Emotional contagion in humans: study of the transmission of positive emotions through endogenous and exogenous odors carried by the body**

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# Résumé

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L'être humain est un animal social qui communique dans son environnement avec ses congénères et d'autres espèces via ses interfaces sensorielles. Lorsque l'on parle de communication, les canaux visuels et auditifs viennent généralement rapidement à l'esprit, mais un autre sens se trouve être hautement adapté au transfert d'informations entre individus. Le sens olfactif possède de nombreux avantages : les molécules chimiques à l'origine des odeurs peuvent -parmi bien d'autres exemples- être émises et perçues dans le noir, rester dans l'environnement en tant que marques odorantes, être transportées sur de courtes ou longues distances, ou bien contourner des obstacles. Ceci fait du sens olfactif une voie privilégiée pour la communication, qui est retrouvée dans pratiquement tout le règne animal, allant des organismes les plus « simples » aux plus complexes. Depuis des dizaines d'années des cas de communication dite chimique sont rapportés chez les invertébrés notamment chez les insectes (e.g., abeilles, papillons), mais aussi chez des espèces de vertébrés tels que les poissons ou les éléphants, en particulier via des molécules appelées phéromones. Au sein des espèces chez qui elles ont été identifiées, les phéromones remplissent des rôles divers : elles sont impliquées dans l'attractivité, l'accouplement, l'alerte face au danger, le lien entre parents et progéniture, les comportements de fuite et d'agression, ou encore la délimitation du territoire.

Chez l'être humain, l'existence de phéromones est encore débattue et les connaissances sur ces odeurs dites sociales restent encore relativement limitées. Néanmoins, l'odeur du corps d'un individu semble être porteuse d'informations de nature très variée à son sujet, et ces molécules une fois captées par d'autres individus, qu'il s'agisse de proches ou d'inconnus semblent causer des effets à la fois cognitifs et physiologiques chez ces derniers. La littérature à ce sujet montre que les êtres humains sont capables de collecter des informations au sujet d'une autre personne sur des traits constants (e.g., génétique, âge, sexe) ainsi que sur des états transitoires (e.g., maladie, stade du cycle menstruel) de celle-ci, en étant exposés à son odeur uniquement. Cette communication et ses effets ont lieu de manière non-consciente, à la fois pour les individus émetteurs de l'odeur ainsi que pour les individus receveurs de celle-ci.

Parmi les états internes transitoires communiqués via le sens olfactif, un facteur a récemment été l'objet d'études prometteuses : les odeurs corporelles semblent être porteuses d'informations sur *les émotions* ressenties par la personne qui les émet. Ces études se sont fortement concentrées sur le cas d'états émotionnels négatifs tels que l'anxiété ou la peur,

mettant de côté les états positifs qui pourtant sont partie intégrante de nos vies quotidiennes, et également porteurs de bénéfices majeurs pour les individus, les groupes, ainsi que pour la société au sens large. En effet, le fait de ressentir et d'exprimer des émotions dites positives est, dans la littérature, expérimentalement corrélé à de nombreux avantages comme par exemple une plus grande motivation, une plus grande satisfaction dans les relations sociales, une meilleure productivité sur le lieu de travail, une meilleure santé physique, ou encore de fortes capacités de résilience.

Outre ces lacunes, une autre zone d'ombre prend forme lorsque l'on s'intéresse à un facteur allant souvent de pair avec nos odeurs corporelles naturelles : les odeurs exogènes. L'être humain se parfume de manière directe (sur la peau) et indirecte (via les habits ou les senteurs ambiantes) depuis l'antiquité, période où l'on retrouve de nombreux témoignages des usages rituels ou bien cosmétiques de substances parfumées. Aujourd'hui, ces pratiques sont encore largement présentes à travers le globe, et ces odeurs exogènes rajoutées par-dessus notre odeur endogène peuvent, logiquement, potentiellement interagir avec celle-ci. Jusqu'ici jamais d'étude n'a été faite sur l'effet du parfum dans le cas particulier de la communication chimique des émotions chez l'humain, et encore moins des émotions positives.

Le but de cette thèse a été de tenter d'éclaircir ces zones d'ombres multiples afin de comprendre si une transmission des états émotionnels positifs via le sens olfactif existait chez l'humain, et quelle potentielle modulation le parfum pouvait avoir sur celle-ci. Pour cela, nous avons mis en place dans une première étude un paradigme expérimental chez des « donneurs », de qui nous avons collecté les odeurs corporelles pendant qu'ils ressentaient des émotions positives ou non, induites à l'aide d'extraits vidéos, puis avons fait sentir ces odeurs dans un deuxième temps à des « receveurs », chez qui nous avons effectué des mesures physiologiques, verbales, et comportementales. Nos résultats montrent que cette transmission semble être possible chez l'humain et qu'il s'agirait même non seulement d'une transmission (e.g., envoi des informations émotionnelles d'un individu A à un individu B) mais d'une « contagion » (e.g., synchronisation entre les états émotionnels des individus A et B), car des indices de l'affect positif des donneurs sont retrouvés chez les receveurs lorsque ces derniers sont exposés aux odeurs des premiers.

Dans une deuxième étude, nous avons repris le même design expérimental en testant cette fois-ci une méthode potentiellement plus efficace et écologique d'induire des émotions : via réalité virtuelle. Cette méthode permet de créer un environnement plus immersif, d'avantage proche des situations réelles hors laboratoire. Dans cette étude 2, les résultats de l'étude 1 n'ont pas été répliqués, ce qui nous a fait prendre conscience de la nature subtile et

hautement dépendante du contexte de ces signaux chimiques. Plusieurs pistes ont été envisagées pour expliquer la non réplication des résultats, notamment concernant des paramètres expérimentaux tels que la conservation des échantillons ou bien l'intensité des émotions générées via réalité virtuelle qui aurait pu être trop importante pour nous permettre d'observer des effets.

Afin de mieux comprendre la nature subtile et contextuelle de ces signaux chimiques, nous avons décidé d'augmenter encore le niveau de « réalisme » en menant une troisième étude faite à domicile, chez les participants. Dans cette étude 3, les donneurs et receveurs vivaient sous le même toit en tant que colocataires ou couples, ce qui nous a permis d'explorer la communication chimique chez des personnes se connaissant, par opposition à nos études antérieures ainsi qu'à la grande majorité de celles dans la littérature, mesurant la communication entre deux inconnus. Additionnellement à la nature de la relation liant donneur et receveur, nous avons également investigué l'impact d'autres paramètres : la durée de cette relation ainsi que les niveaux de sociabilité individuels des participants. Au cours de cette étude 3, nous avons observé des indices suggérant que la communication chimique entre humains est modulée par la nature de la relation liant les deux partenaires communicants, ainsi que par les niveaux de sociabilité de ces derniers.

La dernière étude (étude 4) est une preuve de concept et rend compte du développement méthodologique d'un outil (intitulé ABOV- Analysis of Body Odor Volatiles) permettant de mieux étudier les bases chimiques liées à ce type de communication. En effet, bien que les effets comportementaux en réaction aux odeurs corporelles humaines soient rapportés dans la littérature de façon plus substantielle d'année en année, les bases chimiques sous-jacentes restent encore largement inconnues. L'outil que nous avons développé est une étape vers la compréhension de ces bases, car il permet la captation des molécules volatiles odorantes au niveau du cou et des aisselles de participants, grâce à des polymères qui sont par la suite analysés en GC-MS. Cet outil permet également de résoudre certains points limitants ou sources de biais des approches disponibles jusqu'alors, via par exemple sa méthode de collecte sans contact direct avec la peau, ou bien l'absence d'émission de composés polluants non pertinents. Dans cette étude 4, le dispositif a été testé sur des participants pour évaluer sa capacité à discriminer des différences inter et intraindividuelles connues au préalable, comme par exemple le sexe des participants ou la zone du corps collectée.

Concernant la question annexe de l'ajout du parfum par dessus l'odeur corporelle naturelle, dans les trois premières études le faisceau d'évidences pointe vers un effet non perturbateur du parfum sur la communication chimique des émotions positives, celle-ci ayant été observée en absence et en présence de parfum. Pour certaines mesures verbales, un effet synergique du parfum et de l'odeur corporelle positive a été observé, mettant en avant des caractéristiques de cette dernière.

Finalement, un article hybride mêlant opinion, revue de la littérature et quelques données expérimentales, s'intéresse aux multiples défis et obstacles que doit surmonter, à notre avis, le domaine de la communication chimique chez l'humain (dont tous ont été rencontrés au cours de cette thèse). Cet article aborde également plusieurs pistes de réflexion ainsi que des perspectives pour de futures études.

**Mots clefs** : Contagion émotionnelle, communication chimique, émotions positives, parfum, cognition sociale

# Summary

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Humans are social animals that communicate in their environment through their sensory interfaces with conspecifics as well as other species. When talking about communication, the visual and auditory channels usually come quickly to mind, but another sense happens to be highly adapted to the transfer of information between individuals. The olfactory sense possesses many advantages: the chemical molecules at the origin of odors can -among many other examples- be emitted in the dark or go around obstacles. This makes the olfactory sense a privileged pathway to communicate, which is found in virtually all the animal kingdom, from the "simplest" to the most complex organisms. For decades, cases of so-called "chemical" communication have been reported in invertebrates, especially insects (e.g., bees, butterflies), but also in vertebrate species such as fish or elephants, in particular via molecules called pheromones.

In humans, the existence of pheromones is still debated, and knowledge about these odors of social nature is still relatively limited. Nevertheless, the smell of an individual's body seems to carry a wide variety of information about them, and these molecules, once captured by other individuals, whether relatives or strangers, seem to cause both cognitive and physiological effects in the latter. The scientific literature shows that individuals are able to gather information about another person's persistent traits (e.g., genetics, age, sex) as well as transient states (e.g., illness, stage of menstrual cycle) by being exposed to their scent alone. This communication and its effects take place in a non-conscious way, both for the individuals emitting the odor and for the individuals receiving it.

Among the transient internal states that can be communicated via the olfactory sense, one factor has recently been the subject of promising studies: body odors also seem to carry information about the *emotions* felt by the person emitting them. These studies have been mainly focused on the case of negative emotions, leaving aside positive states that are an integral part of our daily lives, and also carry major benefits for individuals, groups, as well as for society at large.

In addition to these shortcomings, another grey area takes shape when we look at a factor that often goes hand in hand with our natural body odors: exogenous odors. Humans have been perfuming themselves directly (on the skin) and indirectly (via clothing or ambient scents) since antiquity and these odors added on top of our endogenous odor can, logically, interact with it. Until now, no study has been done on the effect of perfume in the particular case of the communication of emotions, and even less of positive emotions.

The aim of this thesis was to try to clarify these multiple shadows in order to understand if a transmission of positive emotional states via the olfactory sense existed in humans, and what potential modulation the perfume could have on it. To this end, we set up an experimental paradigm in a first study with "donors", from whom we collected body odors while they were feeling positive or not, and then made them smell in a second time to "receivers", in whom we carried out physiological, verbal, and behavioral measurements. Our results show that this transmission seems to be possible in humans and that it is not only a transmission but also a "contagion", because indices of the positive affect of the donors are found in the recipients when the latter are exposed to the smells of the former.

In a second study, we repeated the same experimental design, this time testing a potentially more effective and environmentally friendly method of inducing emotions: via virtual reality. The results of Study 1 were not replicated, which made us aware of the subtle and highly context-dependent nature of these chemical signals.

To better understand this, we decided to further increase the level of "realism" by conducting a third study done in the home, where donors and recipients lived under the same roof as roommates or couples, to better understand the impact of the nature of the relationship binding the two communicating partners, as well as the effect of their sociability.

The last study is a proof of concept and reports on the methodological development of a tool (entitled ABOV - Analysis of Body Odor Volatiles) to better study the chemical bases related to this type of communication. This tool allows the capture of odorant molecules at the level of the neck and armpits of participants via polymers, which are then analyzed in GC-MS.

In the first three studies, the evidence points to a non-disruptive effect of perfume on the chemical communication of positive emotions, with even, for some verbal measures, a synergistic potential of perfume and positive body odor that would highlight characteristics of the latter.

Finally, a hybrid article mixing opinion, literature review as well as some experimental data, focuses on the multiple challenges and obstacles that the field of chemical communication in humans has to overcome (all of which have been encountered during this thesis). This article also contains some avenues and perspectives for future studies, which are discussed.

**Key words:** Emotional contagion, chemical communication, positive emotions, perfume, social cognition

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# Abbreviations

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<b>ABOV</b>	Analysis of Body Odor Volatiles
<b>AUT</b>	Alternative Uses Task
<b>BO</b>	Body Odor
<b>EMG</b>	Electromyography
<b>GC-MS</b>	Gas Chromatography-Mass Spectrometry
<b>HMHA</b>	3-Hydroxy-3-MethylHexanoic Acid
<b>LPS</b>	Lipopolysaccharide
<b>MHC</b>	Major Histocompatibility Complex
<b>MIP</b>	Mood Induction Procedure
<b>MUP(s)</b>	Major Urinary Protein(s)
<b>ODD</b>	Old Deodorized and Desensitized
<b>OR(s)</b>	Olfactory Receptor(s)
<b>TAARs</b>	Trace Amine-Associated Receptors
<b>VNO</b>	Vomeronasal Organ
<b>VOC(s)</b>	Volatile Organic Compound(s)
<b>VR</b>	Virtual Reality
<b>WEIRD</b>	Western Educated Industrialized Rich and Democratic
<b>3M2H</b>	3-methyl-2-hexenoic acid

# INTRODUCTION

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## 1 The Social Human as a Chemical Human

### 1.1 A precious tool at our disposal: sociality

To better understand the human species goes hand in hand with better understanding sociality and interactions between individuals. The knowledge accumulated over millennia, the most impressive architectural features and the most surprising microscopical artefacts, the human expansion over every continent on the planet, the unnamable terrors of wars, and the exploration of Mars all come as a result of humans concurring and acting together through their social nature, exchanging information, sharing intentionality and adapting to it.

In fact, this is such a core concept of our nature that when humans are ostracized and lack social bonds, it results in inhibited development of social, emotional, and cognitive skills, as well as poorer well-being (Williams, 2001). On the contrary, when humans benefit from social support and integration, they show better mental and physical health (Taylor, 2011). In a similar way, fostering social relationships results in enhanced longevity in many non-human primate species, including macaques (Brent et al., 2017) and baboons (Silk et al., 2010). Sharing a social space and partaking in social dynamics is thus inherent to our nature but is not the exclusivity of humans or of other primates, it also takes part in most animal species of the animal kingdom with specific dynamics including courtship, inter and intraspecific competition, mating behavior, predator/prey interactions, territoriality, and kin recognition *inter alia*. Mechanisms akin to social behavior might even take place in organisms lacking a nervous system: bacteria moves between colonies and is able to swarm or not, depending on if the strain is familiar or not (Gibbs et al., 2008). A common point links these social aspects: they all involve *communication* – there is always an individual sending a “signal” to a “receiver” who reacts to the obtained information (Wilson, 1979). This involves a socially shared symbol-system or code (Wiener et al., 1972) that can be multimodal in nature and is perceived through the receivers’ sensory machinery. Usually, various sensory channels are engaged simultaneously, especially in highly social creatures living in groups. To communicate a state of sadness for example someone might consciously use language to express that feeling, but

also unconsciously adopt a withdrawn posture, cry, and have a shivering mouth along with a broken voice and a lethargic demeanor. Whether we are aware of communicating or not, this, in a group, would be perceived by other members through their sensorial interfaces which would let them access this affective information, accompanied in most cases by an adapted behavior to the said perceived affective state. As Watzlawick et al. postulated in 1967 in the first axiom of their famous *Pragmatics of Human communication*: “One cannot not communicate” (Watzlawick et al., 2011). As social species, communication is a core concept that is inevitable, allows to better refine our behavior as a group, to attain basic goals and needs, to build communities and survive.

## 1.2 Communicating through chemistry

The visual and auditory modalities are the first ones to come to mind when thinking about communication, they require the sender and the receiver to be within seeing or hearing distance. Touch too requires an even more proximal contact. In situations when these channels can be difficultly exploited, another sense demonstrates its particular utility.

As Synnott opines (Synnott, 1991, my emphases in italics):

“Odour is many things: a boundary-maker, a status symbol, a distance-maintainer, an impression management technique, a schoolboy’s joke or protest, and a danger signal – but it is above all a statement of *who one is*. Odours define the individual and the group, as do sight, sound and the other senses; and smell, like them, *mediates social interaction*”.

Chemical signals are considered the oldest and most widespread form of communication across taxa (Wilson, 1970), and all cellular life-forms are sensitive to chemical information, whether coming from the environment, food, threats, or members of the same or other species. (Wyatt, 2014a). Additionally, olfaction is often described as a sense that cannot be shut (in normal physical conditions) since doing so would result in blocking vital respiratory functions, but closing our eyes or blocking our ears is found to be easier. Because breathing is indispensable, therefore humans are constantly screening the air around them. Air is ubiquitous around us and every organism living inside the atmosphere is in contact with it. Besides its fixed portion (i.e., nitrogen, oxygen, argon, carbon dioxide, water vapor), it also contains traces of many other substances, of natural origin or not, that differ locally and seasonally. These can include dust of mineral and organic composition, pollens, spores, volcanic ashes, industrial pollutants but also volatile compounds that are odoriferous. Notably, every living organism from bacteria (Smit et al., 2005), to plants (Heil and Karban, 2010), to insects (Ali and Morgan, 1990), or primates (Costello et al., 2014; Birkemeyer et al., 2016) emits chemicals into its environment, some of which can be sensed through the olfactory



channel.

The sense of smell relies on the presence of volatile (and less volatile) compounds in the air (and in some cases water) and therefore, besides its ubiquity, inherently comprises numerous advantages: smells can travel through short and long distances, they can stay in a definite place as a scent mark, or on the contrary be carried over air, they can be perceived in dark places when visual signals are hardly interpretable, persist in the environment, and may be dispersed along gradients which can be informative *per se*. Additionally, chemical signals are energetically inexpensive for organisms to produce and can go around obstacles (Krebs and Davies, 1993). Communicating and acquiring information through this chemical apparatus is therefore highly reasonable, even essential when visual or auditory signals would be at disadvantage (such as when a predator or threat is near). This type of signal can also be a support to cues conveyed by other modalities, since communication components can either be redundant or not in meaning, and redundancy reduces environmental noise thus allowing the message to be delivered despite the said noise (Johnstone, 1996).

In this particular “*chemical*” case, communication would involve a sender producing and releasing molecules into the air, that would travel to a receiver’s nose and could be caught by the olfactory receptors of these human or non-human animals. Interestingly, it is relevant to note that smell also happens to be a sensory modality that combines distal (like vision and hearing) and proximal (like taste and touch) perception, informing the receiver about sensory objects (other individuals for example) that are distant but also in direct contact, thus making smell a rather unique sense, fitted for versatile forms of communication.

## 2 Chemosensory Signals in Humans and Other Animals

### 2.1 Pheromones in the animal kingdom

#### 2.1.1 Original definition

In the animal kingdom, chemical communication is closely entangled with the concept of pheromones. *Pheromone* is a neologism composed of the Greek words *Pherein* (φέρειν - to transfer/carry) and *Hormôn* (ὁρμῶν - to excite/stimulate), coined by the German biochemists Peter Karlson and Martin Lüscher. They defined pheromones as “*substances which 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*" (Karlson and Lüscher, 1959). This neologism was proposed the same year that the first chemical characterization of a pheromone occurred (a molecule called bombykol<sup>1</sup>), in the wild silk moth by Nobel prize winner Adolf Butenandt and his colleagues (Butenandt et al., 1959).

Despite this term being adopted in the late 50s, this type of substance had been studied for several decades. The Austrian ethologist and zoologist Karl Von Frisch for example (also later known for his study of the honeybees' *waggle dance*), studied the sensory perception of European minnows by putting the damaged skin of fish into the water and then observing that minnows swam rapidly away, or adopted other behaviors such as shoaling, freezing or increased shelter use (Frisch, 1938). He hypothesized that the damaged skin released a substance (which was later named "alarm substance") that activated anti-predator behavior. In mice, a complex mixture of volatile compounds within urine affects reproductive and social behavior. The major urinary proteins (MUPs) are components of adult male urine that bind to volatile pheromones and regulate their release into the air from urine marks and can act as protein pheromones themselves. They are involved in a myriad of reactions including female attraction (Roberts et al., 2010), synchronization of ovulation in groups of females (i.e., "Witthen effect"), or puberty acceleration in juvenile females (Novotny et al., 1999a, 1999b). Pheromonal effects have been found in many other animals besides mice: female rabbits (*Oryctolagus cuniculus*) emit a pheromone to guide their pups to their mammary glands (Schaal et al., 2003) and blue crabs (*Callinectes sapidus*) mediate their courtship behavior by detecting pheromones through their antennae (Gleeson, 1980). Pheromones secreted by male terrestrial salamanders (*Plethodon jordani*) increase female receptivity (Rollmann et al., 1999) and queen honeybees secrete a mandibular pheromone that inhibits the ovary development of worker bees (Butler et al., 1962). In cichlid fishes (*Neolamprologus pulcher*), agonistic responses and aggressive displays are modulated by pheromones secreted in water (Bayani et al., 2017) and male tilapias (*Oreochromis mossambicus*) convey dominance status to avoid unnecessary cost-intensive fighting encounters (Saraiva et al., 2017).

### 2.1.2 Updated concept

This dissertation would be short to relate the multitude of examples of pheromones and their hypothesized impact, but since the original definition, pheromones have been found to be present in every part of the animal kingdom including in squids, lobsters, goats, elephants, fish, and they have roles only as diverse as their necessity: they rule attraction, mate choice, trail following, interactions between kin and parents/offspring and so on. Pheromones can be volatile or not volatile, soluble or not, large or small, short or long-range, carried to the receiver in air, water, or directly deposited onto their nose (Wyatt, 2014b).

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<sup>1</sup> Impressively, this molecule can be detected by moths up to 10km away

The pheromonal signal can either be composed of one or several molecules, which are released at once or successively. They can be found depending on animal species in the skin, dermal glands, saliva, breath, urogenital secretions, or anal glands for example. They are mostly esters, aldehydes, steroids, or saturated carboxylic acids. This particular category of signal seems therefore to be multiform and its nature uneasily described by a definition that would be strict and non-inclusive. In fact, the variety of molecules acting as pheromones across the animal kingdom suggests that almost any type of molecule released by an organism could act as a pheromone, given that it confers an evolutionary advantage (Wyatt, 2014b).

In the same vein, most pheromonal responses are thought to be “innate” meaning that they do not seem to require learning, are unconditional, “hardwired”. However, sometimes responses have been shown to be modified in subtle and context-dependent fashions, and/or to require specific conditions to be met in critical periods during development to arise (Wyatt, 2014). For example, male moths that have recently mated do not respond to female sex pheromones that would otherwise attract them (Barrozo et al., 2010). The conventional concept of pheromone implying a stereotypical stimulus-response reaction, besides other criteria described above, seems to therefore be too strict for the true way pheromones act. This becomes all the more true when studying the human species, in whom the effects of chemical signals seem to be much more complex. In the majority of cases, a human reaction towards an odor depends on context, personality, individual history, and actual motivation, and is thus hardly stereotypical.

## **2.2 Humans and their chemosignals**

### **2.2.1 Introduction**

So far, no human pheromones have been found, that is: i) chemically identified and ii) shown to have an effect when tested in rigorous bioassays (Wyatt, 2014b). Perhaps the closest case to a human pheromone takes form in a nipple secretion present in lactating mothers' Montgomery's areolar glands, which has been shown to stimulate nipple search and suckling selectively and unconditionally in neonates (Doucet et al., 2009). A positive correlation has also been shown between the number of areolar glands and the neonates' suckling behavior, weight gain in the first 3 days after birth, and speed of lactation onset (Schaal et al., 2006; Doucet et al., 2012).

However, this example aside, convincing examples of pheromones in humans have not been discovered yet, but scientists and scholars have been studying the field of communication nevertheless through the lenses of chemical signals (chemosignals) with interesting discoveries. A chemosignal is a chemical substance produced and released by an organism

(resulting from the combination of endogenous and exogenous factors) that is perceived by surrounding individuals (intra or inter-species) and communicates information.

This signal enters the communication frame in the sense that it passes information coming from a sender to a receiver of that same odor. These emissions are automatic, produced outside of the sender's voluntary control, and cannot be blocked. Even though the existence of pheromones in humans has been subject to debate and sometimes poor methodological design (Wyatt, 2015, 2020), other mammals rely extensively upon chemical communication (Petrulis, 2013), which is why it is very likely that chemical cues are important in our behavior too. Especially given the advantages of such a way of communicating as well as our, regular to say the least, propensity to smell ourselves and the people around us. A survey of more than 400 participants internationally, revealed that 60.64% of people report smelling strangers, 94.34% of people declare smelling their close relationships, and 94.31 and 91.58% of people smell their own hands and axillae respectively (Perl et al., 2020).

Being aware of the odor of our own bodies as well as the bodies of people in our environment seems therefore to be a constant, central phenomenon in human life.

### **2.2.2 Semantics and definitions**

At large, chemicals coming from the outside that provide information through the chemical senses and thus mediate the interaction between organisms are termed semiochemicals, an umbrella term coming from the Greek *semeion* (σημείον – signal), which is a synonym of chemosignal (see Figure 1). Pheromones are one type of semiochemicals, that have evolved to communicate information between two (or more) members of the same species. Regarding intraspecific communication, some signals have evolved to be relevant (i.e., pheromones) and some are contextually learned to be. Thus, all semiochemicals are not pheromones, but all pheromones are semiochemicals. Additionally, if a semiochemical is directed towards members of another species (interspecific communication), then the term allelochemical is used. Both groups are classified into subgroups depending on the effects they have (primer, releaser for pheromones) or to whom they benefit (kairomones, allomones, synomones for allelochemicals).

Another semantical nuance that should be considered, and which is not limited to the chemical senses but relevant to any communication at large, is the difference between a signal and a cue. Often in the literature the two terms are used interchangeably, which leads to confusion. A signal is an evolved way to actively convey information and influence the receiver's behavior, while a cue in contrast is a passive, non-evolved biological or environmental trait that inherently provides information to the receiver (Smith and Harper, 2003; Bradbury and Vehrencamp, 2011). The difference being intentionality: a signal is made by the sender to be received by a receiver, a cue is just collected and advantages the receiver only.

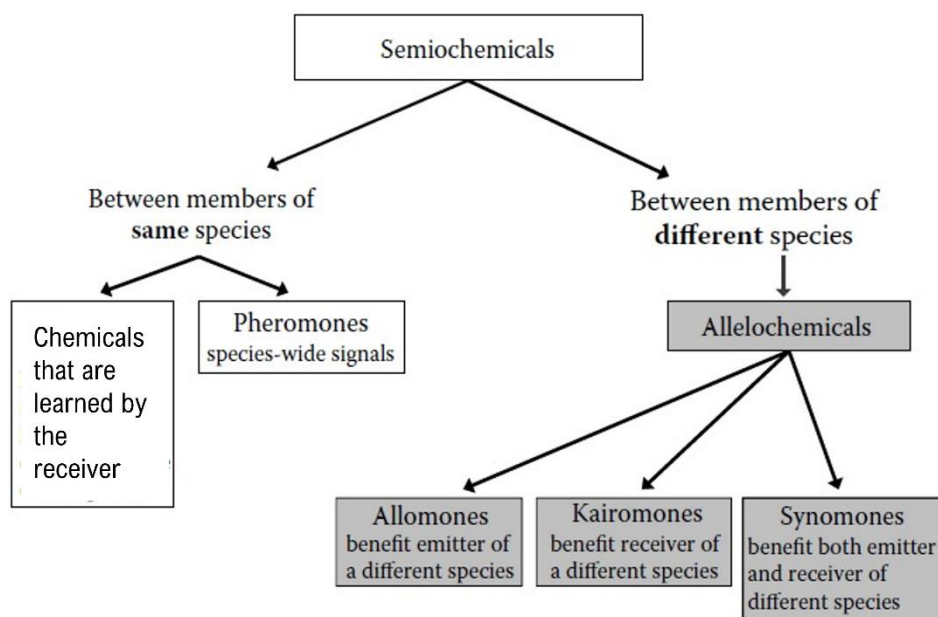


Figure 1: Diagram showing semiochemicals and different subtypes (adapted from Wyatt, 2014)

Organisms use both signals and cues to gather information, and often a cue can evolve to be a signal, in the same way any odor can potentially evolve to become a pheromone.

For the purpose of this dissertation, the technical classification of the chemical information, be it a pheromone, a chemosignal, a chemical cue, a semiochemical, etc., and especially if the molecules involved in human chemical communication have evolved to be or were learned to be, will not be discussed. For the sake of simplicity and independently of semantical debates, we will use the terms semiochemicals and chemosignals as synonyms to try to explore and document how a stimulus of chemical nature emitted by an individual can convey information to, and impact behavior in another individual exposed to it.

# 3 Body Odor Emission

One type of communication, called chemical, therefore exists between individuals of many living species and rules their interactions daily. In humans, volatile molecules emitted by the body, also called *semiochemicals* or *chemosignals* seem to mediate these exchanges. Where exactly is this body odor produced? What is its composition? These questions are an essential step in understanding this mode of olfactory communication and are addressed in the following paragraphs.

## 3.1 Body odor secretion

Humans do not possess a distinct scent gland like some other mammals, but dispose of around 3 million glands concealed in their skin which are capable of producing up to 12 L of fluid a day (Millington and Wilkinson, 1983). These glands, which emit the substrates for our natural body odor, are the following: i) sebaceous, ii) eccrine, iii) apocrine and iv) apoeccrine glands (see Figure 2).

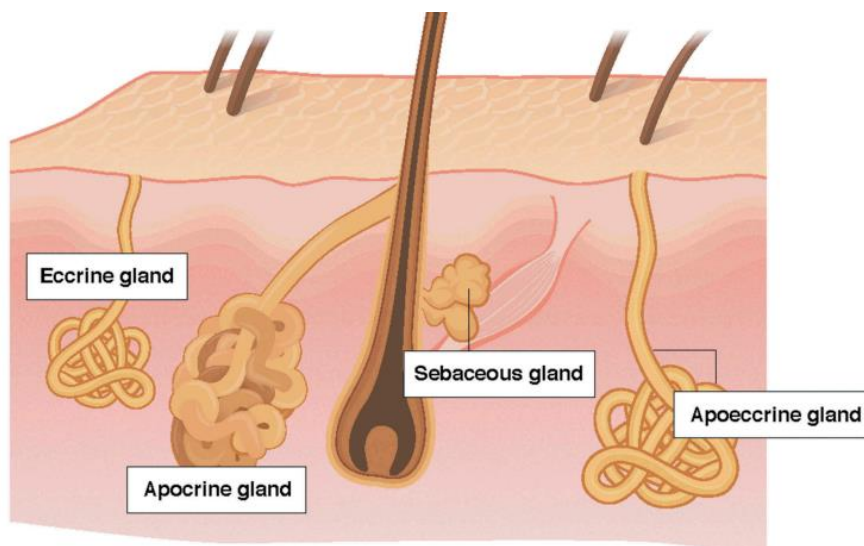


Figure 2: The different types of sweat glands on human skin (from Baker, 2019)

### 3.1.1 Sebaceous glands

*Sebaceous glands* are the exocrine glands associated with sebum. They are present on the forehead, the face and scalp, and absent on the palms and soles of the feet (Nicolaidis, 1974). They are also found in the ear canal (Meibomian Glands), lips, buccal mucosa (Fordyce's glands), nostrils, nipples (Montgomery's glands), eyelids (Meibomian glands), and anogenital region. Their role is to secrete most of the lipids of the skin (e.g., triacylglycerols, wax esters) to permit it to be waterproof and keep its suppleness. Sebum has been speculated to act as a concrete, a carrier compound that would retard the liberation of odorous molecules imprisoned in it (Zouboulis et al., 2008).

### 3.1.2 Eccrine glands

*Eccrine glands* which are referred to as "sweat glands" or merocrine glands, possess coiled tubules that reach the skin surface connecting the secretory part located deep inside the dermis to a sweat pore. Eccrine glands are present in virtually all areas of the body with the highest density in palms, soles, and head and they secrete an aqueous solution of inorganic salts and amino acids that has the role of thermoregulating the body by water evaporation of the said aqueous solution (Sato et al., 1995). Their secretion is sterile, and its primary components include bicarbonate ( $\text{HCO}_3^-$ ), potassium (K), sodium chloride (NaCl), and also minor components such as pyruvate, glucose, lactate, cytokines, immunoglobulins, among others (Bolognia et al., 2012). They are innervated by the sympathetic nervous system (cholinergic fibers) and are primarily activated by changes in deep-core body temperature. The glands that are situated in the palms and soles do not respond to temperature shifts but rather to emotional arousal.

### 3.1.3 Apocrine glands

*Apocrine glands* are the major source of body odors in humans. In the same manner as eccrine glands, they can serve a thermoregulatory role in some species, even if this role is not apparent in humans. Their localization is limited to areas with hair such as the axillae, the anogenital region, mammary alveoli, cheek region, eyelid (Moll's glands) external auditory meatus, scalp, and sternal region (Doty, 1981). Even if they are present in several locations, most of the apocrine glands are located in the axillae, where they produce an odorless, oily, and opaque secretion containing large amounts of cholesterol, proteins, C19-steroid sulfates, and trace levels of C19-volatile steroids (Gower et al., 1994; Spielman et al., 1995). This secretion is what produces the characteristic body odor after transformation by the axillary bacteria (mainly lipophilic and large colony diphtheroids and micrococci). Their secretion is adrenalin sensitive and is triggered by emotional stimulation in humans (e.g., anxiety, stress, fear, pain; Wilke et al., 2007).

### 3.1.4 Apoecrine glands

*Apoecrine sweat glands* are glands that, presenting characteristics of both, cannot be classified as either eccrine or apocrine (Wilke et al., 2007). They are larger than eccrine but smaller than apocrine glands and their secretory portion shows similarities to both glands' secretory coils. They are found in the armpits (in which they can represent up to 50% of the glands) and perianal region. Apoecrine glands are presumed to be the result of eccrine glands that were transformed through puberty and play a large role in sweating, by the secretion of a thin, watery sweat in a continuous way resembling the eccrine's (Wilke et al., 2007). Their innervation is sensitive to cholinergic and adrenergic activity.

### 3.1.5 Which glands release semiochemicals?

Among these glands, the apocrine ones are believed to be the best candidates for the production of possible human semiochemicals for several reasons (Doty, 1981). They i) produce the characteristic odor that we smell when we are close to others, ii) develop during puberty (accompanied by a change in body odor that is also observed in other primates from sexual maturity onwards), are functional only after then, and become nonfunctional after menopause, iii) their activity differs between men and women (McCance, 1938; Kawahata, 1960) with men showing much larger glands than women (although sometimes females possess a higher number of them), and finally iv) their activity is maximal during periods of excitement or stress.

## 3.2 Body odor composition

The odor known as "*body odor*" that can be perceived if close to someone else's skin or if we are in crowded places is a complex mixture of hundreds of chemical compounds including ketones, aldehydes, esters, hydrocarbons, carboxylic acids, alcohols, etc. (Costello et al., 2014). These compounds are transformed from the secretions of the skin glands (which are odorless and water-soluble), through bacterial decomposition present on the skin (e.g., corynebacteria, propionibacteria, staphylococcus) (Leyden et al., 1981; Wilke et al., 2007). This conjunction of the cutaneous bacterial microbiome and skin glands' secretions forms our peculiar endogenous odor (Gower et al., 1994; Troccaz et al., 2004). A fraction of it is genetically (Roberts et al., 2005; Kuhn and Natsch, 2009) fixed (i.e., *primary odor*), and a fraction of it is variable, depending on age (Mitro et al., 2012), diet (Havlicek and Lenochova, 2006), and physiological state (Singh and Bronstad, 2001; Shirasu and Touhara, 2011) for example (i.e., *secondary odor*), or on cosmetic practices (i.e., *tertiary odor*).

Recent studies document nearly 2000 different volatile organic compounds (VOCs), coming out of healthy human bodies, particularly from breath and skin (Costello et al., 2014) Despite



this, most of the research on *axillary* secretions has tended to focus on the presence of a few major compounds, that will be presented hereafter.

### 3.2.1 Steroids, sulfurs, and acids

The first type of the most studied axillary compounds is found in the androgen-derived steroids such as androstenol (5 $\alpha$ -androst-16-en-3-ol), androstenone (5 $\alpha$ -androst-16-en-3-one), and androstadienone (androsta-4,16-dien-3-one) that possess a pungent musk-like odor at high concentrations (Austin and Ellis, 2003). Androstadienone may be the precursor of the more odorous 16-androstene steroids (androstenone/androstenol) after implications of the axillary microflora. These steroids were originally described as key odorants in the axillae odor, however biologically they are present in very low concentrations (Gower et al., 1994) and most probably do not contribute consequently to the overall odor (James et al., 2013).

Several research groups identified almost simultaneously the strongest odorants in the axillary region to be sulfur compounds (Hasegawa et al., 2004; Natsch et al., 2004; Troccaz et al., 2004), of which 3-Sulfanyl-3-methyl-hexan-1-ol is the most important. More abundant quantitatively than sulfurs, some C6-C11 acids have also been reported (Natsch et al., 2006). Among those, the most prominent is 3-methyl-2-hexenoic acid (3M2H) (Zeng et al., 1991), and is present at far higher concentrations than the 16-androstenes. Interestingly, 3M2H is bound after secretion into the glands' lumen to ASOP1 and ASOP2, two carrier proteins that prevent the formation of smell. The characteristic odor only appears after bacteriolysis (Spielman et al., 1995; Jacoby et al., 2004).

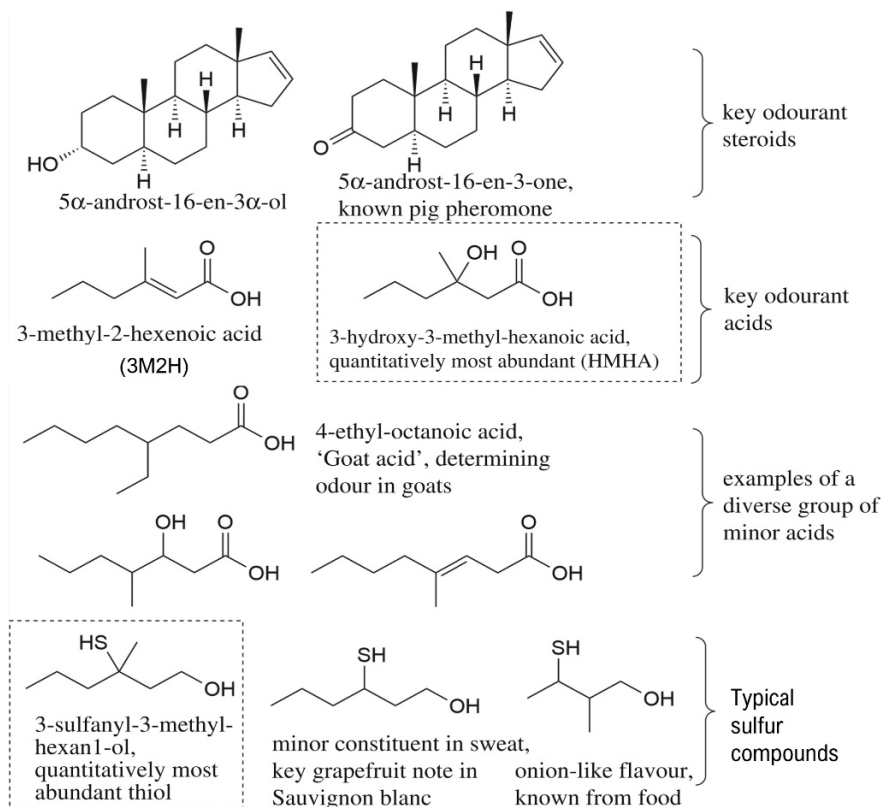
Another closely related acid, the 3-hydroxy-3-methyl-hexanoic acid (HMHA), was later identified as the most dominant human odorant, quantitatively (Natsch et al., 2003).

HMHA and 3M2H have, so far, not been described in any other species than humans. They are key representatives of a broader class of odoriferous acids, all sharing carbon skeletons that are related to the sulfur compounds, which suggests a common origin (Natsch and Emter, 2020).

### 3.2.2 Compounds in an evolutionary context

The components described in the previous paragraphs are particularly remarkable in the sense that their nature and unique chemical structure differ from compounds found in other sometimes strong-smelling parts of the body, usually studied in malodor management (e.g., breath, feet). While the latter are products of unspecific common catabolism, resulting from amino acids being degraded into volatiles by bacteria, fatty acids being transformed into short-chain fatty acids, or ketones and aldehydes by bacterial abiotic oxidation or  $\beta$ -oxidation, the former are not derived from simple byproducts of bacterial catabolism. Axillary odor

compounds are *specific odorants*, released *locally* as *specific precursors*, by *specialized glands*. This, suggests that they had (and may still have) an adaptive function in chemical communication, in an evolutionary context (Natsch and Emter, 2020).



**Figure 3:** Some of the known key axillary odorants. Note the common carbon skeleton of the most abundant acid and sulfur compounds, highlighted in dotted boxes. Adapted from (Natsch and Emter, 2020)

### 3.2.3 Interindividual differences in body odor composition

Some differences in body odor composition between individuals, be qualitative or quantitative, have been reported. For example differences in smells between sexes have been linked to different compounds emitted, the metabolism of glutamine conjugates creates a cheesy rancid odor for men and the sulfur-rich conjugates create an onion-like smell for women (Troccaz et al., 2008). Differences in quantity are also reported: the levels of 16-androstenes have been measured to be 50 times higher in males than in females (Gower and Ruparelia, 1993), and 3M2H is also proportionally more highly concentrated in males than in females (Zeng et al., 1996). Regarding differences between groups or individuals, a single nucleotide polymorphism (538G→A) in the gene ABCC11 was found to be responsible for the transition from a rather strong body odor in Caucasian and African populations to the fainter acidic smell (and interestingly white dry earwax phenotype too) found in Asian populations (Martin et al., 2010).

# 4 Body Odor Reception

## 4.1 Reception capacities

### 4.1.1 Is olfaction an inferior sense?

Human evolution was characterized by the gradual ascendance of vision and reduction of smell, as seen in the anthropological evidence recording diminution of the snout size and eye shift to the central part of the face to facilitate depth of vision (Jones et al., 1992). Additionally, the adoption of an erect posture as well as an arboreal habitat moved the nose away from the rich variety of odors present on the ground, hence diminishing the frequency and/or quality of stimulation.

In Aristotle's hierarchy of the sensorium, smell was considered of low status:

“At the top were the senses of sight and hearing, whose special contributions to humanity were beauty and music; [...] at the bottom were the animal senses of taste and touch, which alone could be abused, by gluttony and lust respectively [...] in between was smell: it could not be abused” (Synnott, 1991).

If Aristotle seemed to classify smell as an inferior sense, Kant did not even bother to discuss it in his aesthetics (Synnott, 1991). In the 18<sup>th</sup> and 19<sup>th</sup> centuries, philosophers and scientists again appraised sight as the “preeminent sense of reason and civilization, [while] smell was the sense of madness and savagery” (Classen et al., 1994). And still today, many people see smell as our least important sense. If you were given a list of things including cosmetics, your passport, phone, car, laptop, and your sense of smell, but you were allowed to only keep one, which one would you choose? In a 2011 survey named “The Truth About Youth” the McCann Worldgroup revealed that 53% of the more than 7000 respondents aged 16-22 and 48% of aged 23-30 would rather lose their own sense of smell if it meant keeping a technological apparatus such as their phone (McCann World Group, 2011).

### 4.1.2 General smell capacities

Although olfaction has been regarded as a “secondary” or “inferior” sense in popular belief, experimental studies show that this is hardly the case and humans possess an extraordinary, if underappreciated, olfactory capacity (Shepherd, 2004). Having adopted a bipedal position deprived us of some smells, but the capacity to cover large distances allowed us to access new ones by discovering new food sources. This retro nasal (i.e., perception of flavor coming from the oral cavity) food-based stimulation was multiplied by the domestication of fire that

allowed Sapienses to consume a whole new panel of possibilities, along with livestock, agriculture, and the use of spices (Sarafoleanu et al., 2009).

Additionally, the human capacity to smell has also been diminished by critics pointing out that the size of the human olfactory bulb is, relative to brain volume, much smaller than bulbs of species considered to be macrosomatic such as mice and dogs. This size difference has thus been brandished as proof of the evolutionary degradation of our smell faculties. Nevertheless, although the olfactory bulbs are indeed smaller in humans, they possess approximately the same number of neurons as macrosomatic species do, with more connectivity (Maresh et al., 2008). Moreover, the olfactory bulb is larger in absolute terms in humans than in these other species, so it likely did not decrease in size during evolution but rather the rest of the brain expanded around it.

In the last decades, the myth of an inferior or poor olfactory sense in humans has been proven wrong, as illustrated by numerous studies, such as those describing the human capacity to detect a single drosophila in a glass of wine via its odor (Becher et al., 2018) or those comparing our olfactory capacities to those of these famous microsomatic species: when comparing smell detection thresholds of some specific compounds, humans have been shown to perform as well or better than other primates, but also as well or better than other mammals. Specifically, for compounds composed of straight-chain aliphatic aldehydes, dogs perform better than humans on short-chain compound detection, but humans outperform them on longer chain compounds, and perform significantly better than rats as well (Laska et al., 2000).

Moreover, after immunity, the second biggest part of our genome is dedicated to olfaction with a large supergene family coding for  $\approx 400$  olfactory receptors (Buck and Axel, 1991; Niimura, 2009). Additionally to these functional genes, recent studies revealed that the number of pseudo olfactory genes is higher in humans than in other species, including macrosomatic ones (Rouquier et al., 2000; Glusman et al., 2001). The fact that these are pseudo genes and therefore not active is not an argument to defend the idea that humans have a poorly conserved or activated sense of smell, since non-coding regions of the genome play an essential role in gene regulation and RNA transcription (Tutar, 2012). Some have claimed (Bushdid et al., 2014), that humans could discriminate many more odors (*one trillion*) than they could discriminate tones (*half a million*) or even colors (*several million*). Not only humans can discriminate an important quantity of odors, but they can do so at very low thresholds. Ethyl mercaptan, an additive used to make unperceivable gases perceivable, is detected by trained humans at concentrations lower than 1 part per billion (ppb; Whisman et al., 1978), something translated to a real-life example by Yeshurun and colleagues (Yeshurun and Sobel, 2010): this would be equivalent to discriminating between two Olympic sized swimming pools, if only one contained three drops of Ethyl mercaptan.

### 4.1.3 Detection of body odor compounds in particular

Regarding the human capacity to detect body odor compounds specifically, Labows and colleagues reported that five compounds related to human body odor could be detected at concentrations ranging as low as 0.18 to 14 parts per million (Labows et al., 1999). Only one ounce (around 30 grams) of androstenone, a molecule found in boar's saliva and also described as a putative human pheromone, was enough to manufacture the 1.5 million scratch-and-sniff samples of the worldwide "smell survey" carried out by the National Geographic magazine in 1987 (Gilbert and Wysocki, 1987). In addition to low thresholds for some compounds, humans have been shown to process subtle differences in body odors: they can recognize the odor of their mothers upon birth, discriminate the odor of familiar people from strangers, and their own odor among hundreds (*see section 5 below*; Lord and Kasprzak, 1989; Macfarlane, 1975; Porter et al., 1986). This particular type of stimuli has also been shown to cause cerebral activation of subcortical regions as well as of areas of the neocortex related to odor processing but also to emotional and attentional processes (Jacob et al., 2001) when presented subliminally (*see section 4.3 below*).

Humans, therefore, seem to possess the capacities, when the relevant context and stimuli are presented, to very performantly detect compounds in the air around them.

## 4.2 Reception structures

### 4.2.1 Olfactory epithelium

The systems involved in the reception of semiochemicals are still a shadow zone in humans. One that logically comes to mind is the olfactory system, which is responsible for the perception of volatile organic compounds and creates the smell sensation, in conjunction with the trigeminal system which is responsible for the processing of cold, pungent, or burning sensations (Hummel, 2000). In this system, the reception happens through the olfactory epithelium, which is located in the postero-dorsal part of the nasal cavity. At the surface of this epithelium, are present olfactory neurons (between 10 and 20 million in humans) expressing olfactory receptors (ORs) at the surface of their cilia. Each olfactory neuron in the nasal epithelium is considered to express only one OR, in a highly specific way for certain specific features but tolerant for others (Araneda et al., 2000).

When one odorant enters the nasal cavity, it binds to several ORs, and one receptor can respond to different molecules, allowing for a combinatorial activation pattern for each compound. Subsequently, the odorant binding will activate G-proteins specific to the olfactory neurons, allowing the chemical information to be transmitted via the olfactory neurons' axons (grouped in afferent nerve fibers) to the olfactory bulb, through the lamina cribrosa.

However, in most animal species where pheromonal processes have been demonstrated, the detection of these chemical signals of particular nature happens in structures specifically devoted to their recognition. Among those, some are speculated to be involved in human reception too and are presented hereafter.

#### 4.2.2 Vomeronasal organ

The main structure that has been taken into account as being the seat of chemosignaling perception is the vomeronasal organ (VNO), a role that it endorses in many mammals including rodents, ungulates, and even some primates (Muller-Schwarze, 2006). Yet, in humans, the VNO does not seem to be a functional sensory organ (Knecht et al., 2001; even though some scholars have claimed it to be, see Monti-Bloch and Grosser, 1991; Monti-Bloch et al., 1994). It is visible in embryos and also as a cognate structure in fetuses (Boehm and Gasser, 1993), but atrophy seems to occur during embryogenesis (Bhatnagar et al., 2002). This organ -if not completely absent in adults- is considered to be vestigial for several reasons: i) it is deprived of sensory cells (Boehm and Gasser, 1993; Boehm et al., 1994), ii) an accessory olfactory bulb that would receive its nervous terminations is absent (Meisami and Bhatnagar, 1998), iii) no neural connection between the VNO and the brain is found, iv) most of the putative genes coding for the VNO receptors found in other species (V1R, V2R, and V3R) are nonfunctional in humans (Meredith, 2001).

The question of the existence or not of a functional VNO in humans, seems to be irrelevant in any case, since its observed absence or presence i) does not change the perception thresholds of some tested body odor compounds, such as 16-androstenes (Knecht et al., 2003; Frasnelli et al., 2011), ii) behavioral effects of chemosignals are still observed in humans (see *section 5*), observations which would not take place if chemosignaling perception relied only on an absent VNO, and iii) at least some pheromones and their effect on behavior or physiology have been shown to depend on the main olfactory system and not on the VNO in non-human animal models (Hudson and Distel, 1986; Dorries et al., 1997; Charra et al., 2012).

#### 4.2.3 Grüneberg ganglion and TAARs

A second olfactory subsystem, called the “Grüneberg Ganglion”, has also been taken into account to play a central role in the perception of semiochemicals in animals. It is a small cluster of neuronal cells first described by the British geneticist Hans Grüneberg in 1973 (Grüneberg, 1973) and has been shown to be involved in chemosensory perception in many mammals. In rodents, it is located at the tip of the nose, close to the naris entry, and its receptors are sensitive to biologically relevant chemical signals such as alarm pheromones (Brechtbühl et al., 2008) and predator odor (Brechtbühl et al., 2013). Therefore, this ganglion has been considered a candidate to play a role in the reception of semiochemicals in humans

as well. Although it is still elusive if primates, including humans, also dispose of a Grüneberg ganglion, some findings suggest that a related organ might exist, at least in human embryos (Grüneberg, 1973).

Recently, a novel class of G protein-coupled receptors named TAARs (Trace Amine-Associated Receptors) was detected on rodent Grüneberg ganglion cells (Fleischer et al., 2007) and also in olfactory neurons (Carnicelli et al., 2010; Wallrabenstein et al., 2013). The TAARs are receptive to endogenous amines that act as pheromones in mice (Liberles and Buck, 2006) triggering avoidance behavior for example (Dewan et al., 2013). TAARs, also present in humans, have thus been proposed as another potential pathway to mediate the detection of human chemosignals, however such propositions remain speculative, much like they are for the Grüneberg ganglion.

#### 4.2.4 An ubiquitous sense

Finally, some studies report the expression of functional extra nasal olfactory receptors, such as in gastrointestinal cells (Braun et al., 2007), sperm (Spehr et al., 2003), or prostate cells for example (Neuhaus et al., 2009). The perception of chemosignals could therefore even be located in other places than one definite specialized organ.

### 4.3 Cerebral processing

Irrespective of which organ or receptor would be responsible for the detection of complex semiochemicals, social odors coming from the body seem to form a distinct category and not share the same processing as “common” odors. First, we will present briefly the networks involved in the processing of classical odors and then we will present the brain structures that have been reported to be activated in response to body odors or body odor compounds.

#### 4.3.1 Classical olfactory networks

Among the central structures involved in the processing of odorants, the olfactory bulb is the first relay in the olfactory pathway. In the bulb, axons of the sensory neurons form synapses with the dendrites of the secondary neurons (i.e., tufted and mitral cells) and interneurons (i.e., periglomerular cells) within the glomeruli. Olfactory information is then transmitted from the olfactory bulb to the ipsilateral primary olfactory cortex (piriform cortex, olfactory tubercle, entorhinal cortex, anterior olfactory nucleus, amygdala; Carmichael et al., 1994; Zhang and Firestein, 2002). It is noteworthy that emotional and olfactory processes are entangled since they share common pathways in the limbic system, and some projections (e.g., olfactory tract

– amygdala) are bidirectional, making olfaction the only exteroceptive sensory modality to possess such connections with the limbic system (Zald and Pardo, 1997).

#### 4.3.2 Experimental reports on body odor processing

The neuronal underpinnings underlying body odor processing were first studied for compounds of the steroid family. Androstadienone was first found to cause the activation of subcortical and neocortex areas not necessarily involved in olfactory processing, such as regions regulating emotional and attentional processes (e.g., prefrontal cortex, hypothalamus, cerebellum, amygdala, cingulate cortex, visual cortex, thalamus) when presented subliminally (Jacob et al., 2001). This same compound was also found to cause differences in hypothalamic activation depending on sex (Savic et al., 2001) and later more exactly to depend on sexual orientation rather than sex (Savic et al., 2005; Berglund et al., 2006). The hypothalamus is involved in the regulation of basic biological functions or needs (e.g., thirst, sleep, fatigue, circadian rhythms), as well as in the hormonal secretion by the endocrine system, and has been regularly reported as recruited during exposure to androstenes.

Subsequently, social semiochemicals were studied by presenting not only one molecule but as a “whole”. These approaches are closer to reality since body odors are far from being monomolecular, but rather are composed of a mixture of hundreds of compounds (*see section 3.2*). Body odors collected directly on people were found to impact networks of the so-called “social brain”, which mediates among others the representation of emotional states in others, emotional attentional processing, or the processing of social stimuli. Structures such as the insula, the precuneus, the anterior and posterior cingulate cortex, the occipital cortex, the angular gyrus or the fusiform gyrus are activated after exposure to the odor of strangers or relatives (Lundström et al., 2008, 2009; Prehn-Kristensen et al., 2009; Lundström and Olsson, 2010; Pause, 2012), instead of the classical networks activated for non-social odors. Furthermore, smelling strangers activates the inferior frontal gyrus (Lundström et al., 2008), a structure involved in social processes as well as action inhibition/execution, while smelling friends activates brain regions involved in the processing of familiar faces and voices such as posterior parts of the retrosplenial cortex (Lundström et al., 2009). Additionally, parts of the reward system can also be activated in response to social chemosignals. For example, primiparous women show activation of the caudate nucleus when smelling the odor of newborns (Lundström et al., 2013), a structure also found to be recruited when socially open individuals smell body odors (Lübke et al., 2014), indicating that these social odors can represent a rewarding stimulus for some categories of people. Furthermore, the body odors collected on people during an anxiety-inducing event (awaiting an academic examination) activate areas in receivers supporting the processing of emotional stimuli (fusiform gyrus), as



well as networks associated with and regulating empathy (precuneus, cingulate cortex, insula; Prehn-Kristensen et al., 2009).

#### 4.3.3 Body odors are not common odors: the relevance of affective and social stimuli

Overall, these results accumulated over the years show the recruitment of heterogenous brain structures, but they all seem to point towards a common aspect: social body odors are not processed in areas recruited for common olfactory processes, but rather in networks of the so-called “social” and “emotional” brain. In particular, and although it surely differs vastly depending on the context in which the body odor is collected, a recent meta-analysis has emphasized the significant convergence of evidence towards the right inferior frontal gyrus (IFG; Dal Bò et al., 2020). According to the authors, the right IFG has been linked to numerous functions such as participating in the empathic response, the perception of facial expressions, the ability to understand others’ emotions as well as being an important hub of the human mirror neuron system. This region is thus implicated in basic and essential aspects of social cognition and communication.

The fact that these olfactory stimuli are handled by brain structures residing outside of the principal olfactory pathway is a phenomenon also found in other sensory modalities, in which stimuli that carry a high evolutionary significance for the individuals seem to be treated with priority processing (Öhman et al., 2001) and recruit subcortical areas not commonly activated otherwise. Stimuli such as faces (Morris et al., 1998) and infant cries (Seifritz et al., 2003) are processed in different ways than stimuli that are perceptually comparable but of limited behavioral relevance. For example, the perception of other humans’ facial expressions takes part in differential processing (via the fusiform face area) when compared with common visual objects (Kanwisher et al., 1997), and social/affective touch, which fosters relationships and bonds, is also processed differently (insular cortex, orbitofrontal cortex) than discriminative touch (classical somatosensory areas S1 and S2) (McGlone et al., 2014).

# 5 The Secrets Concealed in the Odor of our Skin

As discussed previously, all over the animal kingdom different species seem to rely on the odors produced by their bodies to communicate social information to conspecifics. In that sense, humans are animals like the rest, and the odor of our skin also contains information about us, even if we remain largely unaware of such phenomenon. Although the existence of human pheromones still remains speculative *stricto sensu*, the impact of chemosignals on people is less dubious: a large corpus of studies has explored the diverse qualities that could be conveyed via this media, and some of these studies will be presented over the following paragraphs.

## 5.1 The first studies: sexual attraction and partner choice

### 5.1.1 Fertility status and cycle synchronization

The pioneering works regarding human semiochemicals were related to fertility status and its implication in sexual attraction. Martha McClintock, in the early '70s, reported that females sharing the same apartment happened to synchronize the onset of their menstrual cycle with their roommates (McClintock, 1971). An observation that was demonstrated experimentally by other scientists afterwards (Graham and McGrew, 1980; Russell et al., 1980; Quadagno et al., 1981).

Subsequently, this cycle synchronization phenomenon has been tested in dozens of variable samples including lesbian couples (Weller and Weller, 1992), bedouin mothers and their daughters (Weller and Weller, 1997), basketball players (Weller and Weller, 1995), women sharing offices (Weller et al., 1999) and so on, with mixed results. Albeit it is hypothesized that these discrepancies would be caused by the influence of factors not pinpointed yet - among which: time spent together, emotional closeness, and cycle regularity-, it should also be pointed out that the majority of these studies has been criticized for theoretical, statistical and methodological flaws, especially concerning how menstrual synchrony was computed (Wilson, 1987; Schank, 2001, 2002; Yang and Schank, 2006) or the lack of control groups.

Body odors also seem to contain cues of menstrual cycle stage that could be perceived by others, specifically men. In the follicular (i.e., fertile) phase, odors collected on women are rated by men as least intense, more attractive, and more sexy than the odors of the same women in the luteal or menstrual phase (Singh and Bronstad, 2001; Havlíček et al., 2006), and these

cues seem to be long lasting since they can be detected after one week of samples being stored at room temperature (Singh and Bronstad, 2001). These results suggest that men could use the sense of smell to monitor menstrual cycle phases in current or prospective sexual partners.

### 5.1.2 Partner choice and MHC

Body odors have also been extensively studied in the context of partner choice. The major histocompatibility complex (MHC) is a group of genes involved in the immunological recognition of self (i.e., endogenous components) and non-self (i.e., exogenous components) in animal species (Penn and Potts, 1999). The products of its genes play a role in the immune system by binding peptides of foreign origin and then presenting them to the cell surface so they can be recognized by other components of the immune system (Penn, 2002). The MHC is the most studied model of preference for complementarity and shows high diversity (over 200 different alleles in some loci in humans). Since the inheritance of MHC alleles is codominant, offspring of two parents with different alleles will show a higher resistance and improved immune response to a wider spectrum of infections. This immunocompetence feature is thought to be selected in the mating choice process with individuals expressing preferences for people with MHC profiles that differ from their own, and would also serve to prevent inbreeding. This idea took its genesis with pioneering work done by Yamazaki and colleagues (Yamazaki et al., 1976), which reported that mice preferred the odor of conspecifics with dissimilar MHC alleles than their own. Since then, these results have been replicated in numerous vertebrate taxa (Bernatchez and Landry, 2003), and some studies have suggested that this is the case in humans too (Thornhill et al., 2003; Sandro Carvalho Santos et al., 2005).

Some anecdotal reports have been in coherence with such claims, for example the Tucano people from Colombia believe that people have a certain odor and that marriage should happen between two people of different odor categories (Classen, 1992). Furthermore, in experimental studies, experts have even been able to perceptually discriminate different MHC alleles, even if this remained difficult (Wedekind et al., 2007). This pattern of MHC-dissimilarity preferences is reversed in women using hormonal contraception (Wedekind et al., 1995; Roberts et al., 2008), and this is thought to have a significant impact on relationship quality and frequency of breakup (Garver-Apgar et al., 2006). Couples who met while the woman partner was under hormonal contraception show lower sexual satisfaction but higher overall relationship satisfaction (Roberts et al., 2012).

Still, there is an ongoing debate because mating with highly dissimilar individuals may cause an outbreeding effect, that is, disruption of locally selected gene complexes and some studies have reported that couples in their samples did not have a superior MHC dissimilarity than expected by chance (Ihara et al., 2000) or even preference in some cases for similar MHC, depending on the relationship status and contraceptive use (Wedekind et al., 1995; Roberts et al., 2008). Some studies have also reported a preference not for total dissimilarity but rather for intermediary levels of dissimilarity (Reusch et al., 2001; Jacob et al., 2002), and meta-analyses have emphasized that the preference seems to be rather towards MHC-diverse (heterozygous) partners rather than MHC-dissimilar ones for humans and that this is likely conserved in primates (Winternitz et al., 2017).

Taken together, although some results can be context-dependent or modulated by other factors, mate-related odor preferences seem to be associated with genetic heritage (for a review see Havlicek and Roberts, 2009).

### 5.1.3 The particular case of Androstene compounds

It has been suggested that androstene compounds might act as human pheromones and would have a role in sexual attraction (for reviews see Grammer et al., 2005; Mostafa et al., 2012). These compounds: 5 $\alpha$ -androstanol, 5 $\alpha$ -androstenone and androstadienone (see *section 3.2.1*) were originally found to affect mating behavior in pigs, then also found in human sweat and therefore tested as stimuli for studies in humans.

If androstenone is sprayed on one chair in a dentist's waiting room, this odorized chair is significantly more used by women, and less by men, even if this chair is moved every day. Cowley and colleagues (Cowley et al., 1977) asked 183 male and female participants to wear surgical masks infused with androstanol while evaluating opposite-sex individuals. Female, but not male participants, gave better evaluations if exposed to androstanol. Kirk-Smith and colleagues (Kirk-Smith et al., 1978), observed that attractiveness ratings given to female photographs increased if the participants were wearing an androstanol-infused mask. Androstadienone too has been reported to affect mood, skin conductance activity, cortisol levels, and social perception (for a review see Havlicek et al., 2010) especially in women (but see (Ferdenzi et al., 2016a), for evidence of non-sex-specific effects). These components of underarm secretions of men have been said to reduce tension, increase relaxation and stimulate the onset of the next peak of LH in women (Preti et al., 2003).

However, exposure to androstanol and androstenone makes male participants feel less attractive (Filsinger et al., 1985) and some studies show no effect of androstanol on attractiveness (Black and Biron, 1982). The effects, if existing, seem to be highly context-dependent and go

far beyond the original definition of a pheromone that would trigger a specific behavior unconditionally (*see section 2.1.2*). The question of the effects of these “putative pheromones” remains therefore much debated, with research in this area having undergone considerable criticism and controversy (Wysocki and Preti, 2004; Havlicek et al., 2010; Wyatt, 2015, 2020).

## 5.2 Identity, kin and non-kin recognition

Recognizing individuals and differentiating them from one another is crucial for reproductive success and keeping group solidarity. It allows identifying one’s own progeny, as well as to defend resources such as mates, territories, or food from intruders or competitors, while at the same time accepting familiar individuals. Thus, it rules many social dynamics in and outside a group.

### 5.2.1 Telling friend from foe

The *Desana* people of Amazonia have a specific way of distinguishing between tribes. They constantly sniff their environment because they declare that each tribe emits a specific odor, that they are able to detect and follow in their territory. As such, while walking through the forest they use this capacity to smell if another tribe member has been present shortly prior (Classen, 1992).

This anecdotal evidence has been backed up by experimental studies. Relatives can reliably detect the odor of siblings among the odor of strangers of the same age and sex (Porter et al., 1986), the odor of identical twins can be matched by exterior perceivers above chance even if the twins are living apart (Roberts et al., 2005), and we are able to pick out a shirt worn by ourselves out of 100 shirts worn by others (Lord and Kasprzak, 1989).

These discoveries have been taken a step further with analytical chemistry procedures. When analyzing the sweat, urine, and saliva volatiles emitted by 197 adults in an Austrian village, 373 peaks are consistent over time and among these, distinct and reproductive differences can be spotted through sexes and individuals (Penn et al., 2007a), which backs up the idea that humans all possess a very unique chemical fingerprint. This fingerprint has been shown in mice to be unique rather quantitatively than qualitatively. In other words, individual odor signature contains few, if any, unique compounds and what appears to convey individual information in the chemical profile is the relative proportion of volatile compounds (Singer et al., 1997; Schaefer et al., 2002).

### 5.2.2 Sex

Besides the study of the individual chemical signature as a whole, some studies showed an early interest in the possible recognition of one quality composing identity in human body odor: the sex of the individual from which it originates. Pioneering works have reported the explicit ability of participants to perceptually discriminate the odors of men from those of women, without having been trained to do so (Russell, 1976; Hold and Schleidt, 1977).

Nonetheless, these studies have been criticized (Doty et al., 1978) and the assignment of sex seems to be based solely on intensity and pleasantness judgements: body odors that are stronger and less pleasant tend to be attributed to men, and body odors less strong smelling and more pleasant tend to be attributed to women, independently of the true sex of the donor. Regarding chemical profiles, some evidence has supported the idea that discrimination can be made, by finding sex-specific volatile compounds (Penn et al., 2007a), as well as by finding a concentration variation of sex-specific non-volatile odor precursors of axillary sweat (fatty acids and thiols; Troccaz et al., 2009).

### 5.2.3 Age

Another factor that participates in defining interindividual odor signature is age. The odor emitted by our bodies changes during puberty (*see section 3.1*) but also later in life for older people. The apocrine and sebaceous skin glands being under androgenic hormone control, this could contribute to the changes in skin odor since levels of androgen hormones decrease with age (Zouboulis et al., 2007). Some studies have tried to elucidate the chemical profile of the “old age odor”: three compounds (i.e., dimethylsulphone, benzothiazole, nonanal) have been found to correlate with age (Gallagher et al., 2008a). In another example, Haze et al. (2001) also found rapid increases of 2-nonenal (a compound reported to smell like orris, fat and cucumber) in individuals older than 39 years old.

### 5.2.4 Parent-offspring

In the case of parent-offspring bonds, recognizing progeny allows maternal and paternal resources to be distributed to the own offspring, while being kept from the offspring of others. This chemosensory form of recognition is also speculated to facilitate the rapid development of parent-infant attachment, motivating parents to take care of the infant and thus providing food and protection, *in fine* strengthening reproductive success by keeping infants safe. Some examples can illustrate such claims: human infants, for example, possess the ability to recognize their mothers by scent (Macfarlane, 1975; Cernoch and Porter, 1985). In the same way, mothers can recognize their offspring’s odor (Porter et al., 1983; Ferdenzi et al., 2010) even if they have only been exposed to it during time periods as short as 10 minutes post-

partum (Russell et al., 1983; Kaitz et al., 1987). This chemosensory preference of neonates towards body odor cues coming from their mother seems to be acquired during pregnancy, since they also orient themselves towards the odor of amniotic fluid preferably than a control (Schaal et al., 1995). They are also capable of discriminating their own amniotic fluid from an unfamiliar one (Schaal et al., 1998), and this regardless of their feeding regimen (breast or bottle-fed). Conversely, this feat is also possible by mothers and fathers, who are able to discriminate between a sample of their infant's amniotic fluid and a sample of an unrelated one.

If put in contact with nightgowns worn by their own or unfamiliar mothers, newborn infants tend to calm down (Sullivan and Toubas, 1998). In return, the odor of neonates elicits increased responses in neostriatal areas in women (both primiparous and nulliparous) that are linked with reward learning mechanisms (Lundström et al., 2013), suggesting a potential reward mechanism fostering maternal motivational and emotional responses to infants.

### **5.3 Neonates and breastfeeding**

An interesting example, that is probably fostered by parent-infant recognition but that has its own use, is the relationship that neonates have regarding breastfeeding. As said earlier, this is perhaps the closest example so far of a human pheromone. When placed on mothers' stomachs, newborn babies crawl to the breasts of their mothers, and they do not show this type of behavior if the areolas are previously washed (Varendi and Porter, 2001). This would indicate that neonates use the sense of smell and are able to detect volatiles secreted by their mother areolas to guide themselves to be fed. This behavior is observed also in other species such as in rabbits (Coureaud et al., 2003; Schaal et al., 2003). Human babies also show a preference for the odor of lactating breasts, even when they are fed on formula, therefore this preference seems to be independent of previous reward reinforcement (Porter et al., 1991). Examination of the areolas shows that a higher alveolar gland density is positively correlated to faster onset of breastfeeding and suckling activity (Schaal et al., 2006).

### **5.4 The scent of sickness**

#### **5.4.1 History and diagnosis**

Pathological processes, such as infection or metabolic disorders, can modify the profile of volatile organic compounds (VOCs) in body odor either by producing new VOCs or changing the ratio of already existing ones. These changes can be perceived and used as medical diagnosis or sickness detection in social settings. Diagnosis by smell goes back to Hippocrates (460b.c. – 370b.c.) and Avicenna (980-1037), who reported some pathologies to possess

characteristic smells and the usefulness to exploit them. In Middle Ages, smell itself was considered to be the cause of disease, present in the air as *miasmas*. To thwart miasmas, people carried scented pouches, used unguents, or perfumed torches during periods of plagues and pandemics. Since then, the medical profession over centuries has used smell as a diagnostic tool to recognize woes such as gout, yellow fever, scrofula, uremia, typhoid, diphtheria, pellagra, rubella, gastrointestinal problems, respiratory problems and so on (Doty, 1981; Shirasu and Touhara, 2011; Tizard and Skow, 2021).

This “diagnosis by smell” is also attributed to other mammals. Dogs were found to alert their owners of skin lesions later becoming melanomas (Williams and Pembroke, 1989) or basal cell carcinomas (Church and Williams, 2001), and since then they have been trained to facilitate smell-based diagnostics to detect cancerous patients by smelling exhaled breath or stool samples (Sonoda et al., 2011) for example.

In a less organic example, electronic noses are also able to discriminate the odor of pathological organisms such as helicobacter pylori (Pavlou and Turner, 2000) or discriminate cancer cells in vitro (Kateb et al., 2009).

#### 5.4.2 Behavioral impact

The odorous pattern change in VOCs infectious states can therefore be detected, at least by some species, and this may cause a behavioral impact found in social interactions. For example, in rodents, disease is known to alter body odor resulting in a lowered preference for the infected animal during investigation by conspecifics (Ehman and Scott, 2001, 2002). Lipopolysaccharide (LPS), is used to activate the innate immune system and artificially induce an inflammatory response, so that this state and the associated processes can be studied (Beutler, 2009). After LPS exposure, rats show increased avoidance of the injected individuals (Arakawa et al., 2009; Dantzer, 2009).

The olfactory detection of the immune and inflammatory responses has also been shown in humans. After a few hours, participants exposed to LPS had a more aversive body odor than those who had received a placebo (Olsson et al., 2014). These findings have been extended in subsequent studies in which body odors after LPS injection tend to decrease face liking (Regenbogen et al., 2017) and decrease overall person liking (Sarolidou et al., 2020) when presented concomitantly.

Olfactory cues may modify not only avoidance behavior directed towards the sick or unhealthy but also approach behavior if “healthiness” related cues are present/or disease-related cues are absent. Thus, they are likely to have an impact on diverse social phenomena such as exclusion/inclusion but also on mate choice (*see section 5.1.2*).



# 6 The Chemical Transmission of Emotions

Recently, another trait or feature conveyed by the human body odor has received considerable scientific attention in the field of human chemical communication: the potential transmission of emotions and affective states, a question that was explored prior in fields dealing with other animal models. Stress responses for example, have been associated in many major taxa with the release of chemosignals directed to conspecifics or predators (Fanselow, 1985; Zalaquett and Thiessen, 1991; Suh et al., 2004). Could such a mechanism exist and play a role in the human species too?

## 6.1 Introduction – the pioneering studies

A very first evidence of chemosensory communication of emotions in humans originates in a thesis dissertation presented by Patricia Owen (Owen, 1981), entitled *olfactory correlates of induced affect*. In the manuscript, the authors proposed to “investigate the possible emotion-odor interaction by determining whether humans could differentially detect other humans’ odor collected under varying emotional conditions”. For this, they collected, with the help of cotton pads, the odor of 4 women while they underwent mood induction procedures supposed to induce states of relaxation, anxiety, and sexual arousal. These samples were, at a later stage, evaluated by 16 male judges who were able to separate the anxiety-state samples from the relaxation and sexual arousal ones in an “unpleasantness rating” task. For the relaxation and sexual arousal samples the evidence was inconclusive, the authors stating that it may be due to “methodological challenges”. Such methodological challenges are still present today for example the difficulty to create a positive relaxation state or sexual arousal when in an experimental setting.

A few years later, at the turn of the century, came publications that laid the foundation for the future studies of human chemical communication. In a preliminary study, Chen and Haviland-Jones (2000) showed frightening or funny clips to participants (men and women) to induce in them fearful or happy states respectively (Chen and Haviland-Jones, 2000). They then asked other participants to choose the “odor of people when they are afraid”: both men and women rightfully selected the congruent odors of “fearful” men above chance, but participants could not choose the right odor when it came to “fearful” women body odors. Women also correctly chose the “odor of people when they are happy” collected on men and women, however, men

were only successful at identifying the odor of “happy women” and not of “happy men”. More than the identity-intrinsic qualities of the odors (such as age and sex tested in the previous study) they found that the affective state in which body odor donors were, impacted the mood of perceivers of the said odor. Women generally recognized odors better than men which could be the result of better smell sensitivity but also a higher capacity to perceive differences associated with emotionally significant stimuli (Chen and Haviland-Jones, 2000). In a similar study, participants watched either a terrifying or an emotionally neutral control movie while their axillary odors were collected. A triple forced-choice test showed that participants were able to discriminate between the fear and the non-fear axillary pads (Ackerl et al., 2002).

## **6.2 Transmission of negative emotions – a textbook case**

Beyond this conscious identification, there appears to be some unconscious responses and effects generated by these chemosignals as well, and in the following years, several experiments took those findings a step further by exploring the so-called negative states.

### **6.2.1 Are all negative states equal?**

Notably, most scholars have been interested in fear and anxiety. Before proceeding, please note that although both of these concepts share some overlap, and that in the past some theorists have considered them isomorphic, persuasive evidence shows that fear and anxiety are different (Öhman, 2008). While fear is short-lived, present-focused, geared towards a specific threat, and related to avoidance behavior thus facilitating escape, anxiety is long-acting, future-focused, directed towards a broad unspecific threat, and is associated to sustained hypervigilance and prolonged arousal (for a complete discussion see Sylvers et al., 2011). Despite these differences, in the field of human chemical communication researchers have used these concepts rather interchangeably, sometimes using the word fear, sometimes anxiety as well as sometimes stress. Although using these terms as synonyms seems rather incorrect based on the emotional literature, the field has postulated that fear, stress, and anxiety may share a common mechanism by activating the fast stress (i.e., the sympathetic-adrenal medullary) response system (Ackerl et al., 2002; de Groot et al., 2015b). This system releases adrenalin, which then activates the apocrine sweat glands in the armpit region (a phenomenon known as psychological sweating, see Harker, 2013 for a review), and this would be responsible for the chemosignal production. This being noted, we will present the studies with the labels used by the own researchers that carried them.

### 6.2.2 Behavioral and physiological effects

Some groups argued that the emotions created were not strong or real enough and tried to establish acute emotional inductions with real life-like situations. Pause and colleagues, for example, introduced a new method to induce anxiety. They collected body odors on donors just before real-life anxious events (e.g., academic oral examination), and reported effects on subliminal face perception. In females, being exposed to anxiety chemosensory signals diminished the positive emotional priming of facial affect perception (Pause, 2004). With the same inductational paradigm, Prehn and colleagues (Prehn et al., 2006) found that females presented with anxiety chemosignals showed increased startle reflex<sup>2</sup> amplitude in response to auditory stimuli (versus either unused cotton pads or body odors collected during exercise). They interpreted this as the chemosensory anxiety signal priming defensive-like behavior, the startle reflex indicating enhanced vigilance. In a follow-up study, they showed that the observed startle response was potentialized in socially anxious individuals (Pause et al., 2009). In the same fashion of recreating realistic emotional inductions, sweat collected in men during high rope courses also significantly increases the state of anxiety in female participants (versus an exercise condition) (Albrecht et al., 2011) and makes men rate happy faces less positively (Zernecke et al., 2011)

Further repelling the limits of our knowledge, the neural correlates of these so-called “alarm signals” have also been explored. After smelling male sweat samples collected during a first-time tandem skydive, activation of the amygdala was shown (Mujica-Parodi et al., 2009) to take place in receivers, in comparison to when exercise sweat was presented to them. This finding is in line with the role of the amygdala, which is involved in the evaluation of stimuli for potential threat and hence recruited in response to fear-inducing stimuli. The same year, another study showed activation of the insula, thalamus, prefrontal cortex, fusiform gyrus, precuneus, and cingulate cortex in response to an anxiety chemosignal and the authors discussed this semiochemical as activating areas belonging to an empathy-processing network (Prehn-Kristensen et al., 2009).

### 6.2.3 Conclusions

To sum up, there is substantial evidence to assert that anxiety/fear/stress chemosignals are perceived by people exposed to them and that they cause behavioral and physiological adaptations. These adaptations are at least as powerful as ones caused by audiovisual stimuli (de Groot et al., 2014b), and this seems to be true even beyond ethnocultural boundaries (de Groot et al., 2018). As resumed in a meta-analysis in 2017, since the years 2000s and until

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<sup>2</sup> The startle reflex is an unconscious defensive response to sudden and intense stimuli (strong noise or sharp movement for example). It is associated with negative affect, and serves to protect vulnerable parts of the intact body, by reactions such as a whole-body startle or eye blinking.

the time of writing, there were over 25 studies including more than 1700 participants studying the effects of body odors collected in these negative emotional states. The authors concluded that the found effects were veracious and did not show evidence of publication bias (de Groot and Smeets, 2017). This emphasizes the robustness of the combined findings showing that semiochemicals of fear and related states would share a common mechanism; namely the activation of a *fast* stress response system mediated by adrenalin that would stimulate apocrine secretion and allegedly produce semiochemicals as a result. These would then be carried to surrounding individuals and would cause a change of state that would resemble the donors'. There is therefore not only a mere transmission but a *contagion of emotions* through smell. Other negative affective states than the ones previously discussed have been tested with similar results: body odors collected during situations designed to induce disgust also trigger disgust-like states in the receivers (de Groot et al., 2012). The replication of these states goes with the replication of different sensory strategies. Fear chemosignals trigger both fearful facial expressions but also improved sensory acquisition (e.g., increased sniff magnitude, increased eye scanning) and disgust chemosignals trigger both disgusted facial expressions but also sensory rejection (e.g., decreased sniff magnitude, decreased eye scanning, and decreased target-detection sensitivity). In other words, being exposed to emotionally charged body odors creates congruent emotions in the observers. By changing our sensory acquisition, they improve survival: fear-related characteristics allowing us to scan for potential predators and threats, thus preparing us to respond adequately, and disgust to avoid noxious stimuli (Susskind et al., 2008).

These changes are not caused by mere differences in the stimuli intensity or hedonicity since chemosignals and controls are comparable in such scales (Prehn et al., 2006; Prehn-Kristensen et al., 2009; Adolph et al., 2010; Albrecht et al., 2011; Gelstein et al., 2011) and most of the times the stimuli are not even consciously perceived (Chen and Haviland-Jones, 2000; Ackerl et al., 2002; Mujica-Parodi et al., 2009; Zhou and Chen, 2009). The effects remain therefore largely unknown to perceivers.

# 7 Positive Emotions

As developed until now, virtually every study in the field of human chemical communication has been centered around “*negative*” states, encountered in threat response/harm avoidance. Even in the handful of studies that did not study fear, this shift towards negative emotions or states is present (anger: Hatcher, 2016, aggression: Mutic et al., 2016, disgust: de Groot et al., 2012b; dominance: Adolph et al., 2010).

This bias is particularly striking when thinking about *positively valenced* emotions, which have been set aside in this field -sometimes not even mentioned- but this negativity bias is not the monopoly of human chemical communication and is found all over the psychological literature. Why has the positive side of affect been neglected? To understand why this literature gap exists, it is necessary to first dwell on the very particular nature of positive emotions at large, as well as their functions, which will also emphasize why it is fundamental and crucial to explore these states that are an integral part of human functioning and human lives. After definitions and a short explanation of why these states have been majoritarily set aside, we will address their effects on human cognition and physiology as well as their benefits in the long and short term, before finally summarizing the present findings of the effects of positive emotional semiochemicals.

## 7.1 A puzzle for the scientific community

Emotions are mental states, created by multicomponent response tendencies comprising subjective feelings, cognition, attention, facial expressions, cardiovascular and hormonal changes, and these components are unfolded over a short time span (Lazarus, 1991; Tooby and Cosmides, 2008). Positive emotions form a distinct and particular group in the emotional spectrum. They include a range of specific pleasant states, such as joy, contentment, bliss, gratitude, love, interest, pride, or mirth for example. Such states usually arise when our physical and psychological needs are satisfied and when our organisms appraise their current circumstances as safe (Schwarz and Clore, 1983). Based on evolutionary accounts, positive affect has long remained a puzzle, since most theories proclaim that emotions were conserved and shaped because they were adaptive to our ancestors by serving survival. Emotions are characterized by what is called “*action tendencies*” (Frijda, 1986), that is, the urge to act in certain ways, to carry out certain expressive or instrumental behaviors linked to the specific

emotion they are related to. All of these action tendencies prepare the body for future potential action: these emotions were selected through evolution because they helped react in quick and decisive ways in situations where life and limb were threatened. What are then the action tendencies proper to positive emotions, and how are they useful, since by definition they arise when our life is not in danger? This remained problematic to explain for a long period of time, because it seemed difficult to adapt those general emotion theories to positively valenced affect. In contrast with negative emotions' action tendencies which are very stereotypical, action tendencies accompanying positive emotions are described as rather vague and nonspecific. Contentment is linked to the urge of *doing nothing*, joy is linked to the urge of *doing anything*. The theoretical mould proposed to account for emotions made sense for negative ones but did not seem to fit for this end of the spectrum, and therefore scholars often turned down the study of positive states. While negative emotions were shown to correlate with distinct behavioral and neurological states, well-being and happiness have often been treated as the *absence of a strong negative state*. Positive emotions also are harder to elicit in laboratory settings, are thought to be less differentiated and more likely to co-occur with one another (Ellsworth and Smith, 1988; Danner et al., 2001; Fredrickson, 2001). All of these elements have made the scientific literature on negative emotions much more substantial and documented than that of positive emotions. As said in the introductory paragraph of this section, this negativity bias is present in the knowledge of emotions in a broad sense, but is also found in the particular case of chemical communication, in which very little is known about positive affect communication.

### 7.1.1 The birth of a new discipline

In the '90s, some scholars pointed out that most of the animal kingdom research of the 20<sup>th</sup> century was limited to fear and anger because of their explicit contribution to survival (McGuire, 1993). Even though "joy" was described as a "strong" and "basic" emotion in the days of Darwin, limited research was carried out on it until the late '90s and early 2000s. Around that time, the field of *positive psychology* was born, along with the interest of some scientists to study what makes life most worth living, trying to look for elements that cause both individual and societal well-being. In a founding paper of 2000, United Statesian psychologist Martin Seligman and Hungarian psychologist Mihály Csíkszentmihályi, wrote a plea for integrating the study of human well-being and positive emotions into research at the dawn of the century (Seligman and Csikszentmihalyi, 2000). They pointed out that psychologists had been focused on curing the ill and reestablishing the baseline conditions when "things went wrong or pathological", without looking at the other side of the picture and also exploring what happened when "things went well".

### 7.1.2 Solving the mystery: Positive emotions are more than esthetic

A second turning point happened when another important figure of positive psychology brought a significant improvement around the same time: Barbara Fredrickson, based on previous works of her team and other psychologists, proposed a theoretical framework to explain the utility of positive emotions (Fredrickson, 1998, 2001; Fredrickson and Branigan, 2005). This model is called the “*Broaden-and-build*” theory and postulates that positive emotions are adaptive too, but in different ways than negative emotions. They serve us and help our survival, but over longer timescales by *broadening* our mindsets, and over time this expansive awareness allowed our ancestors to *build* resources (physical, social, intellectual, see Figure 4). While negative emotions on the contrary narrow our attentional focus, promoting quick and decisive behavior oriented to urgent stimuli treatment<sup>3</sup>, positive emotions in contrast do not happen in the same circumstances; Because happiness and well-being seldom happen in reaction to life-threatening situations, they do not need to evoke response tendencies as focused and specific. Instead, they allow greater flexibility of thoughts and widen the array of tools at our disposal (Fredrickson, 1998).

This is observed for other social species than humans, in which play for example, a behavior inspired by joy, will allow offspring to build physical and social skills for later in life (e.g., using a flexible branch to catapult oneself as a kid/using these skills for predator avoidance as adults; Dolhinow, 1987). Social play also signals openness to friendly and new interactions, conveying sympathy (Gervais and Wilson, 2005). Laughter is existent in chimpanzees (Berntson et al., 1989) and other great apes when tickled or at play (Provine, 1996). Rats emit vocalizations in response to tickling (Knutson et al., 1998; Panksepp and Burgdorf, 1999, 2000), possibly indicating “joy”, and communicating it seems to be inherently social: “laughter” predicts playfulness in young rats, and young rats prefer to spend time with older rats that laugh more (vs. older rats that laugh less) (Panksepp and Burgdorf, 1999, 2000). Exploration, inspired by interest will build knowledge and intellectual complexity, contentment will refine self and world views. All of these resources accumulated and gathered over time equip organisms for better reactions to future situations, allowing them to draw into the accumulated resources at later time-points.

### 7.1.3 Benefits

In the last decades, the study of positive emotions in humans -although still underrepresented- is growing and has put light on some of their benefits that are impressively diverse. Controlled and longitudinal studies have found links between the extent of positive emotions written by nuns at an early age in their personal journals to later life longevity (Danner et al., 2001).

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<sup>3</sup> An effect sometimes interestingly referred to as “weapon focus”, because witnesses of crimes are often unable to recall details of the crime they observed (perpetrator’s face, clothing, etc.), since their attention was diverted towards the weapon.

Happiness has been positively related to numerous functions such as approach behavior, motivation, effective coping, physical health, strong social support, satisfaction with social relationships, prosocial behavior, productivity in the workplace, and other markers of success (Lyubomirsky et al., 2005). Positive affect is undeniably more than a lack of negative affect or a hedonically pleasant state, is it valuable and useful for individuals and groups.

## 7.2 The broaden-and-build hypothesis

### 7.2.1 The broaden effect

As mentioned earlier, experiencing positive affect is proposed to broaden focus, by shifting our attentional focus from a more local processing style to a more global processing one. Participants who have felt positive emotions recently, tend to show more frequent eye saccades and increased attention towards peripheral visual stimuli (Wadlinger and Isaacowitz, 2006), when asked to list what they would feel like doing, they also show a greater number and variety of actions (vs. a neutral affect group, which in return lists fewer actions than a negative affect group). Positive affect is linked to a greater positive perception of others (Clark and Waddell, 1983), increased trust (Dunn and Schweitzer, 2005), greater cooperation (Rand et al., 2015), and increased overlap between the concept of self and other (Waugh and Fredrickson, 2006). A core aspect of positive affect is that its functioning happens through a particular quality/byproduct: creativity.

### 7.2.2 A particular quality: creativity

Creativity is usually defined as the faculty of generating something both *novel* and *useful* (Runco and Jaeger, 2012), and sometimes *surprising* is added as an additional criterion (Simonton, 2013). Creativity can be seen as taking the form of either a creative mental process, a creative person, or a creative product resulting from the working of the creative process or person (Simonton, 2003). Even if these 3 concepts entail different measurements and approaches, they show fairly respectable intercorrelations (Eysenck, 1995; Carson et al., 2005): which means that creative products tend to come from creative persons using creative processes.

This quality has been put forward as being a key function in the *Broadening* effect of positive emotions (Fredrickson, 1998; Fredrickson and Branigan, 2005). The broadening materializes itself in improved creativity, because creativity *is broadening* by essence. Positive affect has been repeatedly shown to affect cognitive processing (for reviews see Isen, 1993, 1999), more specifically to promote flexibility of thoughts and enhanced creative problem solving, but also improved innovation and thinking especially when tasks are difficult (Carnevale and Isen, 1986; Isen et al., 1987, 1991; Fredrickson, 2001; Isen, 2001). For example, physicians under positive

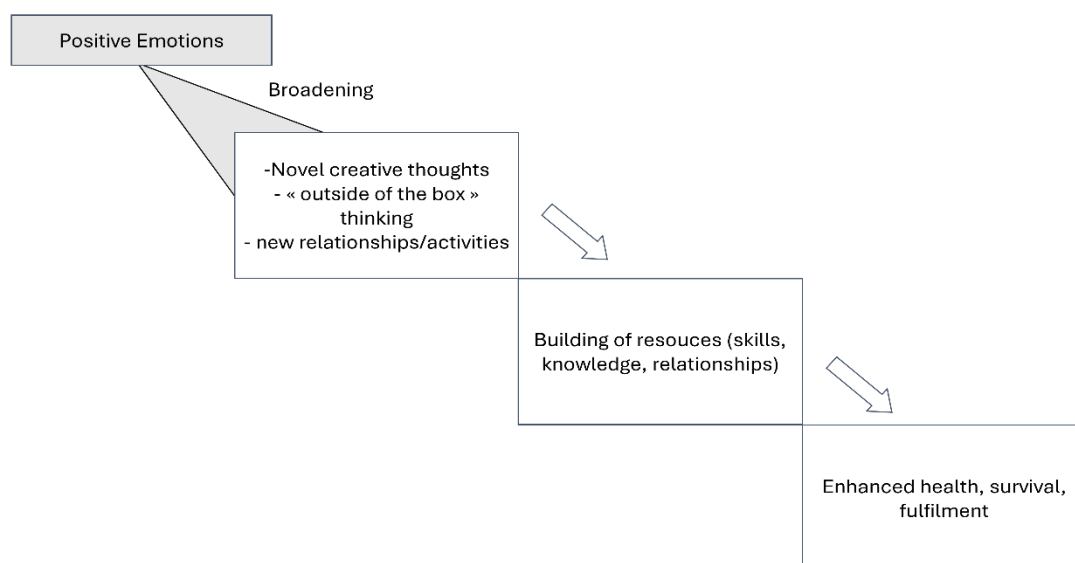


affect show facilitated clinical problem solving by identifying their diagnostic choices earlier, are more likely to go beyond the task by expressing improved interest in other patient cases, integrate material earlier and to a reliably greater extent, show less confusion and disorganization, demonstrate less anchoring and more thought flexibility (Isen et al., 1991; Estrada et al., 1997). Different organizational processes take place in individuals in whom positive affect has been induced, and these differential processes can improve flexibility and integration in problem-solving. In other words, happy people are more creative. It is important to note that for such benefits to happen, mild positive affect such as the one that is experienced daily is sufficient.

### 7.2.3 The build (and undo) effect(s)

Positive emotions, like other emotions, are ephemeral, but broadening out thought-action repertoire punctually allows for the building of durable resources in a durable way. Sharing positive experiences in dyads fosters a greater social bond, in a way that benefits both the individuals (e.g., increased positive emotions, subjective well-being, self-esteem, and decreased loneliness) and the relationship (e.g., improves satisfaction, intimacy, commitment, trust, liking, closeness, and stability) (Gable and Reis, 2010). Experiencing positive emotions also builds physical resources: people counter illnesses more successfully by reducing symptoms and pain (Cohen and Pressman, 2006) and live longer (Danner et al., 2001; Levy et al., 2002). This is perhaps mediated by the power of positive emotions to lift people out of stressed states imposed by negative emotions. As discussed before, negative emotions are highly adaptative in an urgent way hence their very typical action tendencies to react to acute situations, but they are detrimental over long time periods for health. Glucocorticoids, the adrenal steroids secreted during stress responses are critical to adapt to sudden physical stressors but are deleterious if secreted in excess: they disrupt synaptic plasticity, atrophy dendritic processes, compromise the neuron survival ability, and can even lead to neuron death (Sapolsky, 1999a).

By contrast, participants who have been exposed to an anxiety-inducing event and then see movie clips designed to create positive emotions in them, recover faster from the cardiovascular stress response (Fredrickson et al., 2000) than a group viewing a neutral clip, which also recovers faster than a third group watching a sad clip. This is known as the *undo effect* of positive emotions. Positive affect has thus been shown to help resilience and to deal with undoing the noxious effects of negative emotions. It helps us cope with life events and keep a bright view on life, by helping us bounce back from negative emotional experiences (Tugade and Fredrickson, 2004).



**Figure 4:** The broaden-and-build theory of positive emotions. (Adapted from Tugade et al., 2021)

#### 7.2.4 How can we apply this knowledge to the field of chemical communication

As presented in the different sections above, positive emotions are associated with specific cognitive and physiological processes, some of which can prove to be particularly useful when trying to observe a communication of the said emotions between individuals. Since the odors and effects they elicit are hard to describe by language (Lorig, 1999) and even more because body odors as a stimulus, as well as their effects remain non-conscious to receivers (see section 6.2), there is therefore a need to use methods that are implicit and thereby more reliable, instead of introspective self-report measures.

While in psychology directly asking participants how they feel is a common practice, it may not be the best way to proceed (see Baumeister et al., 2007 for a critique), and perhaps studying implicit non-language-related measures of what can be labelled “actual behavior” can prove to be helpful. In that sense, the study of individuals’ *broadening* of thoughts and creative ideas is a pertinent proxy of their levels of present experience of positive emotions and this concept was applied throughout our experiments.

### 7.3 What we already know about positive chemical communication

Positive affect, therefore, is fundamental and necessary for our survival, it impacts our lives in a wide-range panel of aspects, be it individual, relational, or societal. Despite this, very few studies have explored if humans could release and perceive semiochemicals related to those

states. All of them have used, arguably, the term “happy” sweat, instead of talking about positive emotions at large, so this denomination will be used to describe their works below.

### 7.3.1 Explicit discrimination

The first experiment to ever describe the effects of happy sweat found that participants could not explicitly discriminate happy/relaxation sweat and sexual arousal sweat (but they were successful at differentiating anxiety sweat), calling for future experiments to further explore these effects (see section 6; Owen, 1981). These results should only be taken with precaution and as preliminary results given the low sample sizes. A few years later came the pioneering study by Chen & Haviland-Jones (*see section 6.*), which found that participants could discriminate happy sweat from fear sweat and blanks at an above-chance rate when asked to do so (Chen and Haviland-Jones, 2000). This detection result was later replicated but participants, even if able to discriminate happy sweat, were still less accurate at doing so than when the fear sweat was used (Zhou and Chen, 2011).

### 7.3.2 Transmission

To extend those findings, a study by the same group explored the behavioral effects that these emotional body odors could have: happy sweat was found to have no effect on the perception of ambiguous facial morphed expressions, while exposure to fear body odors did shift perception (Zhou and Chen, 2009). The authors concluded that happiness does not carry as much “evolutionary salience” as anxiety and fear, and that therefore the effects of happy sweat were non-existent or marginal (Zhou and Chen, 2009, p. 181).

Since then, happiness-related chemosignals have received only low interest in the literature, with the exception of studies by DeGroot and colleagues. They found that exposure to happy sweat elicited happier facial expressions and a global processing style when compared with fearful sweat (de Groot et al., 2015a). This significant addition to the general knowledge of positive chemosignals showed that, in the same fashion as for negative states, positive ones seem to trigger a partial replication of the state of the donor in the receiver, a mechanism known as emotional contagion (see section 8.3).

In sum, evidence of chemical communication of positive emotions remains scarce, discrepant, and approaches poorly comparable (explicit vs. implicit). As a recent review pointed out:

“overall anxiety, dominance [...] are the most recognized emotions through chemosignals, whereas the demonstration of recognition of happiness is less frequent [...] which makes data less robust and awaiting confirmation” (Calvi et al., 2020).

There is therefore a real need to study such states to better understand them, to allow to (partially) complete the picture of emotional human chemical communication.

# 8 Embodied Emotions and Emotional Contagion – Communicating in context

## 8.1 How to explain the results found in the chemical communication literature?

After having explored the many aspects that make up the positive olfactory communication of emotions in humans, one last piece is missing to complete the picture. Studies in this area, both those on negative emotions as well as the few studies on positive emotions report a common effect taking place: there is a synchronization in the emotional state of a receiver and a donor after the former is exposed to the body odor of the later (see *sections 6.2 and 7.3*). In pragmatic terms, correlates of fear are found in a person exposed to fear semiochemicals, just as correlates of “happiness” are found in receivers who have been exposed to “happy” semiochemicals.

Despite this, some exceptions aside, the majority of studies describe this phenomenon without providing a real interpretation or theoretical framework to account for it, besides the fact that it facilitates the transmission of the emotional signal to the group. Yet, why is there not only a transmission but a synchronization? What is the explanation behind such a phenomenon and what is its utility? To understand and interpret this omnipresent result, we must first understand how our present emotional experience is embodied, and how emotions can be transmitted from one person to another in a social setting. In the following sections, the fundamental notion of emotional contagion will be introduced in a broad sense and then this notion will be applied more precisely to human chemical communication.

## 8.2 Our emotions and thoughts are embodied

### 8.2.1 Introduction to the concept

The human body is involved in the acquisition of attitudes, preferences, and emotions. There is a relationship between bodily expressions of emotions and the way in which emotions are attended to and interpreted, and this relationship is reciprocal. When participants are told to

adopt either a conventional working posture, a slumped posture, or an upright posture (straight back, shoulders held high and back), and subsequently told that they succeeded on a test completed beforehand, their attitude in welcoming the result changes. If the success is received in the slumped posture, participants feel less proud and report a worse mood than participants in the upright or conventional posture (Stepper and Strack, 1993). This finding is generally found all over the literature: when individuals adopt emotion-associated postures, they report experiencing congruent emotions. Vice versa, when individuals experience emotions, their postures adapt accordingly. In other words, our bodies are entirely part of our emotional experience, and our affect is linked to emotional expression: gestures and attitudes can both influence and be influenced by our affective state. Moreover, when individuals' motor movements are inhibited, interference in the experience and processing of emotional information is observed (Niedenthal et al., 2005).

### **8.2.2 Reactivating embodiment**

When reliving or recalling a past experienced state, high cognitive processes will partially reactivate the said state and its associated sensory, motor, and affective patterns (Somatic marker hypothesis; Damasio, 1994). Experiencing a present situation is a lot like reliving past situations in some (and sometimes all) sensory-motor and affective modalities. The perception of an emotional stimulus such as a howling wolf for example while walking in a forest involves a response of fear, fueled by hearing the wolf, seeing the wolf, and feeling consciously afraid of the wolf. Populations of neurons in the modality-specific sensory, affective, and motor systems are highly interconnected and their concomitant activation supports the multimodal experience of a howling wolf in our minds. Later, during our next walks into the forest, just thinking of stumbling into a wolf can reactivate the neural states representing that animal, such as the visual impression of it. That visual impression can subsequently cascade into other systems to complete a full pattern of activation and thus recall our past original experience (Barsalou et al., 2003).

Our bodies being intimately linked to our thoughts and emotions, this reactivation is said to be *embodied*: the embodiment of thinking of the howling wolf might trigger a dry mouth, shaky hands, and increased monitoring of our surroundings. The embodiment of anger might involve tension in muscles used to strike, the activation of facial muscles used to frown, and a rise in diastolic blood pressure. These body changes caused by emotions -or *action tendencies*- are a central part of the emotional experience (Frijda, 1986)

### **8.2.3 Embodiment in a social setting – a shared space of affect**

Embodiment not only takes place when we are exposed to situations or objects, but also will have crucial importance in social settings. In a social situation with interacting individuals, the two (or more) partners must continuously update information about their partners' inner state,

intentions, motivation and affect, in order to be included and participate in the other ones' behavior and to adapt their own. One proposed mechanism to serve a major role in this process is called *embodied simulation* (Frith et al., 2003). When people observe someone else's affective behavior, a mirror representation of it will be activated in the perceiver's brain. The act of performing an action and observing it are thought to activate similar neural networks on both ends. This creates what is called a "*shared space of affect*" between senders and receivers of information and this would be a necessary step to integrate emotional information and therefore establish communication (Cacioppo et al., 2014). Volunteers observing someone else receiving a painful stimulus activate a "pain network", which is also activated when the same volunteers receive a painful stimulation themselves (Morrison et al., 2004). The anterior insula and to some extent the anterior cingulate cortex are activated both when participants smell odors generating disgust and when they watch videos of people experiencing the same emotion (Calder et al., 2000; Wicker et al., 2003).

### **8.3 Emotional contagion – embodiment applied to emotions**

More generally, observing a facial expression or affect activates part of the somatomotor network also activated when people express the same emotion themselves (Carr et al., 2003; Leslie et al., 2004; Hennenlotter et al., 2005; van der Gaag et al., 2007). Recognizing an emotional face, emotional words, emotional music, etc. involves the *embodiment* of that emotion (Adolphs, 2002). As people non-consciously and automatically mimic their interlocutors' expressions of emotions, they often come to feel pale reflections of their partners' feelings. By attending to the stream of moment-to-moment reactions, people are inhabited by the emotional landscape already present in their partners, in a process called *emotional contagion* (Hatfield et al., 1993). Emotional contagion (sometimes called "*primitive empathy*") is defined as:

"the tendency to automatically mimic and synchronize expressions, vocalizations, postures, and movements with those of another person's and, consequently, to converge emotionally (Hatfield et al., 1992, pp. 153-154)"

This process is, in the view of developmental theorists, clearly distinct from more "sophisticated" and cognitive processes such as empathy and sympathy (Eisenberg and Strayer, 1987). Empathy involves identifying or understanding the emotions of another ("feeling for") while emotional contagion involves physically feeling the emotions of another person ("feeling with") (Miller et al., 1995). Primitive emotional contagion happens in three stages the first one being i) mimicry, followed by ii) afferent neural feedback in response to the observer's facial and bodily expression, and finally, iii) corresponding emotions evoked in the observer

(Hatfield et al., 1992, 2014). The process of emotional contagion allows individuals to become synchronized, and enhances the chances of reacting in an adapted manner in social contexts (van der Schalk et al., 2011). When this happens, a shared social space is created between the two ends.

### 8.3.1 Mimicry as the founding base for contagion

“When I wish to find out how wise, or how stupid, or how good, or how wicked is any one, or what are his thoughts at the moment, I fashion the expression of my face, as accurately as possible, in accordance with the expression of his, and then wait to see what thoughts or sentiments arise in my mind or heart, as if to match or correspond with the expression” (Poe, 1844).

In this excerpt of the Purloined Letter, Edgar Allan Poe describes surprisingly precisely a phenomenon that would be studied by science only decades later: facial mimicry. Facial mimicry is conceptualized as an automatic, reflex-like response (Hoffman, 1985; Hatfield et al., 1993). Infants mimic facial expressions of emotion of their caregivers shortly after birth and continue to do so throughout their lives (Hatfield et al., 1992). Mimicking facial expressions would serve the role of facilitating emotion recognition by permitting to access the emotional concept (Niedenthal et al., 2010; Hess and Fischer, 2013). This automatic process would then cascade to higher and more cognitive processes, imitation putting a strong foundation for empathy, permitting communication and helping build social relationships: studies show that in long-lasting marriages, people present similar facial features because of mimicking each other emotional expressions for years (Zajonc et al., 1987). Mimicry also enhances sympathy for the person being mimicked, advances social connection, smoothens interactions (Chartrand and Bargh, 1999; Lakin et al., 2003) and promotes prosocial behavior (Stel and Harinck, 2011). These mechanisms help monads to be integrated into groups of people and strengthen group coherence (Lakin et al., 2003), something crucial for survival in humans and most organisms. Conversely, in cases where social interactions are troubled such as in people with autism spectrum disorders, the automatic imitation of facial expressions is impaired (McIntosh et al., 2006). Additionally, for people in whom facial mimicry is blocked, for example in groups of people having undergone botox injections recently (which rigidifies the muscles), the recognition of emotions in others is impaired (Neal and Chartrand, 2011).

This behavior is also highly adaptive: during their lifespan, humans acquire new skills by observing and then reenacting the actions of others around them through mimicry.

### 8.3.2 Neurophysiological bases of emotional contagion

Neuroimaging studies have explored processes happening during emotional contagion. They show that there is a temporal succession in the flow of affective information, information in the observer being delayed relatively to the information in the sender's brain (Anders et al., 2011). Interestingly this delay decreases over time in an affective exchange period, possibly showing a mechanism of "tuning in" between the perceiver and the sender. While it may initially take time to create this "*shared space*", once it is built, information transfer seems to become faster (Anders et al., 2011). The recruitment of shared networks can be supported by specialized "*mirror neurons*" or even an entire "*mirror system*" that would map correspondences between performed and observed actions. A seminal finding involved the discovery of neurons in macaques' F5 area (premotor area) that not only fired when monkeys performed a goal-directed action but also when they observed the same action being performed by another monkey (Gallese et al., 1996; Rizzolatti et al., 1996). These neurons might therefore be a crucial link<sup>4</sup> between third-person observation and first-person experience, providing a base for social interaction (Frith et al., 2003).

### 8.3.3 Emotional contagion in the context of chemical communication

Studies on emotional contagion have been numerous and varied since the concept was proposed, nevertheless they have focused almost exclusively on visual cues (i.e., facial expressions triggering facial expressions). Yet, in real contexts, an emotional social exchange is unlike to happen via the visual sensory channel only. Social exchanges are multisensory, and partakers are exposed to facial expressions, but also to verbal prosody, postural cues, contextual settings, as well as... smells.

As said above, in embodiment theories, the activation of one or more systems is thought to cascade into other systems to *in fine* reactivate the entire affective experience. Since emotions are integrative responses then it seems logical to contemplate a cross-channel mimicry. As Hawk, Fischer, and van Kleef (2012) describe:

"When individuals experience a combination of emotional states and nonverbal expressions with sufficient frequency, such as feeling happy, smiling, and laughing, later introspection about a stimulus (e.g., another's laughter) can activate dynamic simulations of associated behaviors and feelings. This pattern completion 'fills in' unperceived elements of the original experience [...] and may manifest as overt motor behavior (e.g., smiling) and subjective states (e.g., feeling happy)."

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<sup>4</sup> However, note that there is a disagreement about the exact location of these neurons and if they are a system, as well as if there are specialized neurons dedicated to mirroring or if regular neurons can perform mirroring instead.



In other words, recall of a single sensory modality will reactivate an integrative pattern comprising other modalities; hearing someone's voice laughing on the radio will have a contagious effect not only on our voice. Experimentally, hearing an emotional voice causes facial expressions, as well as self-reported emotions in congruence with the emotion conveyed in the vocalization (Hietanen et al., 1998; Hawk et al., 2012). On the other hand, if the facial expressions of the receivers are blocked when hearing the emotional vocalizations, then their processing is inhibited, as well as the associated subjective states (Hawk et al., 2012).

This reasoning is also applicable to the compiled results in the chemical communication field, which seem akin to those found for other modalities and in other disciplines. Smelling the odor of someone collected during an emotional situation, induces comparable responses in the smeller of this stimulus (Mujica-Parodi et al., 2009; de Groot et al., 2012; Pause, 2012; de Groot et al., 2015a; Lübke and Pause, 2015; Hoffmann, 2019). The donor and receiver's facial expressions and sensory acquisition styles align, and this, through the process of primitive emotional contagion. One person would feel an emotion (such as joy), associated with physiological changes (such as a distinct change in body odor) and these would be picked up by a receiver in a fast, unconscious manner, creating a (partial) reenactment of this emotion in themselves (such as an increase in creativity, a more global processing style, or facial expressions denoting positive emotions). These processes of synchronizing both affective states would allow individuals to share a common affective space, enabling correct emotional recognition, synchronization, processing and so on, only strengthening the exchanged information and building further connection.

## 9 Perfumed Bodies – a Cultural and Biological Phenomenon

Finally, a last aspect to consider to refine our understanding of human chemical communication is found in an element that shapes the very way we perceive endogenous body odors: the use of fragrances or fragranced products. Often very deeply entangled with our natural body odors, the use of exogenous scents accompanies our daily life. Such scents have always been present around human beings and born significant meaning in body embellishment or rituals. They were present in ancient Mesopotamia and pre-Roman Palestine, and today they still accompany us, even on the most remote islands or in the heart of jungles. If humans have perfumed themselves and their environment for so long and if they are animals that

communicate chemically, therefore the addition of perfume is a critical element to take into account for a more comprehensive overview of the chemical communication phenomenon - especially that of emotions, since perfumes create emotions by design. To put it in other words, considering perfume and cosmetic practices is essential to understand how humans communicate chemically, and so at two levels: i) they modify body odor (relevant for all functions of chemical communication) and ii) they induce positive emotions in surrounding people but also in their wearers themselves (especially relevant for the communication of emotions).

### **9.1 Historical and cultural impact of perfume**

In ancient Egypt, scented anointment was used on statues of cults, participants of religious ceremonies but also on mummies (Stoddart, 1990), Cleopatra adorned herself with fragranced oils to seduce Marcius Antonius, and perfumes were valuable enough to dispose of their own deity: Nefertum. Flowers and fragrances were buried along the Pharaoh's sarcophaguses, for a better afterlife (Steele, 1992). This link with the holy and the sacred is perhaps well illustrated by its very own name: perfume comes from the Latin "*per fumus*" [by the smoke], perfume is that which rises above the smoke to reach the sacred realms of the gods. In Roman times too, perfumes and oils were used during one of the central activities of social life: bathing. This perfume use was codified, and bathing was the moment for social interactions such as making business contracts or discussing political matters. Myrrh was thought to be the divine perfume that could be smelled next to Aphrodite, and the god of perfumes was personified in Adonis, her lover. In the Malagasy tribes of the Isle of Mayotte, boys and girls are considered to enter adulthood only after being fumigated with a mixture of burning seaweed, lemon and kapok seeds, as well as coconut oil (Howes, 1987). These odors are coupled with the moral concepts of bad and good and are often related to the sacred. In Christianity, for example, an odor of Sanctity exists, and it was said to adorn the saints even after their death, a concept that is found in other religions as well. This is based on the idea that deities make their presence known through fragrance, as it was thought for the Holy Spirit (Synnott, 1991). Artificial exogenous odors seem therefore to dress our bodies and have a high mystical and esthetical connotation through the ages and history, even becoming social status markers when they are made of limitedly available and scarce ingredients (Classen et al., 1994).

## 9.2 Present times

### 9.2.1 Experimental effects on users

Nowadays, people de-odorize and re-odorize themselves to smell nice, to feel good, to be beautiful and to attract. One does not only have to be clean, but to *smell clean*. A study found that 79% of women and 60% of men in the UK used a deodorant-based product on a daily basis (Roberts et al., 2010). In the same survey, almost half (44%) of the women reported using perfume daily. In 2022, the global perfume industry is estimated to be worth 49 Billion U.S. dollars (Statista, 2022). These practices, highly prevalent worldwide, seem to be more than just olfactory jewelry to adorn the way we are perceived: if semiochemicals are indeed contained and conveyed by body odors, applying such additional odors would, at first sight, seem to reduce the human ability to detect such cues and therefore be problematic. However, the literature suggests that fragrances may not mask entirely endogenous odors and that they could even be chosen to complement them. Participants are able to discriminate individual body odors and they still perform above chance if the samples are perfumed (although success rates are lower than without perfume). Interestingly, discrimination is higher if the perfume used is chosen by the wearer than if it is assigned to them (Allen et al., 2015), which would indicate that fragrance choices are influenced by their interaction with individuals' body odors.

Milinski and Wedekind (Milinski and Wedekind, 2001), found that participants' preference of certain fragrant compounds was correlated to genetic characteristics. They interpreted this phenomenon as an indication that perfumes could amplify genetic cues present in body odors, a finding replicated by Hämmerli and colleagues (Hämmerli et al., 2012) and further developed by Lenochová and colleagues (Lenochová et al., 2012). They explored how fragrance choice could impact attractiveness. Body odors of participants are rated as significantly more pleasant if they are mixed with the perfume of their choice, more than if they are presented with an assigned perfume even if both fragrances are as pleasant when presented alone.

Overall, exogenous odors seem therefore to be chosen in an unconscious and idiosyncratic way to work in tandem with our genetics and enhance the characteristics of our body odor fingerprint, by creating a favourable body odor/fragrance blend.

### 9.2.2 Experimental effects on receivers

“The beauty of fragrance is that it speaks to your heart... and hopefully someone else's”.

Experimental studies seem to echo this Elizabeth Taylor quote by showing that fragrances not only directly modulate the behavior of people using them, but that they may also affect the behavior of others by indirect effects such as mood or perception changes. After perfume use, formally dressed interview candidates are perceived more negatively, while informally dressed candidates are perceived more positively (Baron, 1981). Male participants are judged as more

attractive in photos, after they have put fragrance on than when they put on a placebo substance, even though the observers were not able to smell them (Craig Roberts et al., 2009). This would be explained by a self-confidence alteration by fragrances, something found in other studies where women were perceived by other women as more self-confident during a job interview if they were using perfume (Higuchi et al., 2005). Perfumes therefore seem to impact the perception we give to others, even if this also seems to largely depend on context.

### 9.3 Message in a bottle - the need to include fragranced practices into account

Taken together, it seems that whether we like it or not, humans remain odoriferous beings despite the cleaning routines that are ritualized each day. Although the aforementioned studies have yielded exciting results, they have been focused on attractiveness and partner choice, the most notorious role that comes to mind when talking about body odor, as well as individual discrimination (and therefore genetics). Yet, as discussed previously (*see section 5*) many other individual characteristics can be drawn from smelling the odor of someone else. Cosmetic practices modulate the olfactory perception of cues present naturally, by creating an endogen/exogen blend that could be the result of culture-gene coevolution (Havlíček and Roberts, 2013). A real “literature black hole” therefore remains, since little is known about the role of perfume in persistent traits (e.g., attractiveness/individuality) but nothing is known about its role on states such as sickness or emotions.

## 10 Aims and Hypotheses

With all due respect to philosophers, psychoanalysts, and experimental as well as theoretical scientists who have considered olfaction as an inferior sense, humans remain inherently olfactive entities that communicate constantly through the odor of their bodies, even inheriting the epithet “scented ape” in Stoddart’s famous book of the same name (Stoddart, 1990). The volatile compounds that are emitted by people in the air are present anywhere, anytime, in every place where at least one person is present: in public transports, at the cinema, in a classroom, at a music concert or in the perfumed wake of a stranger who just crossed our path on the street. They are capable of influencing our most basic behaviors in a rapid and unsuspected way.

Yet, this phenomenon that is experienced by the vast majority if not the totality of us, is surprisingly unknown by most. How many times, out of our awareness, our behavior has been

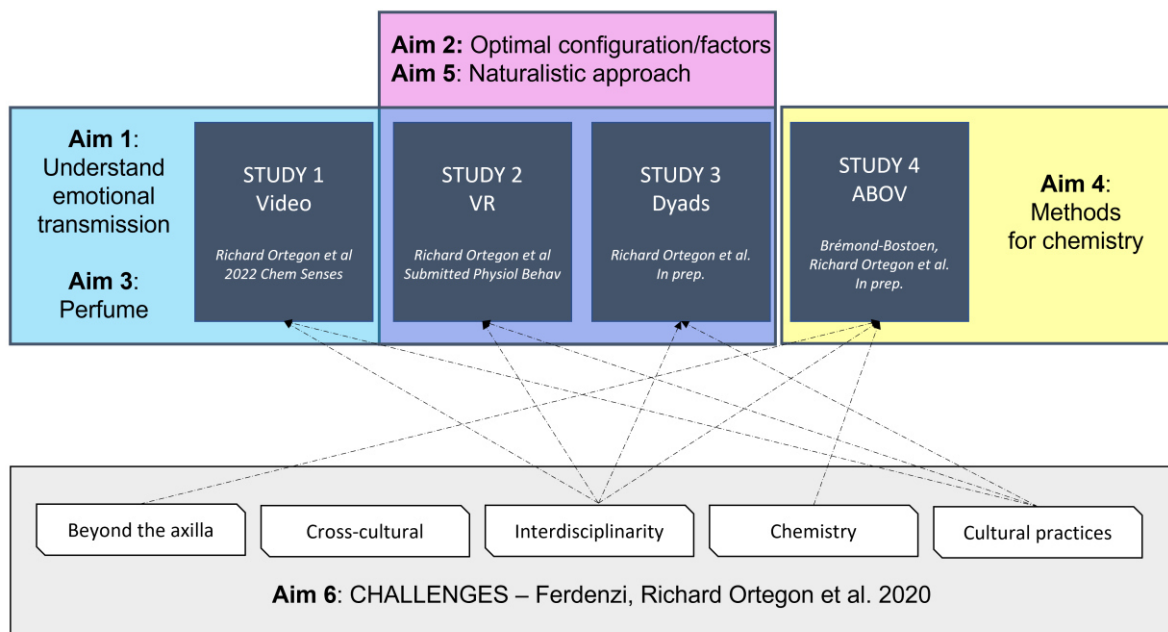
impacted while entering an elevator by smelling the odor of the person that was present in there a few seconds prior? Even though in popular belief clues of this can be found (e.g., a person is said to “smell fishy” when they are lying, emanate “the sweet smell of success” or “smell like a million bucks” in favorable situations), most people remain unaware and unfamiliar with these phenomena. This is rooted in the fact that these effects, despite omnipresent, are subtle, covert, and subject to contextual modulation, in addition to humans not trusting their capacity to extrapolate social information from odors of people (*see section 6*), even though they succeed in doing so with a higher than chance accuracy.

## **10.1 Thesis research problem**

The introductory elements mentioned above help to realize that, in addition to the paucity of “popular awareness”, scientific knowledge and studies are also lacking (and are perhaps surely even one of the causes of said paucity). As a resultant, the chemical communication, of positive emotions in particular, remains uncharted territory. This, despite the crucial impact and central role of positive affect as well as communication for humans, as reviewed in earlier sections. Because it sits at the confluence of several broader domains that are understudied on their own (olfaction vs. other senses, positive affect vs. negative affect, chemical communication vs. other forms of communication), the problem of determining if positive emotions can be transmitted through body odor in humans remains unresolved.

It is therefore compulsory to expand our knowledge when it comes to positive emotions and their communication in connection with the sense of smell. The nature of this topic being integrative and multidisciplinary, as well as the knowledge on it still being limited, a multiplex approach involving psychology, physiology, behavior, chemistry, ethnology, among others is thus necessary. Furthermore, this problem cannot be solved without considering the impact of cultural practices such as the use of cosmetics and perfume, setting up standardized experiments in laboratory settings or exploring more realistic approaches closer to daily-life situations.

On the basis of this problem, I will therefore pose 6 aims, supported by hypotheses (H1 to H5). This thesis is articulated in 5 articles including 4 original articles, and 1 review that will raise the current challenges found by scientists to address the issue of human chemical communication.



**Figure 5:** Overview of the thesis' aims, and the studies implemented to explore them.

## 10.2 Aim 1: Test the existence of a transmission of positive emotions through body odors, and determine if it is an emotional contagion

Given the elements said above, the first step was to test if this phenomenon happened in humans, which was the main aim of this thesis. This was explored through **Study 1**, where donors watched video clips created to induce either a positive or a neutral emotional state in them while their axillary odors were collected with sterile gauze pads. These body odors were then presented to receivers on whom autonomic, verbal, and behavioral responses were measured. Since emotions have conscious (verbal), as well as conscious non-verbalizable and non-conscious components (physiology, behavior), these three levels of measures were implemented to allow us to largely screen and explore potential effects caused by the olfactory stimulus.

These measures were also suited to determine if it was a mere transmission (i.e., the information is passed from a person A to a person B) or rather an emotional contagion in a similar fashion to what is observed for negative states (i.e., person B affective state matches the affective state of person A, after the transmission), using for example creativity tasks because of their robust link with positive affect (*see section 7.2.2*).

This main aim was also later explored in **Studies 2 and 3**. In **Study 2**, the same paradigm was used but this time emotions were induced via virtual reality. In **Study 3**, a similar paradigm still involving a donor and a receiver was carried out, but this time participants did the experiment at home. This allowed us to gather more information about the existence of this effect, as well as the use of indirect measures of positive affect in receivers.

#### **10.2.1 H1: A transmission of positive emotions does exist through body odors**

Because positive emotions are as relevant as negative ones, therefore their transmission should also happen in the same vein as what is found for negative affect. If a semiochemical marker of positive affect exists, then the samples collected in donors during the positive emotional induction should differ from those collected in the control condition, and they could elicit different responses in the receivers. These differences should therefore be observed in **Study 1**, materialized by either different physiological patterns, different verbal perceptions, or different performances on creativity tasks when comparing exposure to both experimental conditions.

To better attain this objective, subsequent experiments were carried out that by design all allowed us to further explore the existence of positive semiochemicals in humans. In **Study 2**, the same measures were implemented therefore the same differences potentially found in **Study 1** were expected. In **Study 3**, only behavior was measured and the differences between conditions should also fall in line with those found for this variable in **Study 1**.

#### **10.2.2 H2: It is not only a transmission but rather an emotional contagion**

If positive emotions are indeed transmitted through body odors in the same way that negative ones are, thus an emotional contagion should also be expected. Signs of a partial replication of the donors' state should be found in the receivers in **Studies 1, 2, and 3**, in the form of increased creativity in the group of participants exposed to the positive chemosignals (relative to the control group). For the verbal and physiological variables, directions of effects can be speculated (more positive evaluation of the positive body odor, reduced heart rate) although these are less obvious than for behavior for several reasons explained in **Article 1**. Nonetheless, all the differences of the positive group (vs. the neutral control) should be coherent with the presence of experienced positive affect in receivers.

### 10.3 Aim 2: Identify the optimal configuration for positive emotional contagion – the underlying factors

It has been suggested that chemosignals in humans act in ways that are less stereotypical and more nuanced than in other animals, because of the richness of contextual elements that accompanies these signals as well as of our communication, processing, and action modes. These contextual factors were part of the object of analysis of **Study 2**, with a change in the emotional induction method. Instead of 2D Videos, virtual reality (VR) was implemented and this more powerful way to induce emotions might change the chemical communication of positive affect, deepening our understanding of how emotions should be induced for an optimal contagion.

In **Study 3**, the objective to identify relevant factors ruling positive chemical communication was further explored with the following matter of substance in mind: are there some typical profiles of “super-communicants”, at the scale of the individual or of a pair of individuals that would represent an optimal paradigm to study the chemical communication of emotions? Among the possible factors, many could be rightfully studied, but we decided to target some of them that we considered relevant: personality, relationship proximity, and learning. These factors were explored experimentally by including participants presenting different sociability levels, living under the same roof either as roommates or as a couple, with varying degrees of cohabitation length, and then measuring how these factors modulated creativity during exposure to emotional chemosignals.

Note that cultural practices especially perfume addition are also essential factors to consider for the optimal configuration to observe positive chemical communication, but this was considered as an aim of its own and will be developed below.

#### 10.3.1 H3: This emotional contagion is subtle and depends on contextual factors

As expected from humans and given the difficulty of isolating semiochemicals, contextual factors such as the method to induce emotions (**Study 2**) or characteristics of the involved individuals (**Study 3**), should affect the chemical emotional contagion. Because these have never been tested before and are in essence exploratory, it is difficult to expect the directions of such changes. However, we pose that human emotional semiochemicals are less stereotypical and unconditional than pheromones, and thus contextual changes should modulate the observed response: the emotional contagion may be enhanced with VR, as well as by receivers' higher levels of sociability, relationship proximity (couples), and increased



duration (long relationships). The underlying justifications are further detailed in each corresponding article.

### **10.4 Aim 3: Investigate the potential modulating effect of perfume**

In this thesis a fundamental interrogation that was addressed and followed every step of our thinking was that of how the use of perfume influences the chemical communication of positive emotions. Because as humans we emit a combination of a natural endogenous odor and of one or several exogenous odors that are chosen, therefore the perception that others have of us is, more often than not, a composite of these two elements. If a chemical communication of positive emotions does indeed take place, then what impact can have this added artificial odor? To investigate this question, in **Study 1, Study 2, and Study 3** we included several conditions with added perfume in our samples of body odors, and we compared the responses of receivers when exposed either to body odors alone, or the odor of the samples with added perfume.

#### **10.4.1 H4: Perfume does not suppress this chemical contagion**

We expected that in **Studies 1, 2, and 3**, perfume addition should not inhibit the establishment of olfactory communication, otherwise, fragrance use would deprive us of precious social information, which is unlikely since cosmetic practices have been conserved through recent evolution and are adapted to our individual genetical heritage (see Perfumed Bodies – A Cultural and Biological Phenomenon). Because this has never been tested before in the context of emotional contagion through body odor, the options of perfume severing the transmission or enhancing it, should not be ruled out.

### **10.5 Aim 4: Implement a methodological solution to better explore the chemical bases of body odor**

An essential element to consider in our understanding of the chemical communication of positive emotions (but also in the field at large), is the chemical bases underlying the observed behavioral and physiological effects. Without this mandatory step, our understanding of such mechanisms remains incomplete. Yet, approaches in the literature are heterogenous and comprise several biases sometimes fundamental such as the use of contact methods that would collect heavy compounds most probably not involved in our object of study.

While browsing the available literature, it stands out that there is a need for methodological improvement to eliminate such biases and collect relevant compounds. This was the main aim of **Study 4**. In this study, there was no emotional induction but rather a study of the chemical

bases correlated to controlled inter- and intra-individual differences, which is a prerequisite for later studying finer-grain differences such as emotional ones. This was done via the implementation of an original and innovative system (ABOV: Analysis of Body Odor Volatiles) that was designed and created specifically to attain this objective and is the result of extensive testing of several techniques since the beginning of the doctorate. Participants wore the ABOV system equipped with adsorbent polymers that were subsequently analyzed by GCxGC-MS.

#### 10.5.1 H5: ABOV will allow measuring basic inter- and intra-individual differences in body odor

ABOV was designed to allow the sampling of VOCs in an efficient manner, while solving some constraints linked to chemical analysis in the field. We postulate that this device will be able to pick up some controlled and known inter-individual (e.g., sex, identity) as well as intra-individual (e.g., sampled body part) differences, for example between the neck and axillary odor.

### 10.6 Aim 5: To study the phenomenon in a naturalistic approach

During this thesis, a longitudinal objective was to perform experiments closer to real-life situations in a *naturalistic neuroscience* approach, while keeping as much as possible the rigor and control of experiments performed in laboratory settings.

**Study 2** was designed in this sense, via the implementation of a new and immersive technique to induce positive emotions: through Virtual Reality. Virtual Reality is a powerful tool to stimulate the sensory channels concomitantly and creates feelings that are more ecologically valid than 2D videos (method used in **Study 1**). After the mood induction via virtual reality, the body odor samples of donors were presented to receivers, and their responses measured in the same fashion as in **Study 1** (i.e., autonomic, verbal, and behavioral creativity tasks). In **Study 3**, this objective was taken further since it was entirely carried out at home by participants, allowing to explore an even greater level of ecological validity. Since most behaviors observed in participants are subject to what is named “behavioral artifacts” such as stress caused by laboratory settings (i.e., “white-coat effect”), or a desire to fulfill the expectations of the experimenters (i.e., subject-expectancy-effect/demand characteristics), putting participants in a familiar and neutral setting should put those biases aside, giving a view of closer-to-real-life effects.

This was an objective in how to approach experiments rather than a “problem to solve”. It was about implementing a way of acting, applied whenever possible, to our experiences and

therefore this objective did not comprise working hypotheses. Nonetheless, we believe that this way of exploring human functioning is essential and should be an aim in every research work or thesis.

### 10.7 Aim 6: Identify the challenges that stand in the way to better understand the chemical communication in humans

In the same vein as the previous aim, aim 6 was inherent to our thesis and did not result from one research question in particular, but rather of our view to carry out research. Therefore, it does not comprise working hypotheses.

Because positive affective states seem to be communicated under the form of an emotional contagion from us to others but also from others to us, it is therefore of crucial importance to elucidate and better delineate those mechanisms that affect people in every social scheme of every day of their lives. To do so, several methodological and theoretical obstacles still need to be surpassed. This dissertation aimed to explore some of those, but evidently, the task is much bigger than that. We thus tried to list and describe in **Review 1** what were, in our view, the principal challenges to overcome as well as putting forward roadmaps for future studies that will hopefully be useful for the field. These challenges were: taking into account other body areas than the axilla, better understanding the chemical bases of chemical communication, employing cross-cultural approaches, studying the impact of cultural practices such as pill or fragrance use, and carrying out integrative studies at the intersection of disciplines with different yet complementary approaches such as social sciences, neuroscience, ethology, and microbiology. This review, published at the halfway point of the PhD project, is the result of many thoughts and observations carried out before and throughout this doctorate, as well as inputs that came from reading literature. It also provided guidelines for how to conduct the experiments in a way to achieve the aims developed above.

# STUDY 1 - VIDEO

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## Preamble

Because evidence regarding a transmission of positive emotions through the olfactory sense in humans was rare, the first step was to ensure that a transmission was possible, in the same way as for negative emotions. Therefore, inspired by previous experiments carried out on fear and anxiety, we developed a donor-receiver paradigm that would be used throughout this PhD thesis. First, in donors, either a positive or a neutral emotional state was induced via videos on different days in a within-subject fashion, while their body odors were collected on sterile cotton gauze pads.

The second step was to present the "emotional" (positive/neutral) body odors to receivers, while physiological, verbal, and behavioral measures were taken in response to them. The latter component, that was longitudinal throughout the thesis, constitutes the originality of our approach: for the first time in the study of chemical communication, creativity measures were introduced to test the hypothesis of emotional contagion of the positive state between donors and receivers, based on the robustly demonstrated link between positive affect and improved creativity.

These body odors were also presented with added perfume to investigate the effect of this factor on communication through the olfactory sense.

# And I'm feeling good: effect of emotional sweat and perfume on others' physiology, verbal responses and creativity (Published – Chemical Senses)

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## Abstract

Emotions can be communicated in social contexts through chemosignals contained in human body odors. The transmission of positive emotions via these signals has received little interest in past research focused mainly on negative emotional transmission. Furthermore, how the use of perfumed products might modulate this transmission remains poorly understood. To investigate human positive chemical communication we explored the autonomic, verbal, and behavioral responses of receivers exposed to body odors of donors having undergone a within-subjects positive or neutral mood induction procedure. These responses were compared with those obtained after exposure to the same body odors with added fragrance. Our findings suggest that positive emotions can be transmitted through body odor. They not only induced modifications at the physiological (heart rate), and verbal levels (perceived intensity and familiarity) but also at the behavioral level, with an improved performance on creativity tasks. Perfume did not modulate the physiological effects and had a synergistic effect on the positive body odor ratings (increased perceived differences between the neutral and positive body odor).

**Keywords:** Chemical communication, positive emotions, body odor, perfume, emotional contagion

## Introduction

A growing body of evidence suggests that there is a communication of social information in humans via cues contained in their biological odors (i.e., chemical communication). This has been observed for information such as gender (Penn et al., 2007a), age (Mitro et al., 2012), health (Olsson et al., 2014), or even sexual arousal (Wisman and Shrira, 2020). Information about emotional states can also be transmitted via this medium. For example, presenting the odor of stress collected on “donors” during first-time skydiving (Mujica-Parodi et al., 2009) and during academic examinations (Pause, 2004) elicits stress-like responses in the “receivers” (e.g., amygdalin activation, facilitated subliminal perception of angry facial expressions).

However, the question of whether the transmission of positive emotional states is also possible has rarely been explored. Indeed positive affect has traditionally been neglected in psychological studies (Seligman and Csikszentmihalyi, 2000), perhaps because positive emotions are believed to be less differentiated, more idiosyncratic, and more difficult to elicit in laboratory settings. In addition, while negative emotions have an adaptive function for survival by modulating responses to threats, positive emotions are not likely to have such direct vital consequences (Pratto and John, 1991). Yet, the impact of positive emotions on health and cognition is major: for example, happier people have more stable marriages, stronger immune systems and are more creative (Lyubomirsky et al., 2005). The field of human chemical communication is no exception to this general trend, with the most studied emotion being negative ones (see de Groot and Smeets, 2017a for a meta-analysis highlighting the capacity of humans to communicate fear, stress, and anxiety via body odor).

Only very few studies have explored “happy” sweat. In the first study, Chen & Haviland-Jones (2000) found that participants could discriminate happy sweat from fear sweat and from blanks at an above-chance rate. Zhou & Chen (2009) found that ambiguous facial expressions (morphed face between happy and fearful) were rated as more fearful when exposed to the fear sweat, while happy sweat had no effect. They also showed that receivers could discriminate happy sweat from neutral control sweat, but that they were less accurate at doing so than when discriminating fear sweat from the control (Zhou and Chen, 2011). Finally, de Groot and colleagues (de Groot et al., 2015a) found that exposure to happy sweat elicited happier facial expressions and a more global processing style, when compared with fearful sweat. This was the first study investigating not only the transmission of positive emotional information to receivers, but also the replication of the donor state in the receiver (i.e., emotional contagion; Hatfield et al., 1993), a process that would favor communication between two individuals by achieving internal state synchronization (Semin, 2007). Indeed, more global processing style has been robustly linked with positive affect (Isen et al., 1985, 1987; Ashby

et al., 1999; Bolte et al., 2003). In sum, evidence of chemical communication of positive emotions remains scarce and approaches poorly comparable (explicit vs. implicit).

Furthermore, the fact that in ecological situations body odors are rarely found alone (Allen et al., 2019) has never been considered before in emotional chemical communication studies. Body odors are an integral part of the sensory image we send to others, impacting our social interactions such as in mate choice (Franzoi and Herzog, 1987; Sergeant et al., 2005). Trying to “control” these endogenous odors with exogenous ones has taken place almost universally since antiquity, with the use of fragrances, deodorant, or soaps. Fragrances could be chosen to complement our natural body odor and genetics (Milinski and Wedekind, 2001; Lenochová et al., 2012), and our individual preferences could be the result of a culture-gene coevolution (Havlíček and Roberts, 2013), enhancing some biologically evolved preferred traits. This is particularly relevant for the studies of positive emotions because perfumes are chosen by their wearers to generate positive feelings in themselves and in surrounding people. Perfumes could then act in synergy with endogenous odors to produce such states. However, some studies have also found that perfume addition alters negatively (although does not suppress) the perception of some traits advertised in body odors (Sorokowska et al., 2016). The cultural practice of wearing perfume could thus also have disrupting effects on biologically evolved signals. In sum, the combination between endogenous body odor and an exogenous fragrance may either have a synergic effect or a disruptive one, by either enhancing relevant characteristics of body odor, or by masking or altering them. Because humans usually emit a combination of biological and artificial odors, investigating their interaction is necessary to fully understand chemical communication.

In this study, the primary aim was to test whether positive emotions can be communicated through chemicals emitted by the body and whether it could take the form of emotional contagion. The secondary aim was to investigate to what extent the addition of perfume can modulate this. We collected sweat from male donors twice, once during a positive and once during a neutral Mood Induction Procedure (MIP), and we presented them to female receivers. Although other studies included both a positive and a negative emotional condition (Chen and Haviland-Jones, 2000; Zhou and Chen, 2009; de Groot et al., 2015a), we deliberately chose not to include a negative one in our design. Indeed, we wanted to avoid a potential contrast effect, where the processing of the negative stimuli would be prioritized over the processing of the positive one (negativity bias) and would thus prevent us from observing an effect of the positive condition. Receivers’ responses were then monitored at three levels: verbal descriptions, peripheral nervous systems’ responses, and performances in behavioral tasks. We hypothesized that the influence of emotional body odors is more likely to remain below the level of consciousness, and should be measurable on physiological and/or behavioral



responses as shown in previous studies (Li et al., 2007; Ferdenzi et al., 2016a). At the behavioral level, we indirectly tested the transmission of positive emotions by using creative problem-solving and divergent thinking tasks. According to the “broaden-and-build” theory (Fredrickson, 1998), positive emotions are expected to increase attentional scope and to allow greater flexibility of thoughts. We hypothesized first that receivers’ autonomic nervous system responses should differ in response to the positive versus the neutral odor, indicating a change in their emotional state (exploratory approach; see Kreibig, 2010, for the difficulty to establish a prediction). Second, we hypothesized that if emotional contagion occurred, receivers should be more efficient in creative tasks after smelling the positive body odor than the neutral one. Third, we expected that positive body odors would elicit higher positive verbal ratings (pleasantness, well-being) and stronger and longer sniffs (Mainland and Sobel, 2006), although it may very well not be the case because being produced in pleasant circumstances does not necessarily imply that a stimulus yields or possesses pleasant qualities in itself (see also de Groot et al., 2015, for an absence of pleasantness difference across conditions). Lastly, the literature on perfume effects is lacking in the field of chemical communication of emotions and our study thus remains exploratory on this question: perfume could either have no effect on chemical communication, erase it (by masking chemical cues), or enhance it due to a synergy between two emotionally positive messages.

## Materials and Methods

### **Odor donor part**

**Participants.** Donors were 21 males (Mean  $\pm$  Standard Deviation: 21.5  $\pm$  2.7 years of age), who declared being heterosexual, of European descent, and non-smokers. Male donors were preferred over female donors because they have larger apocrine glands (Doty et al., 1978) and might thus have the potential to produce more emotion-related chemicals. Sexual orientation and ethnicity were controlled because these parameters have been shown to influence body odor perception (Martins et al., 2005; Martin et al., 2010; Prokop-Prigge et al., 2016). All participants (donors and receivers hereafter) provided written informed consent prior to participation and received monetary compensation. This research was conducted in accordance with the Declaration of Helsinki and was approved by the local Lyon Sud-Est II ethical review board (March 6, 2014).

**Mood Induction Procedure.** All donors attended two emotion induction sessions (within-subjects design), a positive and a neutral one in random order, one day apart. During each induction session, after having been equipped for body odor collection, donors entered a separate room where the experiment was conducted. Induction was performed using short film clips assembled to provide a 30-minute sequence for each condition (for further details, see Supplementary Methods). Donors seated and watched the videos after the experimenters left the room. For the positive condition, donors were seated in groups of 3 which is believed to increase positive emotions thanks to the interaction and sharing of feelings (as seen in de Groot et al., 2015a). They were also given a personalized present (perfume and chocolates) before the induction started (Isen et al., 1987). In the neutral condition, the same donors were seated alone in the room and did not receive any present. To measure the emotional response of the donors during the MIP, we asked them after each excerpt to rate how amused, afraid, happy, sad, surprised, disgusted, angry, neutral and calm they felt during the clips using a paper-and-pencil 10-cm continuous scale from 0 (not at all) to 10 (extremely). Ratings were recorded in centimeters to the nearest 0.1 cm.

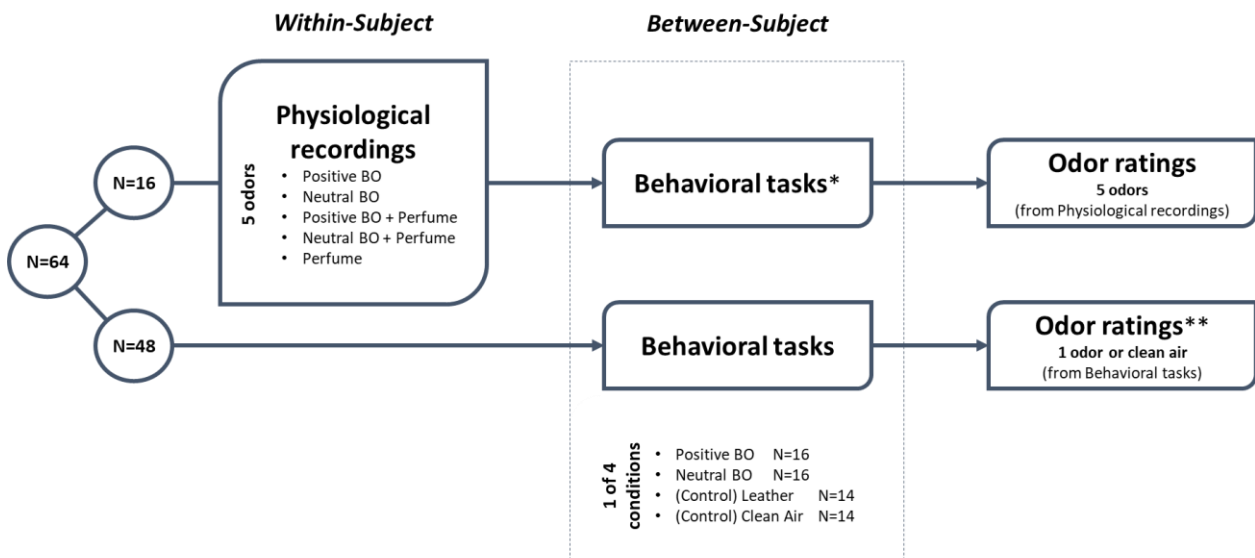
**Body odor collection.** From two days before the first odor collection, donors followed a protocol to prevent odor contamination (details can be found in Supplementary Methods). On collection days, donors had to take a shower just before coming to the laboratory. Experimenters used odorless tape (Urgopore microporous™, Urgo) to attach 10x10cm sterile cotton gauze pads (Sylamed) under each donor's armpit, while wearing nitrile gloves. Donors were then asked to put on a cotton t-shirt (Decathlon, previously washed with a non-perfumed detergent) instead of their personal clothes to prevent odor contamination. At the end of the emotion induction procedure, pads were removed, cut into 1x3cm strips taken from the central area of the pads, placed in aluminum foil and then in one ziplock bag per donor and per emotion condition (positive/neutral), before being stored at -32°C.

**Sample selection for odor presentation.** A selection of the samples was carried out before conducting the following step (presentation to the receivers) based on the emotional ratings provided by the donors after the video clips (see Mood Induction Procedure). As we noticed that emotional induction was not equally efficient in all donors (i.e., average happiness ratings collected during the positive MIP ranged from 2.7 to 9.4 on a scale from 1 to 10), we selected only the body odor samples of the donors who were best responsive to the MIP, to maximize our chances of presenting a chemosignal of positive emotion. Eight individuals fitted the selection criteria of i) average happiness ratings > 5 in the positive MIP and ii) average

happiness ratings  $\leq 5$  in the neutral MIP, and were thus selected. The samples of the remaining ones were not used in the following step of the experiment. Importantly, the fact that body odor samples were limited in quantity and not re-usable (due their instability) constrained the number of receivers that we were able to include in the study.

## **Receiver part**

**Participants.** Receivers were females who declared being heterosexual, of European descent, non-smokers, and using hormonal contraception. They reported not suffering from any psychological, cardiac, respiratory or olfactory diseases. Female receivers were preferred over male receivers because they have a better sense of smell and greater sensitivity to chemosignals of emotion (Brand and Millot, 2001; de Groot et al., 2014b). Sexual orientation and ethnicity were controlled for the same reasons as in donors, and hormonal contraception was also added to limit olfactory variations due to menstrual cycle in spontaneously ovulating women (Navarrete-Palacios et al., 2003). A total of 64 women took part (mean age  $\pm$  SD: 21.6  $\pm$  2.6 years old), either in both the physiological and behavioral tasks (N=16 of them) or only in the behavioral task (N=48 of them) (see distribution in Figure 1). Physiological responses were recorded separately from the behavioral responses, because for physiological recordings participants need to be motionless and calm to collect reliable measurements, which was not the case during the creativity tasks where they were standing and/or moving freely. Both groups did verbal evaluations of the odors they were exposed to either during the physiology session (5 odors) or during the behavioral session (1 odor). Note that some data were lost due to technical problems (see details in Figure 1).



\* Data for 4 participants was lost due to technical issues, \*\* Data for 3 participants was lost due to technical issues. The presented Ns do not include these participants.

**Figure 1: Summary of the experimental procedure.** Participants (N=64) either took part in the physiological recordings followed by the behavioral creativity tasks and the verbal evaluations of odors, or only did the behavioral tasks followed by the verbal evaluations. BO: Body Odor. The data of 4 (\*) and 3 (\*\*) participants was lost due to technical issues (Ns on the figure do not include these participants).

**Olfactory stimuli.** In the physiological recording session, all receivers were presented with 5 odor stimuli: body odors sampled during the positive and neutral MIP with or without perfume added, and perfume alone. The stimuli were presented 3 times each, in 3 blocks comprising the 5 stimuli in a pseudo-randomized order (interleaved with a clean air condition, never in first or last position, to limit olfactory fatigue). These 3 blocks were presented alternatively with blocks of other types of odors (non-body origin), used for another purpose and not analyzed here.

In the behavioral tasks, receivers were exposed either to positive body odor samples, neutral body odor samples, to the odor of leather (Firmenich SA) chosen because of its *a priori* perceptual similarities with human odor or clean air. As a between-subject design was used for the behavioral tasks, the number of different conditions to compare was limited. We therefore decided to include only the conditions related with our main hypothesis (positive versus neutral body odor) and controls, not those related with our secondary question (effect of perfume). With the control odor of leather, we wanted to explore if the mere presence of an odor resembling human body odors could impact creativity performances. We did not do so in

the physiological recordings, since the number of conditions was high and it is already known that the presence of an odor influences physiological parameters.

Preparation of the body odor samples was performed by putting the frozen 1×3cm sweat pad strips obtained in donors at room temperature one hour before the start of the receivers' session. To reduce the effects of interindividual variability, four strips from four different randomly selected donors, combining left or right armpits chosen at random (see Ferdenzi et al., 2009), were placed into a U-shaped Pyrex® tube (VS technologies, France; volume: 10 ml; length: 50 mm; external diameter: 14 mm). Each positive composite body odor and neutral composite body odor was prepared twice, to allow the addition of 2 drops of a male perfume in one of the two samples. The perfume (concentrate of commercially available fine fragrance diluted in Dipropylene-glycol, 10% concentration) was chosen among other perfumes because it received the highest scores of pleasantness in a preliminary test (N=24, 16 women). The “perfume alone” stimulus was obtained by putting 2 drops of the same perfume in a U-tube containing 4 clean 1×3cm strips of gaze. The leather and clean air conditions were obtained by placing 2 mL solution (leather diluted in Dipropylene-glycol, 20% concentration, or Dipropylene-glycol alone from Sigma–Aldrich for the clean air condition) in U-tubes containing scentless polypropylene fabric (twice 1×6 cm; 3M®, Valley, NE, USA). Olfactory stimuli were diffused at an airflow of 1.5 L/min using a computer-controlled olfactometer with time-controlled stimulus onset, and were delivered to the participant's nose through a nasal cannula.

**Physiological recordings.** Heart rate and skin conductance from 16 of the 64 receivers were measured with Equivital EQ02+ Lifemonitor system (Equivital, Cambridge, UK), and amplified by a Dual Bio Amp from AD instruments (Dunedin, New Zealand). The acquisition software was Labchart v8.1.5 (AD instruments, Dunedin, New Zealand). Signals were analyzed in a range of 10-seconds pre- and 10 seconds post-stimulus for the heart rate (as in Delplanque et al., 2009) and 10-second post stimulus for the skin conductance (to get only the event-related responses occurring within a few seconds after the stimulus and not the non-specific ones; Jacquot et al. (2018); Dawson et al. (2007)). High-pass, low-pass filters were added along with smoothing algorithms to eliminate artifacts. A local mean of the points during these 10-second windows was calculated using python scripts developed in-house. For *heart rate*, the mean values of the frequency were computed. For *skin conductance*, responses were detected using the algorithm described in Kim et al. (2004) and then counted in the 10s-post-stimulus window. The basic response basic peak was also measured, as the maximal value of the signal during the very same window. Sniffing behavior of the receivers was also recorded (as in (Ferdenzi et al., 2014, 2015b) This was performed by means of a nasal cannula positioned in both nostrils

and connected to an airflow sensor (AWM720, Honeywell, France). This system was developed in-house to allow us i) to synchronize odor delivery with the participants' respiration, and ii) to record sniffing behavior. The sniffing signal was amplified and digitally recorded at 256 Hz using LabVIEW software®. The maximum airflow (highest point), the area under the airflow curve (volume inspired) and the duration of the sniff (time between the inhalation starting point and the point where the flow returned to zero) were computed for the first sniff following odor presentation.

**Behavioral tests: creativity and problem-solving.** Almost all receivers took part in two behavioral tasks. The first task was the *Guilford's Alternate Uses Task* (Guilford, 1967). In this test, the participants are asked to list as many non-obvious uses as possible for common objects in a limited time and their answers are given scores in terms of fluency, originality, elaboration, and flexibility (for details about scoring and examples, see Supplementary Method). Here, receivers were given 2 minutes per object, which were: *brick, barrel, pencil, shoe, car tire, hanger*. The second task was *Duncker's Candle Problem* (Duncker, 1945). The receivers were brought in front of a table where they could find a box of tacks, a candle, and a box of matches. They were asked to find a way to affix the candle to the wall with the available objects (on a corkboard) in such a way that it would burn without dripping wax on the table or on the floor. The analyzed variable was solving time. The problem was considered as solved if the receivers emptied the book of matches, used the tacks to nail the box to the corkboard and made the candle stand inside the empty box. They were given 10 minutes to solve this problem and the time they spent to find the solution was scored in seconds. The participants who did not find the solution in the maximum allocated time were not taken into account in the time analysis.

**Verbal measures.** At the end of the experiment (after the creativity tasks), the female receivers were asked to evaluate odors on 9-point Likert scales (1 = not at all, 9 = extremely) for how intense, pleasant and familiar they were, and for the extent to which they caused well-being. These evaluations were required for the single odor receivers were exposed to during the behavioral tasks (i.e., either the positive body odor, the neutral body odor, leather or clean air). The 16 participants who underwent the physiological recording were asked to rate the five odors they were exposed to (i.e., the positive body odor with and without perfume, the neutral body odor with and without perfume, perfume alone) and clean air.

**Procedure.** The physiological recording session took part first (before the creativity tasks, for the 16 participants who took part in both types of tasks). The receivers were equipped with the measurement sensors and the nasal cannula and were seated in a comfortable chair in a quiet and well-ventilated room with standardized conditions of light (no windows) and temperature. They were also given white noise, sound-cancelling headphones. The experiment started with 2 minutes of rest to provide a baseline, then the first odor was sent with the olfactometer for 5 seconds, on an expiration to ensure that it would enter the nostrils at the beginning of the next inspiration. The next 60 seconds were odorless to return to the baseline and to avoid olfactory adaptation. Then, the next odor was sent and so on (in a pseudo-randomized order) until all odors were sent (first block out of three). After a 5-minute break, the behavioral tasks started. In the behavioral tasks, the odor condition was attributed randomly, the receivers being blind with regards to the nature of the odor. During the whole duration of the behavioral session, the odor (or clean air) was sent to the receivers' noses by the olfactometer through a nasal cannula, for 5 seconds every 30 seconds. Finally, the receivers rated the odor(s) on verbal scales and were thanked for their participation after a small brief about the purpose of the experiment.

## **Data analysis**

**Preparation of the data.** The receivers' physiological variables that we analyzed were: i) Mean heart rate difference between the 10-second post-stimulus and the 10-second pre-stimulus windows (beats per minute, post- minus pre-), ii) Log-transformed characteristics of the first sniff during odor presentation, namely sniff volume (area under the curve AUC, arbitrary unit) and sniff duration in seconds (between inhalation starting point and the point where the sniff's flow returned to zero), iii) Characteristics of the skin conductance response, namely the log-transformed SC basic peak (in  $\mu\text{S}$ , maximum value of the signal during the 10-s post-stimulus window minus value of the signal at stimulus onset), and number of SC responses (during the 10-s post-stimulus window). The odor ratings of intensity, pleasantness, familiarity and well-being collected after stimulus presentation were used as such. Finally, we analyzed the receivers' performances in the creativity tasks, represented by Alternate Uses Task (AUT) scores of fluency, originality, elaboration and flexibility (see Behavioral tests section) and time to solve the Candle Problem (in sec). The AUT scores were attributed in a double-blind fashion by two independent judges. The scores of both judges on each variable were highly correlated ( $r = 0.70$  to  $0.98$ ), and thus averaged.

There were missing data described as follows. Due to backup issues, 1 block (repetition) out of 3 was lost for 2 receivers (2 out of 48 blocks in total, 4.17%) for the physiological recordings. Due to technical issues, the responses of 4 out of 64 participants were lost for the behavioral tasks, and of 3 out of 48 participants for the odor ratings by the subgroup who only did the behavioral tasks (see Figure 1).

**Statistical analyses.** The physiological variables and verbal ratings made during the physiology session have been analyzed with linear mixed-effects models, using the *lme4* package (Bates et al., 2015) in R (R Core Team 2019, RStudio version 3.6.1). Fixed factors were Condition (Positive/Neutral body odor) and Perfume (With/Without). Subject was used as a random factor. Repetition was also included as a random factor but not retained since it did not significantly improve the models. Model selection was used to select the best models, using the *anova* function. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality. P-values were obtained using Kenward–Roger approximation in the *anova* function of *lmerTest* package in R (Kuznetsova et al., 2017) and non-significant interactions were removed to keep only the best model including the main effects. Post-hoc contrasts were performed using the *multcomp* function of the *emmeans* package in R (Lenth et al., 2020).

The number of SC responses was analyzed with three Chi-square tests to evaluate the effect of Condition and Perfume (for all trials together, and for trials with and without Perfume separately). Because the size of some cells of the contingency table was < 5, a Yates' correction was applied.

For both creativity tasks, we conducted one-tailed t-tests because a clear *a priori* hypothesis was postulated before data collection: smelling positive body odors is expected to increase positive affect and thereby creativity (Isen et al., 1987), compared with smelling neutral body odors. Our target comparison being the positive versus neutral conditions comparison, preliminary analysis comparing performances in presence of the neutral body odor (N=16) with those in the non-targeted conditions was conducted and revealed no significant differences: neither between neutral body odor and clean air (N=14 - AUT Fluency:  $p=0.328$ ; AUT Originality:  $p=0.412$ ; AUT Elaboration:  $p=0.910$ ; AUT Flexibility:  $p=0.439$ ; Candle Problem:  $p=0.144$ ) nor between neutral body odor and leather (N=14 - AUT Fluency:  $p=0.580$ ; AUT Originality:  $p=0.297$ ; AUT Elaboration:  $p=0.510$ ; AUT Flexibility:  $p=0.443$ ; Candle Problem:  $p=0.117$ ). Consequently, in the results section we focus only on the target comparison between positive (N=16) and neutral body odor (N=16). A chi-squared test was also conducted to



compare the frequency of succeeded versus failed attempts during the Candle Problem in the positive versus the neutral condition.

Finally, the odor ratings made after the behavioral tasks (1 odor per participant) were analyzed using Kruskal-Wallis tests. It must be noted that the neutral body odor did not differ from leather or clean air on ratings of familiarity, pleasantness and well-being (all ps >0.05). Only leather intensity was rated higher than all the other odors ( $X^2(3)=22.939$ ,  $p<0.001$ ).

## Results

### Physiological responses

After smelling the positive body odor, receivers had a decrease in mean heart rate (Mean  $\pm$  Standard Deviation:  $-0.957\pm 2.85$ ) which was not found after smelling the neutral body odor ( $-0.050\pm 2.81$ ; Figure 2), as shown by a significant effect of the Condition (Positive vs. Neutral:  $p<0.05$ ; 95% confidence interval (CI) =  $[-1.67, -0.14]$ ; Table 1). The log transformed Skin Conductance (SC) basic peak was not found to be modulated by Condition (Positive:  $-0.860\pm 0.80$ ; Neutral:  $-0.916\pm 0.78$ ;  $p>0.05$ , Table 1) or Perfume (With:  $-0.849\pm 0.79$ ; Without:  $-0.949\pm 0.78$ ;  $p>0.05$ , Table 1). Neither was the number of SC responses (total neutral:  $N=61/27/4/0$  for 0/1/2/3 responses respectively; and total positive  $N=60/18/12/2$ ;  $X^2(3)=7.808$ ,  $p>0.05$ ) even when analyses of only trials with perfume ( $X^2(3)=5.303$ ,  $p>0.05$ ) and without perfume ( $X^2(3)=3.302$ ,  $p>0.05$ ) were conducted. Regarding the olfactomotor responses, larger sniff volumes and longer sniff durations were found when body odors were presented with perfume (log-transformed Volume: With perfume  $-0.35\pm 0.33$  and Without  $-0.44\pm 0.30$ ;  $p=0.002$ ; 95% CI =  $[0.03; 0.13]$ ; log-transformed Duration: With  $0.27\pm 0.20$  and Without  $0.20\pm 0.14$ ;  $p<0.001$ ; 95% CI =  $[0.04; 0.11]$ ; Table 1), which is usually observed with more pleasant odors.

**Table 1.** Physiological and olfactomotor responses as a function of Condition (Positive vs. Neutral body odor) and Perfume (With vs. Without). Results of the linear mixed models with Condition and Perfume as fixed factors and Subject as random factor (intercept). For all variables, the best model was *Variable ~ Condition + Perfume + (1|Subject)*, therefore the effect of the interaction was not tested (see Methods). *P-values < 0.05 are in bold*

Variable	Main effects and interactions	Statistics	P-values
Heart Rate	Condition	F(1,166.03)=5.496	<b>p=0.020</b>
	Perfume	F(1,166.03)=0.334	p=0.564

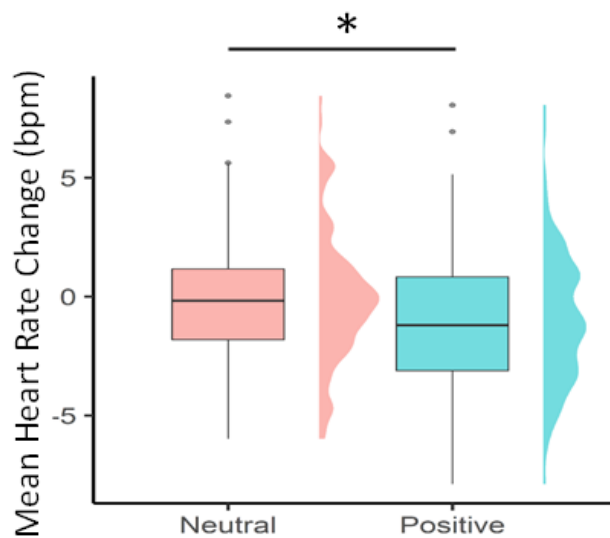
	Condition×Perfume	-	-
Skin Conductance basic peak	Condition	F(1,61.237)=0.044	P=0.835
	Perfume	F(1,60.352)=1.360	P=0.248
	Condition×Perfume	-	-
Sniff volume	Condition	F(1,166)=0.0004	P=0.984
	Perfume	F(1,166)=9.788	<b>P=0.002</b>
	Condition×Perfume	-	-
Sniff duration	Condition	F(1,166)=0.028	P=0.866
	Perfume	F(1,166)=21.090	<b>P&lt;0.001</b>
	Condition×Perfume	-	-

When asked to explicitly evaluate the stimuli they were exposed to during the physiological recordings, the participants rated the positive body odors as more intense than the neutral body odors (Positive:  $4.09 \pm 2.59$ , Neutral:  $3.16 \pm 2.11$ ; Main effect of Condition:  $p < 0.05$ , 95% CI = [0.29; 1.58]; Table 2). The Condition×Perfume interaction was also significant ( $p < 0.05$ , Table 2) because positive body odors were rated as more intense only when combined with perfume (Figure 3). They were also rated as more familiar (Positive:  $4.5 \pm 2.63$ ; Neutral:  $3.47 \pm 2.17$ ; Main effect of Perfume:  $p < 0.05$ ; 95% CI = [0.14; 1.92], Table 2; Figure 3). Finally, when the stimuli were presented with perfume, they were perceived as more pleasant (With perfume:  $4.91 \pm 1.78$ ; Without perfume:  $3.50 \pm 2.20$ ;  $p = 0.002$ ; 95% CI = [0.57, 2.25]; Table 2), more intense (With:  $5.53 \pm 1.83$ ; Without:  $1.72 \pm 0.89$ ;  $p < 0.001$ ; 95% CI = [3.17, 4.46]; Table 2), more familiar (With:  $5.25 \pm 2.13$ ; Without:  $2.72 \pm 2.08$ ;  $p < 0.001$ , 95% CI = [1.64, 3.42]; Table 2), and tended to elicit higher levels of well-being (With:  $4.46 \pm 1.74$ ; Without:  $3.67 \pm 2.22$ ;  $p = 0.06$ ; 95% CI [0.04, 1.67]; Table 2).

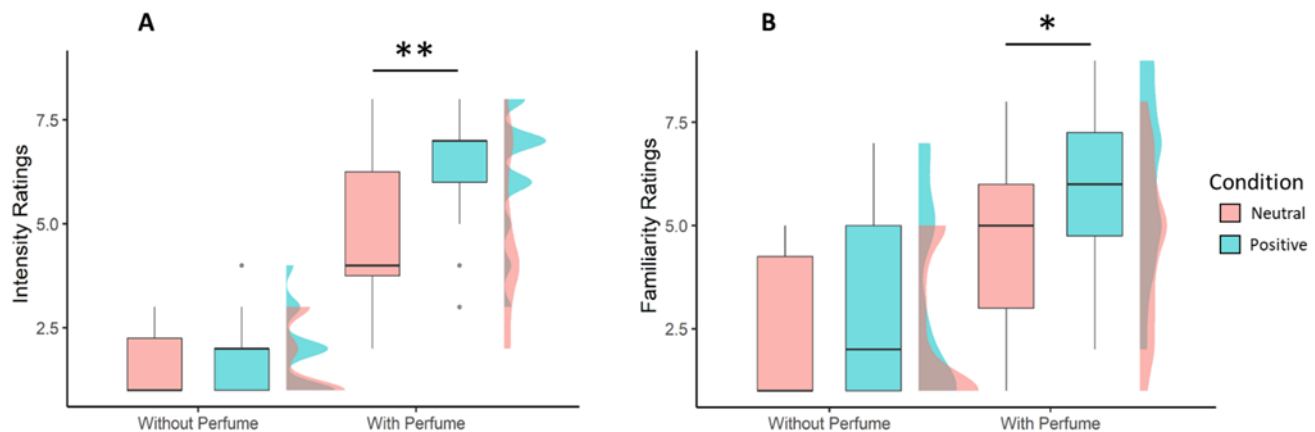
**Table 2.** Odor ratings as a function of Condition (Positive vs. Neutral body odor) and Perfume (With vs. Without) (N=16). Results of the linear mixed models with Condition and Perfume as fixed factors and Subject as random factor (intercept). The effect of the interaction was tested only when the interaction was present in the best model (see Methods). P-values < 0.05 are in bold.

Variable	Main effects and interactions	Statistics	P-value
Pleasantness	Condition	F(1,46)=0.454	P=0.504
	Perfume	F(1,46)=11.340	<b>P=0.002</b>

	Condition×Perfume	-	-
Well-being	Condition	F(1,46)=0.541	P=0.466
	Perfume	F(1,46)=3.657	P=0.062
	Condition×Perfume	-	-
Intensity	Condition	F(1,45)=8.508	<b>P=0.005</b>
	Perfume	F(1,45)=140.710	<b>P&lt;0.001</b>
	Condition×Perfume	F(1,45)=5.445	<b>P=0.024</b>
Familiarity	Condition	F(1,45)=5.476	<b>P=0.024</b>
	Perfume	F(1,45)=32.992	<b>P&lt;0.001</b>
	Condition×Perfume	-	-



**Figure 2: Female receivers' autonomic responses during the presentation of male body odors collected during Positive and Negative mood induction (N=16).** Boxplot of mean heart rate change between the 10 second post-stimulus and the 10 second pre-stimulus window, in beats per minute (Bpm) for the neutral and positive condition (\*:  $p < 0.05$ , see statistics in Table 1).

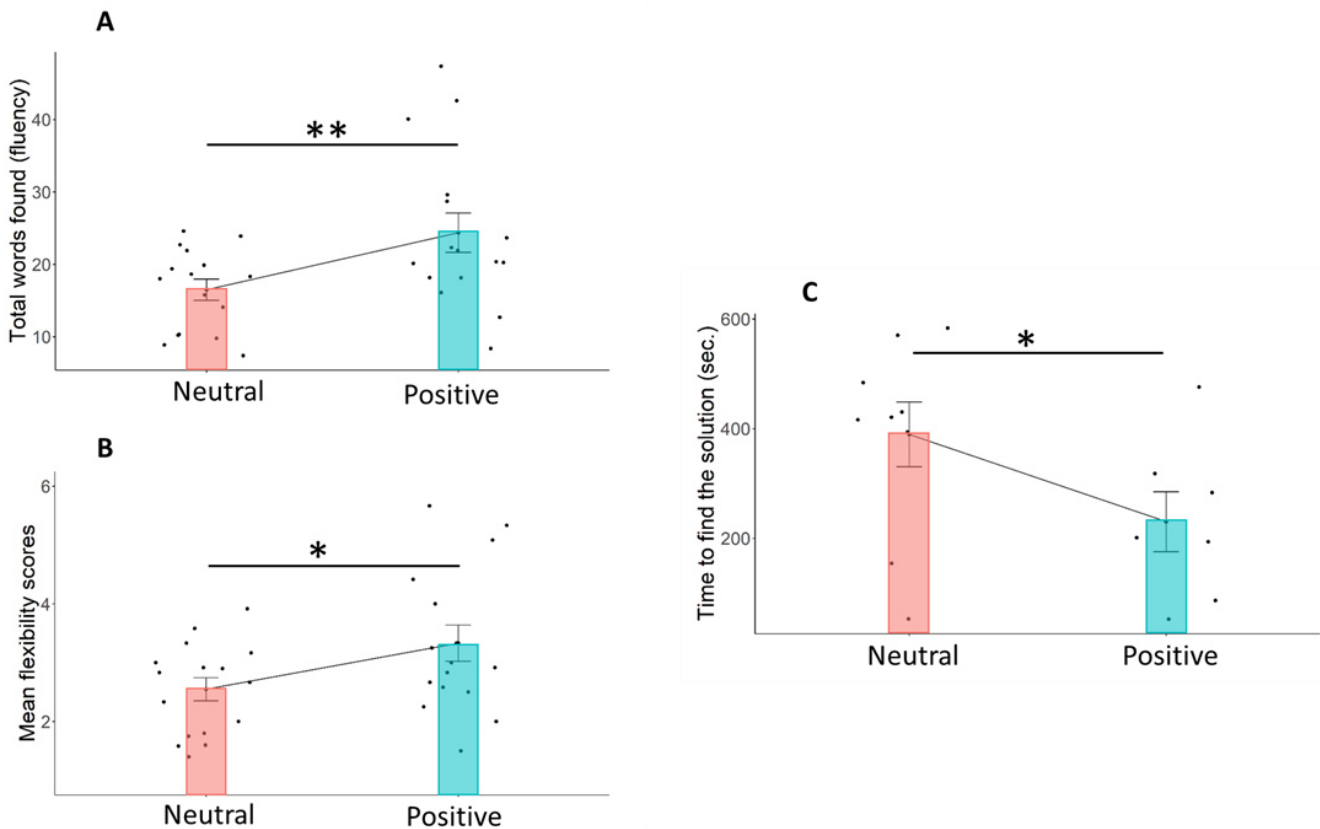


**Figure 3: Female receivers' verbal responses during the presentation of male body odors collected during Positive and Neutral mood induction (N=16). A) Boxplot of the intensity ratings (1-9) for neutral and positive body odors, without and with perfume (Condition×Perfume interaction:  $p < 0.05$ , see statistics in Table 1). B) Boxplot of the familiarity ratings for neutral and positive body odors, with and without perfume. \*:  $p < 0.05$ , results of post-hoc contrasts between Positive and Negative Conditions.**

### Behavioral responses

Receivers' responses in both behavioral tasks revealed consistent results. In the first task, the Alternate Uses Task, the group exposed to positive body odors found significantly more alternative uses (higher Fluency) than the group receiving the neutral body odor (Positive:  $24.37 \pm 10.87$  words, Neutral:  $16.50 \pm 5.83$ ,  $t(30) = 2.553$ ,  $p = 0.008$ , 95% CI = [1.58, 14.17]; Figure 4A). They also displayed higher Flexibility, i.e. they used more varied categories of uses (Positive:  $3.33 \pm 1.23$  categories, Neutral:  $2.54 \pm 0.78$ ,  $t(30) = 2.152$ ,  $p = 0.018$ ; 95% CI = [0.04, 1.53]; Figure 4B). Both groups did not differ on the Originality ( $t(30) = 1.290$ ,  $p = 0.103$ ; 95% CI = [-0.06, 0.27]) or Elaboration ( $t(30) = 0.651$ ,  $p = 0.260$ ; 95% CI = [-0.27, 0.14]) of their responses. In the second task, participants had to solve The Candle Problem in a limited time. Out of 16 participants in each group, 9 found the solution in the allowed time in the neutral condition (7 failed) and 7 in the positive condition (9 failed). This difference between the two observed frequencies was not significant ( $\chi^2(1) = 0.125$ ,  $p = 0.724$ ). Among those who did find the solution, those who were exposed to the positive body odor found the solution faster than those who smelled the neutral one (Positive:  $230.43 \pm 144.75$  seconds, Neutral:  $389.67 \pm 177.22$ ;  $t(13.94) = 1.978$ ,  $p = 0.037$ ; 95% CI = [-332.01, 13.53]; Figure 4C). Let us recall that the effect of perfume was not investigated in these tasks.

When asked about their explicit evaluation of the odor they had just been exposed to, no differences were found between the positive and the neutral body odor regarding intensity, familiarity, pleasantness and well-being (all ps >0.05).



**Figure 4: Female receivers' behavioral responses in creativity tasks during the presentation of male body odors collected during either a Positive or a Neutral mood induction.** A) Total number of words found per participant in the Alternate Uses Test in the presence of the positive and neutral body odors (N=16 per condition). B) Mean flexibility scores for the AUT in the presence of the positive and neutral body odors (N=16 per condition). C) Mean time to find the solution to the Candle problem, in seconds (in participants who successfully solved the problem: N=9 out of 16 for the neutral condition, N=7 out of 16 for the positive condition). Means  $\pm$  Standard Error of the Mean in all graphs.

## Discussion

The aim of this research was to explore whether positive emotions could be communicated between humans through body odors and if this transmission could take the form of an emotional contagion between an emitter and a receiver. We also explored for the first time whether perfume could modulate emotional contagion, since ecologically speaking body odors are uncommonly found alone. We showed that exposure to chemosignals of positive affect collected in donors impacted receivers' responses, in line with our hypotheses and previous work (Chen and Haviland-Jones, 2000; de Groot et al., 2015a). Moreover, there was concordant evidence that positive affect may transfer from one individual to another through this route (emotional contagion, Hatfield et al., 1993), since we recorded increased performances in two different creativity tasks in presence of the positive body odor. Indeed, it has been extensively documented that performance on those tasks is affect-dependent and facilitated if one is experiencing positive affect (Isen et al., 1985, 1987). Finally, perfume increased stimuli pleasantness and had a synergic effect by revealing differences in perceived intensity between positive and neutral body odors that did not reach conscious perception in the absence of perfume.

At the physiological level, heart rate was modulated by the positive body odors compared with the neutral ones. There was a deceleration of the mean heart rate after participants smelled the positive body odor: such a decrease has been reported before with odors considered as pleasant (Alaoui-Ismaili et al., 1997; Bensafi et al., 2002). This may be related to the positive valence of the odor, even though it did not reach awareness since the positive odor did not receive higher pleasantness ratings. Heart rate deceleration has also been linked before to positive emotional states, through the measure of vagal tone. Vagal tone is a core component of the parasympathetic nervous system activity (Porges, 1995); it decreases heart rate and predicts increases in positive emotions (Kok and Fredrickson, 2010). Reciprocally, increases in positive emotions predict heightened vagal tone (Kok and Fredrickson, 2010). This provides support to the fact that positive emotions have a role in countering the deleterious effects of negative emotions (e.g., increased blood pressure and heart rate in response to stressors) by acting as a brake and by allowing the organism to return to a physiological baseline (Stephoe et al., 2005; see also the "undo" effect of positive emotions: Fredrickson, 1998a). The fact that most participants (97%) reported not to smelling anything when presented with body odors alone and that no perceived differences were found in the "without perfume" condition (they were forced to provide ratings anyway) suggests that chemosignals of positive affect may alter physiology and cognition at a subliminal level. This is consistent with previous studies on human chemical communication, where body odors are consistently rated as very low in

intensity, if not perceived at all (Mujica-Parodi et al., 2009) and have subliminal effects on perception and behavior.

Most importantly, when using creativity-related tasks as an indirect measure of positive affect transfer, we showed that the group smelling the positive body odor was significantly more efficient in these tasks than the neutral odor group. They had higher fluency and higher flexibility scores in the AUT and found the solution to the Candle problem more quickly. Note that for the AUT, originality and elaboration scores remained unaffected by Condition, probably due to the time constraints, which can have detrimental effects on creativity (Amabile, 1979). Also, participants in the positive group did not find the solution to the Candle problem more often than the control group (perhaps because the allowed time –fixed for experimental reasons- might not have been sufficient to discriminate between them) but when they did find a solution, they were significantly faster. This has been observed before: after a positive emotional induction, medical students do not solve medical problems more often than the control group, but they do it faster and put more effort into solving them (Isen et al., 1991). Taken together, the physiological and behavioral results are consistent and suggest that emotional contagion may have occurred at two levels in the experimental setting, even though the design only provides indirect evidence of it. Respectively at the physiological and behavioral levels, low heart rate (Ekman et al., 1983) and better performances at creative problem-solving tasks (Isen et al., 1987) have been linked with experiencing happiness or positive affect. This is the first time an effect on creativity has been shown in receivers exposed to emotional body odors.

Regarding the role of fragrance that we tested only on ratings and physiological responses (not behavior), we found that adding perfume to body odors did not interfere with heart rate and skin conductance responses, but that it had a synergic effect with the positive emotion at the perceptual level. Indeed, perfume increased positive body odor intensity compared to the neutral body odor, while both odors were perceptually similar (and mostly not consciously perceived at all) when presented unperfumed. This suggests – for the first time in the context of emotional communication – that fragrance use may not be detrimental to chemical communication within human social networks, in accordance with previous findings on discrimination between individuals (Allen et al., 2015). This points out to the fact that, even if the olfactory background changes, the emotional chemosignals contained in body odors may have such a relevance that they still remain effective. Additionally, our results show that perfume could even, in some cases, facilitate the perception of some characteristics inherent to the emotional body odor (at least with the particular perfume and concentration we used). This facilitating effect could be specific to the communication of positive states. Here, body odors received higher positive ratings (pleasantness, and a tendency for well-being) when

mixed with perfume, which was corroborated by a more intense sniffing behavior (sniff duration and volume) than without perfume: therefore, the synergic effect we found might only take place if the intrinsic qualities of the exogenous (perfume) and endogenous (body) odors are consistent, allowing an easier discrimination by repetition of coherent information without redundancy. In the future, whether such a perceptual synergy would influence the behavioral outcomes we found in creativity tasks should be tested.

To conclude, this study constitutes a significant step forward in understanding the chemical communication of positive emotions in humans and on its modulation by exogenous fragrances. We provided evidence in favor of the presence of chemosignals of positive emotions in human body odor, of the modulation of receivers' physiology and behavior in response to these chemosignals and of a likely replication of the positive emotional state in the receivers. Future research is needed to confirm these conclusions. For example, because of technical constraints our study had to be conducted in a single-blind fashion: although maximum precautions were taken to prevent observer-expectancy, a double-blind design is recommended in the future. In addition, as an initial approach of the question, we limited our study to female receivers responding to male odors of about the same age. Investigating other combinations of sex (and age) characteristics would provide a more ecologically valid picture. Sample sizes were quite small in our study, and future investigations should enhance statistical power by using larger sample sizes. Regarding perfume, investigating its effects on negative emotion communication could be useful, especially in situations where disruption of such a communication could be beneficial (e.g., stress contagion during exams or in confined situations, etc.). Finally, future research could extend the investigation in social situations closer to real contexts, in which olfactory signals co-occur with other sensory stimuli and in which multisensorial integration takes place. While negative emotional contagion serves the adaptive function of alerting conspecifics about dangerous situations, positive emotional contagion also has adaptive advantages: it allows communities to build social interaction, inciting them to explore new approaches about situations and ideas, and promoting global communication. Sharing positive emotions helps us build resources and contributes to defining us as a social species.



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# STUDY 2 - VR

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## Preamble

Several valuable lessons could be learned from **Study 1**. First, the receivers reacted differently to positive and neutral control chemosignals, as measured by physiological, verbal, and behavioral patterns, suggesting the existence of semiochemical markers of positive emotions. Second, the observed effects fell in line with what would be expected if the said semiochemicals caused an emotional contagion: receivers showed a reduced heart rate as well as improved performances in creativity tasks. These lessons in mind, we sought to go further by exploring how the intensity of the emotional induction could modulate the chemical communication. Thus, this second study was carried with a highly similar methodology, except for one crucial point: the way the emotions were created. Since in the previous study videos were used, and that in some donors this induction procedure did not have an effect strong enough (their samples were not included in the receiver part), we decided this time to address this by exploring a higher level of realism and naturality in **Study 2**, by generating emotions via a promising tool: virtual reality. Would the observed effects in receivers prove to be stronger if caused by more intense emotions in donors?

Additionally, although effects of positive chemosignals were found in **Study 1**, the fact that positive emotional chemical communication in humans had only been studied and reported once before (de Groot et al., 2015a) prompted us to attempt to confirm these conclusions and findings in **Study 2**.

# Investigating the human chemical communication of positive emotions using a virtual reality-based mood induction (Submitted – Physiology & Behavior)

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## **Abstract**

Humans can communicate their emotions to others via volatile emissions from their bodies. Although there is now solid evidence for human chemical communication of fear, stress and anxiety, investigations of positive emotions remain scarce. In a recent study, we found that women's heart rate and performance in creativity tasks were modulated by body odors of men sampled while they were in a positive vs. neutral mood. However, inducing positive emotions in laboratory settings remains challenging. Therefore, an important step to further investigate the human chemical communication of positive emotions is to develop new methods to induce positive moods. Here, we present a new mood induction procedure (MIP) based on virtual reality (VR), that we assumed to be more powerful than videos (used in our previous study) to induce positive emotions. We hypothesized that, consequently, given the more intense emotions created, this VR-based MIP would induce larger differences between the receivers' responses to the positive body odor versus a neutral control body odor, than the Video-based MIP. The results confirmed the higher efficiency of VR to induce positive emotions compared with videos. More specifically, VR had more repeatable effects between individuals. Although positive body odors had similar effects to those found in the previous video study, especially faster problem solving, these effects did not reach statistical significance. These outcomes are discussed as a function of the specificities of VR and of other methodological parameters, that may have prevented the observation of such subtle effects and that should be understood more in-depth for future studies on human chemical communication.

## **Keywords**

Chemical communication, virtual reality, positive emotions, body odor, perfume, emotional contagion

## Introduction

Humans are able to communicate information of social nature to people surrounding them via complex signals of chemical nature (chemosignals, Doty, 2010) emitted by the body (Lübke and Pause, 2015). Information from a *donor* (or *emitter*), perceived by a *receiver* via the olfactory channel, may concern for example identity (Penn et al., 2007a), sex (Schleidt et al., 1981), age (Mitro et al., 2012), diet (Havlicek and Lenochova, 2006), sickness (Olsson et al., 2014), aggression (Mutic et al., 2016), or competition (Adolph et al., 2010). Transient negative emotional states can also be communicated in this manner, such as sadness (Gelstein et al., 2011), disgust (de Groot et al., 2012), and especially fear and anxiety (Pause, 2004; Prehn et al., 2006; Mujica-Parodi et al., 2009; Haegler et al., 2010; Dalton et al., 2013; de Groot et al., 2014a, 2014b). This has been confirmed in a recent meta-analysis (de Groot and Smeets, 2017). For the chemical communication of positive emotional states, however, evidence remains much more scarce and disparate results were found (de Groot et al., 2015a).

In a recent study, we investigated humans' ability to communicate a range of positive feelings via their axillary odor (Richard Ortegón et al., 2022). We found converging evidence for the transmission of positive emotions from male donors to female receivers, and that this escaped conscious awareness, as is often observed in chemical communication studies (Lundström et al., 2008; Mujica-Parodi et al., 2009). Rather than a mere transmission, it is an emotional contagion that seems to have taken place (i.e., a partial replication of the state of the donor in the receiver, Hatfield et al., 1993). Indeed, the receivers exposed to the body odor of donors having experienced positive feelings (i.e., positive body odors), showed signs of being in a positive emotional state themselves, such as reduced heart rate (Kok and Fredrickson, 2010; Kok et al., 2013) and improved performance on behavioral tasks known to be modulated by positive affect (i.e., creative thinking/problem solving tasks, Isen et al., 1985, 1987). A secondary aim of that study was to investigate perfume's interaction with this chemical communication of positive emotions. Indeed, although body odors are rarely found alone in ecological situations (Havlíček and Roberts, 2013) and the use of fragrance is nearly universal since antiquity (Classen et al., 1994), the possible modulation of interpersonal chemical communication of emotions remains unexplored to date. In Richard Ortegón et al. (2022), adding perfume did not suppress the effect of positive body odors on heart rate, and acted in synergy with positive body odors for some of the variables studied (increased perceptual differences between positive and neutral body odors).

Although this feeds the meager existing literature with new arguments in favor of a chemical communication of positive emotions in humans, a methodological challenge persists. Indeed, the contrasted results of previous studies may be due to the fact that inducing positive

emotions in the laboratory remains challenging: for example, in the study described above, the positive mood induction implemented with videos was successful in only 38% of the odor donors. Developing new and more efficient methods to induce positive mood is thus an important step to better understand the human chemosignalling of positive emotions. This is the main aim of this article.

Emotion elicitation in laboratory settings can be considered as lacking ecological validity (Parsons, 2015) and is not fully equivalent to that experienced in daily life. Controlled mood induction procedures (MIP) used in the laboratory implement a variety of means, varying in realism. These means, *inter alia*, include: autobiographical recall (Mills and D'Mello, 2014), music (Västfjäll, 2001; Juslin and Laukka, 2004), pictures (IAPS: Bradley and Lang, 2007), short clips/movies (Gross and Levenson, 1995; Hewig et al., 2005), and self-referential statements such as the Velten procedure (Velten, 1968; Kenealy, 1986). A comparison of several of these MIPs suggests that the more senses are engaged, the more efficient MIPs are (Baumgartner et al., 2006; Zhang et al., 2014). As a consequence, a promising pathway to increase MIPs efficiency could be the use of virtual reality (VR). This tool is indeed pertinent because it is closer to everyday life stimulations than many of the pre-existing MIPs, due to the fact that it can recruit visual and auditory channels but also provide tactile return via controllers as well as vestibular sensations for example. VR allows deeper feelings of “immersion” and “presence” (see Steuer, 1992; Baños et al., 2004) which have been reported as important for being closer to real-life daily situations. Furthermore, it has been shown to be a successful tool for inducing emotions, including positive ones (Riva et al., 2007; Gorini et al., 2011; Baños et al., 2012; Diemer et al., 2015; Felnhofer et al., 2015). It thus makes it a promising instrument for studies in the field of human chemical communication of emotions, in which it has never been implemented before.

In the present study, we thus tested a new method to induce positive emotions, namely a VR-based MIP. Apart from the type of MIP (VR activities instead of 2D video clips, to allow for a more realistic setting), the design of the experiment was similar to our previous experiment (Richard Ortégón et al., 2022). We collected axillary sweat from donors after a positive and a neutral VR-based MIP, the former being designed to elicit positive emotions and the latter to not create any vivid emotion. Then, receivers were exposed to these body odors and their responses were monitored at different levels: autonomic nervous system responses, verbal conscious ratings, and behavioral tasks involving creative problem-solving and divergent thinking tasks, based on the “broaden-and-build” theory (Fredrickson, 1998). This theory links creativity to positive affect, an association robustly found in the literature (Isen et al., 1985,

1987, 1991; Estrada et al., 1994; Ashby et al., 1999; Fredrickson and Branigan, 2005). We first hypothesized that compared with the Video-based MIP we previously used, a more realistic and immersive procedure using VR-based MIP would elicit stronger emotions in donors. Second, we hypothesized that, as a consequence, a stronger emotional contagion would occur in receivers exposed to body odors sampled during a VR-based MIP. Especially, it can be expected that this emotional contagion is expressed as previously through the receivers' physiological responses (decreased heart rate after having smelled the positive body odor), but also through their verbal and behavioral responses (better performance in creative tasks when exposed to the positive body odor). Finally, in the physiological session, a condition where perfume was added to the sampled positive and neutral body odors was implemented. In line with our previous study, no disruptive effect of perfume is anticipated.

## Methods

### **Part 1. Odor collection**

#### **Participants (donors)**

Donors were 10 males (mean age  $\pm$  SD: 24.0  $\pm$  4.4 years old) who declared being heterosexual, of European descent, and non-smokers. Male donors were preferred over female donors because they have larger apocrine glands (Doty et al., 1978) and might thus have the potential to produce more emotion-related chemicals. Sexual orientation and ethnicity were controlled because these parameters have been shown to influence body odor perception (Martins et al., 2005; Martin et al., 2010; (Prokop-Prigge et al., 2016). All participants (donors and receivers hereafter) provided written informed consent prior to participation and received monetary compensation. This research was conducted in accordance with the Declaration of Helsinki and was approved by the local Sud Méditerranée III ethical review board (May 13, 2019).

#### **Virtual environment and stimuli**

Donors took part in two sessions each, one with a positive MIP and one with a neutral one, on two different days. Two virtual environments were created in Visual Studio with Unity 2017.4.20f1. For the *positive condition*, participants stood in a virtual homely and warm living room surrounded by mountains and lakes. In this home environment, they were given the possibility to take part in one or more activities successively, among 3 games available from

Steam store (<https://store.steampowered.com/>): Google Earth VR by Google – a game to explore the world through Google Earth in virtual reality, TiltBrush – a 3D painting game by Google, and Guided Meditation by Cubicle Ninjas – an application that allows to meditate in virtual environments) and ten 360° videos (including landscapes of beaches, mountains, videos of puppies or northern lights for example). For the *neutral condition*, participants stood in a virtual room, which was an empty replication of the real experimental room. This virtual room was equipped with a screen where the participants were given the opportunity to watch 2D clips (those used as a neutral MIP in our previous research, Richard Ortégón et al., 2022). and/or to participate in a not very interesting construction game (developed in-house) in which they had to stack wooden blocks to build a pre-defined architectural structure. In both conditions, participants were allowed to perform as many different activities as they wanted for 30 minutes. They were free to repeat or interrupt them according to their wishes, as to give them a personalized experience.

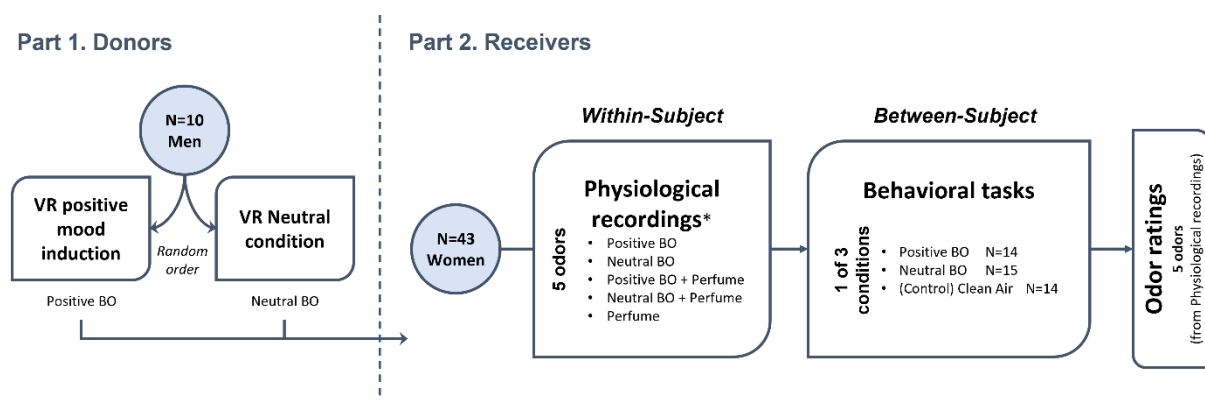
## **Body odor collection**

From two days before the first odor collection, donors followed a protocol to prevent odor contamination (details can be found in Supplementary Methods). Body odor collection took place on mornings only, so as to minimize potential emotional events before the collection. Additionally, donors had to take a shower just before coming to the laboratory. After having washed their armpits with odorless soap (Le Petit Marseillais, Johnson & Johnson, Issy-les-Moulineaux, France), they were asked to put on cotton t-shirts (Decathlon, Villeneuve d'Ascq, France), previously washed with a non-perfumed detergent (Le Chat Sensitive 0%, Henkel, Düsseldorf, Germany), instead of their personal clothes to prevent odor contamination. On these t-shirts, 10x10cm sterile gauze pads (Sylamed) were affixed to the armpit zone via stainless steel snaps. At the end of the emotional induction, pads were removed, cut into 1x3cm strips taken from the central area of the pads, placed in aluminum foil and then in one ziplock bag per donor and per emotional condition (positive/neutral), before being stored at -32°C.

## **Procedure**

Donors attended the two MIP sessions (neutral/positive) in random order one day apart (within-subjects design) (Figure 1). Upon their arrival, they put the prewashed cotton t-shirt on. The experimenters then placed facial Ag/AgCl EMG electrodes on the right *zygomaticus major* to record the number and intensity of contractions during the session as to get an objective

measure of positive affect. Then, participants put the VR headset (HTC Vive, HTC France Corporation, Paris, France) and headphones on to undergo the emotion induction procedures. To measure the emotional response of the donors during the MIP, they were asked after each excerpt or activity to rate how amused, afraid, happy, sad, surprised, disgusted, angry, neutral and calm they felt during the activities using continuous virtual visual analog scales ranging from “not at all” to “extremely” (then converted to 0-100 scores) and presented inside the virtual home environment. For each condition, an internal timer limited the session to 30 minutes, at the end of which participants were informed to exit the virtual activities, to go back to the home environment again and to end the session.



**Figure 1. Summary of the experimental procedure.** Donors (N=10) underwent a positive mood induction procedure and a neutral one, in a random order two days apart, during which their body odor was sampled. Receivers (N=43) took part in physiological recordings during which they were exposed to both positive and neutral body odors, then in behavioral creativity tasks in one of the odor conditions, and finally in verbal evaluations of all odors. BO: Body Odor. Skin conductance data of 10 (\*) participants was lost due to technical issues.

## Part 2. Odor presentation

### Participants (receivers)

Receivers were 43 women (mean age  $\pm$  SD: 22.2  $\pm$  2.7 years old) who declared being heterosexual, of European descent, non-smokers, and using hormonal contraception. They reported not suffering from any psychological, cardiac, respiratory, or olfactory diseases. Female receivers were preferred over male receivers because they have a better sense of

smell and greater sensitivity to emotion chemosignals (Brand and Millot, 2001; de Groot et al., 2014). Sexual orientation and ethnicity were controlled for the same reasons as in donors, and hormonal contraception was also added to limit olfactory variations due to the menstrual cycle in spontaneously ovulating women (Navarrete-Palacios et al., 2003). All of the receivers took part on the same day in a 3.5-hour session which included: physiological recordings, behavioral tasks, and verbal ratings (Figure 1).

## Stimuli

In the physiological recording session, all receivers were presented with 5 conditions (positive body odor, neutral body odor, perfume alone, positive body odor with added perfume, and neutral body odor with added perfume; within-subjects design). The stimuli were presented 3 times each, in 3 blocks comprising the 5 stimuli in a pseudo-randomized order (interleaved with a clean air condition, never in first or last position, to limit olfactory fatigue and cleanse the tubing). In the behavioral tasks, receivers were exposed either to positive body odor samples, neutral body odor samples, or clean air (condition attributed randomly, between-subjects design). Due to time and material limitations, no condition with perfume was included in the behavioral tasks. For the verbal ratings, all odors previously used in the physiological session were rated by all receivers (Figure 1).

Preparation of the body odor samples was performed by putting the frozen 1×3cm sweat pad strips obtained in donors at room temperature one hour before the start of the receivers' session. To reduce the effects of interindividual variability between the 10 donors, 4 strips from 4 different donors (chosen in a pseudo-randomized manner), combining left or right armpit chosen at random (Ferdenzi et al., 2009), were used for each receiver, and this composite stimulus was changed every half-day of experimentation. This stimulus was placed into a U-shaped Pyrex® tube (VS technologies, France; volume: 10 ml; length: 50 mm; external diameter: 14 mm). Each positive composite body odor and neutral composite body odor sample was prepared twice, to allow for the addition of 2 drops of a male perfume in one of the duplicated samples. For the perfume-only condition, 2 drops were dropped into an unused 1×3cm sterile gauze pad strip. The perfume (concentrate of a commercially available fine fragrance diluted in Dipropylene-glycol, 10% concentration) was chosen among other perfumes because it received the highest scores of pleasantness in a preliminary test (N=24, 16 women). Olfactory stimuli were diffused at an airflow of 1.5 L/min using a computer-

controlled olfactometer with time-controlled stimulus onset and were delivered to the participant's nose via a nasal cannula.

## Measures

**Physiological recordings.** Donors' facial muscular responses were measured converted and amplified via an 8-channel Procomp+ amplifier (Thought Technology, Montreal, Canada). Receivers' heart rate, skin conductance response, and facial muscular responses were measured with Equivalant EQ02+ Lifemonitor system (Equivalant, Cambridge, UK), and amplified by a Dual Bio Amp from AD instruments (Dunedin, New Zealand). The acquisition software was LabChart v8.1.5 (AD Instruments, Dunedin, New Zealand). Signals were analyzed in a range of 10-seconds pre- and 10 seconds post-stimulus for the heart rate and 10-second post-stimulus for the skin conductance. High-pass, low-pass filters were added along with smoothing algorithms to eliminate artifacts. A local mean of the points during these 10-second windows was calculated using scripts developed in-house with Python (v.3.7; Van Rossum and Drake, 2009). For *heart rate*, the mean values of the frequency were computed. For *skin conductance (SC)*, responses were detected using the algorithm described in Kim et al.(2004) and then counted in the 10s-post-stimulus window. The basic response basic peak was also measured, as the maximal value of the signal during the very same window. EMG recordings (256 Hz sampling rate in donors, 1000Hz sampling rate in receivers) were done via Ag/AgCl electrodes on the *zygomaticus major* and the *corrugator supercilii* muscles (only *zygomaticus* for donors and both *zygomaticus* and *corrugator* for receivers), because these muscles have been extensively used in psychophysiological research as markers of positive and negative emotions, respectively (Tassinari et al., 2007). Since the aim of EMG measure in donors and receivers was not the same, the analyzed time windows were also different: for donors, they were 30 minutes long (equivalent to one induction session) and for receivers the analyzed portion was the 10-sec post stimulus one. The number of peaks for each respective time window was computed by means of in-house Python scripts, and the area under the curve was calculated for the detected peaks. The sniffing behavior of the receivers was also recorded. This was performed by means of a nasal cannula positioned in both nostrils and connected to an airflow sensor (AWM720, Honeywell, France). This system was developed in-house to allow us i) to synchronize odor delivery with the participants' respiration, and ii) to record sniffing behavior. The sniffing signal was amplified and digitally recorded at 256 Hz using LabVIEW software®. The maximum airflow (highest point), the area under the airflow curve (volume inspired), and the duration of the sniff (time between the inhalation starting point and



the point where the flow returned to zero) were computed for the first sniff following odor presentation.

***Creativity and problem-solving tasks.*** All receivers took part in two different behavioral tasks. The first task was Guilford's Alternate Uses Task (Guilford, 1967). In this test, the participants are asked to list as many non-obvious uses as possible for common objects in a limited time and their answers are given scores in terms of fluency, originality, elaboration, and flexibility (for details about scoring and examples, see Supplementary Method). Here, receivers were given 2 minutes per object, which were: brick, barrel, pencil, shoe, car tire, hanger. The second task was Duncker's Candle Problem (Duncker, 1945). The receivers were brought in front of a table where they could find a box of tacks, a candle, and a box of matches. They were asked to find a way, with the available objects, to affix the candle to the wall (on a corkboard) in such a way that it would burn without dripping wax on the table or on the floor. The analyzed variable was solving time. The problem was considered as solved if the receivers emptied the book of matches, used the tacks to nail the box to the corkboard and made the candle stand inside the empty box. They were given 10 minutes to solve this problem and the time they spent to find the solution was scored in seconds. The participants who did not find the solution in the maximum allocated time were not taken into account in the time analysis.

***Verbal measures.*** At the end of the experiment (after the creativity tasks, Figure 1), the female receivers were asked to evaluate the experimental odors on 9-point Likert scales (1 = not at all, 9 = extremely) for how intense, pleasant and familiar they were, and to the extent to which they caused well-being.

## **Procedure**

The physiological recording session took part first. The receivers were equipped with the measurement sensors and the nasal cannula and were seated in a comfortable chair in a quiet and well-ventilated room with standardized conditions of light (no windows) and temperature. They were also given white noise, sound-canceling headphones. The experiment started with 2 minutes of rest to provide a baseline, then the first odor was sent with the olfactometer for 5 seconds, on an expiration to ensure that it would enter the nostrils at the beginning of the next inspiration. The next 60 seconds were odorless to return to a baseline and to avoid olfactory adaptation. Then, the next odor was sent and so on (in a pseudo-randomized order) until all odors were sent (first block out of three). After a 5-minute break, the behavioral tasks started.

In these tasks, the odor condition was attributed randomly, in a double-blind fashion. During the whole duration of the behavioral session, the odor (or clean air) was sent to receivers' noses by the olfactometer through a nasal cannula, for 5 seconds every 30 seconds. Finally, the receivers rated the odors on verbal scales and were thanked for their participation after a small brief about the purpose of the experiment.

## Data preparation and analysis

### ***Donors' facial EMG responses.***

The facial EMG activity was analyzed with linear mixed-effects models, using the *lme4* package (Bates et al., 2015) in R (R Core Team 2019, RStudio version 3.6.1). Condition (Positive/Neutral body odor) was used as a Fixed factor and Subject was used as a Random factor. Note that here and below for the other variables analyzed similarly, stimulus Repetition was also included as a random factor except in the cases when it did not significantly improve the models. Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality, and when it did, outliers were removed to improve the quality of the model. P-values were obtained using Kenward–Roger approximation in the *anova* function of *lmerTest* package in R (Kuznetsova et al., 2017). Post-hoc contrasts were performed using the *multcomp* function of the *emmeans* package in R (Lenth et al., 2020).

***Donors' emotional ratings.*** The donor's evaluations of how they felt, recorded after each video/activity during the VR-based MIP, were averaged by emotion and by session (positive, neutral) for each donor.

How “neutral” and “happy” the donors felt were compared with the average ratings collected in our previous study using Video-based MIP, using Welch t-tests. Comparison between the positive and the neutral MIP for the “neutral” and “happy” ratings in the present study were also conducted, using Welch t-tests.

***Receivers' physiological responses.*** The receivers' physiological variables that we analyzed were: i) Mean heart rate difference between the 10-second post-stimulus and the 10-second pre-stimulus windows (beats per minute, post- minus pre-), ii) Log-transformed characteristics of the first sniff during odor presentation, namely sniff volume (area under the curve AUC,

arbitrary unit) and sniff duration in seconds (between inhalation starting point and the point where the sniff's flow returned to zero), iii) Characteristics of the skin conductance (SC) response, namely the log-transformed SC basic peak (in  $\mu\text{S}$ , maximum value of the signal during the 10-s post-stimulus window minus value of the signal at stimulus onset), and number of SC responses (during the 10-s post-stimulus window), iv) the facial EMG number of contractions (10-s post-stimulus window) and intensity of contractions (area under the curve AUC) for the *zygomaticus major* and *corrugator supercilii*.

As for the donors' facial EMG analysis (see above), linear mixed-effects models were used with Condition (Positive/Neutral body odor), but also Perfume (With/Without) as Fixed factors and Subject as a Random factor. Here, a model selection procedure was conducted to select the best models, using the *anova* function, where the non-significant interactions were removed to keep only the best model including the main effects. Only the number of SC responses was analyzed differently, with three Chi-square tests to evaluate the effect of Condition and Perfume (for all trials together, and for trials with and without Perfume separately). Because the size of some cells of the contingency table was  $< 5$ , a Yates' correction was applied.

**Receivers' performances in the behavioral tasks.** The receivers' performances in the creativity and problem-solving tasks were the Alternate Uses Task (AUT) scores of fluency, originality, elaboration and flexibility (see Behavioral tests section) and time to solve the Candle Problem (in sec). The AUT scores were attributed in a double-blind fashion by two independent judges. Scores of both judges on each variable were highly correlated ( $r = 0.70$  to  $0.96$ ), and thus averaged.

For both creativity and problem-solving tasks, we conducted one-tailed Welch t-tests because a clear *a priori* hypothesis was postulated before data collection and was already found in our previous research. Namely, smelling positive body odors is expected to increase positive affect and thereby creativity (Isen et al., 1987) compared with smelling neutral body odors. Our target comparison being the positive versus neutral conditions comparison, a preliminary analysis comparing performances in presence of the Neutral body odor with those in the control condition revealed no significant differences between Neutral condition ( $N=15$ ) and clean air ( $N=14$ ) (AUT fluency:  $p=0.680$ ; AUT originality:  $p=0.330$ ; AUT elaboration:  $p=0.950$ ; AUT flexibility:  $p=0.700$ ; Candle Problem:  $p=0.209$ ). Consequently, thereafter we focus only on the target comparison between Positive ( $N=14$ ) and Neutral conditions. A Chi-square test was also conducted to compare the frequency of succeeded versus failed attempts during the Candle Problem in the positive versus the neutral condition.

**Receivers' odor ratings.** The raw receivers' odor ratings of intensity, pleasantness, familiarity, and well-being were used in the data analysis.

The odor ratings made after the behavioral tasks were analyzed using linear mixed-effect models with Condition (Positive/Neutral body odor) and Perfume (With/Without) as Fixed factors and Subject as a Random factor, using the same procedure as for the physiological responses (see above).

**Missing and removed data.** For donors, saving issues resulted in the loss of the EMG recordings of 2 participants for the neutral MIP, and 1 for the positive MIP. For receivers, due to technical issues, the sensor measuring SC responses did not allow us to record the signal of the first 10 participants. Additionally, technical faults of the acquisition system happened during some trials, and some trials were also removed if artefacts were found after visual inspection. In total: 22 trials for the SC (0.05%), 32 for the heart rate (0.06%), 25 for the sniff (0.04%) and 31 for the EMG (0.06%) were removed or not analyzable. During data analysis, several outliers were deleterious for the quality of some of the statistical models detailed in Table 1. After being identified by visual inspection of the graphs of residuals and of Cook's distances, they were removed before recomputing the final model.

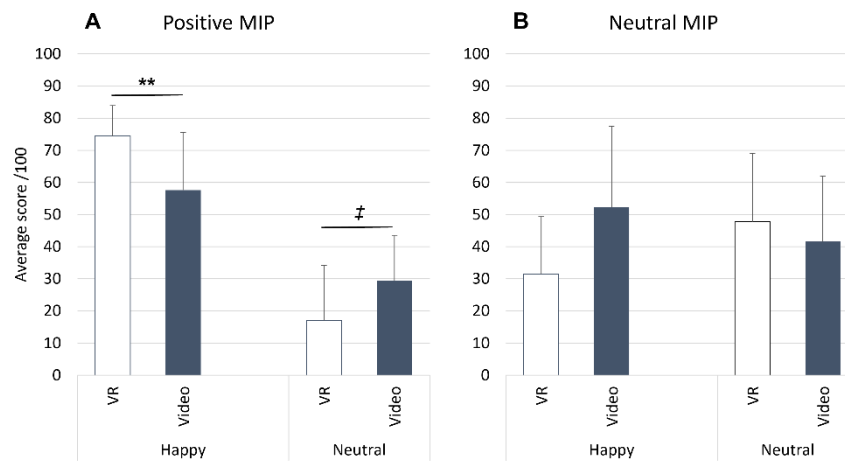
## Results

In this section, we first tested whether the VR-based induction we developed was efficient to induce positive emotions in the odor donors, and whether it would be more efficient than the Video-based induction we used previously in Richard Ortegón et al. (2022) (illustration in Figure 2). Second, we tested whether the different types of responses of the receivers (physiological, motor, verbal and behavioral) would vary as a function of the odors they were exposed to. Notably, we tested the effect of Condition (smelling body odors collected during the positive MIP versus during the neutral condition, illustrated in Figure 3), and in some cases the effect of Perfume (body odor with or without perfume, illustrated in Figure 4).

## Donors: Emotion induction efficiency

The average happiness ratings per donor that were collected during the positive VR-based MIP induction were all above 50 on a 0-to-100 scale and ranged from 52 to 87 depending on the individuals. This means that, based on self-reports, the VR-based MIP induction was efficient in inducing a positive state in all donors (N=10, 100%), which is a major improvement compared to our previous study with Video-based MIP, where mood induction was efficient in only 8 donors out of 21 (38%). Note that donors were independent in both studies and had similar characteristics. The significance of this progress was further assessed by comparing the mean “happy” and “neutral” ratings between both studies. During the positive induction (Figure 2A), donors provided higher happiness ratings with the VR-based MIP (Mean  $\pm$  Standard Deviation:  $74.42 \pm 9.52$ ) than with the Video-based MIP ( $57.64 \pm 17.93$ ) (Welch t-test,  $t(28.495) = 3.399$ ,  $p = 0.002$ ; 95% confidence interval (CI) = [6.68, 26.89]). They also reported feeling marginally less neutral (VR:  $17.02 \pm 17.10$ ; Video:  $29.47 \pm 14.06$ ; Welch t-test,  $t(15.026) = 2.002$ ,  $p = 0.064$ ; 95% CI = [-0.81, 25.67]). During the neutral condition (Figure 2B), no differences between studies were found, either for “happy” or “neutral” ratings ( $p > 0.05$ ). The mood induction based on VR was thus better at inducing positive emotions when compared to the Video-based MIP used in our previous study (Richard Ortegón et al., 2022).

In the present study, the manipulation of our experimental conditions was successful since happiness ratings were higher in the positive VR-based MIP than in the neutral VR-based condition (Positive:  $74.42 \pm 9.52$ , Neutral:  $31.44 \pm 17.91$ ;  $t(13.71) = -6.701$ ;  $p < 0.0001$ ; 95% CI = [29.20, 56.76]). This result is supported by the participants' non-verbal behavior. Indeed, the donors had more EMG peaks for the zygomatic muscle during the positive than during the neutral condition (Positive:  $101.21 \pm 103.39$ , Neutral:  $33.88 \pm 45.48$ ; Condition main effect:  $F(1, 99.41) = 14.68$ ;  $p = 0.0002$ ; 95% CI = [21.8, 68.6]). They also had higher AUC (Positive:  $3589.96 \pm 3399.95$ , Neutral:  $1009.80 \pm 813.28$ ; Condition main effect:  $F(1, 102.06) = 38.67$ ;  $p < 0.0001$ ; 95% CI = [1318, 2553]) for this muscle whose activity is known to correlate with positive emotion (see Supplementary Figure S1).



**Figure 2: Male donors' verbal ratings during the VR-based (current study) and the Video-based (previous study) Mood Induction Procedures. (A) Ratings during the positive mood induction (0-100). (B) Ratings during the neutral mood induction (0-100). Means  $\pm$  Standard Deviations. †:  $p < 0.10$ , \*\*:  $p < 0.01$ .**

## Receivers: Responses to the positive vs. neutral body odor

### Physiological responses.

No main effects of Condition or Perfume on mean *heart rate* and no Condition $\times$ Perfume interaction were significant ( $ps > 0.05$ , see Table 1).

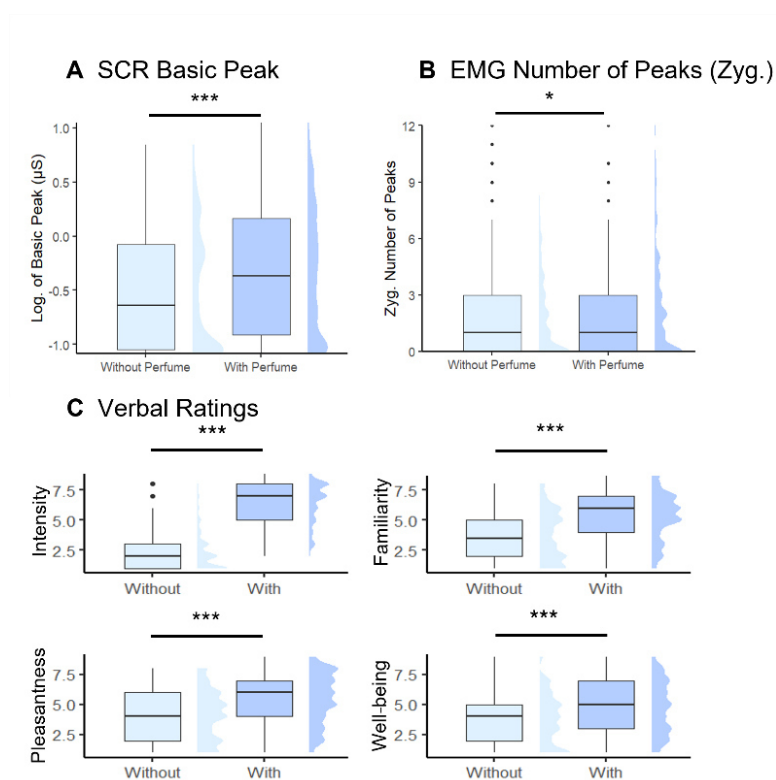
**Table 1.** Physiological and olfactomotor responses as a function of Condition (Positive vs. Neutral body odor) and Perfume (With vs. Without). Results of the linear mixed models with Condition and Perfume as fixed factors and Subject (and in some cases stimulus Repetition) as random factor (intercept). Zyg.= zygomaticus major, Corr. = corrugator supercilii. P-values < 0.05 are in bold.

Variable	Main effects and interactions	Statistics	P-values
Heart Rate	Condition	F(1,432.49)=0.284	P=0.594
	Perfume	F(1,431.22)=1.390	P=0.239
	Condition $\times$ Perfume	-	-
Sniff volume	Condition	F(1,429.09)=0.518	P=0.472
	Perfume	F(1,429.12)=2.596	P=0.108

	Condition×Perfume	-	-
Sniff duration	Condition	F(1,437.17)=0.007	P=0.934
	Perfume	F(1,437.27)=0.006	P=0.937
	Condition×Perfume	-	-
SC basic peak	Condition	F(1,252.84)=1.230	P=0.268
	Perfume	F(1,252.09)=13.997	<b>P=0.0002</b>
	Condition×Perfume	-	-
EMG Number of Peaks	Zyg. Condition	F(1,425.50)=0.093	P=0.761
	Zyg. Perfume	F(1,425.41)=4.984	<b>P=0.026</b>
	Zyg. Condition×Perfume	-	-
	Corr. Condition	F(1,416.34)=0.041	P=0.839
	Corr. Perfume	F(1,417.32)=0.994	P=0.319
	Corr. Condition×Perfume	-	-
EMG Peaks AUC	Zyg. Condition	F(1,431.48)=3.317	P=0.069
	Zyg. Perfume	F(1,431.33)=0.431	P=0.512
	Zyg. Condition×Perfume	-	-
	Corr. Condition	F(1,348.18)=0.268	P=0.605
	Corr. Perfume	F(1,348.33)=1.761	P=0.185
	Corr. Condition×Perfume	-	-

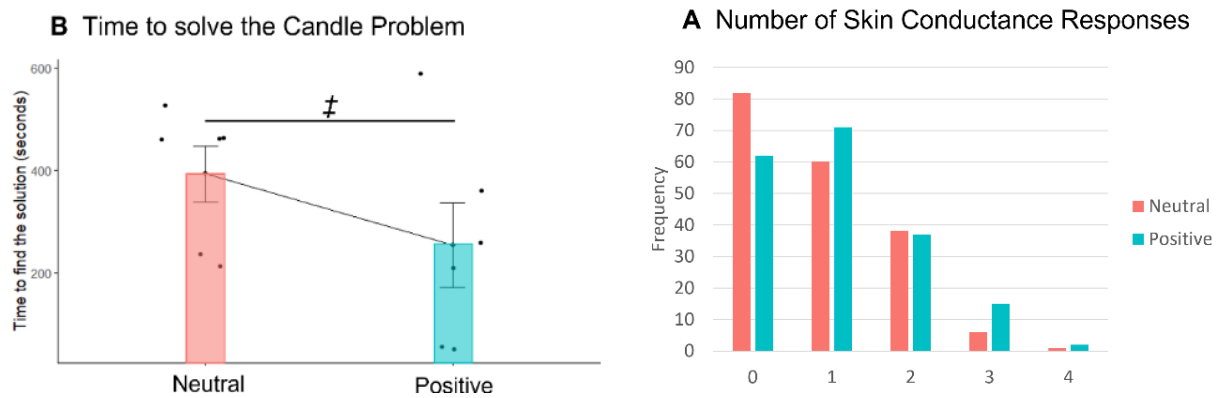
The best models were *Variable ~ Condition + Perfume + (1/Subject) + (1/Repetition)*, except for heart rate for which the best model was *Variable ~ Condition + Perfume + (1/Subject)*.

The analysis of the log-transformed *Skin Conductance (SC) basic peak* (Table 1) revealed a significant effect of Perfume ( $p=0.0002$ , Figure 4A) but no effect of Condition nor of the Condition $\times$ Perfume interaction. Higher SC peaks were found when perfume was present ( $M_{\log}\pm SD= -0.331 \pm 0.59$ ) than when body odors were presented alone ( $-0.500 \pm 0.60$ ). Chi-square tests on the *number of SC responses* (Neutral: N=82/60/38/6/1 for 0/1/2/3/4 responses respectively; Positive: 62/71/37/15/2) did not show any dependence between the Condition and the number of responses (despite a tendency:  $X^2(4)=7.905$ ,  $p=0.095$ , Figure 3A). A similar conclusion was found when i) only trials without perfume on the one hand ( $X^2(4)=3.895$ ,  $p=0.420$ ), and ii) only trials with perfume on the other hand ( $X^2(3)=6.642$ ,  $p=0.084$ ), were analyzed separately.



**Figure 3. Effect of the factor Perfume on female receivers' responses** (independently of the factor Condition). (A) Skin conductance Basic Peaks ( $\mu S$ ) in response to donors' body odors without and with perfume. (B) Number of Peaks detected for the zygomaticus major muscle in response to donors' body odors without and with perfume. (C) Verbal responses for perceived intensity, familiarity, pleasantness, and well-being in response to donors' body odors without and with perfume. \*:  $p<0.05$ , \*\*\*:  $p<0.001$





**Figure 4. Effect of the factor Condition (neutral vs. positive) on female receivers' responses.** (A) Number of skin conductance responses to the neutral and positive body odors ( $N=33$  receivers, 374 trials; Chi-square test:  $X^2(4)=7.905$ ,  $p=0.095$ ). (B) Mean time to find the solution to the Candle problem, in seconds (in participants who successfully solved the problem, Neutral,  $N=6$  out of 15; Positive:  $N=6$  out of 14). Means  $\pm$  Standard Error of the Mean. ‡:  $p<0.10$ .

### Motor responses

There were no main effects of Condition or Perfume and no interaction on log-transformed *sniff volume* nor on log-transformed *sniff duration* ( $ps>0.05$ , see Table 1).

Regarding EMG responses, there was only a significant main effect of Perfume on the number of peaks for the *zygomaticus muscle* ( $p=0.026$ , see Table 1, Figure 3B), which was higher when the body odors were presented with perfume ( $2.53 \pm 3.43$ ) than without ( $2.15 \pm 3.34$ ). No main effects of Condition or Perfume and no interaction were significant for these peaks' AUC ( $ps>0.05$ , see Table 1). As for the *corrugator muscle*, we found no main effects of Condition or Perfume and no interaction on the number of peaks nor on peaks' AUC ( $ps>0.05$ , see Table 1).

## Verbal ratings

A significant effect of Perfume was found (no effect of Condition and no interaction) on all verbal ratings (see Table 2, Figure 3C). When presented with perfume, body odors were perceived as more intense ( $6.45 \pm 1.70$  vs.  $2.30 \pm 1.60$  without perfume;  $p < 0.0001$ ; 95% CI = [3.71, 4.60]), more pleasant ( $5.48 \pm 2.12$  vs.  $4.13 \pm 2.06$  without;  $p < 0.0001$ ; 95% CI = [0.77, 1.93]), more familiar ( $5.38 \pm 2.06$  vs.  $3.69 \pm 2.08$  without;  $p < 0.0001$ ; 95% CI = [1.10, 2.28]) and as inducing more well-being ( $4.70 \pm 2.21$  vs.  $3.69 \pm 2.12$  without;  $p = 0.0009$ ; 95% CI = [0.43, 1.60]).

**Table 2.** Odor ratings as a function of Condition (Positive vs. Neutral body odor) and Perfume (With vs. Without). Results of the linear mixed models with Condition and Perfume as fixed factors and Subject as random factor (intercept). The effect of the interaction was tested only when the interaction was present in the best model (see Methods). P-values < 0.05 are in bold.

Variable	Main effects and interactions	Statistics	P-values
Intensity	Condition	F(1,124)=0.138	P=0.711
	Perfume	F(1,124)=341.890	<b>P&lt;0.0001</b>
	Condition×Perfume	-	-
Pleasantness	Condition	F(1,124)=2.023	P=0.157
	Perfume	F(1,124)=21.087	<b>P&lt;0.0001</b>
	Condition×Perfume	-	-
Familiarity	Condition	F(1,124)=2.554	P=0.113
	Perfume	F(1,124)=32.182	<b>P&lt;0.0001</b>
	Condition×Perfume	-	-
Well-being	Condition	F(1,124)=2.203	P=0.140
	Perfume	F(1,124)=11.623	<b>P=0.0009</b>
	Condition×Perfume	-	-

The best models were *Variable ~ Condition + Perfume + (1|Subject)*

## **Behavioral tasks**

No differences were found between the group exposed to positive body odors and the group receiving the neutral body odor, in any of the behavioral tasks.

In the Alternate Uses Task, both groups did not differ on Fluency (Positive:  $3.44 \pm 1.08$ , Neutral:  $3.64 \pm 1.21$ ,  $t(26.94) = -0.480$ ,  $p=0.682$ ; 95% CI = [-0.92, Inf]), Originality (Positive:  $0.67 \pm 0.22$ , Neutral:  $0.64 \pm 0.17$ ;  $t(24.77) = 0.372$ ,  $p=0.360$ ; 95% CI = [-0.10, Inf]), Elaboration (Positive:  $0.47 \pm 0.15$ , Neutral:  $0.56 \pm 0.19$ ;  $t(26.40) = -1.530$ ,  $p=0.931$ ; 95% CI = [-0.21, Inf]) or Flexibility (Positive:  $3.27 \pm 0.98$ , Neutral:  $3.51 \pm 1.16$ ;  $t(26.74) = -0.592$ ,  $p=0.721$ , 95% CI = [-0.92, Inf]).

In the Candle Problem, 6 participants out of 15 exposed to the neutral condition found the solution in the allowed time (9 failed), while they were 6 out of 14 in the positive condition (8 failed). The difference between these two observed frequencies was not significant ( $X^2(1) = 0.00$ ,  $p = 1.000$ ). Among the participants who did find the solution, problem solving time did not significantly differ between the groups (Figure 4B), although there was a tendency for the positive group to find the solution quicker (Positive:  $254.50 \pm 202.40$  seconds, Neutral:  $393.16 \pm 133.22$  seconds,  $t(8.648) = -1.402$ ,  $p=0.098$ ; 95% CI = [-Inf, 43.52]).

## **Discussion**

This research addresses an important challenge for the understanding of human chemical communication of positive emotions. Namely, it aimed at developing a new method to induce positive moods in participants whose body odor is collected to examine its behavioral effects on receivers. Indeed, although first evidence suggests that positive emotional contagion can happen via volatile chemicals emitted by the body, it remains difficult to induce positive emotions in the laboratory (Richard Ortegón et al., 2022). In the latter study for instance, the axillary samples of only 8 out of 21 donors could be used for the experiment because the positive induction was not effective enough in 13 of them. Therefore, we used a similar design but replaced 2D videos by VR activities. VR is an innovative and more immersive approach to induce intense emotions.

An important methodological finding was that the VR-based MIP was significantly more efficient at inducing the desired positive emotional state in donors than our previously used video-based MIP. Such a comparison has never been done before in the context of chemical communication, but is consistent with previous research showing that VR is efficient in inducing such states (e.g., Baños et al., 2012; Herrero et al., 2014). However, although we expected

that a stronger emotion would trigger stronger differences in receivers' responses to the positive versus the neutral condition, in the present study we could not replicate the findings of our previous work. Indeed, while anteriorly we found that receivers exposed to an emotionally positive body odor had a reduced heart rate, were more performant on creativity tasks, and were able to verbally differentiate it from a neutral control (Richard Ortegón et al., 2022), here no significant differences were found for those variables. This was despite the efficiency of the VR-based MIP that was expected to even lead to stronger physiological and behavioral effects (but see de Groot et al., 2021 for a non-confirmation of this intuitive thought in the context of chemical communication of fear). The fact that this was not the case and that we only found several marginally significant effects (more skin conductance responses and faster problem-solving in presence of the positive odor compared with the neutral one, Figure 4) could be explained by several factors.

It is possible that, instead of triggering more intense positive feelings, VR may rather have elicited more consensual responses between individuals than did videos in our previous research. When comparing the happiness ratings of the 8 donors selected in the video study (based on successful emotion induction) with the ones of all donors in the present VR experiment, no differences occur (Figure S3). This means that, i) using a selection of donor samples, although not optimal due to loss of samples, can approximate the results of a more efficient MIP, and ii) instead of expecting stronger effects it would have been more reasonable to expect similar effects to our previous study. As this was however not the case, other factors specific to the VR experiment may have accounted for the near absence of effect of the odor condition.

VR has the advantage to provide a higher level of immersion than images or music alone, but it also constitutes what we can call a *supranormal stimulus*, with out-of-the-ordinary scenarios unattainable in real-life settings where participants fly in the air or paint in space, for instance (as it was the case here). These supranormal situations could trigger stronger emotions than necessary for chemical communication to happen optimally, especially since most of the participants had never used a VR headset before (anecdotal evidence from discussions with them). Indeed, as suggested by Isen (1999) intense positive affect may have a different impact on cognition (in kind, and not in magnitude) than mild affect, because an intense emotion could distract or demand too much attention. In our study, it could be that the VR situation was too intense for the donors overall, in the positive as well as the neutral condition. This hypothesis came to us after having examined the arousing ability of the body odor samples. Indeed, participants in the VR-based MIP showed twice more skin conductance responses to the odor samples than in the Video-MIP (one or more SCR responses in 61% of the trials versus 34% of the trials in the Video-MIP;  $X^2(1)=35.7$ ,  $p<0.0001$ , Figure S2A). Interestingly, this was

applicable not only to the responses to the positive odor samples but also to the neutral ones (Figure S2B). Although only a direct comparison of VR- and Video-based protocols in the same participants could provide reliable answers, we can formulate some speculations. With VR the contrast between the positive and the neutral condition might be insufficient to trigger observable differences in the physiological/behavioral outcomes. Although this assumption is not supported by the explicit emotional ratings (Figure S3), it cannot be excluded that other aspects of the emotional response are in play, such as the donors' level of arousal (not recorded here). It could also be hypothesized, as evoked elsewhere (de Groot et al., 2021), that an increase in eccrine sweat due to a more intense emotion could dilute the active compounds responsible for the behavioral effects observed previously with a less powerful emotion induction. Finally, there is also a possibility that other compounds are produced during VR-induction compared to Video-induction and that these have a masking effect on the active compounds. In the future, a finer knowledge of the chemical bases of human chemical communication would help interpreting these results.

Some methodological parameters of the experimental designs could also explain the discrepancies of results between our two studies. The time between body odor samples collection and their utilization for receivers was longer in the VR experiment ( $\approx$ 5.5 months) compared with the Video experiment ( $\approx$ between 1 week and 1.5 months), and although microbial transformation is significantly reduced at  $-32^{\circ}\text{C}$ , it is not unlikely that this longer storage length led to modifications in the sample composition. Consistently with this hypothesis, there were four times more participants who reported being able to perceive something when presented with the body odor samples in the VR experiment (11.63% versus 3.33% in the video experiment). Although storage duration up to 6 months at this same temperature seems to have no effect on perceptual ratings of body odors sampled for 24 hours (pleasantness, attractiveness, masculinity; Lenochova et al., 2009), this does not exclude the possibility that chemical cues of emotional state may have been altered during storage, especially since our sampling was considerably shorter (30 min) and emotional cues are more subtle than less transient information such as masculinity. Two other experimental parameters may also have contributed to the different outcomes obtained in both studies. For the positive MIP in the Video experiment, participants took part in groups of 3 (which is believed to amplify the experienced positive emotion) but this was not technically possible to implement in the VR experiment (individual sessions). Additionally, in our previous work, but not in the present study, the participants received a personalized gift during the positive MIP. This may have had an additional positive influence in the Video study, even though the gift was found to have mitigated success (anecdotal evidence from participants' post-experiment debrief interviews).

As to the possible effect of fragrance on the chemical communication of positive emotions, we found no interaction. When presented with added perfume, the body odors were rated as more intense, pleasant, familiar, and caused more well-being than when they were presented alone, as in our previous study. These results were expected, since the perfume used was pre-selected to be pleasant, and was clearly perceivable by contrast with the body odors which most of the time were not consciously perceived. Presented with perfume, the body odors also were associated to a higher basic peak amplitude in the skin conductance recordings (in accordance with the overall odor's higher intensity: (Bensafi et al., 2002)), and a higher number of contractions of the major zygomatic muscle (in accordance with the more positive valence: Tassinari et al., 2007). In our previous study, we found a synergic effect of the fragrance (higher intensity and familiarity of the positive body odor vs. the neutral one when they were presented with perfume, while no difference occurred when presented alone). This was not observed here, in accordance with the absence of differences between conditions on the different variables investigated.

To conclude, although the present study did not reveal significant evidence of a chemical communication of positive emotion through human body emissions, it is very likely that some methodological choices in this study account for its inability to reveal a phenomenon that truly exists. Several previous works support this position. They provide evidence that body odors of positive emotion can be explicitly discriminated from body odors collected in a neutral state (Chen and Haviland-Jones, 2000; Zhou and Chen, 2011), that they differ in their chemical properties (Smeets et al., 2020) and most importantly that they elicit different behavioral responses even if not consciously detected (e.g., happier facial expressions: (de Groot et al., 2015a; higher creativity: Richard Ortegon et al., 2022). Importantly, the patterns of results for the creativity task obtained in the latter study and the present one are extremely similar, which is an element of confirmation (Figure S4). In addition, not only humans, but also other animal species display behavioral changes in response to human positive versus neutral body odors (more stranger-directed behaviors in dogs: (D'Aniello et al., 2018); less head lifting behavior in horses: Sabiniewicz et al., 2020). Therefore, we believe that the chemical communication of emotion is characterized by physiological and behavioral effects that are difficult to observe in laboratory, and that some methodological choices prevented us from revealing these effects, which are subtle and probably modulated by the context, in the present study. This leads us to formulate some recommendations for future studies in this field. Given that inducing positive emotions in the laboratory is uneasy, VR is undoubtedly interesting for its very consensual effects (less waste of time, energy, and money due to less odor sample loss than with videos that are not systematically successful). However, for its use to be optimal, it may *first* be worth controlling for previous experience of the donors with VR since in novices it might constitute

an experience that is too much out of the ordinary, even in the neutral condition. *Second*, increasing the contrast between neutral and positive conditions by using videos in the former and VR in the latter is an option to be considered. *Third*, not only measuring the level of arousal of the odor donors during emotion induction (by recording electrodermal responses for instance) is recommended, but also future studies should investigate the respective weight of the effect of arousal (high, low) and valence (positive, negative, neutral) of the induced emotion, in order to better understand how these two major components emotion (Russell, 1980) are involved in human chemical communication. Finally and more generally, research on human chemical communication would benefit from further methodological investigations of parameters that are susceptible to affect the observability of a chemical communication, such as storage temperature and duration (see Gomes et al. (2020) for first evidence), among others.

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# STUDY 3 - DYADS

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## Preamble

Although the results found in **Study 1** could not be replicated, some patterns consistent with our hypotheses were observable nonetheless in **Study 2**. This led us to consider that a primitive emotional contagion did in fact exist through the olfactory sense, but that our subject of study, emotional semiochemicals, were even more subtle and sensitive to many contextual elements than firstly expected. This could explain why despite the fundamental importance of such signals in human life, research is so few and only relatively recent in this field. Perhaps only when many more experiments will have been conducted, and the contextual elements governing these phenomena will have been pinpointed, then real human *pheromones* will be found and proven to work in a consistent, repeatable, and robust way (if the specific conditions are required).

With this in mind, we decided to continue the double approach (factors of variation, closer to real-life) initiated in **Study 2**, taking it one step further. In **Study 3**, other contextual factors were explored (relationship type, duration, sociability, perfume use), both in donors and receivers, while the degree of ecological validity was also increased with an experiment taking place entirely at home by participants themselves.

The data has been fully collected but is still being analyzed, so here the reader is introduced to how this experiment was conducted, what variables were studied, and how they were treated in a preliminary version, including preliminary results and a preliminary discussion.

# Factors influencing the chemical communication of positive emotions in humans: Insights from an at-home experiment (In prep.)

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## **Abstract**

Humans can transmit the emotions they are feeling to surrounding people via volatile organic compounds contained in their body odor, in a process known as primitive emotional contagion. This has been shown repeatedly for negative emotional states, and more recently for positive emotional states. However, this particular form of communication remains still poorly understood and many factors that could influence it have yet to be identified. In this study, the influence of several factors such as the nature and duration of the relationship in which the emotional contagion takes place as well as the sociability of the individuals or the addition of perfume on the body odor were explored. To do so, participants in dyads (either couples or roommates) took part successively in an experiment entirely carried at their own home. First, one participant of the dyad took part in an emotion induction procedure (either positive or a neutral control) while their body odor was collected. In a second step, their body odor was presented to their partner while they performed behavioral tasks to measure the impact of these emotional chemosignals on behavior. In addition, both individuals of the dyad completed questionnaires on their relationship duration as well as on their individual degree of sociability. In order to study the potential modulation by cosmetic practices, these same odors were also explored when presented to partners with added perfume.

## **Keywords**

Chemical communication, positive emotions, body odor, perfume, sociability, emotional intelligence, relationships

## Introduction

Humans, like other species, communicate information to their conspecifics via volatiles contained in their body odor and processed through the olfactory system (Lübke and Pause, 2015). Among the most relevant information for the individual's survival and social interactions, emotions have recently been shown to be possibly transmitted via chemosignals (de Groot et al., 2012). There is redundant evidence that the body odor of an individual ("donor" or "emitter") experiencing fear, as well as other negative emotions, influences the physiology and cognition of perceiver (or "receiver") individuals (de Groot and Smeets, 2017). This communication seems to occur in a non-conscious way, has chemical underpinnings that are just beginning to be explored (Smeets et al., 2020), and often takes the form of a primitive process of replicating partially the donor's state (emotional contagion: Hatfield et al., 1992). Although positive emotions have been much less explored in general, and in the field of human chemical communication in particular (despite their function in survival and flourishing; see discussion in Richard Ortegón et al., 2022), there is increasing evidence that their transmission through chemicals emitted by the body is likely (de Groot et al., 2015a; Richard Ortegón et al., 2022).

To better understand this recently studied form of non-verbal communication in humans, we would gain from elucidating the contextual factors of variability of such a phenomenon, of which the nature and amplitude of impact are still ignored. To study, isolate, and control these factors would help obtaining reliable, robust, and repeatable results, which is sometimes lacking in the field of chemical communication (Wyatt, 2015, 2020). Some factors have been pinpointed and discussed, such as the nature and the intensity of the emotional induction procedures (de Groot et al., 2020; Richard Ortegón et al., submitted), or the personality of the receivers. The latter factor is probably of prime importance as it is in other forms of communication (Cunningham, 1977; Campbell and Rushton, 1978). Are some individuals "*super-communicants*", namely who are more likely to pick up and process chemosignals present in their surrounding air and to display adaptive responses to them? For example, in a study on the ability to explicitly identify happiness and fear in body odor samples, Haviland-Jones et al. (2016) found important interindividual differences with some individuals being "super-detectors" while others were "anosmic for the chemosignals". How does personality and/or event experience contribute to these abilities?

Several studies have started to explore these questions. First, it has been shown that socially anxious receivers exposed to anxiety chemosignals showed an increased startle reflex response in response to a sound (a defense mechanism linked to negative stimuli) compared with non-anxious subjects (Pause et al., 2009). Socially anxious participants were also found to engage more neuronal resources during early pre-attentive stimulus processing and to

display earlier information processing when exposed to anxiety chemosignals than normo-anxious individuals (Pause et al., 2010). On the opposite side of anxious individuals, some people seek and like to take part in social situations: individuals ranking high in “social openness” were found when exposed to non-emotional body odor, to display stronger activations (vs. less socially open participants) in brain regions linked with social perception and recognition of emotions (Lübke et al., 2014)(e.g., inferior frontal gyrus, caudate nucleus which is part of the reward system). This suggests that these stimuli are subjectively perceived as more positive and relevant by these individuals who are more outgoing, assertive, decisive, sociable and therefore more able to initiate and maintain social contact.

When it comes to positive emotions communicated through chemosignaling, the role of sociability levels is probably highly relevant, although never studied. Indeed, sociable and extrovert persons seek social contact, while introverts shy away from it (Costa Jr. and McCrae, 1988). As a result, introverts communicate less than extroverts (Borg and Tupes, 1958; Carment et al., 1965), more specifically, they tend to speak less in dyads or groups of people (Bem and Allen, 1974; Shaw, 1976; Cheek and Buss, 1981). Additionally to extroversion/introversion, another aspect worth exploring was added to the measure of social capacities: emotional intelligence. Emotional intelligence is the ability or tendency to perceive, understand, regulate, and harness emotions adaptively in the self and others (Mayer and Salovey, 1997; Schutte et al., 1998). People with high scores of emotional intelligence show more cooperative behaviors towards partners, are more empathetic, satisfy more partners in relationships and marriages, as well as have higher social skills. (Schutte et al., 2001), characteristics which would be expected from “socially competent” people. Given the elements above, it is possible that very sociable individuals (extroverted and showing high levels of emotional intelligence), as they take part more often in social interactions, would be more likely to detect (not necessarily explicitly) and respond to emotional cues contained in body odors. This would be comparable to an expert who displays differential processing of stimuli linked to their area of expertise (Lübke et al., 2014).

Another aspect has barely been explored yet: how previous exposure with the donor and how the context of exposure could modulate chemical communication. Studies investigating the chemical communication of emotions always use pairs of donor-receiver who are strangers to each other. However, it is possible that the level of familiarity, represented by the duration of the relationship between a donor and a receiver, as well as the type of relationship (sexual partners, friends, colleagues, etc.) modulates the chemical communication between them, as it does for other forms of communication (Owen, 1984; McDaniel and Andersen, 1998). One study investigated the potential effect of familiarity on the explicit perception of chemosignals: using olfactory perception tasks in couples, Zhou & Chen (2011) showed that the ability to

detect emotional changes in axillary sweat odor is higher when the samples come from a partner (compared with a stranger), and increases with the number of years the couples had spent together. Whether such phenomena extend to behavioral effects of emotional odors remains unexplored to date.

The aim of this experiment was to investigate the variability of the chemical communication of positive emotions, as a function of individual factors that we identified above as potentially relevant: personality (sociability) and relationship characteristics (type and duration). To do so, we used a similar protocol as in our previous study (Richard Ortegón et al., 2022) to test the chemical communication of positive emotions. This protocol consists in inducing a particular state (positive, neutral) in body odor donors before exposing receivers to these odor samples while they perform creativity tasks. Performance in creativity tasks is used as a proxy of positive emotional contagion because creative problem-solving and divergent thinking have been robustly found to be impacted by positive affect (Isen et al., 1985, 1991; Estrada et al., 1994). One of the original features of this study is that the protocol was not implemented in the laboratory, but in the participant's home. This methodological choice was made to try to overcome the difficulties of inducing emotions in the laboratory (especially positive ones), by putting the participants in familiar conditions where they feel comfortable, while also increasing ecological validity. Dyads of participants were recruited, differing in their relationship's nature (either couples or roommates) and duration (either short, <2 years, or long, ≤4 years). Each participant's sociability was measured through questionnaires of extraversion and emotional intelligence. We also included a condition where the body odor samples were sprayed with perfume (as body odors and perfume are often encountered together in everyday life), to investigate how it could modulate chemical communication. In this study where both participants of the dyads acted as body odor donors and as receivers, we expect emotional contagion to occur, indicated by increased performances in creativity tasks in presence of the positive body odor versus the neutral one (as in Richard Ortegón et al., 2022). This emotional contagion may be enhanced by the receivers' level of sociability, and by the relationship proximity (couples) and increasing duration (long relationships) provided experience has a role in shaping responsiveness to chemosignals of emotion.

## Methods

### **1.1. Participants**

Nineteen dyads took part in this study, i.e. 38 participants (mean age  $\pm$  SD: 26.33  $\pm$  4.27 years old) who have been living together as either couples or roommates for a period of time ranging between 0 and 2 years (hereafter called "short relationships") and between 2 and 4 years

(hereafter called “short relationships”) (see detailed sample size and characteristics in Table 1). The participants declared being non-smokers, and not to suffer from any olfactory disorders. Inclusion was possible only for participants having a house or apartment large enough to allow the assignment of two rooms specifically for the experiment (see Section 2.5.), that did not include the kitchen (to avoid food-related odors) and one of which has a window to allow for ventilation. All participants provided written informed consent prior to their participation and received monetary compensation. This research was conducted in accordance with the Declaration of Helsinki and was approved by the local Sud Méditerranée III ethical review board (May 13, 2019).

**Table 1.** Dyad characteristics for each duration (short/long) and nature (roommates/couple) group. N=number of participants, n=number of dyads.

	<b>Short</b>	<b>Long</b>	<b>Total</b>
<b>Couples</b>	N=14(n=7) Age: 26.77±4.21	N=14(n=7) Age: 26.89±3.52	<b>N=28(n=14)</b> <b>Age: 26.83±3.86</b>
<b>Roommates</b>	N=4(n=2) Age: 21.75±0.86	N=6(n=3) Age: 27.17±5.48	<b>N=10(n=5)</b> <b>Age: 25±5.02</b>
<b>Total</b>	N=18(n=9) Age: 25.59±4.28	N=20(n=10) Age: 26.97±4.19	<b>N=38(n=19)</b> <b>Age: 26.33±4.27</b>

## 1.2. Questionnaires

**Relationship's characteristics.** Each member of the dyad was asked to indicate the nature of the relationship with their partner (couple or roommates). Additionally, they reported how long they had known their partner and how long they had been living together. In order to limit biases linked to dyads going through a bad patch at the time of the experiment, they were also asked how good their relationship is currently, how close they feel to their partner and how often they communicate face to face.

**Sociality.** To measure participants sociality, the McCroskey's Introversion Scale (Richmond and McCroskey, 1989) and the Emotional Intelligence Scale (Schutte et al., 1998) were used. The first one, based on Eysenck's (1970) extraversion-introversion scale, is designed to determine relative levels of extraversion/introversion and is composed of questions about how people behave during social experiences (e.g. "Do you like to mix socially with people?"). The second one measures the respondent's ability to interpret other's emotions and to manage their own emotions (e.g., "I am aware of the non-verbal messages other people send"). Both questionnaires were used to measure different yet complementary aspects that are part of sociability.

## 1.3. Donors: body odor collection

**Emotion Induction Procedure EIP.** All participants attended two emotion induction sessions (within-subjects design), a positive and a neutral one in random order, one day apart. During each induction session, after having put on the t-shirts used for body odor collection, they watched on the web interface short film clips assembled to provide a 30-minute sequence for each condition. These clips were used successfully in past experiments to induce the desired states (for further details, see Richard Ortegón et al., 2022). To measure the emotional response of the participants during the EIP, they were asked to rate after each excerpt how amused, afraid, happy, sad, surprised, disgusted, angry, neutral and calm they felt during the clips using a visual analogue continuous scale ranging from "not at all" to "extremely" (then converted to 0-100 scores).

**Body odor collection.** From two days before the first experimental day and until the end of the procedure, participants followed a protocol to prevent odor contamination (details can be found in Supplementary Methods). Just prior to odor collection, participants were asked to wash their axillae with unperfumed soap (Sanex Sensitive 0%), and then to wear one of the cotton t-shirts (Decathlon) sent in the package and pre-washed with unperfumed detergent (Le Chat sensitive, 0%), instead of their clothes to prevent olfactory contamination and to serve as collection media. At the end of the EIP, participants were told to wear nitrile gloves, to take off their t-shirt before putting it in an annotated ziploc bag and to leave it on the table for the other participant's use. A new t-shirt was used for each participant and each condition.

#### **1.4. Receivers: Odor presentation and behavioral tasks**

**Odor stimuli.** When in the receiver position, participants were exposed to the t-shirt that had just been worn by their donor partner, either without any additional odor (Without perfume condition), or to that same t-shirt after perfume addition (With perfume condition). For the latter condition, the participants used nitrile gloves to spray perfume once on the axillary area of their partner's t-shirt, with a 5mL flask through a disposable paper cylinder (d=8, h=10.5cm) used to control i) the spraying distance and ii) the sprayed surface. The perfume was chosen because it had received the highest pleasantness scores in a pre-test (N=29) where it was tested along with other fragrance compositions created specifically for the study. In order to control for potential confounding factors, participants were asked to rate the pleasantness and intensity of the perfume during the experiment on a 1 (= not pleasant/intense at all) to 9 (= very pleasant/intense) scale, and also the perceived gender associated with the perfume on a 1 (= very masculine) to 9 (=very feminine) scale. They were also asked to score the pleasantness and intensity of the body odors alone, on the same scales used for the perfume (1= not pleasant/intense at all to 9 = very pleasant/intense).

**Creativity and problem-solving tasks.** All receivers took part in 4 different behavioral tasks, that were each repeated 4 times, once for each condition (neutral body odor, positive body odor, neutral body odor with perfume, positive body odor with perfume). On each new repetition, the stimuli words changed.

The first task was the Guilford's *Alternate Uses Task* (Guilford, 1967). In this test, the participants are asked to list as many non-obvious uses as possible for common objects in a limited time (for details about scoring and examples, see Supplementary Method). Here,

receivers were given 2 minutes per object, which were 8 different words in total: brick, barrel, pencil, shoe, car tire, hanger, pan, journal. Two 2 stimuli words were given in each session. Their fluency (i.e., number of alternative uses found, after filtering out irrelevant answers) was measured.

The second task was a *metaphor generation task* (based on Kasirer and Mashal, 2018). Here participants were given an incomplete sentence (e.g., being ashamed is \_\_\_\_ ) and they had to complete it by finding a new original and creative way to express the concept. Per session, they had 1 minute to generate 4 metaphors , which corresponds to 16 different metaphors in total. Each answer was scored depending on its originality, as determined by two independent judges, without awareness of the condition. A non-creative metaphor or literal expression was given 1 point (e.g., being ashamed is to be shameful), transparent metaphors were given 2 points (e.g., being ashamed is wishing a wall would rise up), and “novel” metaphors were given 3 points (e.g., being ashamed is being a knight without a kingdom to serve). The score for one condition was the average score of the four metaphors of the condition.

Participants also had to solve a third task, which was a series of *riddles* (8 different ones in total) taken from previous experiments on creativity (e.g., Beaty et al., 2014). In each session, they were asked to solve 2 riddles within a 2-min slot per riddle. The solving accuracy was scored out of 2 (1 point if correct, 0 if incorrect).

The fourth and last task used to measure creative divergent thinking was the *Chain Free Association Task* (based on Isen et al., 1985). Here, after a first word was given to the participants (e.g., “wax”), they had to type another word this first word made them think of (e.g., “candle”), and so on (“candle” leads to “flame”, etc.) until they had completed a 10-word chain. A total of 30 starting words were available. They had 4 minutes to form a maximum number of word chains, and this number was recorded as the score.

Before all the creativity tasks, an example page was first shown to the participants with dummy stimuli words and example answers, so that they could get familiarized with each task.

## 1.5. Procedure

**Material, installation and data recording.** The participants received all the necessary instructions and material for the experiment (unperfumed soap, prewashed t-shirts, perfume bottle, gloves, paper cylinder and cardboard boxes) in a parcel sent via postal service. The experiment was entirely implemented online web platform where, thanks to a unique code previously sent by email, the participants could follow step-by-step the instructions (written and filmed) and take part in the different tasks. The participants were told to use one room for the



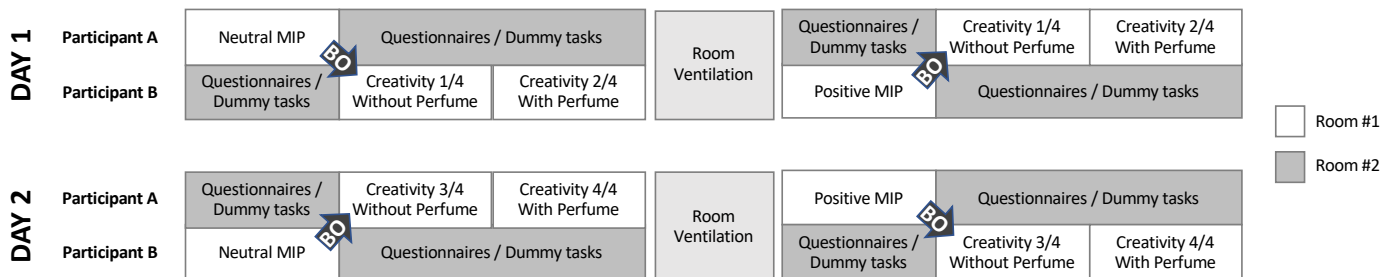
EIP/behavioral tasks, another one for the questionnaires, and to not communicate with their partner about the experiment until the end of the procedure. At any given moment of the experiment, they could contact the experimenters by phone if needed, to ask questions or if they encountered a problem. At the very end of the experiment, the participants filled a short survey designed to identify any difficulty or error that could have occurred and had to upload two photographs of how they installed the setting, from two different angles, for verification purposes (Figure 1C).

**Procedure.** The experiment took part over 2 days, in 2 different rooms of the same home. On day 1, participant A (donor) underwent the Neutral EIP by wearing a cotton t-shirt while watching the videos, in the dedicated room. Participant A then left the room after leaving the worn t-shirt on the table, and let participant B (receiver) take place in that same room. There, participant B had to install the experimental setup by putting the t-shirt on top of a cardboard box we provided (21x13x18cm). The participants were told to turn the t-shirt inside out and to put both the axillary areas of the t-shirt at the center of the cardboard box (Figure 1A). They then had to adjust the height of the box by stacking books underneath it until they could rest their chin on the box without discomfort while still being able to see their computer screen well (instructions illustrated with a picture, Figure 1B). This was set to standardize as much as possible the distance between the nose and the body odor. Once ready, participant B took part in a first session involving the 4 creativity tasks while exposed to the body odor alone. At the end of this session, they had to spray (with nitrile gloves) the fragrance on the t-shirt (see Section 2.4. Odor stimuli; note that the gloves and paper cylinder used to do so had to be thrown away out of the experimental room, just after spraying the perfume). They then continued with the second session, involving the same creativity tasks but with different stimuli, while being exposed to the body odor with added perfume. The “with perfume” condition was always performed after the “without perfume” condition, in order to avoid room ambient contamination of the “without perfume” condition with potential residues of perfume in the air. During the time participants were taking part in the EIP or the creativity tasks, the other participant was kept busy in the other room with standardized tasks, i.e. questionnaire completion (see Section 2.2.) interleaved with dummy tasks (memory/attention tasks, not analyzed). After careful room ventilation (by opening the window for at least 15 min until the perfume was not perceivable anymore), the participants switched roles, participant B being the donor and undergoing the Positive EIP, and participant A being the receiver.



**Figure 1.** (A,B) Pictures used to indicate to the participants how they are supposed to set the experimental installation up (model setting). (C) Example of a setting put in place by a participant.

The exact same procedure was repeated the day after, in such a way that at the end of Day 2, both participants have been donors and receivers in each of the 4 conditions (Positive and Neutral EIP, each With and Without Perfume). To do so, as illustrated in Figure 2, on Day 2 Participant B first acted as a donor while undergoing the Neutral EIP, and Participant A then acted as a donor while undergoing the Positive EIP. Note that the Positive EIP always took part after the Neutral EIP to avoid potential residues of chemosignals of positive emotions to remain in the air and influence the next task. The duration of experiment was of about 3 hours per day.



**Figure 2.** Experimental design for a dyad over the 2-day experiment. EIP: Emotion Induction Procedure; BO: Body Odor. Both members of the dyad (participants A and B) serve as donors twice, i.e. in the neutral and the positive conditions. They also serve as receiver of the other member's BO twice (BO collected during the positive EIP and BO collected during the neutral EIP). BO were presented alone, and then added with perfume.

## 1.6. Data preparation and analysis

**Relationship information.** The length of cohabitation was judged as more exact and used over the declared length of acquaintance, because dyads having known each other for long periods of time but not living under the same roof would not have had comparable amounts of shared time and therefore comparable exposure to each other's body odor. The arbitrary 2-year threshold was chosen to allow the inclusion of roommate dyads with duration lengths comparable with couple dyads. Based on this threshold, cohabitation lengths were transformed into "short" and "long" categories, and the relationship type (roommates or couples) was used as such.

**Sociability.** Because the scores of the two scales used to measure *sociability*, i.e., extraversion and emotional intelligence scales, were correlated (Pearson correlation coefficient=0.44), a composite score was computed to reduce the number of variables by adding the individual z-scores to each scale. Statistical analyzes were conducted on a categorial variable separating "low sociability" (scores<0, N=16 participants) and "high sociability" (scores>0, N=22 participants).

**Emotion ratings.** Participant's evaluations of how they felt, collected after each video excerpt during the EIPs (see Section 2.3.), were averaged by emotion and by session (positive/neutral) for each participant.

**Creativity performances.** A global creativity score per participant per condition (Positive/Neutral, With/Without Perfume) was computed by adding the normalized scores of the four creativity tasks (detailed in Section 2.4.). Indeed, each creativity task being scored on different scales, scores were normalized to 1 in order to allow the same weight to all tasks, 1 being the maximum score, namely either the maximum possible (*Alternate Uses Task*, *Chain Free Association Task*) or the best performance among the participants' scores (*Metaphors*, *Riddles*). The global creativity score was thus comprised between 0 and 4.

**Missing and removed data.** Technical issues on the web interface and the server resulted in the loss of 1 day for 4 participants: 4 neutral conditions (5.26%) and 4 positive conditions

(5.26%). Because one participant declared afterwards to be misophonic, and that the videos were thus uncomfortable to watch, the behavioral responses of their partner were excluded (unsuccessful EIPs' effects).

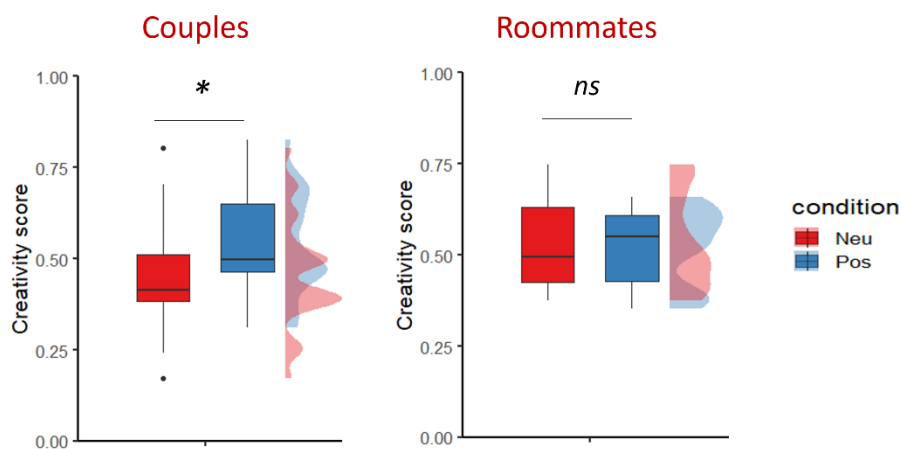
### **Data analysis.**

First, a control analysis was conducted to evaluate the success of the EIPs, i.e. whether donors felt happier in the Positive than in the Neutral EIP, and more Neutral in the Neutral than in the Positive EIP. The mean "happy" and "neutral" ratings obtained during the neutral and positive EIPs were compared using Welch t-tests.

Second, we aimed at testing whether creativity (our proxy of emotional contagion) was higher in the Positive than in the Neutral condition and whether this could be modulated by several factors: Perfume, Sociability, Relationship type and duration. Linear mixed-effect models were conducted using the *lme4* package (Bates et al., 2015) in R (R Core Team 2021, RStudio version 4.1.2), with the global creativity score as a dependent variable, with Condition (Positive/Neutral body odor), Perfume (presence/absence), Sociability (high/low), Relationship type (couples/roommates), and Relationship Duration (long/short) as fixed factors, and with Subject as a random factor. The *dredge* function of the *MuMin* package (version 3.5) was used on the complete model to help determine the best model where non-significant factors and interactions were removed. The best model was selected based on model comparison through lowest corrected Akaike's Information Criterion and associated weight/delta/. P-values were obtained using Kenward–Roger approximation in the *anova* function of *lmerTest* package in R (Kuznetsova et al., 2017). Post-hoc contrasts were performed using the *multcomp* function of the *emmeans* package in R (Lenth et al., 2020). Visual inspection of residual plots did not reveal any obvious deviations from homoscedasticity or normality, and when it did, outliers (identified by Cook's distances) were removed to improve the quality of the model.

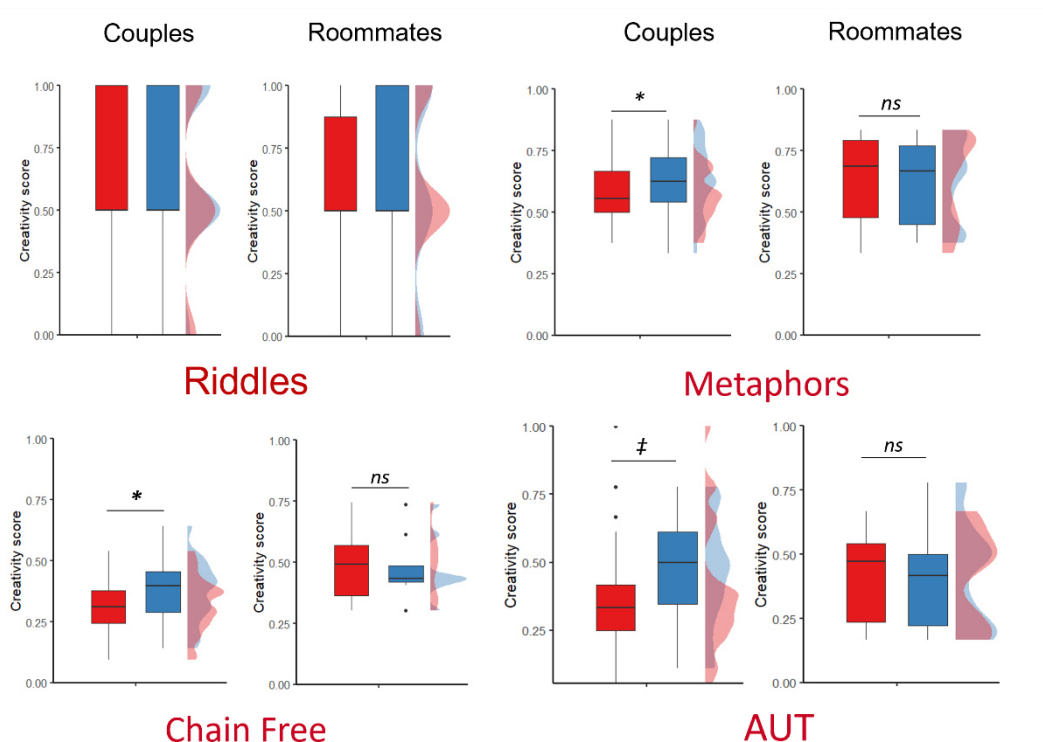
## Preliminary results

On the exhaustive model, linear mixed model effects showed a significant effect of Condition ( $F(1, 108.622) = 4.85, p=0.0297$ ). The creativity scores were higher in the positive condition than in the neutral one (Mean $\pm$ SD, Pos:  $0.526\pm 0.14$ ; Neu:  $0.48\pm 0.13, p=0.030$ ). A main effect of Relationship Type was also found ( $F(1,33.472)=4.830, p=0.0350$ ). We explored separately how creativity in the positive and the neutral condition were impacted in these groups. In couples, there was a significant difference between the positive and the neutral condition, with higher scores after having been exposed to the positive body odor (Pos:  $0.518 \pm 0.15$ ; Neu:  $0.458 \pm 0.13, t(103.72) = 2.328, p = 0.011$ , see Figure 3), which was not found in the roommates group (Pos:  $0.545 \pm 0.15$ ; Neu :  $0.546 \pm 0.13 ; t(37.09)=-0.019, p=0.508$ , see Figure 3)



**Figure 3. Global creativity scores for the couples and roommates in the positive and neutral conditions.** As measured by mean performances over 4 different creativity tasks\*:  $p < 0.05$ .

Looking more in depth, when considering each behavioral task independently for couples, we generally observed the same pattern of significance as for the global creativity score, except for the riddles (see Figure 4). Indeed, there was an increase of creativity in the positive (vs. neutral condition) for the “Chain-Free Association Task” (Pos:  $0.378\pm 0.12$ , Neu:  $0.33\pm 0.13, t(97.74)=1.830, p=0.035$ ) and the “Metaphor generation Task” (Pos:  $0.604 \pm 0.14$ , Neu:  $0.561 \pm 0.12, t(99.521)=1.760, p=0.041$ ) in couples. There also was a trend in the AUT, with a higher score in the positive condition, though it did not reach significance (Pos:  $0.433 \pm 0.23$ , Neu:  $0.419\pm 0.21, W=1657.5, p=0.054$ ). For roommates, we did not find significant differences between creativity performances after exposure to the positive body odor (in contrast with the neutral one), no matter what creativity task was explored.



**Figure 4. Individual creativity scores per task, for couples and roommates in the positive and neutral conditions. ‡:  $p < 0.1$ ; \*:  $p < 0.05$ .**

Additionally, a main effect of Sociability was found ( $F(1, 33.948)=6.955, p=0.0125$ ), with higher creativity performances for participants with lower levels of sociability. However, we did not find any significant effect of the Condition within sociability levels in the couples, except a trend for high sociability individuals in couples (Low/Positive  $0.552 \pm 0.11$ , Low/Neutral:  $0.516 \pm 0.12$ ,  $t(50.085)=1.1259, p=0.131$ ; High/Positive  $0.479 \pm 0.15$ , High/Neutral:  $0.404 \pm 0.12$ ,  $W=414, p=0.078$ ). The same was true for roommates (Low/Positive:  $0.635 \pm 0.09$ ; Low/Neutral:  $0.533 \pm 0.21$ ,  $t(4.052) = 0.896, p=0.420$ ; High/Positive:  $0.523 \pm 0.16$ ; High/Neutral:  $0.550 \pm 0.11$ ,  $t(26.891) = -0.55981, p=0.580$ ).

Finally, we did not find an effect of Perfume ( $F(1,106.085)=0.0404, p=0.841$ ), nor of Relationship duration ( $F(1,33.825)=0.549, p=0.464$ ) on creativity scores, and these factors as well as their interactions with other factors did not appear to be part of the best models.

## Preliminary discussion

This research aimed to further explore the chemical communication of positive emotional states between humans. More specifically, it was designed to better understand the effect of several potential modulating factors on the said communication. These factors concerned

individual (sociability) as well as relationship characteristics (length, type) and the use of perfume.

In virtually every study on chemical emotional contagion, participants are exposed to body odors of strangers that they have never met. Here, we explored what could happen when the two individuals were familiar with each other. We showed that the type of relationship might be a crucial factor to control, and that perhaps humans show different reactions depending on the relationship they have with the body odor emitter.

In our preliminary results, we found that in couples a positive emotional contagion happened, as indicated by increased creativity when smelling the positive body odor of their partner, versus a neutral control. This appears to be a robust result since it was found in almost all the types of creativity tasks that we used (metaphors, chain-free, trend for the AUT), except one (riddles). For the riddles, the binary nature of the response (either false or true) may not be discriminant enough to observe the effects of the positive semiochemicals, which are often subtle. In roommates, this difference between conditions was not found, thus no elements allowed to conclude in favor of emotional contagion. This does not necessarily mean that a transmission did not happen, but rather that a synchronization between donor and receiver was absent or could not be measured.

These results also shed light on previous experiments in the literature. In one study, Zhou and Chen (2011) found that familiarity shaped the ability to unconsciously discriminate emotional changes in body odors (higher discrimination in couples vs. strangers) and that this ability increased with the number of years a couple had spent together. Here, our results seem to confirm the effect of proximity, this time by showing that it not only facilitates discrimination, but also the impact of emotional semiochemicals, and the behavioral changes caused by them. However, unlike this previous study, we did not find evidence for time spent together to modulate the chemical communication.

Going beyond the discrimination abilities, emotional contagion has only been reported between strangers in chemical communication studies so far (see meta-analysis de Groot and Smeets, 2017a), which goes against the idea of an effect that would take place between very close persons only. Of course, one cannot rule out the option that the effects found in the literature would have been even greater if they had been tested on familiar dyads, but, this seems incompatible with our lack of results in roommates who are already people closer than strangers. One option is that perhaps this phenomenon is not linear but follows a U-curve. Perhaps humans show an increased sensitivity/responsiveness towards people they do not know because they represent an unknown and unpredictable element that they must probe. With people that they already know and spend time with regularly (roommates, friends), the levels of attentional focus may be lower, and increase again with very close people such as a

romantic partner. In a romantic relationship, it may be more necessary to be more attuned to partners' odors and emotions, along the fact that spending time closely under different intense emotional states (such as being naked during a sexual relationship) could provide more experience of the partner's odors, as a training exercise. However, we did not find any effect of the relationship duration, which would be expected for a learning effect.

Another element to take into account when comparing these results with the ones found in the literature is that they have in the vast majority been obtained for negative states. Such studies are also often realized in highly controlled experiments in laboratory settings, which can cause stress and not feel natural enough, a bias that here we tried to prevent. In laboratories, with less ecologically realistic approaches, the stressful context may increase the states of vigilance of the participants towards sensory stimuli. Especially highly relevant and salient ones such as human social odors, all the more if they are markers of negative states, thus allowing a chemical emotional contagion to take place independently of familiarity.

In this study, we also tested the effect of the participants' levels of sociability. Since sociable persons seek social contact, while introverts shy away from it, we hypothesized that highly sociable individuals would be the most likely to detect and respond to emotional cues contained in body odors. No evidence in favor of this was found so far, except a trend for emotional contagion in highly sociable individuals in couples, which was not found in other groups of participants. Further analyses will be needed to confirm or infirm this hypothesis.

Finally, a secondary objective was to examine the effect of perfume also as a modulating factor. In this study, we found no differences for the samples with added perfume, suggesting that, as in previous studies, perfume is not an obstructing factor to this type of emotional communication.

These results should be taken carefully before drawing firm conclusions, since they are only preliminary, and the entirety of the data is still being analyzed. Perhaps because of the still low sample sizes, especially among roommates, the emotional contagion could not be observed. Furthermore, because of the design of the experiment which was carried out at home and because every donor acted as a receiver and vice-versa, participants (even if told to not communicate about the experiment with their partner) were obligatorily aware of the nature of the stimuli used (i.e., body odors). Body odors are usually perceived relatively negatively, a bias that was countered in our previous experiments by telling the participants what they were smelling only after the end of the experiment. Here, these qualities attributed consciously and non-consciously to body odors could not be controlled. Perhaps this positive emotional contagion was not observed in roommates because they cognitively were disturbed by a negative perception of their roommates' body odor, while couples did not. Indeed, it has been



shown before that the body odors of partners are rated as less unpleasant than those of strangers (Stevenson and Repacholi, 2005). Nevertheless, this research presents a novel method of evaluating the capacity of human body odors to communicate and modify others' emotional states and opens up interesting perspectives to further explore the factors that rule this essential human function.

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# STUDY 4 - ABOV

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## Preamble

A missing key link to thoroughly understanding positive semiochemicals and their effects is to know what causes them at the molecular level. In the field, more and more studies report effects on receivers but few focus on their origin, that is, they are interested in chemosignal effects but not in the chemosignal itself. This is surely not due to a lack of interest by scientists but rather to the technical difficulties and biases encountered when dealing with analytical chemistry in human chemical communication.

This observation drove us to carry out extensive testing with different methodologies available in other fields (e.g., solvent extraction, different polymers, VOC traps, etc.) *in fine* enabling us to develop a tool allowing to collect, measure, and identify the VOCs present on the human skin. This device was named ABOV (Analysis of Body Odor Volatiles) and was designed to help solve some of the current problems faced when collecting human body odor. ABOV was tested during an experimental phase in **Study 4**, and the data is collected but still under analysis. Nevertheless, the reader can find in the following pages details about the proof-of-concept and how the said experiments were carried out. Please note that this device was tested here to measure known inter- and intra-individual differences and not emotional state differences, but the former represents a first step and a prerequisite for the latter.

# A novel system of direct headspace skin sampling to study human body odor Inter- and intra-individual differences (In prep.)

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## Introduction

Human bodies release chemicals, including Volatile Organic Compounds (VOCs) produced mainly through the action of skin bacteria on skin secretions. Even if the origin and the biosynthetic pathways of these compounds are not fully understood yet, there is increasing evidence that they are the basis of chemical communication in humans (Roberts et al., 2020). Namely, social information can be communicated through airborne chemicals produced by an emitter's body and perceived by a receiver's olfactory and/or trigeminal system. For example, there is convincing evidence for mother-infant communication in the context of breastfeeding, via chemicals produced by the mother's breast (Doucet et al., 2009). Chemical communication of emotions is increasingly documented in humans (de Groot and Smeets, 2017; Richard Ortégón et al., 2022). In addition, information relevant to mate choice has been reported to be conveyed by body odor, such as genetic background (Wedekind et al., 1995; Roberts et al., 2005; Winternitz et al., 2017), fertility status (Singh and Bronstad, 2001), health status (Olsson et al., 2014; Sarolidou et al., 2020), age (Haze et al., 2001; Mitro et al., 2012) or even personality (Sorokowska et al., 2012). However, the mechanisms of such communication are poorly documented to date. One of the major challenges to better understand human chemical communication is the knowledge of body odor chemical composition (Ferdenzi et al., 2020).

In humans and other mammals, chemical communication has been investigated more recently than in other organisms (plants, insects). *In the past two decades, the chemical composition of human scents has received increasing interest in areas such as medical diagnosis or forensics (see review in Ferdenzi et al., (2020) but more rarely in the field of psychology and affective neuroscience (Smeets et al., 2020).* Our aim in the study presented here was to develop a method suited to further investigate the chemical bases of behavioral effects of human body odor, such as those reported so far in the literature. For instance, women's body odor is more attractive during the fertile phase of the menstrual cycle (Singh and Bronstad, 2001): what are the chemical underpinnings? And are there chemical markers of gender, infection, emotions? First attempts to answer these questions can be described here.

Using a 2-dimensional Gas Chromatography coupled with Mass Spectrometry (GC×GC-MS) analysis of polydimethylsiloxane (PDMS) stir bars placed in flasks containing axillary pads, (Smeets et al., 2020) identified chemical compounds that differentiated emotional states (happy, fearful and neutral). Chemical compounds associated with stress have also been

described (Prete et al., 2019) using solid-phase microextraction (SPME) fibers placed in breath and saliva headspace followed by GC-MS analysis. Penn et al. (2007) investigated chemical profiles of saliva, urine and axillary sweat, using for the latter GCMS analysis of PDMS stir bars applied in contact with the skin, and identified individual and gender-specific markers. Gender, but also age differences were investigated by Gallagher et al. (Gallagher et al., 2008a) who evaluated with GC-MS the VOCs produced in two body locations (upper back and forearm) using two complementary sampling techniques (non-contact SPME inside a closed environment formed near the skin with a glass funnel, and solvent extraction of skin secretions performed directly on the skin). Certain chemical compounds were found to vary with age and site of collection (but no differences were found between men and women). Variations with age were also evidenced by Haze et al. (2001), after headspace dynamic sampling of t-shirts back area with Tenax columns followed by GC-MS analysis. Such studies, however, remain rare and the methods and results are heterogeneous. Not only is more research needed, but it is also essential to refine the methods according to the specific aims of the research. Regarding the context of human chemical communication, two weaknesses of the current approaches can be identified: sample contamination with external odors and the inadequate representativeness of the body volatiles, that would be present on the human skin but not responsible for causing observed behavioral effects.

The first problem encountered when investigating the chemicals naturally produced by an organism, is the contamination by unwanted external odors. These occur at all levels of the chemical analysis process (Nonnamaker, 2021): at the levels of i) the emitting organism (e.g. compounds related to smoking, the use of perfumed cosmetics, drugs, diet, pollutants, etc.), ii) the adsorbent device (e.g. cotton pads or swabs have been shown to release numerous compounds), iii) the collection procedure (e.g. molecules present in the environment and/or emitted by the experimenter and/or the potential collection device), iv) the storage and shipping of the samples, v) the extraction method (e.g., desorption, solvent extraction) and vi) the GC column itself. Of course, restriction protocols are usually applied on the body odor donor and the experimenter, and many precautions are taken, such as ventilating rooms or wearing gloves, but additional efforts can be made. One interesting option is to reduce the number of steps to a minimum. For example, instead of sampling body odor on pads or t-shirts and then using an intermediate step before running the GC analysis (like headspace analysis with stir bar, Tenax column or SPME fibers as in (Smeets et al., 2020), (Haze et al., 2001) or (Curran et al., 2010a)), *in situ* odor collection on the body with a device that can be directly desorbed in the GC column should be favored. This would solve the problem of possible contaminants present in cotton pads (obvious in our preliminary explorations and reported in the literature,

e.g. in Kücklich et al., 2017). This would also limit the risk of losing part of the compounds that are already present in very small quantities.

The second drawback is the fact that the collected chemicals may not be representative of the airborne molecules that elicit behavioral effects when presented to the receivers' nose. Among the studies mentioned earlier in introduction who limited the number of intermediate materials between the body emissions and the GC column, some used contact methods (solvent poured on the skin in Gallagher et al. (2008a), stir bar rolled over the skin in Penn et al. (2007). In many other instances, like for forensic or health applications, human body odor sampling is performed by putting sorbent materials in direct contact with the skin, such as stir bars (Soini et al., 2006), sorbent cylinders (Cuzuel et al., 2017), sorptive tape (Riazanskaia et al., 2008), SPME fibers (Dormont et al., 2013b), or glass beads (Bernier et al., 1999). These are usually analyzed directly in GC-MS (e.g. thermal desorption of the stir bars/SPME fibers). However, these contact approaches are likely to adsorb compounds that are not volatile at naturally occurring body temperature or that are purely contaminants (cosmetic residues for instance). This leads scientists to analyze and interpret compounds that are actually not among those of interest, namely – in the context of human chemical communication – those responsible for behavioral effects after having been transported by air from an emitter to a receiver. There is thus increasing interest for more ecological procedures that require both working on headspace close to the odorant source and without using an intermediate carrier. This is the case in two studies mentioned above, in which a SPME fiber was placed in a headspace formed by breath in a bag, by saliva in a vial (Preti et al., 2019) or by skin emission in a glass funnel placed on the skin (Gallagher et al., 2008a). Other devices based on the same principle can be mentioned, such as the Scent Transfer Unit STU and the Human Scent Collection System HSCS (Furton et al., 2015), SPME fibers in the headspace obtained by putting the subjects' arm in a Nalophane bag (Mochalski et al., 2014), the Passive Flux Sampler PFS where a stainless steel petri dish creates a headspace over the skin of the palms and forearm (Sekine et al., 2007), stir bar above a human cell culture (Yamaguchi et al., 2018) or sorptive tape, a non-invasive thin-film headspace sampling fitted out just above the skin with a PDMS membrane (Jiang et al., 2013).

Although these direct non-contact sampling methods are very promising, a few improvements are required so that they can be implemented satisfactorily in chemical communication paradigms. First, they remain uneasy to use in the axillary region (the most studied odor source) given its configuration. Second, they cannot easily be used on moving subjects, for

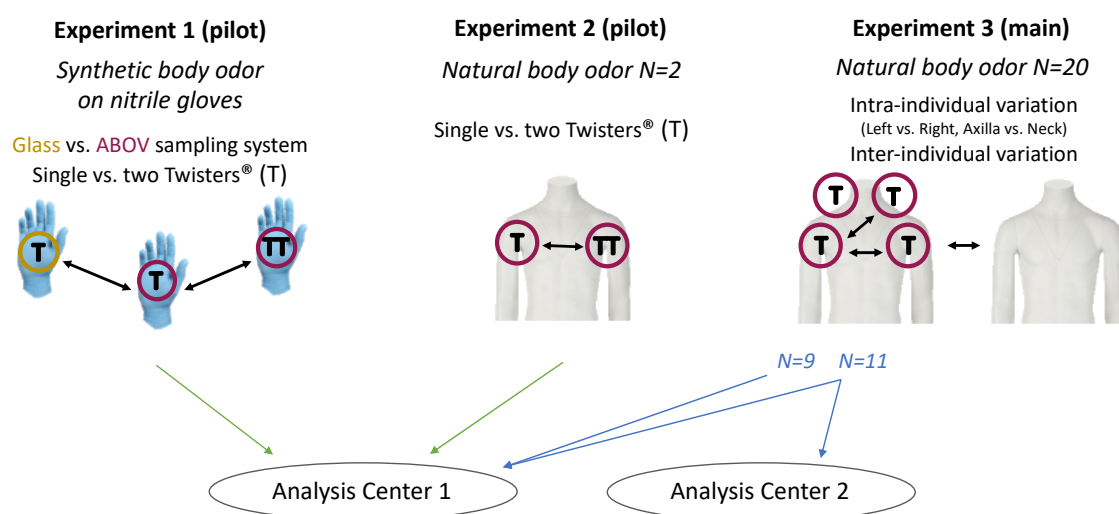
example during a behavioral task. For some, they also happen to fully isolate the concerned body part in anaerobic conditions, modifying the microbial action and therefore possibly the sampled compounds. In this article, we introduce a new sampling device named ABOV (Analysis of Body Odor Volatiles), designed to best meet the various aforementioned constraint. ABOV consists of drilled stainless steel half-spheres that hold on the body thanks to adjustable cotton belts and are equipped with several places for stir bars and single-use adsorbent polymer soft cylinders (both being used for human body odor sampling: Cuzuel et al., (2017); DeGreeff et al., (2011)). In addition to reducing sample contamination with external odors and increasing the representativeness of the body volatiles compared to other methods, ABOV was also designed to 1) be as chemically neutral as possible (no emissions coming from the sampling system itself), 2) interfere as little as possible with the activity of the skin bacteria, 3) be easy to use and to clean, 4) be adaptable to various adsorbent types, 5) be worn comfortably by human participants while they are performing tasks, and even if movement is required while doing them, 6) be potentially adaptable to various body parts, including the axilla, and 7) allow to sample two different body parts simultaneously. Using stir bars and GC-MS analysis, we conducted methodological verifications in Experiment 1 and 2 (pilots), regarding the interactions between two adsorbing devices placed simultaneously in a half-sphere, and regarding the chemical neutrality of the half-sphere compared with glass (on artificial and natural body odor). In the main Experiment (3), we used ABOV to investigate inter- and intra-individual differences (side of the body; odor sources axilla and neck). We hypothesized that chemical profiles between the left and right sides of a given individual would be more similar than chemical profiles of different odor sources of a given individual and that within-subject variability in chemical profiles would be smaller than between individuals. Further, we were aiming at exploring whether specific chemicals would be responsible for differences between axilla and neck and between men and women.

## **Materials and Methods**

### **Conceptual experimental design**

We conducted three experiments (Figure 1): two pilots (Experiments 1 and 2) and one main experiment (Experiment 3), all using the newly developed ABOV system. Experiment 1 was performed with an artificial body odor with two aims: 1) to test whether using a single or two adsorbents (stir bars: Twisters®) simultaneously has an impact on their chemical profiles, and

2) to test the inert character of the ABOV device by comparing its performances with those of a glass vial. Experiments 2 aimed at testing again the possible influence of one Twister® over the other but with a natural body odor collected in situ on two female donors. Finally, Experiment 3 was conducted on 20 donors to test the ability of our system, namely Twisters® placed in the ABOV, to reveal possible intra- and inter-individual differences. This was performed by comparing the chemical profiles collected on both sides of the body (left versus right), on different body parts (axilla versus neck), and between individuals. In experiment 3, half of the samples were analyzed in two different laboratories using different equipment.



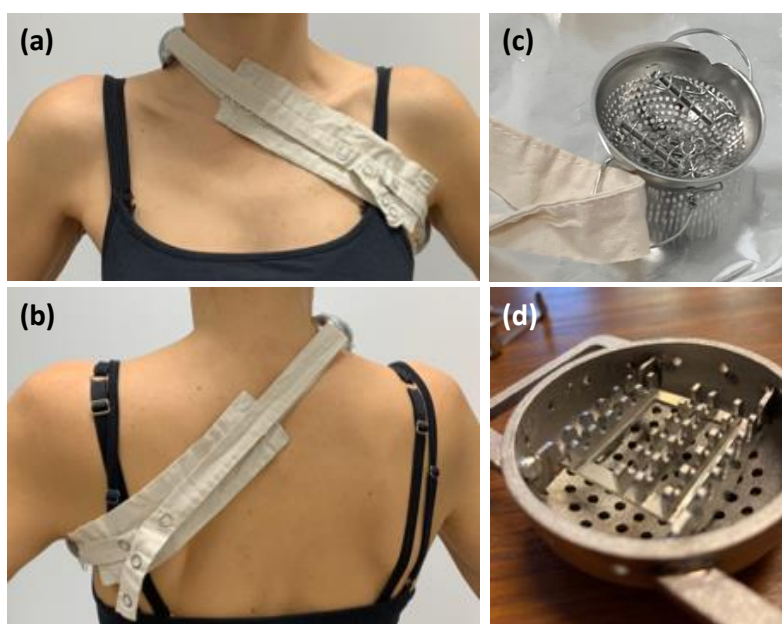
**Figure 1.** Overview of the experimental design.

## **Sampling Material**

*Adsorbent device.* Volatile compounds have been captured using Twisters® (Gerstel, Mülheim, Germany). Twisters® are magnetic stir bars covered with a polydimethylsiloxane (PDMS) phase of 20 mm length x 0.5 mm thickness.

*In situ collection device ABOV.* The ABOV device consists of 1) two stainless steel half-spheres (tea ball-like), placed on the skin and holding the adsorbents above the skin (not in contact) for sampling different locations on the body (originally intended for the armpit and neck), and 2) two 100% cotton belts adjustable with snaps connecting the two half-spheres, one on the

chest side and the other on the backside (Figure 2a,b). The prototype used in the present study was made in house with tea balls equipped with metallic springs (diameter 0.5 mm, length 25 mm) inside which Twisters® were positioned (and to which they are magnetized, Figure 2c). The improved and latest manufactured version of ABOV (not used in the present article) is based on a rack system that allows a universal use for Twisters® 10 and 20 mm length, as well as other adsorbent devices such as Powersorb® (Action Europe, Sausheim, France) (Figure 2d).



**Figure 2.** Collection device ABOV (Analysis of Body Odor Volatiles). **(a)** Front and **(b)** back view of the device positioned to sample the axillary and the neck. **(c)** Detailed view of the half-sphere with Twisters® positioned in the metallic springs. **(d)** Latest version of the ABOV half-sphere (for future studies, not used in the present study) after technical improvement of the device.

*Procedure of use.* Before odor collection, Twisters®, which are reusable, were cleaned using a Gerstel TC2 Tube Conditioner (280°C under nitrogen flow at 70 ml.min<sup>-1</sup> for 120 min) and stored in clean 1.5 ml glass micro vials equipped with caps with borehole in silicone/PTFE (Roth, Lauterbourg, France). The half-spheres were thoroughly cleaned with acetone (CAS 67-64-1, 99.9% purity, Roth, Lauterbourg, France), dried in a desiccator, and then stored in a closed clean glass jar until use. Cotton belts were washed in a cotton laundry net with a fragrance-free detergent (Le Chat Sensitive 0%, Henkel, Düsseldorf, Germany), dried in a dedicated dryer, and then stored in aluminum foil in a closed zip-lock bag. Nitrile gloves were systematically worn by the experimenter when cleaning and handling clean material to avoid

odor contamination and the experimenter was requested to wash hands and wrists with fragrance-free soap before putting them on. Before each scent collection, the workspace was cleaned with alcohol and then protected by aluminum foil on which all the experimental material was placed. The collection room was ventilated before collection for 5 to 10 min. The ABOV device had to be ready to be positioned on the odorant source (cotton frames attached to the half-spheres, leaving only one opening). To limit external olfactory contamination, the micro vials containing the Twisters® were opened right before placing them carefully inside the ABOV half-sphere, and just before positioning the ABOV device on the odorant source. As the polymer on the Twister® can easily be damaged or contaminated, using fingers protected by nitrile gloves was preferred over tweezers (the neutrality of the nitrile gloves in terms of odor contamination was tested in Cuzuel et al., 2017). After odor collection, ABOV was removed from the odor source and placed on the aluminum foil, the Twisters® were removed from the half-sphere and put directly back in their corresponding micro vials that were maintained closed during odor collection. They were then placed in a box and found stable when stored at about 4°C for at least 14 days before GC-MS analysis (Soini et al., 2006).

## **Odorants**

*Synthetic body odor (Experiment 1).* A mixture of synthetic compounds, representing functional groups of interest in human body odor were used: Undecane (Alcane; CAS number: 1120-21-4); D-limonene (Terpene; 5989-27-5); Octanal (Aldehyde; 124-13-0); 6-methyl-5-heptenone (Ketone; 110-93-0); Tetradecane (Alcane; 629-59-4); Octanoic acid (Carboxylic Acid; 124-07-2); Nonanoic acid (Carboxylic Acid; 112-05-0) (provider: Sigma Aldrich).

*Natural body odor (Experiments 2 and 3).* Two female participants (aged 26 and 43 years old) took part in Experiment 2 and 20 participants (9 men and 11 women; mean age  $M \pm$  standard deviation  $SD = 27.8 \pm 11.15$ ; range 19 - 53 years old) were involved in Experiment 3. They were non-smokers. All participants provided written, informed consent before participation and received monetary compensation for their time and potential inconveniences. The experiments were conducted in accordance with the Declaration of Helsinki and were approved by the local Sud Méditerranée III ethical review board (May 13, 2019). Starting two days before body odor sampling, participants were asked to refrain from drinking alcohol and eating food that is empirically known to influence body odor quality (such as garlic, spicy food, asparagus, cabbage). They also had to strictly avoid the use of any perfumed product (soap, perfume,

creams) and to use instead a perfume-free soap (Sanex 0%, Colgate-Palmolive, New York, USA) and deodorant (Cadum Micro-Talc Compressé Sans Parfum, L'Oréal, Paris, France) given to them by the experimenter. On the day of the experiment, participants came to the laboratory in the morning without wearing makeup or any kind of deodorant and after having showered with the non-perfumed soap. They were asked to wash the sampling areas with the perfume-free soap, to dry them with a cotton cloth, and to put a 100% cotton white tank top on that they would wear throughout the odor sampling. Cotton cloth and tank tops were previously washed with a fragrance-free detergent, Le Chat Sensitive 0%, Henkel, Düsseldorf, Germany.

## **Procedures**

*Experiment 1 (Pilot).* This experiment started by sampling the environment of the room for 40 min (measure called the “blank”), with the ABOV prototype equipped with one PDMS-Twister® and placed on a nitrile glove (the absence of additional contaminants when using the nitrile glove was measured by (Cuzuel et al., 2017)). Second, a similar sampling was performed with a glass half-sphere equipped with a PDMS-Twister® at the bottom (maintained thanks to a magnet attached to the outside). Third, a sampling of the synthetic body odor was then performed. Three new nitrile gloves were each odorized with 10 µl of the synthetic mixture described above and were sampled for 40 min either with an ABOV system equipped with one Twister®, with an ABOV system equipped with two Twisters® or with a glass half-sphere equipped with one Twister®. This procedure allowed us to test whether using a single or two Twisters® has an impact on the volatile trapping efficiency for each twister, and thus on their chemical profiles (first aim), as well as the inertness of the ABOV device compared with glass (second aim). To do so, we compared the GCMS profiles of the Twisters® from the three sampling systems.

*Experiment 2 (Pilot).* In this experiment, the environment (“blank”) was sampled for 40 min simultaneously with the participant's odor collection by placing an ABOV equipped with one Twister® and another ABOV equipped with two Twister® in a remote corner of the room on aluminum foil. Two female donors took part and were sampled on their two armpits simultaneously. Each armpit received an ABOV with one or two Twister®. After 20 min, sides were switched (i.e. the ABOV on the left armpit was put on the right armpit and vice versa) to limit potential side-related differences in VOC production, and sampling lasted for 20 more minutes. This exact same procedure was then repeated with the same set-up, with two



Twisters® in each ABOV. This procedure allowed us to test the possible influence of one Twister® over the other during natural body odor collection, by comparing their GCMS profiles.

*Experiment 3 (Main).* In the main experiment, 20 male and female odor donors were sampled simultaneously on both armpits and both sides of the neck, thanks to 4 ABOV systems each equipped with one Twister®. The environment (“blank”) was sampled simultaneously with the participant's odor collection: the whole procedure took 40 min. This procedure was designed to investigate the intra-individual differences (as a function of odor source, and side of the body) as well as inter-individual differences based on the participants' body odor chemical profiles (see details in the Statistical Analyses section).

## **GC-MS analysis**

### ***Analysis Center 1.***

Samples of all experiments were analyzed at the Platform for Chemical Analyses in Ecology (PACE) at the Centre d'Écologie Fonctionnelle et Évolutive, Montpellier, France. The analysis was performed for a total time of 31 min per sample (without cooling time). We used a gas chromatograph (GC, Trace TM 1310, Thermo Scientific TM Milan, Italy) coupled to a mass spectrometer (ISQTM QD Single Quadrupole, Thermo Scientific TM Milan, Italy). Separation was executed by a DB-WAX capillary column (30 m, 0.25 mm internal diameter, 0.25 µm film thickness). Samples were handled with a Multi-Purpose Sampler (Gerstell, Mülheim, Germany) and desorbed with a double stage desorption system, composed of a Thermal Desorption Unit (TDU) and a Cold Injection System (CIS) (Gerstell, Mülheim, Germany). Samples were desorbed splitless at a temperature of 250°C for 5 minutes on the CIS trap cooled at -80°C by liquid nitrogen. Then, the CIS trap was heated to 250°C with a 1:4 split ratio for 2 minutes to inject the compounds into the column. The carrier gas used was helium at 1 ml.min<sup>-1</sup>. The oven temperature was held at 40°C for 1 minute, increased from 40°C to 180°C at a rate of 6°C.min<sup>-1</sup> and from 180 to 220°C at 20°C.min<sup>-1</sup>, and finally held for 5 minutes. The temperature of the transfer line and the ion source of the mass spectrometer was 250°C and 200°C respectively. The acquisition was from 38m/z to 350m/z, at a 70eV ionisation energy. Xcalibur TM software (Thermo Scientific TM Milan, Italy) was used for data processing. Mass spectra were identified by matching the mass spectra with data of mass spectrum databases (NIST 2007, Wiley Registry Ninth) and personal laboratory bank. Retention index (RI) for each compound was calculated following injection of a series of n-alkanes (Alkanes standard

solution, 04070, Sigma-Aldrich) in the same GC-MS, and RI were then compared to data from libraries and published compounds databases (e.g. Adams, 2007, Pubchem, <https://pubchem.ncbi.nlm.nih.gov/>).

### ***Analysis Center 2.***

In experiment 3, N=11 participants (6 women, 5 men) were sampled using two Twister® instead of only one, allowing for an analysis in both Center 1 (see above) and Center 2 (Twistaroma, 300 bvd Sébastien Brant 67412 Illkirch, France) for comparison purposes.

The extracted volatile compounds were desorbed from the stir bars in a Thermal Desorption Unit TDU 2, Gerstel) connected to a Cooled Injection System (CIS, Gerstel) of the GC-ToFMS system. Desorption in the TDU was done in splitless mode with a temperature program from 40°C (1min), at 120°C/min to 250°C (8 min hold) using helium as carrier gas. The desorbed compounds were focused in the CIS on a glass liner packed with Tenax TA (Gerstel) at -30°C. Finally, the trapped compounds in the CIS were rapidly transferred to the analytical column by increasing the temperature of the trap from -30°C to 300°C at 12°C/s.. The desorption and injection procedures were fully automated using a Gerstel MPS-XT autosampler and operated using Gerstel MAESTRO software. All analyses were performed on an Agilent 7890B GC (Agilent Technologies, Wilmington, DE, USA) coupled to a BT-TOF mass spectrometer (Leco Corporation, St. Joseph, MI, USA). The column used was a DB-HeavyWax with dimensions 30 m x 0.25 mm x 0.25 µm df (Agilent Technologies, Folsom, CA, USA). The column oven was temperature programmed starting at 40°C for 2 min, then increased at a rate of 5°C/min to 260°C and maintained at 260°C for 1 min. The carrier gas was helium, at a flow of 1.2 mL/min. Ionization was done by electron impact at 70 eV, scan range was from m/z 30 to m/z 300 and acquisition speed was 5 spectra/s (30 Hz). The interface temperature was 300°C and the ion source was maintained at 250°C

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# REVIEW 1 - CHALLENGES

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## Preamble

During the presented **Study 1**, **Study 2**, **Study 3**, and **Study 4**, many obstacles, points of interest, precautions to be taken, and observations following the results arose, which also blended with the numerous reflections carried out throughout as well as at the beginning of this PhD thesis.

All these elements are crystallized in **Review 1**, in which we address and discuss what are, in our opinion, the main challenges still standing in the way of the field of chemical communication. The considerations around these five challenges were also the occasion to show experimental data collected previously (by Dr. Camille Ferdenzi), which made this hybrid review revolve around human attractiveness, a thematic distinct yet very complementary to positive emotions. Furthermore, the recommendations compiled here are applicable to the quest for a better understanding of human attractiveness through olfaction, but also apply (and should be extended) to understand positive emotional chemosignals and their effects, and even chemical communication at large.

*Note that if needed for comfort this article is also accessible to read online at:  
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# Interdisciplinary challenges for elucidating human olfactory attractiveness (Published – Philosophical transactions of the Royal Society B.)

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## Abstract

Many species use chemicals to communicate. In humans, there is increasing evidence that chemicals conveyed by the body are extremely important in interpersonal relationships. However, many aspects of chemical communication remain to be explored to fully understand this function in humans. The aim of this article is to identify relevant challenges in this field, with a focus on human attractiveness in the context of reproduction, and to put forward roadmaps for future studies that will hopefully extend to a wider range of social interactions. The first challenge consists in not being limited to body (mal)odours from the axilla. Preliminary data on how the odour of the face and head is perceived are presented. Second, there is a crucial need to increase our knowledge of the chemical bases of human chemical communication. Third, cross-cultural approaches must not be overlooked, because they have a major input in understanding the universal and culture-specific aspects of chemical communication. Fourth, the influence of specific cultural practices such as contraceptive and fragrance use is likely to be prominent, and therefore needs to be well described. The fifth and last challenge for research projects in this field is the integration of different disciplines such as behavioural sciences, social sciences, neurosciences, and microbiology.

### **Keywords (3-6 words)**

Olfaction, Human attractiveness, Sex differences, Culture.

## Introduction

The human body conveys a complex mixture of hundreds of chemical compounds (alcohols, carboxylic acids, ketones, aldehydes, esters, hydrocarbons, etc.), which are transformed from precursors secreted by excretory skin glands (Leyden et al., 1981; Wilke et al., 2007) through the action of skin bacteria (*Corynebacteria*, *Propionibacteria*, *Staphylococcus*) (see Natsch & Emter, this issue) and which constitute body odour. This chemical blend has a fixed fraction, which is genetically determined (Roberts et al., 2005; Kuhn and Natsch, 2009) and used as a marker of individuality (Penn et al., 2007a; Marchal et al., 2016). It also possesses a variable fraction, which depends for example on diet (Havlicek and Lenochova, 2006; Fialova et al., 2016), age (Mitro et al., 2012) or physiological state (Singh and Bronstad, 2001; Olsson et al., 2014). There is empirical and societal evidence that odours produced by human bodies are not just some unwelcome emissions that a large proportion of individuals from many societies try to eliminate with the help of hygienic and cosmetic practices: They are sought, and they clearly affect daily interactions with others, especially the close ones. Scientific studies back up these observations by providing solid reasons to believe that chemical communication occurs in humans, i.e. communication through chemicals emitted by an emitter's body and perceived by a receiver through the olfactory and/or trigeminal systems.

Mother-infant communication, for example, is likely modulated by chemicals produced by the mother and perceived through the olfactory system of her baby. Indeed, mothers' areolar glands produce secretions that are attractive to newborns (Doucet et al., 2009) and that are positively associated with breastfeeding success (Doucet et al., 2012) (see Schaal, this issue). But human chemical communication has been most extensively studied in the context of mate choice, mostly by investigating perceived attractiveness and preferences for a potential reproductive partner. Studies using self-reports show that body odour is rated as a key factor in a person's attractiveness when compared with several sensory and behavioural characteristics of a potential partner (Herz and Inzlicht, 2002), although mainly in female raters (Herz and Inzlicht, 2002; Havlicek et al., 2008). Studies in patients with olfactory disorders show that olfactory loss has serious adverse effects on the quality of social interactions (see Hummel, this issue), such as partnership insecurity or decreased sexual activity (Croy et al., 2014). It must be pointed out here that a significant part of the research in this area has been driven and even drifted by the fascination of the scientific community as well as the public by pheromones. In particular, many studies have focused on the behavioural effects of male steroid compounds, such as androstadienone. But the scientific justification for such a focus - to the detriment of all the other components of human biological odour - is highly debatable (Wyatt, 2015) and, although androstadienone is likely to have psychological effects (Jacob and McClintock, 2000; Bensafi et al., 2004), it does not seem to meet the concept of a sex

pheromone (Hummer and McClintock, 2009; Ferdenzi et al., 2016a) (see also Wyatt, this issue). In sum, while pheromones have been defined (Karlson and Lüscher, 1959) and identified in several animal species (insects (Butenandt et al., 1959) and mammals (Schaal et al., 2003; Roberts et al., 2010)), their existence in humans has only been speculated and not rigorously demonstrated. In addition, their functional processing has been a subject of debate. Namely, the widespread belief that they would be processed through the accessory (vomeronasal organ VNO) rather than the main olfactory system has been challenged by the fact that i) occlusion or absence of VNO in humans has no effect on putative pheromone perception (Frasnelli et al., 2011) and that ii) in other mammals (e.g., rabbit) pheromones are processed through the main (not the accessory) olfactory system (Hudson and Distel, 1986; Schaal et al., 2003; Baxi et al., 2006).

Another section of research in this area provided significant advances in understanding human chemical communication by postulating that human body odour carries specific and relevant information about the individuals, which is transferred from one individual to another (chemosignalling; see Lübke and Pause, 2015). Based on previous literature in non-human animals (e.g., Yamazaki et al., 1976), perceptual studies in humans have revealed preferences for biological odours that provide cues to biological quality of a potential sexual partner with regards to genetics (including the major histocompatibility complex MHC), reproductive status and health. People have been shown to prefer and choose MHC-dissimilar mates based on their body odour (Wedekind et al., 1995), at least in some populations (Chaix et al., 2008), a mechanism believed to favour the production of MHC-heterozygous offspring who are more resistant to pathogens (see also Havlicek, this issue, and Croy, this issue). This outcome is also served by a preference for MHC-diverse (heterozygous) mates, which has been shown to be a more robust phenomenon in a recent meta-analysis (while mixed evidence was found – notably as a function of samples' ethnical heterogeneity – for MHC-dissimilarity) (Winternitz et al., 2017). Preferences for other indicators of mate fitness, which have been evolved because of their beneficial effects on the offspring (biological quality, contribution to child care), seem to be mediated by body odours. For example, women within the fertile phase of the menstrual cycle prefer the body odours of men with greater body bilateral symmetry (indicating a better developmental stability, which is a marker of good physical condition) (Thornhill and Gangestad, 1999), and for socially dominant men (Havlicek et al., 2005). Men's preference for women's cues of fertility is another adaptive phenomenon that seems to be (in part) mediated by body odour, as shown by men's preference for odour samples collected during women's fertile phase of the menstrual cycle (Singh and Bronstad, 2001; Kuukasjarvi et al., 2004). Additionally, human body odour communicates information about health status (see Olsson, this issue), which is one aspect of mate fitness. Compared with healthy donors, the odour of

sick persons is more aversive (Olsson et al., 2014) and more intensely activates brain networks involved in odour processing (Regenbogen et al., 2017). Information about body condition related to nutritional state is also conveyed by body odour (Fialová et al., 2019), as well as about gender (Doty et al., 1982; Chen and Haviland-Jones, 1999) and age (Mitro et al., 2012). Finally, body odours are involved in the communication of emotions (see also de Groot, this issue; Pause, this issue; meta-analysis in (de Groot and Smeets, 2017) and of personality traits (such as dominance and neuroticism) (Sorokowska et al., 2012), both of which being involved in the initiation and maintenance of romantic relationships (Mahmut and Croy, 2019).

In spite of these numerous pieces of evidence regarding the existence of a chemical communication in humans, especially in the context of mate choice, the mechanisms of such a communication are poorly documented to date. The aim of this article is to identify in the following sections five relevant challenges in the field and to put forward potential avenues for future studies to better understand chemical communication. The context of mate choice is used as a background here because it is the most largely documented, probably due to the fact that reproduction is a fundamental function in living organisms and to the rich evolutionary theoretical framework available in this domain. However, it must be kept in mind that the identified challenges also apply (and should be extended) to other social contexts. Current knowledge is almost exclusively based on one odour source, the axilla, and on several unpleasant odorous compounds (“malodours”): Challenge 1 therefore consists in going beyond malodours from the axilla. Especially, odour sources that have a behavioural relevance in interactions with the actual or a potential mate (such as the hands or the face) should clearly be within the scope of investigation. We started facing this challenge and provide some new data on the perception of head/face odour from men and women. Challenge 2 consists in increasing our knowledge of the chemistry of human body odour. Most of the studies mentioned in the previous paragraph use perceptual approaches, and little is known about the chemical bases of human chemosignalling. Exploring how this question was studied until today reveals several limitations, as well as heterogeneity and relative paucity of investigations. Challenge 3 is a warning against confining investigations to the usually studied WEIRD populations (Western, Educated, Industrialized, Rich, and Democratic countries) (Henrich et al., 2010b) and an explicit incentive to extend them to different cultures, which to date has only been done occasionally. This allows testing to what extent hypothesized mechanisms of odour-based attractiveness may be common to the human species and to identify cultural specificities. About cultural specificities, two major aspects constitute Challenge 4: contraception and fragrance use. These very widespread practices seem to interfere with or complement natural chemical communication. Finally, significant advances in the field will be possible only with the combined efforts from different disciplines: This constitutes Challenge 5.

This last challenge presents how the conjunction of behavioural sciences, social sciences, neurosciences, and microbiology will help increasing our understanding of human chemical communication.

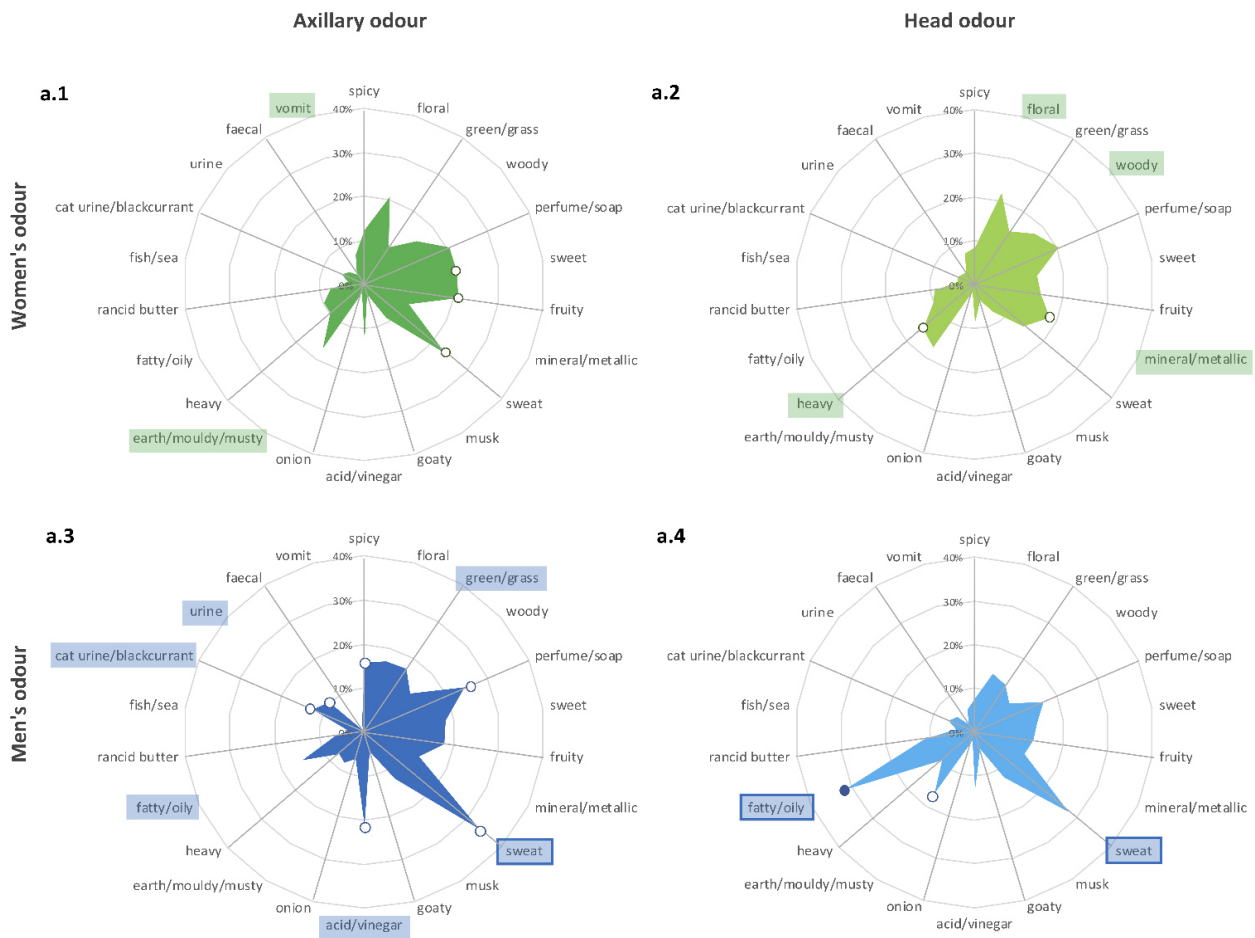
### Challenge 1: Beyond the axilla

Although many areas of the body produce a smell, most studies on human chemical communication have investigated odours from the axilla. This can be explained in part by the belief that axilla has taken over the communication role from the anogenital region due to the upright human posture (Pawłowski, 1999), but also by cosmetic motives (necessity to understand the formation of malodours to better neutralize them), and by the fact that in adults it is one of the most odorous body regions (richest in apocrine sweat glands) and one of the easiest to collect (discreet sampling, limited contamination by exogenous odours). Other odour sources, largely ignored so far, may be relevant though.

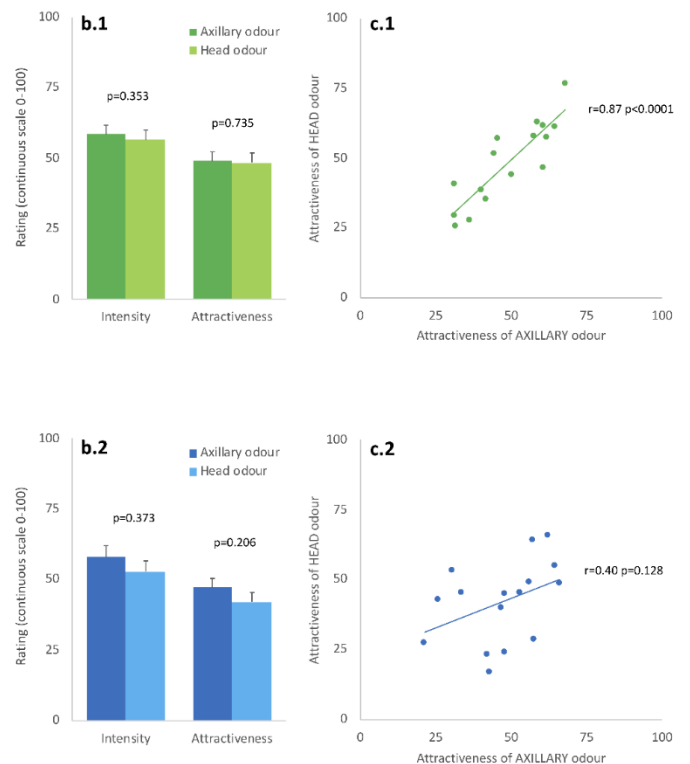
For example, the perception of vaginal and breath odours has been occasionally investigated as a function of hormonal status and gender. Vaginal odours were found to have lower intensity and unpleasantness during the late follicular phase (near ovulation) of female donors, compared to the other phases of the menstrual cycle (Doty et al., 1975). The authors however raise some doubts regarding a possible function of vaginal odours in attraction because they remained in the unpleasant pole of hedonic valence even around ovulation. Breath odour of men and women were categorized as male or female at a better than chance frequency (Doty et al., 1982), which seems to be driven by the propensity to rate male odours as more intense and less pleasant than female odours (see also (Hold and Schleidt, 1977)). Another study found that individuals can be discriminated on the basis of olfactory cues from their hands; female raters' performance in this task was improved when the two donors were genetically unrelated, and differed on their diet (Wallace, 1977). More recently, a comprehensive approach consisted in comparing the responses of men exposed to women's tears *versus* a control saline solution (Gelstein et al., 2011). Without conscious perception of an odour, tears caused men's sexual arousal to decrease, which was associated with a decrease in physiological arousal and in the activation of the cerebral substrates of sexual arousal (but see (Gračanin et al., 2017a) and the following debate (Gračanin et al., 2017b; Sobel, 2017)). Another study from the same group (see Sobel, this issue) focused on a widespread social practice: greeting by handshaking (Frumin et al., 2015). This behaviour may be used to sample conspecifics' chemosignals since participants increased the sniffing of their own hands after a handshake. How hand sniffing behaviour after greeting a person of the opposite sex could be related with evaluation processes of a potential reproductive partner is

an aspect that should be investigated further. Finally, other body odour sources have been investigated for other purposes than studying human attractiveness to conspecifics. These studies often favour analytical views of the emitted odour over behavioural approaches. Their aims range from *i*) managing malodorous emanations (e.g., from feet (Caroprese et al., 2009), urine (Troccaz et al., 2013), flatus (Ohge et al., 2005), but also related to aging (Haze et al., 2001), *ii*) diagnosing diseases (e.g., cancer, from breath (Bajtarevic et al., 2009)), *iii*) forensic applications (e.g. odours from hands (Curran et al., 2010a), internal organs (Dubois et al., 2019)), to *iv*) understanding the spreading of diseases (due to blood-sucking insects attracted by human hand odour (Bernier et al., 2000) or feet odour (Verhulst et al., 2013)).

Returning to body odour attractiveness, it is crucial to consider odours that may be meaningful during interactions with the partner, namely odours emitted by body parts that are sampled voluntarily or – more likely – in a non-conscious manner. This includes more particularly the head (face, hair, neck, mouth), the hands, the axilla and the genital areas. Here, we present the results of a perceptual study comparing the odour of the head and of the axilla (for Methods details see Supplementary Material). Young heterosexual adults, of European descent and non-smokers, took part either as donors (N=16 men and 16 women, including 8 non-pill users and 8 pill users) or as raters (N=16 men and 17 women, including 9 non-pill users and 8 pill users). Donors followed a strict food/hygiene protocol and sampled the odour of their axilla and their head (face, neck, and scalp) over 6 days. Raters evaluated the attractiveness and intensity of opposite-sex odour samples on continuous scales, and described them by choosing the most appropriate terms among a list of both positive and negative descriptors from a list of 22 items (Table S1). Qualitative variations can be described as a function of gender (Fig. 1.a, descriptors highlighted by colours). Men's odours were perceived as sweatier than female samples (axilla and head), but also more fatty/oily (head). Women's axillary odours were more earthy/mouldy/musty and smelled more like vomit than male samples, and their head odour was more floral, woody, heavy and mineral/metallic. Odour sources also differed (Fig. 1.a, descriptors highlighted by dots).



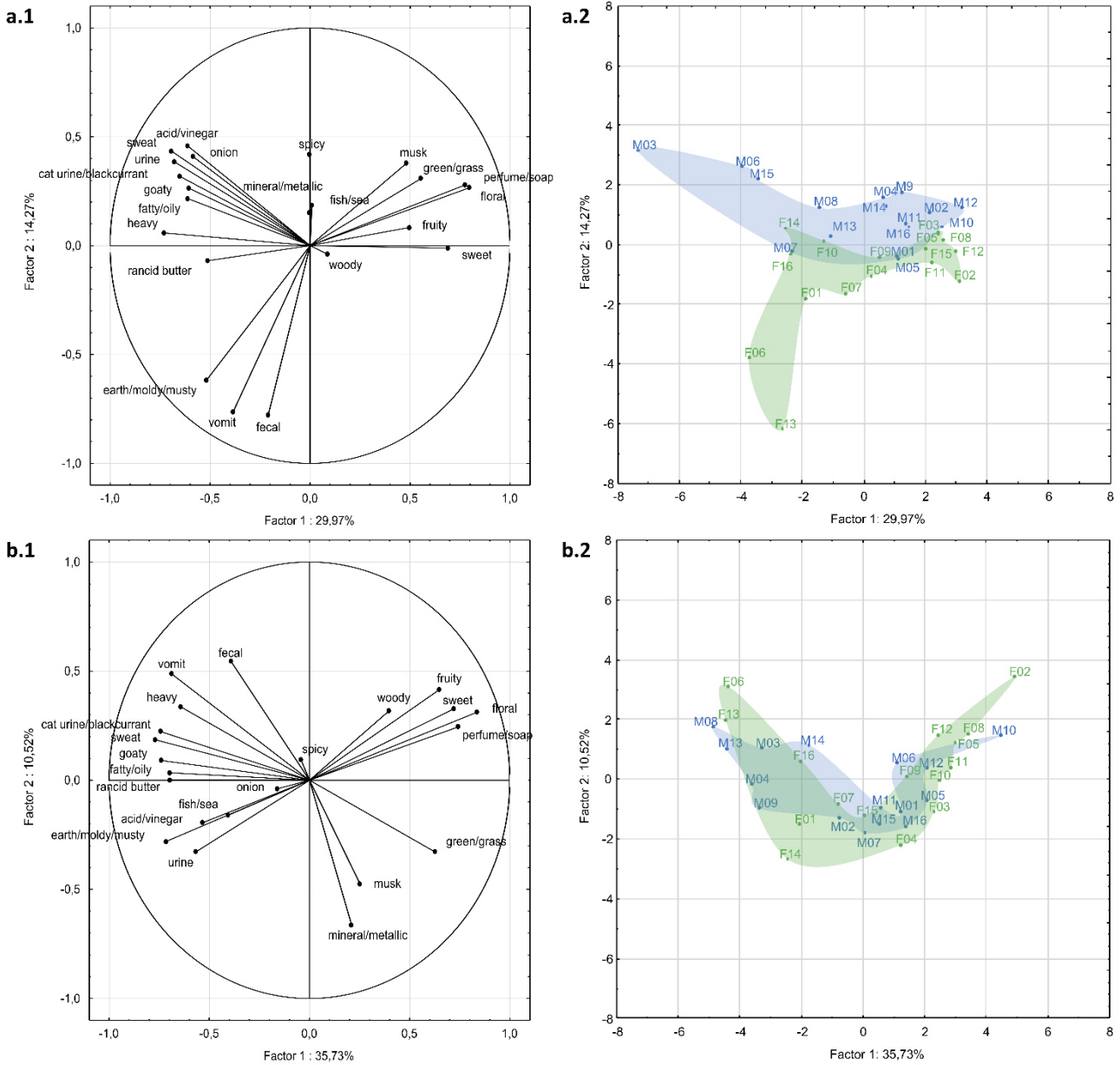
**Fig. 1** Perception of human body odour from the axilla and head of women (top, green, N=16) and men (bottom, blue, N=16). **(a)** Descriptive profiles (in percentage of times each descriptor was chosen): terms differing by more than 5% between men and women are highlighted (in green when higher in women, in blue when higher in men) and frames indicate a difference >10%; terms differing by more than 5% and 10% between head and axilla are indicated by empty and plain dots respectively. **(b)** Average intensity and attractiveness ratings (Mean ± SEM) for axillary and head odours, compared by paired-sample t-tests. **(c)** Pearson correlations between axillary and head odours' attractiveness





Compared to axillary odour, head odour was heavier and more mineral/metallic in women, and more fatty/oily and earthy/mouldy/musty in men. On average, head and axillary odours did not differ in intensity or attractiveness, which were moderate (Fig. 1.b). A principal component analysis (PCA) conducted on the individual's qualitative profiles showed that the highest part of the variance (30% and 36% for axilla and head odours respectively, first factor) was explained by valence as shown by the contribution of descriptors such as "floral", "perfume/soap" vs. "sweat", "heavy", "cat urine" (see Fig. 2.a.1 and 2.b.1). The second factor (14% and 11% of the total variance respectively) could be interpreted as pathogenic threat, since for both odour sources the terms related to organic decay "vomit" and "faecal" contribute importantly to this dimension (Fig. 2.a.1 and 2.b.1; in opposition to "mineral/metallic" for head odour, Fig. 2.b.1). Examination of how odour donors are represented in these 2-dimensional spaces (Fig. 2.a.2 and 2.b.2) suggests that there is a higher variability between individuals, i.e., spatial distance between them, with regards to the negatively connoted descriptors (left side of the graphs) than for the positive descriptors (right side of the graphs). This was true both for head odours (bottom graph, Fig. 2.b.2) and even more for axillary odours (top graph, Fig. 2.a.2) for which men and women seem to present different patterns of unpleasant features. The diversity in body odour quality between individuals may thus rest upon chemical compounds that are rather unpleasant, especially in the axilla. A relevant question for research in the coming years is whether olfactory attractiveness is based on some (to be defined) pleasant attributes, or on the absence of some (to be defined, too) unpleasant attributes that are cues of poor health / of other unwanted features in a reproductive partner, or on both (the second option being supported by the fact that diversity is higher within the unpleasant pole of descriptors).

Interestingly, head and axillary odour attractiveness were highly correlated in women ( $r=0.87$ ,  $p<0.0001$ ) and significantly less in men ( $r=0.40$ ,  $p=0.128$ ; Fig. 1.c; comparison between  $r$ s:  $p=0.028$ ). It cannot be excluded that a bias could have accounted for these results: a potential greater use of perfumed cosmetics in women may have homogenized the olfactory signature of different body parts (through residual compounds diffusing all over the body for example, despite the hygienic restriction protocol we applied) rendering axillary and head odour more similar than in participants using less fragrant products. But another possibility that would be worth exploring in the future is that the odour of the head could convey different cues than the axilla in male donors. Some of the most interesting questions to address in the future are: which information is conveyed by each odour source? by which mechanisms? and which odour source has more weight in determining the attractiveness of a potential reproductive partner?



**Fig. 2** Principal Component Analyses on the descriptive data of (a) the axilla and (b) the head odour of women (green, N=16) and men (blue, N=16). The figures represent the projections of the variables (descriptive terms, a.1 & b.1) and of the cases (odour donors, a.2 & b.2) on the first bi-dimensional spaces that explained nearly half of the variance.

Associated with another set of studies showing that odours of the breast, a body area rich in sebaceous glands as is the face, may serve mother-infant communication (Doucet et al., 2009, 2012), the unique data presented above support the idea that more effort should be made to investigate odours produced in the facial area due to their potentially relevant informative content. While axillary odours mostly originate in the bacterial transformation of compounds conveyed by apocrine sweat, the face and scalp possess a high concentration of sebaceous glands (and some apocrine glands) and probably host a different microflora, which is likely to result in odours differing in quality compared to the axilla. Whether these odours differently impact potential partners' attractiveness remains to be tested, with comprehensive approaches including the testing of behavioural effects. Qualitative measures using descriptive terms is a useful approach to investigate the sensory profiles of body odours (see also (Allen et al., 2018)), but also to describe their intra- and inter-individual variations (gender differences, variations according to hormonal status), and eventually to link the odours' perceptual and chemical profiles.

## Challenge 2: Body odour chemistry

In humans and other mammals, the study of chemical communication is much more recent than in other organisms such as plants or insects (Dudareva, 2004). In the last two decades, the chemical composition of human scents has received increasing interest in areas such as medical diagnosis (Bajtarevic et al., 2009) and disease prevention (Dormont et al., 2013b; Verhulst et al., 2018), forensics (Curran et al., 2010a; Dubois et al., 2019), emergency search (Agapiou et al., 2015), and more occasionally in the field of cognitive psychology and affective neuroscience (e.g. communication of emotions (Williams et al., 2016; Stönner et al., 2018)). The chemical underpinnings of human chemical communication remain mostly unknown, likely because explorations of the characteristics of human scent using analytical chemistry are very heterogenous and generally confined to very specific issues such as malodour management (Haze et al., 2001; Natsch et al., 2005; Starckenmann et al., 2005).

The chemicals emitted by the human body are volatile organic compounds (VOCs, which are targeted when investigating communication through the olfactory system), but also semi- and non-volatile compounds that emanate from the skin, urine, sperm, vaginal secretions, sweat and breath. Various sampling methods have been used to analyse human body odour (see Dormont et al., 2013b for a review), including i) solvent extraction, where compounds are collected on a medium (e.g., cotton, gaze, glass) and then extracted with a solvent (e.g., hexane, dichloromethane, ether), ii) solid-phase micro-extraction (SPME) and stir-bar sorptive extraction (SBSE), where volatiles are trapped on an adsorbing polymer coated on a small

glass fibre or a stir bar, and then liberated by thermal desorption for analysis, and iii) other types of VOC-traps for the dynamic headspace adsorption on various porous polymers (e.g., Tenax, Porapak Q). Analysis is then often performed with Gas Chromatography - Mass Spectrometry (GC-MS), which combines the excellent resolutive capacity of GC with the power of MS for structure identification (usually assisted by the use of mass spectra databases). GC-MS is particularly adapted to highly volatile compounds of low molecular weight and polarity (as are most of animal scent compounds). Alternatives include liquid chromatography LC-MS (Hooton et al., 2016) more adapted for detection of non-volatile compounds, proton-transfer-reaction PTR-(Q or QTOF)-MS (Williams et al., 2016) allowing for real-time quantification of VOCs (see Williams, this issue), selected ion flow tube SIFT-MS (Turner et al., 2008), or multi-capillary column-ion mobility spectrometry MCC-IMS (Ruzsanyi et al., 2012). Each method has its advantages and drawbacks, such as isolation of irrelevant compounds with solvent extraction (compounds that are not volatile at natural body temperature) or SPME (artefacts originating from the trapping polymer) (Prada et al., 2011). Choosing the most suited technique must be carefully weighted (Drea et al., 2013) depending on the studied substrate (human scents are complex and diverse) and the pursued goal (e.g., understanding individual's full chemical signature for forensic applications *versus* investigating olfactory detection of airborne attractive compounds). Indeed, two different methods may provide very different outcomes, as shown for example by a comparison of SPME and solvent extraction, which revealed only 15 molecules in common (against 92 and 58 compounds found with each technique respectively (Gallagher et al., 2008a). To comprehensively and exhaustively understand human body odour, using complementary techniques and comparing them as it has been done in plant science (Agelopoulos and Pickett, 1998; Tholl et al., 2006) can prove to be useful (Gallagher et al., 2008a; Prada et al., 2011; Dormont et al., 2013b; Kücklich et al., 2017), although inevitably costly and time-consuming.

To date, the knowledge about the chemical composition of human body odour remains heterogeneous and incomplete. Diverse methods are used for sampling (collection time from a few minutes to several hours; during daytime or night-time; contact or non-contact; diverse media such as sterile gauze, cotton, wool, viscose, glass beads, t-shirts (Curran et al., 2006; Preti et al., 2006; Birkemeyer et al., 2016)), and for analysing (see above). Outcomes are therefore hardly comparable, which is worsened by the small number of donors involved and by the large number of VOCs found (Agapiou et al., 2015). These VOCs are sometimes listed without discussing their origin: it has been estimated that nearly one third of the molecules reported in mammals are either misnamed or not likely to have been produced by the studied organisms (Charpentier et al., 2012), therefore emphasizing the need for a critical attitude towards the origins and roles of the compounds found. The complexity and fluctuations of

human body odour (due to diet, physiological state, interindividual genetic variability, and exogenous compounds introduced by using drugs and cosmetics) constitute a serious challenge. Exogenous compounds related to fragranced cosmetics are difficult to eliminate even with a specific hygiene protocol before sampling (Labows et al., 1979; Gallagher et al., 2008a) and others are due to contaminations of the samples at every stage of the processing, indicating that special precaution should be taken to diminish this risk (Drea et al., 2013). In sum, more research is needed in this area, always with extreme care at all stages of processing especially regarding undesirable contamination, and standardization of methodologies would be welcome. To do so, recruiting volunteers having a natural/perfume-free lifestyle could help obtaining more relevant chemical profiles. Also, repeated measures in time for a given individual would be helpful. Replications of previous studies are needed too, as in other fields of science, which could be facilitated by open-access practices (Drea et al., 2013) that allow for cross-analyses and reduction of redundant experiments. Finally, significant progress could be achieved on chemical profiles characterization with the help of new generations of artificial noses, namely electronic devices mimicking the nose and detecting odorants through sensors. The field of artificial olfaction has recently achieved a significant expansion, and offers increasingly performant devices based on bio-inspired sensors (Barbosa et al., 2018). Historically used for quality control of the environment or of food and beverages, artificial noses are increasingly employed in disease diagnosis and could very well extend their applications to detection of body odour compounds.

### Challenge 3: Cross-cultural studies

The study of how body odours may be involved in human reproductive function should not be limited to the usually studied WEIRD populations (Henrich et al., 2010b). Including different populations allows testing to what extent hypothesized mechanisms of odour-based attractiveness may be common to the human species, and to describe cultural specificities. For example, it has been proposed that if human body odour contains compounds that are relevant in human attractiveness, then olfactory receptor genes responsible for their detection would be highly conserved in the human species (Wyatt, 2015). In light of this, the extensively studied putative pheromones androstenone and androstadienone seem to be poorly credible candidates. Indeed, at least one in five people cannot detect them (Amoore, 1991; Ferdenzi et al., 2016a) and strong genetically-based interindividual variability has been described for their perceived quality (Keller et al., 2007). In line with this, a significant part of the population (80–95% of Asians, *versus* 0–3% of Europeans and Africans) possesses a non-functional variant of the ABCC11 gene, which has a key function in the formation of body odour, resulting in the absence of androgen (and carboxylic acid) compounds and to a much weaker body odour

(Martin et al., 2010). These molecules may thus not be as relevant in human mate choice as scientists once thought.

Considering the more complex body odour in its entirety, cross-cultural studies remain scarce. Anthropologists have pointed out ethnicity-related differences in body odour judgments, such as the fact that white and black people perceive the other group as “foul-smelling” (Classen, 1992). A proposed explanation was that such an olfactory classification of people demarcates social groups and contributes to maintaining boundaries between them. However, whether this has biological and perceptual grounds remains under-studied to date probably because this is an ethically sensitive topic. A few studies compared Asian, African and Caucasian people on several aspects, though. African participants were found to have the largest apocrine glands and highest levels of sweat secretion, while Asian participants have fewer apocrine glands and a lower level of axillary odour (Hart, 1980). The emission of some carboxylic acids also differs between ethnic groups (Prokop-Prigge et al., 2016), and differences related to donors’ ethnicity were reported in terms of pleasantness and intensity ratings (Parma et al., 2019), which are likely genetic, although diet- and hygiene-related influences cannot be excluded.

Cultural norms and practices may indeed influence body odour emission and perception. For example, rules of interpersonal distances during social interactions (theory of proxemics (Hall, 1966)) vary according to culture (Sorokowska et al., 2017) and may have a role in chemical communication, as hypothesized in some cultural comparisons of body odour perception (Schleidt et al., 1981; Ferdenzi et al., 2008). Cultural variations do also exist in emotional responses to odours (Ferdenzi et al., 2013; Sorokowska et al., 2018) and in the language used to evoke odours (see Majid, this issue). Cultural variations in cosmetic and drug practices may also be influential, as detailed hereafter.

#### **Challenge 4: Pill and fragrance use**

Cultural practices are known to interact with body odour emission and perception: hormonal contraception and cosmetic practices are among the most significant ones. Using hormonal contraceptives seems to cause counter-adaptive effects, such as inverting preferences related to the immune system (preference for the smell of individuals with a similar MHC (Roberts et al., 2008), while the reverse could be expected in naturally cycling women on the basis of some studies (Wedekind et al., 1995); but see (Winternitz et al., 2017)). Studies using various smells (Caruso et al., 2001; Doty and Cameron, 2009) and body odours (Lundström et al., 2006) show that olfactory sensitivity of pill users is equivalent to that of non-pill users in the luteal (non-fertile) phase of their menstrual cycle, both groups having lower sensitivity than non-pill users

in the follicular (fertile) phase of their cycle. The same pattern occurs for body odour emission, with body odour attractiveness being highest around ovulation (Singh and Bronstad, 2001) and lowest in the luteal phase and in women using the pill (Kuukasjarvi et al., 2004). Hormonal contraception use is very widespread in Western societies (41% of French women aged 15-49 years (Bajos et al., 2014)) and its influence on mate preferences (Alvergne and Lummaa, 2010) and more largely on the brain and behaviour (Pletzer, 2015) is being increasingly studied. Therefore, how it interferes with olfactory attractiveness of a partner and how initiation/cessation of it impacts the relationship deserves more attention in the future.

Another practice that might influence chemical communication is the ancient and widespread use of fragranced daily hygiene products. Masking or embellishing people's body odour is one of the major functions of this practice, but the nature of perfume-body odour interactions is complex and to date not fully understood, all the more so as most studies on human chemical communication require perfume removal in donors to focus on the biological odour and to limit exogenous variations in body odour samples. There are chemical interactions with perfume depending on the person's natural odour type (Ostrovskaya et al., 2002), potentially leading to the formation of new aromatic compounds (Behan et al., 1996). There is some evidence that fragrance has a disruptive effect on judgments of masculinity (Allen et al., 2016), personality traits (Sorokowska et al., 2016) and gender (Lindqvist, 2012), and that it modifies other social judgments such as perceived likeability and friendliness (Gaby and Zayas, 2017). Some experiments support the idea, however, that fragrances may interact with body odour in a complementary manner. Individual's natural olfactory signature is conserved even when they use perfume, as shown by a discrimination task (Allen et al., 2015) and the use of fragrance creates individually-specific odour mixtures leading to the maintenance of the interindividual variability (Lenochová et al., 2012). Comparing people's own perfume *versus* a fragrance imposed by the experimenter, several studies show that people choose perfumes in an individual fashion to complement their own natural scent (Lenochová et al., 2012; Allen et al., 2015). This is very consistent with the fact that individual preferences for perfume ingredients (for use on self) correlate with a person's MHC genotype (Milinski and Wedekind, 2001; Hämmerli et al., 2012). Perfumes selected for oneself may thus enhance the individual genetic/olfactory signature (see also Havlíček and Roberts, 2013 for a discussion of perfume-body odour interaction being an example of culture-gene coevolution), and the selection of perfume by a biologically related individual (sister vs. girlfriend or oneself) enhances the attractiveness of the perfume / men's body odour blend (Sobotková et al., 2017). Human body odour is very complex in itself, and understanding the hardly predictable perceptual quality that emerges when it is mixed with a perfume represents an additional significant challenge for the field of human chemical communication. In the future, a particular

attention should be paid to the fact that not only conscious processes (as measured by raters' verbal responses, in the studies cited above), but also non-conscious processes, are likely to result in fragrance-related changes in social behaviours. To finally widen the scope of investigation, other hygienic practices may be worth considering to understand the impact of human behaviours aimed at odour control, such as how, and how often people wash their body.

### **Challenge 5: Interdisciplinarity**

Inputs from different disciplines is obviously required to understand chemical communication. Beyond the necessity to multiply analytical chemistry approaches (discussed in Challenge 2), other approaches using measures of overt behaviour, theoretical frameworks of the social sciences, neuroscientific methods and analysis of the skin microbiome will undoubtedly be beneficial to the field.

Human chemical communication has been studied using mostly verbal descriptions of how body odour samples are perceived, either with rating scales (pleasantness, intensity, attractiveness, etc.) or with preference tasks (see Introduction). Indirect tasks have also been used, requiring social stimuli (e.g., faces (Ferdenzi et al., 2016a), real persons (Saxton et al., 2008)) to be rated after being primed by or in the presence of a body odour or a body odour compound. However, how chemosignals influence our biology and cognition, and ultimately our behaviours, is likely to be a covert process, which is not necessarily measurable with conscious verbal methods. Future research would certainly gain in developing paradigms to measure overt behaviours. For example, motor behaviours are sometimes (but rarely) measured, especially when language is lacking: e.g., head orientation of infants towards odours spatially distributed (Marlier and Schaal, 2005), or reach-to-grasp action towards an object in children with autism (Parma et al., 2013). Other motor behaviours appear to be relevant, such as odour sampling behaviours, measured indirectly, e.g., by recording the frequency with which someone brings his/her own hand near the face after hand-shaking (Frumin et al., 2015), or directly, e.g., by recording airflow variations in the nostrils (sniffing behaviour (Mainland and Sobel, 2006)). The latter, however, has never been used to our knowledge in the context of social communication in humans (but see (Jaenig et al., 2018) for non-human hominids). Ideally, behaviours displayed in real social interactions (e.g., speed dating experiment, see (Saxton et al., 2008)) and indicating attraction or repulsion towards someone would be very informative. However, although being highly ecologically valid, such approaches face numerous experimental biases, such as uncontrolled sensory and behavioural factors inherent to the interacting person. Therefore, crafty alternatives could be



developed, such as associating the diffusion of body odours with artificial standardized individuals, using virtual avatars (Kim et al., 2015) or physically present manikins (Endevelt-Shapira et al., 2018).

Besides these methodological perspectives in terms of outcome variables, taking advantage of the theoretical frameworks provided by social sciences would help having a more integrated view. Some models have been proposed to conceptualize social interactions, such as the perceptual model of intergroup relations (PMIR) (Xiao et al., 2016). The PMIR can be fed with several existing research on human body odour from various disciplines (Ferdenzi et al., 2016a), to explain how olfaction mediates the interactions between group belonging (gender, culture/ethnicity, religion, social status) and intergroup perception/relationships. Although this model can be recruited for many types of social interactions (colleagues, friends, strangers, etc.), in the case of reproduction and mate choice, gender-related aspects are of major interest. Indeed, this framework can help modelling how one's particular biological odour influences his/her gender identity (e.g., level of gender conformity/nonconformity (Novakova et al., 2013)), as well as the reverse, i.e., how one can modulate his/her gender identity by manipulating the odour blend conveyed by his/her body (through hygienic and cosmetic practices). This in turn may have implications for the relationships with other individuals, depending on their gender (e.g., implications for sexual orientation). Tightly related to this, the concept of stereotype is also worth considering as it may have a considerable influence on body odour perception. Gender stereotypes have seldom been investigated in the field of social olfaction (see (Sczesny and Stahlberg, 2002) for perfumes, and (Mutic et al., 2015; Parma et al., 2019) for body odour), despite being a potential significant source of cognitive modulation of body odour perception.

To understand the mechanisms by which chemicals emitted by a potential mate influence receivers' responses, we need to have a better knowledge of the central processing of these chemosignals. The neural networks involved in the perception of social chemosignals have been explored mostly for androstadienone, which was found to activate – even in the absence of conscious perception – a brain network that is not exclusively associated with olfaction and that is related to social cognition and attention (Jacob et al., 2001; Gulyás et al., 2004). Differences were found in the hypothalamus as a function of perceiver's sex (Savic et al., 2001) and sexual orientation (Savic et al., 2005; Berglund et al., 2006), and interpreted as being the underpinnings of sex-differentiated behavioural responses. In more naturalistic approaches, it was found that body odours induced increased neural activity in a large network including cingulate cortex, occipital and angular gyri, but not the primary olfactory areas (Lundström et al., 2008). Different networks are recruited depending on the origin of the body odour: network for processing fearful stimuli (stranger *versus* friend odour) (Lundström et al., 2008), kin

recognition (sister *versus* friend odour) (Lundström et al., 2009) and rewarding stimuli (infant's odour) (Lundström et al., 2013). More directly related with body odour attractiveness, exposure to sadness tears (Gelstein et al., 2011) and to body odour of sexually aroused donors (Zhou and Chen, 2008) modulate activations in the brain substrates of sexual arousal (namely fusiform gyrus and hypothalamus). Further research is needed to identify the neural networks involved in body odour attractiveness processing, considering for example other odour sources than the axilla (see Challenge 1).

While neuroscientific approaches provide an invaluable methodological asset to understand how receivers process potentially relevant chemosignals, there is a need to better understand how these chemosignals are produced and the mechanisms by which they convey information that is relevant to mate choice (and more generally to other social interactions). In this perspective, analytical chemistry has been identified as key discipline in Challenge 1, but biochemistry and microbiology are at least as important. Indeed, microorganisms are key contributors to the formation of human body odour. Precursor molecules that are present in the (odourless) secretions of skin glands (apocrine, eccrine, apoecrine, and sebaceous glands) are transformed through enzymatic activity of the resident bacteria into compounds that are more or less volatile. This process has been mostly explored for one production site: the axilla (Leyden et al., 1981; Labows et al., 1982; Zeng et al., 1991; Gower et al., 1994; Natsch, 2013; Troccaz et al., 2015). The main families of bacteria identified on the skin are Coryneform bacteria, Propionibacteria and Staphylococci (Leyden et al., 1981; Natsch, 2017), with more men having a coryneform-dominant microflora (two thirds, vs. one third of the women) (Jackman and Noble, 1983). Different types of bacteria have been found to produce different compounds, resulting in various odour types: Corynebacteria are responsible for the production of carboxylic acids (such as 3-methyl-2-hexenoic acid and 3-hydroxy-3-methylhexanoic acid) and androgen steroids (such as 5 $\alpha$ -androst-16-en-3-one, 5 $\alpha$ -androst-16-en-3 $\alpha$ -ol and 4,16-androstadien-3-one) that contribute to a typical pungent axillary odour, while a more acid and sulphur-like odour is given by Staphylococci through the production of short-chain fatty acids and thio-alcohols (such as 3-methyl-3-sulfanylhexasan-1-ol) (Leyden et al., 1981; Gower et al., 1994; Starckenmann et al., 2005). The axilla is an ideal field of exploration in this regard because it contains a high concentration of all types of skin glands, hosts a dense population of microorganisms and produces numerous volatile compounds. Other odour-producing areas of the body, however, are likely less prolific and thus more difficult to investigate, but they probably constitute an unescapable challenge for future research in human chemical communication. Deeper explorations would also be welcome regarding individual differences but also factors of variations in time and their potential influence on interpersonal behaviour.

## Conclusion

Chemical communication in humans is a relatively new field of research, with most of the research effort being concentrated in the last two decades. Major advances have been made, but many aspects of remain poorly understood for various reasons, including the fact that this is a recent topic, that focus has been made on some odours to the detriment of others, and on some social contexts to the detriment of others (e.g., mate choice vs. other types of social interactions such as parent-child, friends etc.) and that researchers are facing numerous technical, methodological and disciplinary limitations. The challenges developed in this article do not concern blank areas of research, which shows that progress is being constantly made. Rather, they are destined to provide guiding principles for future studies contributing to elucidate the social function of odours in various contexts of social interactions.

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# GENERAL DISCUSSION

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## 1 Recontextualizing

### 1.1 Introduction

During the course of this thesis, numerous concepts were approached, intertwined, jostled, connected, and I hope piqued your curiosity as much as they piqued mine during my own journey into the world of chemical signals in humans. Our species being social by nature and using its senses to navigate and interact with its environment, it seems *prima facie* evident that we communicate everywhere, always, with everyone around us. Today, we even communicate perhaps more than ever, in a society in which sending messages to someone else thousands of kilometers away is as easy as opening a computer or a mobile phone: the other side of the world is as far as our fingertips. Communication is now global, intercultural, instantaneous, fast, and connected. Yet, these communication modes are still very recent in the grand scheme of things, and our human ancestors evolved to communicate in close small groups of several dozens of individuals at most (Dunbar, 1993). In these tribes, where reading or writing concepts as complex as we are able to do now was not an option, and the use of language was limited or inexistent, it was necessary to make others understand one's own intentions and feelings in a clear, unequivocal way. How to make someone aware that an action they just performed hurt us or on the contrary filled us with joy? Emotions are inherently anchored into our functioning, promoting survival and/or reproductive success. They help us overcome problems or address them (Frijda, 1986; Lazarus, 1991). At a social level, they have been categorized as serving two functions: generating new relationships and consolidating them or maintaining a social position at the expense of others (Fischer and Manstead, 2008). Therefore, communicating emotions shapes our whole status and place in a group, strategically shifting between social bonding and social power.

Emotional communication is, in the wild, multimodal although very often thought of and studied only in audiovisual terms. One of the most poorly known and yet constantly active means of communicating our emotional states could be through the olfactory sense via the molecules continuously emitted by every organism.

## 1.2 The invisible walls on the way

### 1.2.1 Untouchable untastable inaudible invisible – on the difficulty to approach the olfactory stimulus

Still, a lot is to be understood from our endogenous odors. Even though a lot of progress has been made - mostly in the last 40 years - odors in general are still understudied in comparison with stimuli coming from other modalities, and when they are, research is mainly devoted to perfumery, malodor control, food products, and what Cain has called “Industrial endeavors” (Cain, 1978). It is as if there was an intangible barrier<sup>5</sup> standing in the way that prevents and limits the exploration of olfactory-related themes by humans, something that here I will refer to as “*invisible walls*”. In the study of sociality and communication, this *invisible wall* is, again, found when entering the realm of olfaction: of the natural function of body odors, much less is known than what is for face perception or auditory communication for example.

One of the reasons is perhaps the difficulty to manipulate the signal: while videotaping visual, auditory, and even tactile exchanges is easily doable for them to be explored later in controlled settings, doing the same for olfactory cues right away proves itself to be more complicated. Moreover, the controls needed for olfactory studies focused on molecules with such fine and subtle effects are also much more complicated to achieve. While a stimulus without noise, without a visual component, or a condition without taste or tact is not difficult to imagine, an environment without any odor much less so. Every single experimental material used, as well as every experimenter, diffuses an odor<sup>6</sup>. Such odors are of course most often weak, but not negligible when studying the effects of *subliminal* odors such as the ones explored here, that happen to work in non-conscious ways and are therefore hardly noticeable too.

Likewise, even accessing the signal can be challenging. For example, Li and colleagues (2002) in a study of sea lampreys spent more than two years condensing over one ton of water from specimens held in tanks to collect approximately 30 mg of the purified “signal” to be able to study it – about one drop.

### 1.2.2 The morality of body odors

A second *invisible wall* is found when dealing with *body* odors specifically. These cannot be treated in the same way as more *classical* odors because they are linked to our very essence. This strong bond between our sense of inner self and its odoriferous nature perceivable from the outside has been a closely monitored aspect, body odors being usually associated with filth, only one step away from moral filth (Soo and Stevenson, 2007). Body odor and personal cleanliness have acquired a moral dimension, emphasized with the hygienist movement in the 19<sup>th</sup> century after discovering that germs could spread infections, then establishing a link

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<sup>5</sup> Perhaps methodological, perhaps philosophical, moral or psychological

<sup>6</sup> As an example, during the measurements with the ABOV system we even had to get rid of the furniture in the room to try to collect as few irrelevant VOCs as possible.

between infection and strong odors emanating from a body. Smelling strong means not having cleaned oneself and thus is associated with being lazy or careless and risking disease for oneself and others. In his article “Presenting the self, the social body and the olfactory: managing smells”, Low reports that in some places in Asia the absence of body odor has been a selection criterion for obtaining civil service jobs and that in Japan the presence of body odor was a reason to disqualify someone immediately from military service (Low, 2006). This response, even if fluctuating over eras<sup>7</sup>, is rather recent; an example can be found in a famous letter from 1796, in which Napoleon wrote to Joséphine “Ne te lave pas, j’accours et dans huit jours je suis là [Do not bathe, I’m coming and in eight days I will be there]” (de Tourtier-Bonazzi and Tulard, 1981). Not bathing supposedly would increase the emperor’s pleasure upon reunion. There are numerous other historical examples of people not washing without being bothered in the previous centuries (at least in the western world). This tendency to view (strong) body odor as something immoral or foul seems to be a cultural and acquired response: adults strongly dislike axillary odor, but not children (Soo and Stevenson, 2007). Surely, biology does not take into account cultural morality and there is a need to surpass this taboo to do more and better research.

## 2 The Smell of Emotions

In a world where the odor of our ancestor’s bodies was more omnipresent and surely less sanitized, works suggest that this medium in addition to other nonverbal ways to communicate, was one of the keys of human social dynamics and still continues to do so. This field is flourishing and will hold many surprises, but the outlines are already taking shape around the communicative function of body odors when it is a matter of negative states. Feeling a (negative) emotion is associated with a quick modification of internal physiological, chemical, and cognitive states, thus modifying metabolism and skin glands’ activity, in fine changing the odor emitted by bodies (de Groot et al., 2017), in a relatively quick way (12 minutes are enough, see Haviland-Jones et al., 2016). This salient modification of volatile organic compounds would then be carried through the air into surrounding individuals’ noses, a communication mode extensively studied in other species such as insects in which it is referred to as “pheromonal”. These VOCs would bear an informative quality for receivers, who would adapt their behavior in response to them in a non-conscious way. In the case of negative emotions

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<sup>7</sup> Even though this is likely to have been facilitated after the hygienist movement lately, aversion for body odor has been reported in earlier times too. The pleasant-unpleasant quality of body odor being highly impacted by culture, therefore no absolute truths can be said.

and for humans, the receivers would see their internal state change to match that of the donors', in a process known as primitive emotional contagion. This synchronization of affective states would provide a "bridge" between the two organisms to allow communication by facilitating information transfer, emotional recognition, and so on. Thereby, the literature shows numerous examples of emotional contagion happening through body odors for negative emotional states such as stress, anxiety, or fear (e.g., de Groot and Smeets, 2017; de Groot et al., 2014; Haegler et al., 2010; Pause, 2004; Prehn-Kristensen et al., 2009).

## 2.1 The sweet smell of positive affect

What still remains to discover is whether similar modifications occur for positive affective states. Passing on an anxiety message when a predator is near is an efficient, rapid, and advantageous way of communicating to others that danger is imminent and that they should be prepared, thus increasing survival of the group. However, is communicating positive emotions sensible when no danger is near?

It would appear so, positive emotions participating into our survival by allowing us to acquire and consolidate social, intellectual, material resources which can be drawn upon later on (Fredrickson, 1998, 2001). Therefore, it does not seem too hazardous to think that positive states too, could and should be communicated quickly to individuals around us, signaling that the moment is propitious for calm and stress comedown. When a predator, danger, or threat is near, the group should be alerted quickly and the signal should be clear for optimum survival in a hostile environment; When the threat is nowhere to be seen/heard/smelled, then this safe situation in a welcoming environment should also be signaled in an unequivocal and rapid way, allowing individuals to perform actions that will make them *flourish* (see Ryff and Singer, 2000). Negative emotions are highly adaptive but are useless and even dangerous in the long term, if experienced too intensely, too often or for too long they can have disastrous fall downs (Sapolsky, 1999b). Communicating positive emotions can be a soothing message, for conveying "calm *after* the storm". They are also, independently of negative ones, sources of numerous benefits described in the introductory section of this thesis, that are highly adaptive to individuals but also to the group, and therefore spreading them seems rather reasonable to multiply the said benefits.

### 2.1.1 Lessons on emotional transmission and emotional contagion

This was the possibility that was explored in the course of this thesis, building on top of the exciting yet still too scarce proofs of a positive emotional contagion through olfaction. Our main thesis aim was to test if a transmission of positive emotional states was possible through body

odors. For that, we conducted a first study, **Study 1**, in which we observed that the body odor of donors having felt positive emotions had an impact on several levels on receivers smelling it. First, this odor alone, not coupled with visual or auditory cues, was sufficient to decrease receivers' heart rate, a well-documented effect of positive affect (Kok and Fredrickson, 2010). Second, at a verbal level, this odor also was rated differently than a neutral body odor control, receivers evaluating it as more familiar and intense. Third, the positive odor could modulate participants' complex behavior as measured by creativity tasks. Regarding the third behavioral result, only one study has been interested before in cognitive modifications caused by a positive body odor in humans. They found a modification of facial expressions as well as of global/local processing style in receivers (de Groot et al., 2015a), in a direction that is coherent with markers of positive emotional contagion (i.e., happier facial expressions, more global processing style).

Here, the thought was taken a step further, and the behavioral impact was measured at a higher level, on broad functions that are used daily by all individuals: our capacity to solve problems and to think creatively. In our study, receivers also showed markers of positive emotional contagion in the form of increased creative potential. On average, they showed what was expected of people in a positive affective state by finding more alternative uses for common objects, in more different categories in the AUT, as well as finding more quickly the solution of the Candle Problem, two tasks designed to measure creative thinking/problem solving. This is the first time that complex behaviors such as these have been shown to be impacted by chemical communication.

In **Study 2**, such an emotional contagion was not replicated. However, although they did not reach significance, several patterns were found to be close to those observed in Study 1, especially those for the Candle Problem. In **Study 3**, only creativity tasks were used as a proxy for emotional contagion, and again participants were found to be more creative in the positive than in the neutral condition, suggesting that an emotional contagion had taken place.

Therefore, in this study first elements were provided in favor of our **first hypothesis** (a transmission of positive emotions does exist through body odors), and **second hypothesis** (it is not only a transmission but rather an emotional contagion). Elements were found backing up the possibility that a positive emotion can be transmitted through the body odor of humans (i.e., differences between positive and neutral body odors for physiology/verbal responses) and that a process of primitive emotional contagion has taken place (coherence between these modifications and those expected for positive feelings.).

It is interesting to note that all these effects entirely happened outside conscious awareness, since none of the receivers declared to have smelt anything (with a few exceptions). Yet, we

found evidence of the impact of positive semiochemicals over three different levels in receivers: physiology, verbalization, and behavior. This has also been reported repeatedly for the transmission of negative emotions.

In general, conscious processes are intentional, controllable, effortful, while non-conscious processes by contrast are characterized by being unintentional, uncontrollable, and relatively effortless (minimal attentional resources are required) (Bargh, 1994). The brain needs to encode large quantities of information, coming from a complex physical world, producing complex stimuli, in complex contexts. Moreover, this perception of the world is multisensory, and the brain must respond to the constant bombardment of a multitude of information coming from interdependent sensory systems. Non-conscious processes would serve the role of attending in a rather effortless way to this flow of information, something not possible with conscious perception, which is in contrast much more limited in capacity. Therefore, much of our perception and knowledge of the physical world is built outside the conscious field. For example, non-conscious and automatic processes immediately and unintentionally evaluate the positive or negative valence of all incoming novel stimuli (Duckworth et al., 2002). It is these processes of information selection and sharing between non-conscious and conscious spheres, which result from the pressure and selection imposed by evolution, that the human brain uses to navigate through the complexity of the world at the lowest possible cost.

This astronomical amount of information, if consciously available, would be overwhelming and thus prevent us from functioning. This rationale is also true for the emotional contagion of emotions through body odors. If we were conscious of synchronizing our emotional state with most of the people we cross paths with every day, it would be extremely costly in attentional and mental resources, and our mind would be constantly distracted by it. Consciously and lengthily analyzing emotional changes also seems illogical and deleterious in contexts where split-second decisions are necessary for survival (transmission of negative emotions) or in contexts in which spontaneity and creativity are needed (transmission of positive emotions).

### 2.1.2 Lessons on optimal configuration for emotional contagion through body odors – insights from a naturalistic approach

Here, since both **Aim 2** (Identify the optimal configuration for emotional contagion) and **Aim 5** (study the phenomenon in a naturalistic approach) were explored together through **Studies 2** and **3**, and that **Aim 5** did not comport working hypotheses but was rather a way of performing experiments, we will present our findings for both aims conjointly.

After having shown evidence in favor of positive chemical communication (**Aim 1**), the second step was to examine what factors could impact this phenomenon. For this, we chose to use particular approaches. Ever more neuroscientists are trying to perform science closer to what

happens in the *real world*, by contrast with what happens in *laboratory settings*, in a novel approach called naturalistic neuroscience. Historically, to be studied, simple stimuli and the reactions to them have been isolated from bodily and social contexts. The underlying epistemology being that reducing the number of variables allows easier inductive inferences. However, studying complex stimuli like the biological and neural mechanisms shaping animal behaviors is inherently wired to social and contextual factors, and thus should be done in real life or approaching to real-life, naturalistic conditions (Zaki and Ochsner, 2009; Maguire, 2012; Tikka and Kaipainen, 2014). Certainly, when animals perform or observe actions in “the wild” they do it in ways that differ from what can happen in laboratories, there is thus a need to now export neuroscience to the field, as ethologists do (**Review 1**, Challenge 5). With that aim in mind, a virtual reality method was implemented in **Study 2** to create emotions closer to those that can arise in real-life settings, immersing the participants in a 3D world by contrast with the previously used 2D video method of **Study 1**. In this study, the previous results were not replicated, even though VR proved to be significantly more efficient at inducing the desired positive emotional state in donors. However, some effects were observed in coherence with the results of **Study 1** (see *Discussion section 2.1.1*). The fact that these expected effects were only marginally significant lead us first to confirm that the positive emotional semiochemicals we are dealing with, appear to be subtle and perhaps easily impacted by external factors of which the majority is still unknown, in coherence with **Hypothesis 3** (This emotional contagion is subtle and depends on contextual factors). Secondly, this led us to discuss some methodological choices that could have prevented to observe an emotional contagion, such as sample storage length<sup>8</sup> as well as the supposed influence of social settings (donors seated in groups of 3 for the positive induction to foster emotional experience in **Study 1** vs. seated alone in **Study 2**). This body of conclusions helped to document **Hypothesis 3** objectives of research, by underpinning some components that might diminish the chemical communication of positive emotions (e.g., experienced “realism”, arousal, unfavorable social settings).

In continuity with a view to generate situations closer to reality (**Aim 5**), **Study 3** was implemented in an original and entirely at-home way. To our knowledge, this is the first and only study on the chemical communication of emotions in which the receiver phase did not take place in a laboratory. This naturalistic aspect could have had an impact on the emotional induction. The fact that the participants were alone at home in a familiar and relaxing context could have facilitated the fact of “letting go”, thus allowing them to feel subjective affective states more easily (but this remains to be verified after analysis). Furthermore, this study was

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<sup>8</sup> Which was longer in the virtual reality experiment than in the video experiment, thus possibly causing changes in sample composition



also conducted specifically to explore the repercussion of several factors. In a real social interaction happening between two or multiple individuals, one of the factors that logically should regulate the chemical communication of positive emotions (**Hypothesis 3**) is the nature of the relationship that unites the individuals partaking in it, as well as their own individual characteristics or experience. Among the numerous concepts entangled with the elements cited above, we chose to focus on 3: relationship proximity, learning, and personality. They were measured respectively by the relationship type our participants were in (couples/roommates), as well as their relationship duration (long/short), and sociability levels (high/low).

From the point of view of body odors in general, perception is modulated by whether they are the perceivers' own odors, those of close people such as relatives or partners, or those of total strangers; Body odors of strangers are judged as more unpleasant than one's own odors or those of close people (source effect Stevenson and Repacholi, 2005), illustrating the well-known relationship between stimulus familiarity and pleasantness also found in other modalities (i.e., mere exposure effect; Zajonc, 1968).

In this study, we found elements in favor of an influence of the relationship type, couples being subject to positive emotional contagion while roommates were not. We discussed this finding as increased attention to emotional modulations as a function of proximity. Perhaps humans are more sensitive to emotional changes of people they are close to, and next to whom they daily live close emotional situations. However, this goes against the results found in the literature of chemical emotional contagion, which have all been obtained on dyads of strangers. Thus, we proposed based on preliminary results so far, a non linear relationship: emotional contagion may be higher between strangers and very close people, while levels of transmission are lower in middle levels of proximity. Another option to not rule out is the fact that perhaps emotional states are transmitted in strangers only because of the "stressful" unknown settings in which they are studied (i.e., laboratories), thus increasing hypervigilance, something that would not be observed in normal settings. The latter point confirms the need to explore these cues or signals in ecological situations (**Aim 5**).

### 2.1.3 Lessons on perfume addition

Regarding the effects of perfume that was studied transversally throughout **Study 1**, **Study 2** and **Study 3**, several conclusions could be drawn that alimnt **Hypothesis 4** (perfume does not suppress chemical communication). In the first study, perfume addition to body odor samples did not cause a disruption in the communication of positive emotions (i.e., differences between effects of positive body odor and neutral body odor control when presented alone were conserved when body odors were presented with perfume). In some particular cases,

perfume seemed to be even an enhancer for some internal characteristics of the positive odor: when presented with perfume, this odor becomes even more familiar and intense than the neutral control also presented with perfume. The fact that perfume does not abolish the transfer of cues contained in body odor echoes previous results showing that participants are able to discriminate between individuals even after the addition of perfume to their body odor samples (Allen et al., 2015; Gaby and Dalton, 2019). Here, however, much more labile traits were tested, emotions being quick and momentaneous changes unlike individuality which is a persistent background trait. This is the first time that the effect of the perfume is tested in the framework of the chemical communication of the emotions.

The second equally interesting effect was the synergy between the positive body odor and perfume. Since the positive body odor visibly communicated positive states (**Hypothesis 1 and 2**), and the perfume was selected to be pleasant (as in real life situations) and thus had positive characteristics as well, then the congruent combination of the two may have made certain characteristics of the mixture more salient. With the neutral body odor, the two objects being incongruent in nature, the same synergistic effect is not found. Further experiments are needed to better refine our understanding of this phenomenon.

Since the effect of perfume was a transversal question in this dissertation, we sought to replicate these results in **Studies 2 and 3**. In **Study 2**, again no effect of perfume was found (although the differences between the positive and neutral stimuli could not be replicated, therefore if there was a potential effect of perfume, it would not have been observable on the modulation of said differences). In **Study 3**, perfume had, again, no detrimental effect on the emotional contagion of positive emotions, at least in the preliminary results.

Taken together, these results point to a non-detrimental overall effect of perfume addition to the transfer of subtle and labile traits such as emotions (consistent with **Hypothesis 4** - perfume does not suppress chemical communication), and even sometimes to the complementarity between perfume and body odor. In the much more known thematic of attractiveness, the influence of perfumes and their potential synergistic effects have been explored more thoroughly. For example, some studies show that perfume choices are made to complement our genetics (Milinski and Wedekind, 2001). Despite the fact that emotions are not a genetic trait per se in the same way as individuality, they still remain a biological phenomenon and thus some perfume choices could complement some emotions more and others less. Since the perfume that was used in these experiments was chosen because it was the most pleasant one among a selection during a pre-test, it is therefore a perfume liked by the majority of the population, which does not mean by everyone. Indeed, the olfactory sense and the preferences in this modality being highly variable, it is necessary to explore in the future what could happen with perfumes chosen by the participants (donors) themselves and

not imposed by the experimenters as it was done here. These discussions again echo the field of human attractiveness where results show that body odors are more liked when presented with perfumes chosen by their wearers (or relatives), and that this configuration (vs. a forced perfume) facilitates individuality discrimination (Allen et al., 2015; Sobotková et al., 2017).

## 3 Limits

The aforementioned research encompasses some limits, that we ought to note, principally concerning the naturalistic approach to study our participants, as well as the lack of knowledge on how to handle semiochemicals, and the characteristics of the tested populations.

### 3.1 Naturality means uncertainty

Over the course of this thesis, we posed as an aim to explore populations in conditions closer to their own regular living conditions. On two levels, first by inducing emotions that would feel more “real” to the participants than the ones caused by a screen in an unknown laboratory room, and second, by later exploring chemical communication directly in their homes.

Even though we encourage this type of testing, which we consider particularly relevant concerning the social and affective domain, getting experiments “out of the laboratory” means inevitably making concessions over control. This was particularly striking for **Study 3**, in which participants were alone at home. Although the maximum possible elements were controlled, such as asking them feedback during/at the end of the experiment, asking them to take photos of their experimental setting, imposing a specific room for experiments, standardizing material, or being available on the phone for any questions at any moment., the level of control was indisputably less high than when experimenters are in the same room as participants. This is a drawback that is necessary to accept, in exchange for some insights into how the human mind and body function in their natural conditions. In many ways, the stimuli used in experimental science do not resemble the complexity and dynamics of stimuli found in real-life. Despite this, science has solved numerous problems by tightly controlling experimental settings and adopting a reduced number of variables as well as simple, isolated stimuli. We argue that both views are compatible and should be used in conjunction to complete one another.

### 3.2 Semiochemicals: a user guide

Human semiochemicals still remain a mystery for the most part. As mentioned earlier (*see Discussion section 1.2*), the nature itself of the olfactory stimuli makes it uneasily handled. It is difficult to obtain (whole experiments on several dozens of participants in this thesis were needed “just to” obtain our stimuli), difficult to provide experimental controls (i.e., an environment without any odor), but also very little is known about how to collect and handle chemosignals.

Most studies in the field, including ours, collect these molecules via gauze pads placed directly onto the participants' skin. This, unavoidably, also collects heavy, non-volatile compounds. Such compounds might be relevant and involved in other types of social interactions with very close social contact (e.g., romantic and sexual relationships). However, logically such heavy compounds should not be involved in the mechanisms of our object of study: everyday social communication between individuals and even strangers, the same that everybody encounters profusely every time one walks on the street.

Additionally, when the stimulus is collected and because body odors are volatile, evanescent, and subject to bacterial alteration, it is very often frozen to preserve it. Here again, little is known so far about the effects of freezing. Most studies do so based on an experiment that suggested that freezing did not change body odor perceptual qualities for at least up to 6 months (Lenochova et al., 2009). This was tested on persistent traits such as masculinity, attractiveness, and pleasantness. In this thesis too, the temperature was chosen as  $-32^{\circ}\text{C}$  based on this, but perhaps finer qualities such as states that are changing (e.g., emotions) are impacted differently or more quickly by freezing. Especially when dealing with non-conscious tasks (vs. conscious verbal discrimination). In **Study 2**, one possibility for the lack of replication was the storage length, which was longer than in other experiments (5.5 months vs. 1.5 months) and of which little is known in the context of emotional chemosignals. Furthermore, some laboratories keep their samples at diverse degrees of temperature, going from  $-32^{\circ}\text{C}$  all the way to  $-80^{\circ}\text{C}$ , which also makes it difficult to compare results.

### 3.3 We are weird and odd

#### 3.3.1 The male-female paradigm

As is customary in this field, only males were used as donors and females as receivers (with the exception of the dyad experiment). Yet, if a communicative phenomenon of emotions exists, then it seems logical that the entire population would have access to this evolutionary advantage. It might be arguable to consider sex differences for sexual chemosignals, but there is no good reason to do so for emotions. Even though gender differences are observed in emotional processes and expressions between men and women (e.g., females expressing emotions more intensely than males, and males inhibiting their emotions more; Brody, 1985) this seems to be caused by social factors rather than biological mechanisms (Manstead, 1992). An extrapolation is thus made from a sub-part of the population in only one configuration (men communicating emotions to women), and even if these choices were taken and justified by the relatively recent field of human chemical communication as well as the even more recent and exploratory nature of experiments about positive semiochemicals, it is now necessary to study the impact of gender and sex on these behaviors.

The same is true for other controlled parameters in our samples: sexual orientation but also ethnicity.

#### 3.3.2 A very western slice of humanity

Limiting research, by choice or by mere automatic sampling bias, to subpopulations and then extrapolating the found results to the whole human species is a problem encountered widely in research (Henrich et al., 2010a) where only so-called WEIRD (Western European Industrialised Rich and Democratic) populations are studied. As Henrich and colleagues say, these conclusions are drawn upon a "thin, and rather unusual, slice of humanity" and cannot be generalized to every other slice without questioning (**Review 1**).

Great examples can be found in other parts of experimental research, illustrating how easily one can sometimes take erroneous conclusions if extrapolated only from WEIRD populations in olfactory research. Sorokowska et al. (2013) compared the olfactory thresholds for an odorant (n-butanol) between a traditional forager-horticulturalist society of the Bolivian Amazon, the Tsimané, and Germans. In this study the authors declare that both groups were not familiar with n-butanol. The results are impressive: even the most sensitive German was outperformed by 25% of the Tsimané individuals, making them much more sensitive than the average German. The authors underline the fact that these results are even more striking when considering the background of both samples: Germans were healthy, nonsmokers, with good socioeconomic background and regular professional health care, while none of the Tsimané

had access to a permanent physician or nurse<sup>9</sup> and they showed recurrent upper respiratory tract illnesses.

Thus, there seems to be a non-negligible difference in olfactory functioning between populations living in conditions far from those of the participant with whom science is built. This difference has been observed for “classical” odors, but anecdotal evidence has also been reported for differences in perception of odors of body origin for a long time by anthropologists. For the Dassanetch, a population living in Ethiopia and part of Kenya, the odor of menstrual blood is considered odorless, as all odors coming from the body, because they are neutral and natural, and for the Desana in the Amazone, the same odor of menstrual blood is considered to attract snakes and to threaten crops (Almagor, 2016)

Because in our sample only WEIRD people were included and their perception of body odors and the value they attach to them is inherent to the culture they live in, as well as of the relative richness of their olfactory environment, therefore close attention should be paid to other types of population before generalizing these results as a global mechanism. To counter this WEIRD bias, a first step was taken by de Groot and colleagues, who studied the chemical communication of emotions in a non-Caucasian sample of particularly interesting comparison (de Groot et al., 2018). Most East Asians (80-95%) carry the A/A allele of the ABCC11 gene causing fewer precursors as well as a lower quantity of emitted VOCs than Caucasians (0-3% A/A). Since in this thesis we have presented the link between emitted volatiles and emotions, then it would not seem surprising to expect a reduced ability in East Asian populations to *transmit* emotions via their chemical senses but also to *perceive* them. Their results, on the contrary, show that non-Caucasian receivers exposed to emotional chemosignals are impacted by them, emulating the emotional states communicated as it has been observed before, and this outside of awareness. This tested only the receiving end of the transmission, and still needs to be explored what would happen if the donors were also East-Asians.

Interestingly, during this PhD thesis a similar experiment was originally planned in Asia to further explore this last question as well as the points developed above, by testing the potential communication between donors and receivers of both origins. Regrettably, this had to be canceled due to the Covid-19 pandemic but is an ensemble of questions that just remains pending.

Additionally, intercultural differences exist not only in the odor production and perception but also in emotional expression, with some cultures controlling their intensity more than others (Matsumoto and Ekman, 1989). This difference in expression is linked to the value attached to emotions, which varies depending on culture. In individualist cultures such as in the west, high

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<sup>9</sup> The professionals being a few hours or few days away by boat

arousal emotions are more valued, while in collectivist cultures more present in the east, low arousal emotions are more valued and thus preferred (Lim, 2016). Furthermore, cultural practices also impact odor evaluation (Ayabe-Kanamura et al., 1998) as well as cosmetic use, hence why it is crucial to better cartography these aspects (**Review 1**).

### 3.3.3 Aseptic adults in big cities

A fact noted by Roberts and colleagues (Roberts et al., 2020a) and cleverly summarized by a second acronym of their own invention is the fact that the WEIRD populations (and thus those tested in our studies) are very generally also ODD, that is: Old (i.e. adults), Deodorized and Desensitized. Old because chemical communication plays a major role during childhood (see *Introduction sections 5.2.4 and 5.3*), but the vast majority of the subjects studied are adults. Most of them shower every day, change their clothes just as often, wear them only once, and remove their hair recurrently or even permanently with the help of lasers destroying the air follicles, which reportedly minimizes the buildup and diffusion of odor. All of these practices to heavily deodorize oneself can also impact the skin microbiome, which is a key factor in the production of body scent and probably of human semiochemicals. The ODD participants also live in polluted areas, caused by important industrial and human activity (the majority of our sample came from Lyon - the 3rd largest city in France) with a considerable impact on their olfactory capacities, according to some studies collected by Roberts and colleagues. They cite the example of a study by Hudson and colleagues (Hudson et al., 2006), who compared two groups of participants coming from Mexico, those from Mexico City, the heavily polluted capital, and those from Tlaxcala, a state considered to be geographically similar but relatively less polluted. In their study the authors report that the inhabitants of Tlaxcala are able to detect common odors (coffee, orange drink) at lower concentrations, to discriminate better between two perceptually similar odors, and present a lower percentage of poor olfactory function than inhabitants of the capital.

### 3.3.4 Conclusions

Logic would suggest that if less ODD populations were tested, or populations coming from societies that are not WEIRD, then the olfactory apparatus being more sensitive as well as the environment being oriented towards rich olfactory stimuli might have caused even stronger results, but we cannot be sure without testing. In addition, the majority of conclusions showing an advantage of non-WEIRD and non-ODD populations are drawn from perceptual thresholds, and these are different from a functional approach such as an emotional transfer. Still, one cannot ignore the fact that olfactory performances seem to be strongly impacted by

geographical and cultural contexts, and therefore their impact must be taken into account in order to fully understand the emission and especially the perception of body odors and *in fine* the chemical communication of emotions.

In sum, more efforts are needed in this direction to rule out effects caused by biology from those caused by culture. Not to shed light on the importance of one over the other, but rather to better understand the fundamental links between them, their dynamics, and the contexts where they act, thus allowing our models to be closer to reality, a global and multicultural one.

## 4 Future Horizons

Giving insights for the future is something that was started in the course of this thesis via **Review 1**, in the form of some major challenges that need to be addressed in this field, and recommendations to solve them. The recommendations were written for the future, but also applied in the present, throughout this thesis. These listed challenges point towards exploring other areas of the body than the axillae, since many other parts of the body are meaningful (perhaps more obviously than the axillae) during social interactions. Among these, particularly relevant are the head (mouth, face, hair, neck) which is close to others' noses, the hands with which we greet, hug, and touch people around us, as well as the genital regions involved in sexual encounters. Note that, interestingly, those zones are also the ones that we usually perfume with diverse cosmetic products, which is unlikely to be a coincidence. A few experiments have tried to adventure beyond the axilla by exploring amongst others the perceptual evaluation of vaginal scent (Doty et al., 1975), sex discrimination by hands' odor (Wallace, 1977), or the influence of women tears' semiochemicals on men's sexual arousal (Gelstein et al., 2011). Here, we also follow that direction in **Study 4**, in which we collected participants' axillary, as well as neck odor.

Other challenges have been aborded more extensively elsewhere in this manuscript such as better refining and adapting our knowledge of the chemical bases of human body odor, which for now is limited (*see Discussion section 4.3* for further development), designing cross-cultural studies (*see Discussion section 3.1* for further development), or combining methods and expertise from multiple fields such as ethnology, social sciences, or neuroscience.

In addition to the challenges outlined in the opinion paper (**Review 1**), some other remaining aspects, which are not necessarily challenges but rather perspectives will be covered in the following lines.



## 4.1 Minimizing interventions

Most of the studies in the field of chemical communication in humans for experimental reasons use any kind of media to collect the signal and present it to the receivers, such as gauze pads or sensors on the body. It is likely that the manipulation of the donors may change their behavior, as well as the quantity or quality of the secreted volatiles. This is more obvious in a non-human animal where manipulation by an experimenter or an external intervention can modify the signal by causing stress for example, which is why for studies in zoological models, precautions are taken to great extents to disturb the animals as little as possible. It is tempting for many of us to think that humans are animals apart and that putting gauze pads under our arms while talking with experimenters wearing white coats in immaculate laboratories is a parameter that our faculties can ignore, but it is highly unlikely.

In order to discover a potential pheromone in the human species, it is necessary to proceed with the same caution and candor as with a “newly discovered mammal” (Wyatt, 2015). Thus, it is necessary to be as free as possible from interventions to refrain from perturbing the natural secretion of semiochemicals. While studying pine snakes and their ability to recognize predators and prey from olfactory cues alone, some scientists have for example collected signal by using the bedding material of their specimens without having to manipulate the subjects especially for chemosignaling use (Burger, 1990).

One step was taken in this direction in this thesis by using an entirely at-home experiment which minimized experimenters’ interventions during the body odor collection, while also putting participants in their everyday familiar setting. However, this is only a first step that entailed some limitations (see Discussion section 3.1), and this proposition can and should be exploited in the future, with for example studies conducted in small rooms where the VOCs emitted by donors stay in the air while a second person (the receiver) enters the room subsequently.

## 4.2 Inter-species communication

Another aspect that should be explored is the fact that since communication shapes our very most basic interactions with other individuals of our species and allows us to position ourselves in the big web of exchanges, but humans do not only communicate with themselves. This type of phenomenon has been shown for many other species of the animalia regnum (see *Introduction section 2.1*) but also in the plantae and fungi regna (e.g., Hare, 2011; Kochert, 1978). Since virtually every part of life is subject to these exchanges of information, it does not seem surprising then to observe mechanisms between species and kingdoms in close contact as for example between insects and plants (Bell and Cardé, 2013).

Humans living on the surface of almost the entire globe and being at the top of the food chain, always invading other species territories, therefore their interactions have always been

frequent and close with many species. Yet, very little is known so far about humans' chemical interactions with them, especially in terms of emotions. The first ones that come to mind are the domesticated species that went with humans through convergent evolution such as dogs or cats.

In a first study of its genre, Siniscalchi et al. (2016) tested the reaction of dogs to human chemosignals of fear. Dogs, exposed to fear semiochemicals showed a lateral asymmetry to sample the odors (left nostril preferentially used), as well as a higher cardiac activity. In continuity with this idea, testing “happiness” human body odors, D’Aniello and colleagues showed that golden retrievers and labradors exposed to them show fewer and shorter owner directed behaviors, more stranger directed behaviors and a lower heart rate, while in the fear condition they display more stressful behaviors and a higher heart rate (D’Aniello et al., 2018). In horses, exposure to emotional human chemosignals also induces sympathetic and parasympathetic changes indicating emotional activation (Lanata et al., 2018). Although the small samples in some studies as well as the rarity of them makes the results preliminary, these results are consistent with what would be observed if an emotional contagion existed between species. Since these species (horses and pet dogs) are known to possess performant olfactory capacities, therefore their models are excellent to study human emotional chemosignaling. New discoveries should also be found while studying other species close to humans, which surely have also evolved to react finely to human emotional cues in particular places where important cohabitation happens.

This could turn to be particularly enlightening when considering among many others: pets’ well-being, domesticated farm animals’ welfare and productivity (e.g., for example pigs seem to be sensitive to intraspecific positive and negative emotional contagion in reaction to human interventions; Reimert et al., 2013), as well as reaction to human emotional chemosignals during handling of animals involved in experimental research.

### 4.3 Exploring the chemical bases

The chemical underpinnings of human chemical odor still remain mostly unknown, and when studies are done several problems arise (e.g, heterogenous methods, impact of pollutants, molecules cited without verification of origin, etc – see **Review 1, Challenge 2: body odor chemistry**). Those of the volatile (or less volatile) molecules involved specifically in chemical communication are even more of a shadow zone. There is thus a necessity to isolate and identify such molecules, which is an unavoidable and essential step to discover “real human pheromones” (Wyatt, 2015). So far, several studies have explored the impact that emotional human body odor could have on behavior, cognition, perception, neural activity, etc. (see

*Introduction sections 6. and 7.3*), and this number is growing. Still, only a handful, if not less, have tried to link these effects to actual molecules.

As this field progresses forward, elucidating the chemical signature behind the observable effects that emotional semiochemicals have will be compulsory and will make this field progress of a giant step. When single molecules or a mixture of compounds will be underpinned, they will be easily tested in bioassays. For now, exception made of a handful of exceptions, the chemical communication of emotions remains a black box similar to that of the behaviorist movement in 20<sup>th</sup> century psychology.

With this idea in mind, a novel and original device named ABOV was entirely imagined and conceived during this PhD thesis (**Study 4**). ABOV offers several solutions by i) being as chemically neutral as possible (no emissions from the sampling system itself), ii) interfering as little as possible with skin bacteria activity (by not creating an enclosed space), iii) being easily cleaned, iv) being versatile in the use of adsorbent polymers, v) allowing participants to perform tasks and move freely during collection, vi) used on various body parts (see **Review 1, Challenge 1: Beyond the axilla**), and finally vii) permitting the sampling of two body parts simultaneously. We are confident that this device will prove to be efficient and helpful to our future studies and will hopefully participate in better refining our knowledge of the chemical bases involved in positive emotional chemical communication, as well as other aspects (e.g., attractiveness, sickness, individuality etc.).

Furthermore, another element that for now is almost totally unknown is the dynamics aspect of the emotional semiochemicals. Are they emitted quickly or not? Is their secretion constant or rather important following the initial stimulation and then drops over time? Is there a plateau in their emission? All of these aspects remain questions to be answered. Currently, sampling times of 20 to 30 minutes are generally used in experiments and are sufficient to observe effects, for both negative and positive emotions. One of the rare studies to have investigated the subject is a study by Haviland-Jones and colleagues in which they compared two collection times of 12 and 24 minutes for emotional semiochemicals (Haviland-Jones et al., 2016). If the secretion of the chemical signal is constant, then a longer period should logically imply a greater amount of signal collected. However, as emotions are brief and changing events, a longer collection period may also cause other emotions to be felt (even briefly) and thus a more ambiguous signal *in fine*. In their study, no difference was found between the two collection periods for perceptive verbal tasks, suggesting that 12 minutes is sufficient. This also poses some interesting biological problems that they discuss: 12 minutes seems to be a period too short for proteins to be made *de novo* and then secreted from the skin cells. This would imply according to the authors that proteins are surely "prepackaged", waiting for an activation signal to be released (in a similar fashion as neurotransmitters). This dynamical question will surely be answered with the help of chemical studies. A promising tool for this is found in proton-

transfer-reaction mass spectrometry (PTR-MS), which allows for real-time monitoring of volatile molecules in the air, and has been successfully used to analyze human skin odor before (Veres et al., 2013; Williams et al., 2016).

#### 4.4 A palette of emotions

As for now, the chemical communication of emotions is a fertile burgeoning field and during the course of this thesis were reported some studies having explored this thematic. One aspect that can be noted down is that for now, studies have explored first emotions that are described as “basic” (see Ekman, 1992). In the prevailing domain of negative ones: anger, anxiety, disgust, fear. In the domain of positive ones: “happiness” or here in this thesis “positive emotions” at large.

It is useful to note that, this corpus aside, in all positive chemical communication studies researchers employ the term “happiness” chemosignals. The reasons for this are never explicitly stated but seem logical: happiness is shorter and hence easier to use, while also appealing a particular emblematic emotion that speaks to everyone unlike the umbrella term positive emotions that can be blurrier. We argue that this shortcut might be appealing but should not be taken, since the two concepts are not interchangeable. Happiness is only one among the numerous positive (not necessarily basic) emotions such as pride, joy, love, gratitude, interest, contentment, awe, hope and many more. For positive emotions, the limits seem to be less clear than for negative ones: their physiological activation patterns are less distinct, the words used to recall them are more intercorrelated suggesting a higher degree of blending, their facial expressions are less stereotypical and unique (Fredrickson, 1998). Additionally, a positive emotion is often co-occurrent with another one (e.g., one might be happy and grateful at the same time because of a hopeful event), something less frequently seen for negative emotions where one of them usually overcomes the rest (e.g., being angry about someone being rude). In experimental studies, it is very unlikely that researchers have induced only one positive emotion (in fact a majority of them use almost only laughter inducing material, which is a very limited approach to happiness).

Therefore, for now, we believe that only the so-called basic emotions have been studied for negative states (and even then, most probably studies interested in anxiety/fear/stress have measured the same state, *see discussion in Introduction section 6.2.1*), while researchers studying happiness have rather studied most probably a blend of positive emotions. Convinced of this, in our studies we have deliberately tried to induce a blend of positive emotions, by using videos or games inspiring contentment, happiness, gratitude, altruism and so on. This is why we employ this larger term in our work, and further research should be carried to unravel what states exactly are being studied and if each basic positive emotion implies different reactions

or if they share a common mechanism at large.

As emotional research advances, the list of basic emotions is being widened by the very same scientists who have conceptualized and described the existence of basic emotions. Now, some evidence is being presented in favor of core distinctive patterns of awe, amusement, contentment, desire, pain, relief, sympathy, or embarrassment in both facial and vocal expressions in cross-cultural studies (Cordaro et al., 2016, 2018). Thus, as research advances and methods as well as theories are being refined, our understanding of if those distinctive bodily patterns also take the form of distinct chemosignals should be explored. Fear communicated by the olfactory sense has been shown to cause very distinct sensory acquisition patterns than disgust for example (de Groot et al., 2012). Is this true for positive emotions, that seem less specific and more likely to co-occur with one another? (see *Introduction section 7.1*). Will other, more “complex” emotions such as serenity, boredom, jealousy, loneliness, fascination, respect, triumph also be communicated through odors the same way they have been shown to be expressed through audiovisual cues?

#### **4.5 Conclusions**

Still many parameters are to be discovered, and numerous other questions still unresolved or unexplored would have deserved to be mentioned here in more detail such as the impact of status or power in a relationship on emotional contagion through body odors (Hsee et al., 1990), are people with a high hierarchical status less susceptible to contagion? Do they send stronger cues? How can these olfactory signals or cues impact people’s well-being in the workplace (Johnson, 2008), especially in careers with numerous social interactions every day, all the more if those are often emotional such as for nurses or sellers (Omdahl and O’Donnell, 1999)? What are the ethical aspects to understand such a powerful non-conscious phenomenon, and can this be manipulated in perhaps malicious ways by some individuals? This thesis fell short of narrating all the byways, accessory concerns, and exciting ideas connected to chemical communication because this field is so diverse and wide, but this is surely the reason why it will hold many surprising results in the future.

## 5 Final Conclusion

In reaction to some events, our emotions come to change in a conscious and directed way, while in other cases our emotions transition in a totally unconscious way without an apparent triggering event. Sometimes, in the company of some people, we feel relaxed and at ease, reassured by their mere presence and without any word, while in the company of other people we feel some kind of anxiety and uneasiness. With some people, we can communicate easily and feel like we are in tune, while with others this connection does not seem to be there. What could explain these reactions that at first glance seem to be “intuitive”? What makes the landscape of our emotions change in unperceivable ways? Emotions are particularly adaptive and serve primordial roles in the survival and the good functioning of organisms. To perceive them and know how to take advantage of them is a talent that optimizes these functions and allows humans to build an essential and rich set of social dynamics. In particular, positive affect encompassing emotions such as joy, gratitude, love, happiness, optimism, or bliss to name only a few, is part of our daily lives and provides important benefits for individuals and societies and makes life worth living.

During the course of this thesis, we explored the use of body odors as a medium in humans to communicate social information to surrounding individuals, and in particular information about positive affective states. Humans are able to perceive molecules in the air associated with these positive affective states (in the same way as they do for negative states) and, in a non-conscious way, to adapt to them by partially replicating the state they have just perceived via a process known as primitive emotional contagion. Individuals exposed to body odors collected from donors who have undergone a positive emotional induction show physiological, cognitive and behavioral modifications compared to what is observed when they are exposed to control body odors. These changes, even if impacted by contextual factors, are not disrupted by the addition of an exogenous odor and bring the state of mind of the two communicating individuals into coherence and allow them to establish or reinforce an already existing relationship, promoting the exchange of affective information and even promoting the synchronization of neural activity.

These olfactory exchanges are made very often, every day, and in every place we go; they allow us to identify ourselves in a given group and to know how to react in certain situations, while granting and diffusing precious benefits for both our mental and physical health. In the Bantu language spoken by some African populations, the word *ubuntu* means that a person

becomes a person only through other people<sup>10</sup>. This view is shared by neuroscientists, the human brain is shaped by its continuous interaction with others, strangers and relatives, and this impacts a myriad of processes (Hari and Kujala, 2009). Perhaps this is why we sometimes prefer to listen to music in large groups, where positive emotions can be captured and reflected, rather than alone in front of a computer; or why we like to go to the cinema, rather than watching a movie alone at home. In these social contexts where emotions seem richer and more intense, maybe our sense of smell helps us to be “contaminated” by what surrounds us, amplifying the experience. By better understanding what automatically and primitively shapes our emotions in social interactions, we can regain power, becoming more resilient towards stress or allowing ourselves to be more susceptible to positive influences. Although these olfactory effects happen beyond our awareness, knowing that they exist and how to best exploit them gives us more control over them and makes us aware of the importance of these subtle yet very important parts of our daily life.

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<sup>10</sup> Interview of Desmond Tutu, New Scientist, April 2006

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# APPENDIX

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## Supplementary Material Study 1

### **Stimuli for emotion induction**

*Positive emotion* induction was performed using 11 film clips, including movie bloopers, humorous sketches, videos of happy babies, dancing crowds and altruistic videos (evaluated during a pilot session, N=9). These were chosen to induce a variety of positive emotions such as joy, happiness, gratitude, amusement or serenity. For the *neutral condition*, 10 clips were chosen with excerpts of chemistry classes, videos of people gardening and documentaries about geology and mussel farming. Documentaries have been used before in other studies to keep participants in a neutral emotional state, as they do not comport any vivid emotion but are interesting enough for the donors not to be bored (Frumin and Sobel, 2013). For each condition, the clips were assembled to provide a 30-minute sequence.

### **Body odor collection protocol**

From two days before the first body odor collection and until the second odor collection, donors were asked to avoid eating food with strong odors (garlic, onions, asparagus, etc.), consuming alcohol and exercising too much. They were also asked to use only scent-free hygiene products (deodorant Sanex Zero™, and shampoo/soap Colgate-Palmolive) that the experimenter provided. Odor sampling during emotion induction was performed only in the morning to limit the accumulation of other types of emotional sweat stemming from daily activities.

### **Alternate Uses Task Scoring**

Receivers' fluency was computed as the mean number of alternative uses found per object for each receiver across the 6 objects. Originality was estimated by comparing each response to the total amount of responses for the same object, by all receivers. Responses that were found 5% of the time or less, were counted as unusual and attributed 1 point, responses that were found 1% or less of the time were counted as unique and were given 2 points. All the other

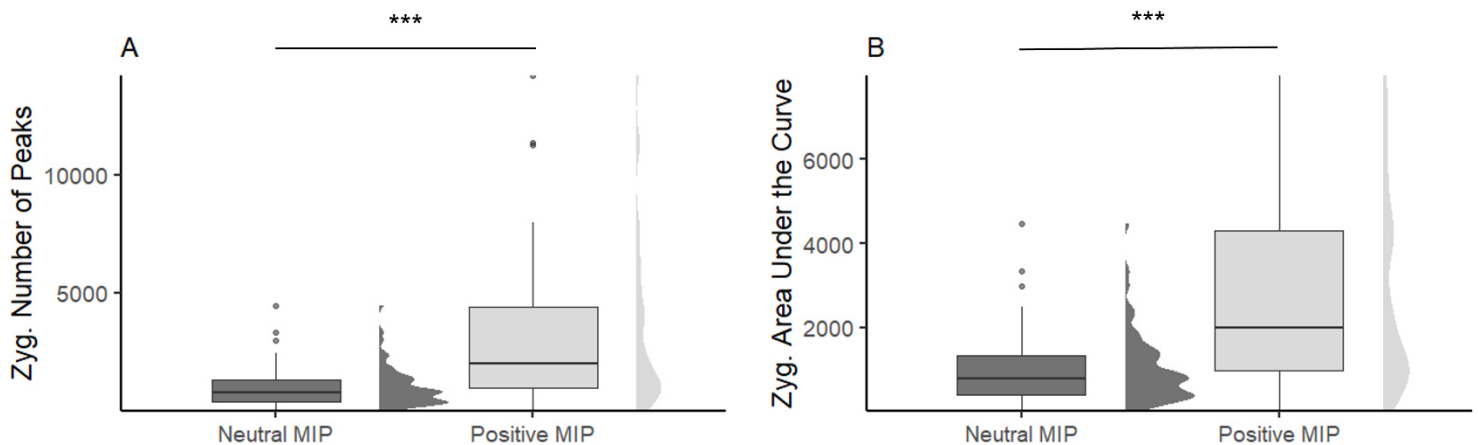
responses (found >5%) were considered usual and given 0 points. Elaboration was obtained by giving 1 point to each element of detail the receivers included in their answer (e.g, for the word *car tire*: “protection” was given 0 points because it has no added precisions, as “a protection for cars during Formula 1 races” was given 2 points for the “for cars” and “during Formula 1 races” elements). Finally, flexibility was computed by classifying each response in general broader categories, and then counting for each subject the mean number of different categories given (e.g., for the word *brick*, “tie it to something so it sinks” and “use as a paperweight” are in the same category, i.e., weight).

## References

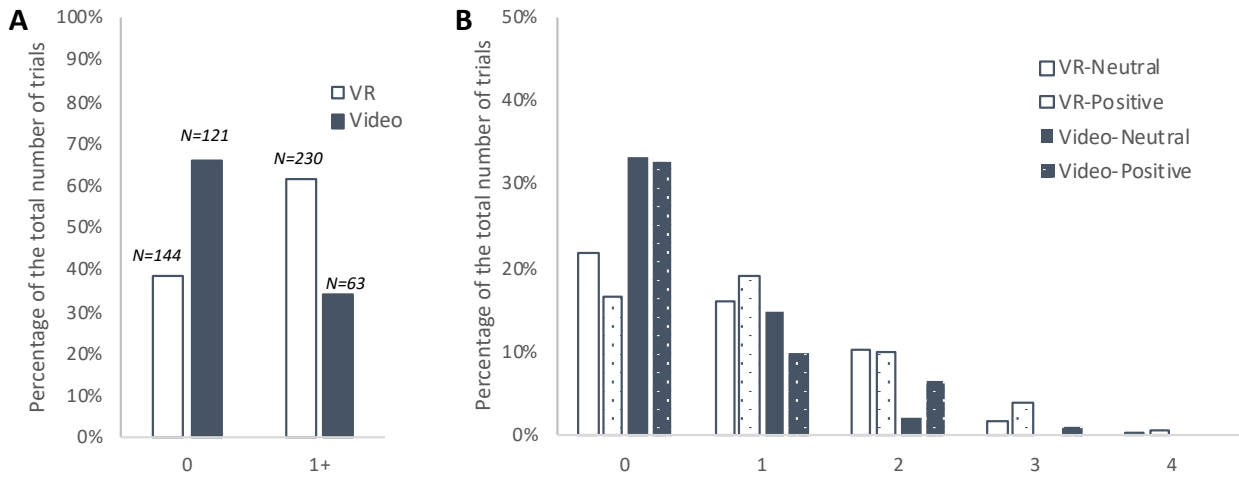
Frumin, I., Sobel, N., 2013. An Assay for Human Chemosignals, in: Touhara, K. (Ed.), *Pheromone Signaling*. Humana Press, Totowa, NJ, pp. 373–394.  
[https://doi.org/10.1007/978-1-62703-619-1\\_27](https://doi.org/10.1007/978-1-62703-619-1_27)

# Supplementary Material Study 2

## Figures

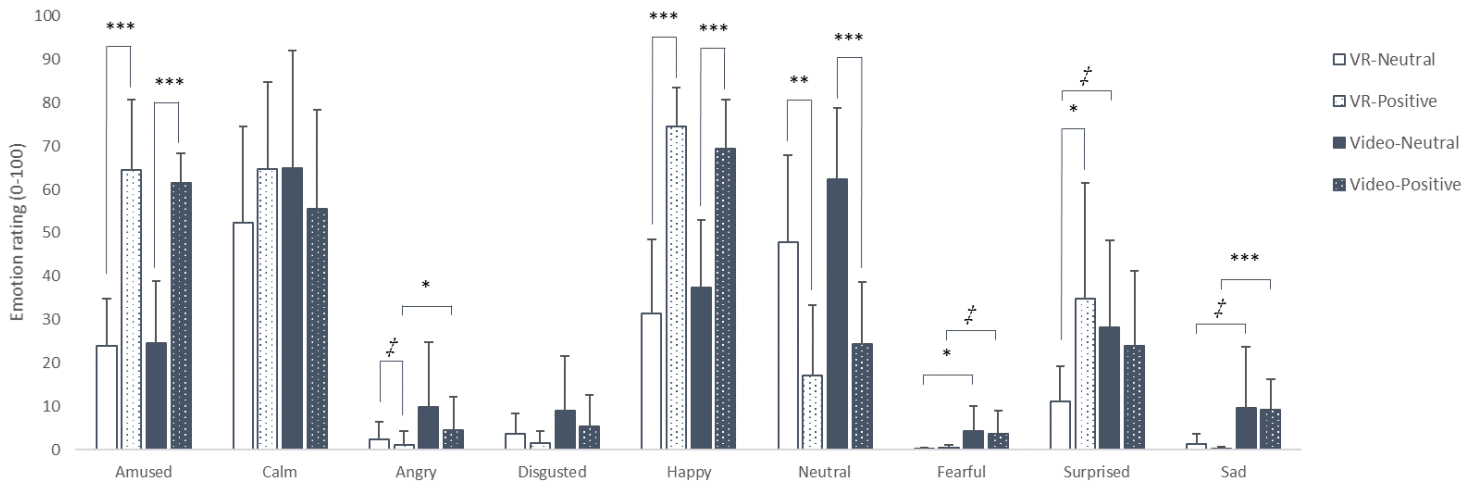


**Figure S1: Donors' EMG responses during the Neutral and Positive Mood Induction Procedures. (A) Number of detected peaks for the zygomatic major muscle. (B) Area Under the Curve for the detected zygomatic major peaks. \*\*\*:  $p < 0.001$ .**

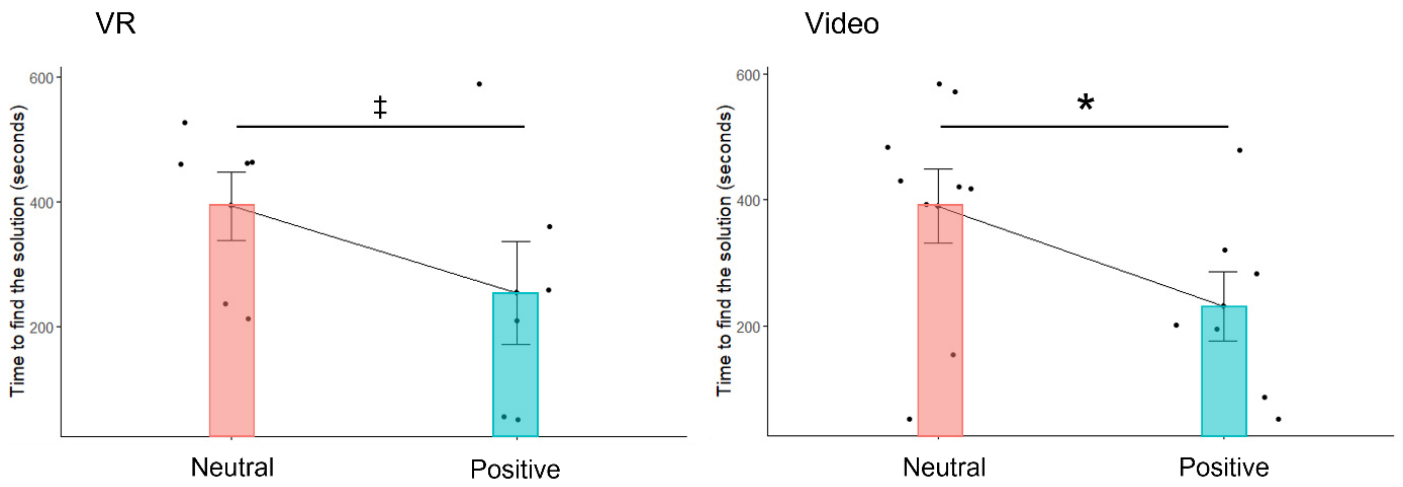


**Figure S2: Donors' number of skin conductance responses (SCR).** (A) Overall view of the percentage (and raw number) of trials with zero SCR versus one or more (1+) SCRs during mood inductions with Virtual Reality (VR) and with Videos (Chi-square test on the raw numbers:  $\chi^2(1)=35.661$ ,  $p<0.0001$ ). (B) Detailed view of the percentage of trials with zero to four SCRs during Neutral and Positive Mood Induction Procedures using VR or Videos.





**Figure S3: Donors' average emotional ratings on 0-100 scales** (Mean, Standard Deviation). Comparisons uncorrected for repeated testing (Wilcoxon/t-tests) between Neutral and Positive conditions within the VR and within the Video inductions, and between VR and Video procedure within the Neutral and within the Positive conditions. If corrected, the differences for the Amused, Happy and Neutral scales are conserved, as well as the VR Positive vs Video Positive comparison for Sadness. ‡:  $p < 0.10$ , \*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$



**Figure S4: Comparison of receivers' performance during Duncker's Candle Problem, in the VR and Video experiment.** Mean time to find the solution to the Candle problem, in seconds (in participants who successfully solved the problem, VR: Neutral, N=6 out of 15; Positive: N=6 out of 14; Video: Neutral, N=9 out of 16, Positive: N=7 out of 16) Means  $\pm$  Standard Error of the Mean.  $\ddagger$ :  $p < 0.10$ , \*:  $p < 0.05$ .

# Methods

## **Body odor collection protocol**

From two days before the first body odor collection and until the second odor collection, donors were asked to avoid eating food with strong odors (garlic, onions, asparagus, etc.), consuming alcohol and exercising too much. They were also asked to use only scent-free hygiene products (deodorant Sanex Zero™, and shampoo/soap Colgate-Palmolive) that the experimenter provided. Odor sampling during emotion induction was performed only in the morning to limit the accumulation of other types of emotional sweat stemming from daily activities.

## **Alternate Uses Task Scoring**

Receivers' fluency was computed as the mean number of alternative uses found per object for each receiver across the 6 objects. Originality was estimated by comparing each response to the total amount of responses for the same object, by all receivers. Responses that were found 5% of the time or less, were counted as unusual and attributed 1 point, responses that were found 1% or less of the time were counted as unique and were given 2 points. All the other responses (found >5%) were considered usual and given 0 points. Elaboration was obtained by giving 1 point to each element of detail the receivers included in their answer (e.g, for the word *car tire*: "protection" was given 0 points because it has no added precisions, as "a protection for cars during Formula 1 races" was given 2 points for the "for cars" and "during Formula 1 races" elements). Finally, flexibility was computed by classifying each response in general broader categories, and then counting for each subject the mean number of different categories given (e.g., for the word *brick*, "tie it to something so it sinks" and "use as a paperweight" are in the same category, i.e., weight).

## **References**

# Supplementary Material Study 3

## **Stimuli for emotion induction**

*Positive emotion* induction was performed using 11 film clips, including movie bloopers, humorous sketches, videos of happy babies, dancing crowds and altruistic videos used successfully to induce positive emotions in previous studies (Richard Ortegón et al., 2022). These were chosen to induce a variety of positive emotions such as joy, happiness, gratitude, amusement or serenity. For the *neutral condition*, 10 clips were chosen with excerpts of chemistry classes, videos of people gardening and documentaries about geology and mussel farming. Documentaries have been used before in other studies to keep participants in a neutral emotional state, as they do not comport any vivid emotion but are interesting enough for the donors not to be bored (Frumin and Sobel, 2013). For each condition, the clips were assembled to provide a 30-minute sequence.

## **Body odor collection protocol**

From two days before the first body odor collection and until the second odor collection, donors were asked to avoid eating food with strong odors (garlic, onions, asparagus, etc.), consuming alcohol and exercising too much. They were also asked to use only scent-free hygiene products (deodorant Sanex Zero™, and shampoo/soap Colgate-Palmolive) that were provided to them.

## **Alternate Uses Task Scoring**

Receivers' fluency was computed as the mean number of alternative uses found for each receiver across the 6 objects. Note that besides fluency scores of originality, elaboration and flexibility of the answers can also be calculated. Given that all measures are inter-correlated, especially with fluency (Cohen and Oden, 1974; Plass et al., 1974; Hebert et al., 2002; Runco, 2010), and that the measure of fluency has been found before to be impacted by positive chemical communication (Richard Ortegón et al., 2022), for simplification purposes only this measure was used in this experiment.

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# Supplementary Material Review 1

## SUPPLEMENTARY METHODS

This article presents data from an experiment divided in two studies (1 and 2, detailed below). Study 1 is part of a larger study aiming at creating a database of facial and vocal stimuli (GEFAV (Ferdenzi et al., 2015a)) and at comparing facial, vocal and olfactory attractiveness in the same individuals (unpublished): only a small fraction of the data related to olfactory attractiveness is presented here, whereas Study 2 was used in its entirety for the present article. Both protocols have been approved by the Committee on Research Ethics of the Faculty of Psychology and Education Sciences at the University of Geneva.

### Participants

In both studies, participants were heterosexual, of European descent, and non-smokers, and were aged between 18 and 36 years old. They were recruited through notice posting and word-of-mouth, mostly among university students. Those who provided body odour samples are called “donors” and those who rated the odours are designated as “raters”. All participants provided written informed consent and received cash or course credits for their participation.

*Study 1 (main study).* 79 participants, including 39 men and 40 women were involved as donors. Among the women, 22 were using hormonal contraception (“pill users”) and 18 were not (“non-pill users”): for the latter, body odour collection was performed during the estimated follicular phase of their menstrual cycle (see estimation procedure in (Ferdenzi et al., 2009)).

Raters, about half of which being also odour donors, were 38 men and 55 women including 29 pill users and 26 non-pill users among which 12 were estimated in the fertile phase of their menstrual cycle.

*Study 2 (follow-up descriptive study).* Due to time constraints for the evaluation session, a subset of Study 1 donors was selected to obtain 32 donors in total (16 men and 16 women, including 8 fertile non-pill users and 8 pill users). Selection was performed with the aim to reduce the sample size while keeping a good representation of the range of attractiveness: therefore, roughly every other sample was retained on the distribution of male and female attractiveness separately (attractiveness here being the average of short- and long-term attractiveness ratings, see Procedure below). Raters were 16 men and 17 women, including 9 non-pill users (1 fertile) and 8 pill users, and were independent of odour donors. Note that due to limited sample size, the factor “pill use” was not considered in the data analysis.

## **Procedure**

*Body odour collection.* Donors had to follow strict behavioural guidelines from 2 days before and during the 6-day sampling procedure. Especially, strong foods, alcohol, cigarette smoke and the use of perfumed cosmetics were to be avoided. Participants had to use a non-perfumed shower gel (Alterra® parfümfrei, Rossmann) and a non-perfumed deodorant (Mum® sensitive care, Doetsch Grether AG) that we provided. They had to wear a cotton t-shirt (Sunshirts.ch) for 6 consecutive nights and in the mornings, they had to gently rub their face, neck and scalp with a 20x20cm cotton cloth, thereby providing a composite sample of these areas of the head. The instruction sheet was illustrated with 6 different photographs of a person performing the head odour collection. T-shirts and cloths were previously washed in the laboratory with a non-perfumed washing powder (Omo® Sensitive, Unilever). During the day,

the t-shirt and the cloth were kept in two separated zip-lock bags, under the participant's pillow. On the 6<sup>th</sup> morning, the bags containing the samples had to be dropped before noon in a dedicated box in the laboratory, and were subsequently cut (axillary area separated from the rest of the t-shirt), wrapped in aluminium foil, placed in a ziplock bag and stored at -28°C. There was no major infringement of the instructions to report according to a questionnaire on the participants' behaviours during the testing period. In addition, the length of index and ring fingers of the participants' right hand was measured to the nearest 0.1 mm using Vernier callipers, directly on fingers (see details of the procedure in (Ferdenzi et al., 2011)).

*Odour rating.* The samples were left 2 hours at room temperature before the testing sessions started. After the ratings of Study 1, the samples were frozen again, and re-used in the rating session of Study 2. Although refreezing is usually avoided (because of the samples instability due to their biological nature), no major change in body odour samples perceived quality has been reported with repeated thawing (Lenochova et al., 2009); moreover, all samples received exactly the same treatment which makes it possible to compare them. Gender-separate sessions were organized, namely one testing day for donors of each sex who evaluated all opposite-sex samples. They took place in a well-ventilated room with 8 individual boxes and computers. The samples were presented in 250 ml open glass jars wrapped and covered with aluminium. Head samples were evaluated before axillary samples that were intuitively thought to be more intense (although ratings showed that it was not the case), and individual samples were presented in random order within these two categories. All samples were placed on a central table and participants picked the sample they were instructed to evaluate via an E-Prime interface.

In Study 1, raters evaluated the olfactory samples of 20 opposite-sex donors (i.e., 40 stimuli) during a single 1-hour session. Each odour sample was evaluated by minimum 18 and maximum 30 opposite-sex raters. Ratings on continuous visual analogue scales (recoded from 0 to 100 later on) were collected for short-term attractiveness ("For a short-term relationship,



could you personally be attracted to this man / woman?") and long-term attractiveness ("For a long-term relationship, could you personally be attracted to this man / woman?"). Note that ratings of pleasantness, masculinity for male samples, femininity for female samples, and trustworthiness were also collected but are not presented here. In Study 2, raters evaluated the olfactory samples of 16 opposite-sex donors (i.e., 32 stimuli) during a single 1-hour session. They had to evaluate the attractiveness and intensity of the samples using the same continuous scales as in Study 1, and to describe them using a list of 22 descriptors, with the Check-All-That-Apply method, i.e., by choosing the most appropriate terms in the list. The descriptive terms were compiled from different sources (Wedekind et al., 2007; Troccaz et al., 2015) reporting descriptions of body odours by experts (perfumers), trained raters and untrained evaluators with their own personal vocabulary. The final list was chosen to cover a wide spectrum of positive and negative qualities while remaining easy to use by untrained raters (Table S1).

## **Data analysis**

Data were analysed using Statistica v.12. Significance level was set at  $p < .05$ .

*Study 1 (main study).* Opposite-sex ratings were averaged for each odour sample (mean of 18 to 30 raters; ratings were missing when no odour was perceived). After checking that the variables were normally distributed (Kolmogorov-Smirnov tests), Pearson correlations were computed between 2D:4D ratio and mean ratings of attractiveness (short-term and long-term separately). Note that short- and long-term attractiveness were highly correlated (axilla:  $r=0.96$ ,  $N=79$ ,  $p < 0.0001$ ; head:  $r=0.97$ ,  $N=77$ ,  $p < 0.0001$ ).

*Study 2 (follow-up descriptive study).* The descriptive data was analysed as follows. First, the frequency of each descriptor was computed, for each donor sex separately, as the number of times this descriptor was chosen for that particular odour source (e.g., “floral” has been ticked 56 times for all female head samples together, and 41 times for all male head samples together; see absolute frequencies in Table S1) relative to the maximum number of times a descriptor can theoretically be chosen ( $16 \text{ donors} \times 16 \text{ raters} = 256$  times for women’s odours and  $16 \text{ donors} \times 17 \text{ raters} = 272$  times for men’s odours, which results in a percentage of occurrence of the term “floral” of 22% in female samples and of 15% in male samples). To compare male and female samples, and head and axillary samples, differences of percentages were computed and highlighted when superior to 5% and 10% difference in Figure 1. Second, two principal components analyses (PCA) were conducted, on head and axillary samples separately, using the raw number of times each descriptor has been chosen for each individual odour sample. The first two factors that explained near half of the variance have been considered for interpretation (see Figure 2), and variables (descriptors) as well as cases (male and female donors) have been represented on this bi-dimensional space. Third, to analyse the ratings, opposite-sex responses were averaged for each odour sample (mean of 14 to 17 raters; ratings were missing when no odour was perceived). After checking that the variables were normally distributed (Kolmogorov-Smirnov tests), paired-sample t-tests were conducted to compare head and axillary odour attractiveness and intensity, and Pearson correlations were computed between attractiveness of odours sampled from the head and the axilla.

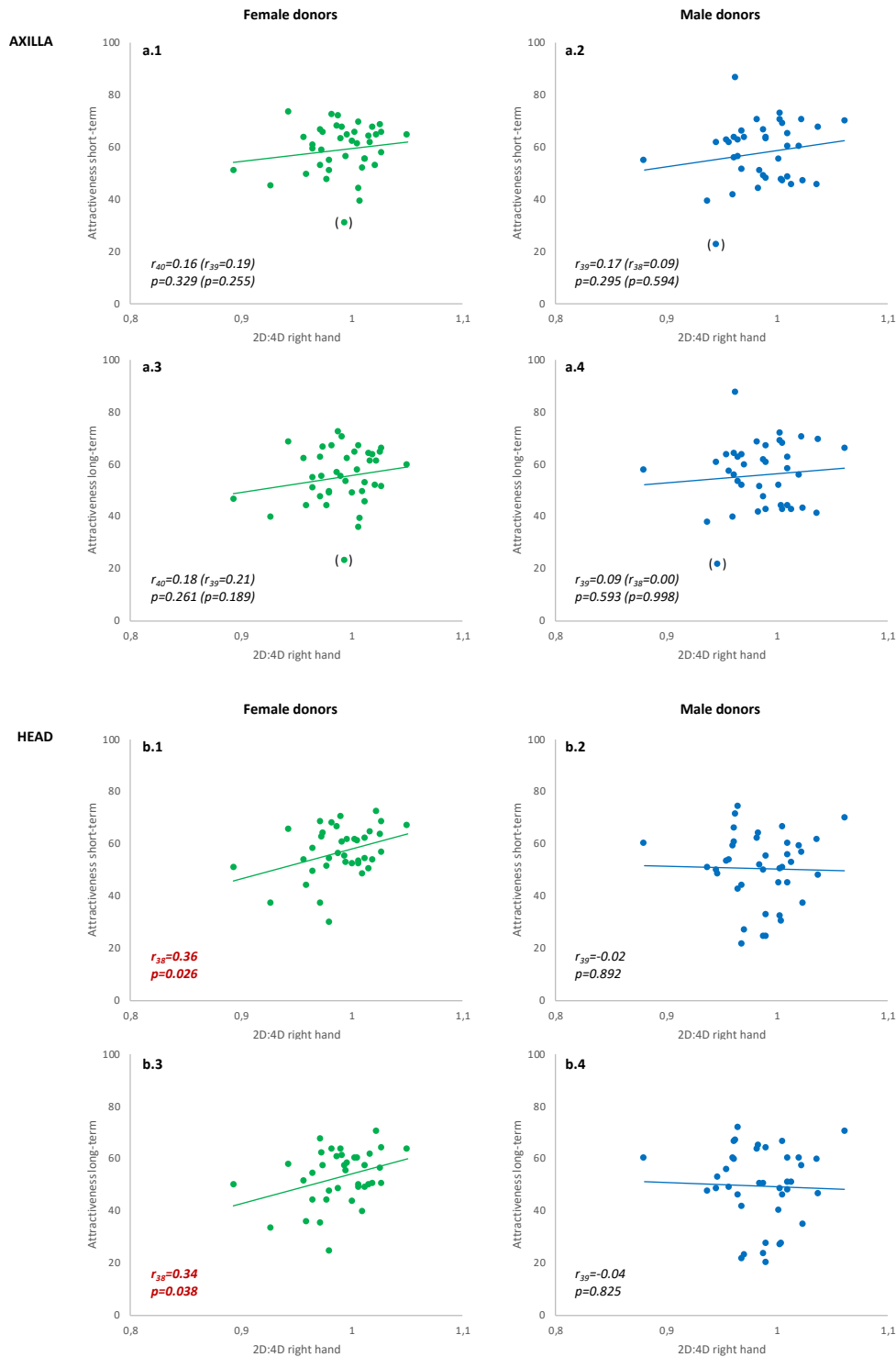
## SUPPLEMENTARY TABLE

**Table S1.** List of 22 descriptors used to describe body odours, in English and in French, which was the language of the experiment. *A priori* valence of the terms is indicated, as well as their source (a: Wedekind et al 2007 in *Evolutionary Psychology* (Wedekind et al., 2007); b: Troccaz et al 2015 in *Microbiome* (Troccaz et al., 2015)), and their absolute frequency for each sample category (female and male axillary and head odours).

Descriptors (English)	Descriptors (French)	Valence	Source	Absolute frequency			
				Women's axilla	Men's axilla	Women's head	Men's head
floral	fleuri	positive	a	53	46	56	41
fruity	fruité	positive	a	54	49	38	36
green/grass	vegetal/herbe	positive	a	26	47	37	38
mineral/metallic	minéral/métallique	positive	a	28	46	47	38
musk	musqué	positive	a	23	39	19	37
perfume/soap	parfum/savon	positive	a	53	69	53	50
spicy	epicé	positive	a,b	32	50	22	23
sweet	sucré	positive	a	53	51	36	41
woody	bois	positive	a	39	43	45	32
acid/vinegar	acide/vinaigre	negative	a,b	33	68	22	44
cat urine/blackcurrant	pipi de chat, cassis	negative	b	14	37	11	20
earth/mouldy/musty	terre/moisi/renfermé	negative	a	44	25	44	49
faecal	fécal	negative	b	7	1	9	6
fatty/oily	gras/huile	negative	a,b	25	42	26	88
fish/sea	poisson/mer	negative	a	9	11	10	16
goaty	chèvre	negative	b	6	15	10	13
heavy	lourd	negative	a	25	24	39	28
onion	oignon	negative	b	5	17	4	7
rancid butter	beurre rance	negative	b	19	25	23	40
sweat	sueur	negative	a	61	97	37	83
urine	urine	negative	a,b	11	28	9	14
vomit	vomi	negative	b	18	5	19	15

## SUPPLEMENTARY FIGURE

**Figure S1.** Correlation graphs between 2D:4D ratio and mean ratings of attractiveness (short-term and long-term separately) for **(a)** axillary odour and **(b)** head odour, in female (left) and male donors (right). Pearson rs with Ns in subscript, and p-values are provided on the graphs. One man and one woman received extremely low attractiveness ratings of their axillary odour (outliers, i.e., rating lower than the mean minus 3 standard deviations; dots within brackets on the graphs): results without these outliers are reported within brackets.



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