

HUMAN OLFACTION AND MATE CHOICE

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To my parents,

*For never allowing me to hide behind self-doubt,
and insisting I go on every adventure.*

*For always being in the stands,
and putting ice in my veins.*

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ABSTRACT

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Coren Lee Apicella

Prevalent beliefs in both scientific and popular culture are 1) humans have a poor sense of smell, and 2) smell plays a minimal role in social behavior. However, this consensus is shifting with researchers even suggesting olfaction influences mate choice. Still, studies of odor-based communication in humans remain inconclusive because of poorly designed experiments, scant replication studies, and publication bias. Thus, the goal of this dissertation was to return to first principles and build a solid foundation for the study of human olfaction and mate choice. Chapter 1 provides a rich overview of human olfaction and odor-based communication, revealing the poor methods used in studies of pheromones and body odor. Chapter 2 investigates the impact of a putative female pheromone, copulin, on men's mating psychology, using rigorous methods (e.g., a placebo-controlled, odor-masking design) and a large sample ($n = 243$ men). The findings reveal that when the limitations of prior pheromone research are addressed, there is no evidence that copulin is a pheromone. Chapter 3 asks whether some individuals smell more or less attractive to the opposite sex. Studies of mate choice from an evolutionary perspective often begin by investigating whether individuals of one sex agree on the attractiveness level (e.g., facial attractiveness) of individuals of the opposite sex. For comparison, a uniform methodology was used to assess agreement in judgments of physical and vocal attractiveness, modalities in which evidence of shared preferences is generally accepted. No differences were discovered between modalities. Therefore, to the extent shared preferences exist for faces and voices, there is also evidence of shared preferences for body odors. Chapter 4 examines the relationships

between independent multisensory judgments of attractiveness (i.e., face, voice, and body odor attractiveness). For men, modalities of attractiveness did not covary. However, in women results indicate weak covariances between all modalities. Moreover, a latent general attractiveness factor (i.e., common fitness correlate) modestly contributed to covariances between modality-specific attractiveness. Together, these findings suggest historical views of human olfaction as unimportant were misguided. In fact, the evidence demonstrates body odor plays a similarly important role to physical and vocal attraction in human mate choice.

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CHAPTER 1: THE EVOLUTION OF HUMAN OLFACTION AND ITS ROLE IN MATING

“Odors have a power of persuasion stronger than that of words, appearances, emotions, or will. The persuasive power of an odor cannot be fended off, it enters into us like breath into our lungs, it fills us up, imbues us totally. There is no remedy for it.”

— Patrick Süskind (2001), *Perfume: The Story of a Murderer*

In the last sixty years, research interest in human odor-based communication has grown tremendously. Yet despite an abundance of studies, whether or not smell influences human social behavior is still largely a mystery. This chapter will 1) provide a rich overview of the research history of human olfaction, and 2) explore the role of smell in mate choice. The quality of studies will be investigated throughout, highlighting the unsettling conclusion that most findings on human odor-based communication and mate preferences are questionable. Finally, this chapter concludes by summarizing the experiments that are presented in chapters two, three, and four, which employ rigorous methods to answer fundamental questions with the goal of building a strong foundation for future research on human olfaction and mate choice.

Human Olfaction

Since the beginning of recorded history, and likely earlier, odors have been associated with primal lust and bacchanalian sexual frenzy. In ancient Greece, the sweat of wrestlers was collected after fights and mixed with creams and oils to be sold as aphrodisiacs (Pickenhagen, 2017). King Xerxes of the Persian empire had virgins complete twelve months of scented oil and perfume treatments before being presented to him (Esther II, 12). Dabney (1913) argued that perfumes, since time immemorial, have been used to stimulate lecherous thoughts. Even today, perfume advertisements commonly incorporate some of the most overtly sexual images used in modern marketing (see Figure 1).

Yet, the allure, intoxication, and sensuality often linked to fragrances seems at odds with the widespread popular and scientific belief that smell is unimportant to humans. Indeed, adults consistently rank smell as the least important sensory system (Enoch et al., 2019), and a large survey of young adults ($n = 7,000$) found that 1 in 2 would rather sacrifice their sense of smell than their phone or laptop (McCann Worldgroup, 2012). However, we know that smell plays a significant role in eating behaviors (for reviews see, Boesveldt, 2017; Boesveldt & Parma, 2021), harm avoidance (e.g., fire detection) (for review see, Parma et al., 2017), religious experience (e.g., incense burning) (Burenhult & Majid, 2011; McHugh, 2012), medicine (e.g., smell has been used to identify certain diseases, such as typhoid fever) (Albuquerque et al., 2020; Geck et al., 2017; Wnuk & Majid, 2014), and social communication (e.g., mate choice) (for review see, Pause, 2017). Furthermore, we now know that the loss of smell presages diseases such as Alzheimer's (Murphy, 2019), Parkinson's (Marin et al., 2018) and, more recently, COVID-19 (Hannum et al., 2020). In fact, there has been a dramatic increase in requests to join olfactory dysfunction support groups, such as AbScent, since

the beginning of the COVID-19 pandemic. Many of the discussions in these groups focus on increased dangers, such as food poisoning, and inability to detect gas leaks or fires, associated with smell loss (Jarvis, 2021). Moreover, members in these groups commonly commiserate over decreased pleasure and quality of life, frequently citing loss of flavor perception as a cause¹ (for reviews see, Rozin & Gohar, 2011; Seo et al., 2021). Additionally, smell loss is connected to depression (Croy & Hummel, 2017), obesity (Peng et al., 2019), reduced sexual satisfaction (Schäfer et al., 2019), and fewer sexual relationships (Croy et al., 2013). So, although life without smell may seem less daunting than life without vision, hearing, or even smart technology, it would undoubtedly be challenging and less pleasurable.

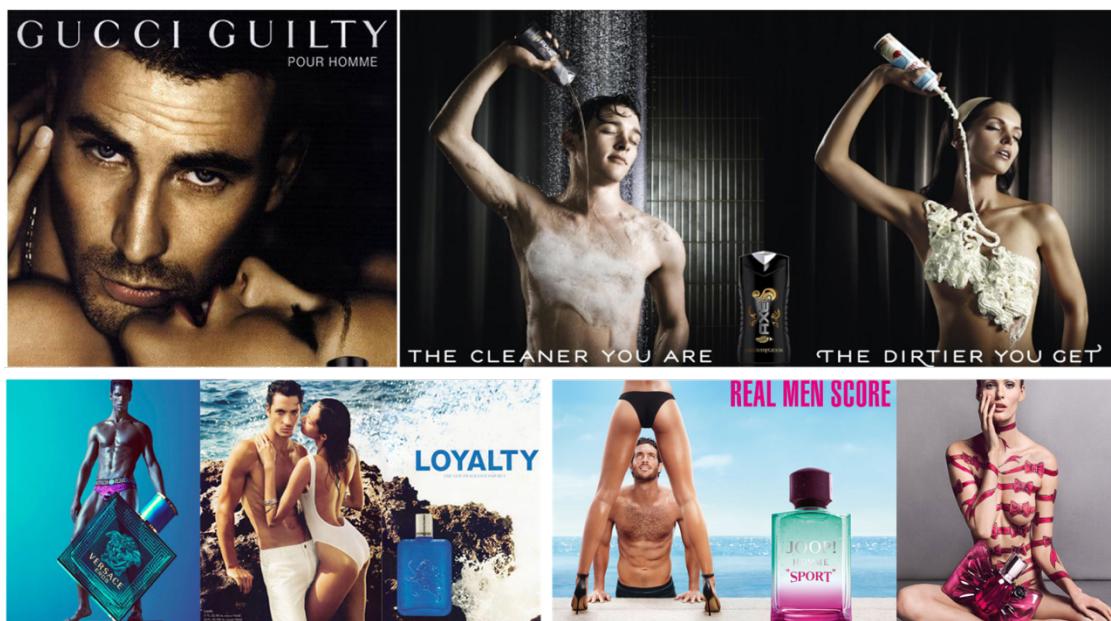


Figure 1. Overtly sexual modern perfume advertisements.
 Top: Gucci Guilty Pour Homme, 2011; Axe, 2012
 Bottom: Versace Eros, 2012; Express Loyalty, 2012; Joop Homme Sport, 2016; Viktor and Rolfe Bonbon, 2014

¹ Flavor perception is the combination of both olfactory and gustatory inputs.

I. Is the sense of smell functionally vestigial in humans?

Systems of internal chemical communication, such as cellular communication via neurotransmitters, differ little from external chemical communication between members of the same, or even different, species. Chemical communication is sometimes considered as old as life itself because intracellular chemical communication existed within prokaryotic cells before eukaryotic cells evolved (Stoddart, 1990). Today, chemical communication is considered ubiquitous among living organisms and many social behaviors are known to be influenced by olfactory information² (for reviews see, Albone, 1984; Brown & Macdonald, 1985; Brown, 1979; Doty, 1976, 1986; Graziadei, Muller-Schwarze, & Mozell, 1977; Halpin, 1986; Shorey, 1976; Vandenbergh, 1983). Yet a prevalent view in both scientific and popular thought is human behavior is not affected by smell. Instead, our sense of smell is thought to be diminished (McGann, 2017; Shepherd, 2004). Tellingly, many celebrated thinkers, such as Descartes, Kant, Schopenhauer, and Freud, described smell as uncivilized, vulgar, coarse and important only to less evolved animals (for review see, Le Guérer, 2002). A desire to differentiate humans from “inferior” animals may partially explain the persistence of the idea that humans possess a weakened olfactory system (Le Guérer, 1994), despite evidence that our olfactory repertoire has been greatly underestimated (Parma et al., 2017; Schaal & Porter, 1991; Shepherd, 2004).

During the 19th century, French neuroanatomist Paul Broca categorized species as either osmotic or non-osmotic based on the relative importance of olfaction to other

² This paper uses general terms, such as information, in lieu of cue or signal. Many researchers in the literature reviewed herein use signal and cue interchangeably, while others debate which term is appropriate. We will not enter into this debate but will define both because their distinction is important. A signal evolved for communication between a sender and a receiver, whereas a cue is any feature of the world that can be used to guide behavior (Smith, Harper, & Harper, 1995). For example, an organism releases CO₂, and CO₂ guides mosquitoes to the organism’s location. CO₂, in this case, is a cue because its release did not evolve to convey location to mosquitoes.

sensory inputs in driving their behaviors (Broca, 1879). Broca's categorizations were soon modified into a continuum ranging from anosmic (i.e., non-smeller; e.g., cetaceans) to macrosmatic (i.e., great sense of smell; e.g., rodents, carnivores, ungulates) (Turner, 1890). Humans were classified as microsmatic, meaning they exhibit a diminished sense of smell. Later researchers exaggerated this classification until smell was considered functionally vestigial with little ecological significance in humans (e.g., Herrick, 1924; Lassek, 1958; Negus & Straatsma, 1958). Interestingly, humans were initially categorized as microsmatic, in part, because of the socio-political climate of France. At the time, the Catholic Church was increasingly threatened by secularization. Clergy within the French senate denounced academic institutions and prominent researchers, such as Paul Broca (Schiller, 1979). Rather unsurprisingly then, Broca's scientific conclusions were sometimes colored by the religious politics of the time. For example, Broca proposed that the human olfactory bulb was sacrificed during evolution to make room for a larger frontal lobe that could house the soul's capacity for free will (Broca, 1879).

The categorization of humans as microsmatic persisted for years, despite the fact that the classification was not determined by any direct tests of olfactory acuity (e.g., Herrick, 1924; Turner, 1890). However, when olfactory acuity is measured, data suggests that humans are able to detect a large array of volatile chemical stimuli (Bushdid et al., 2014). Moreover, olfactory stimuli are demonstrated to influence mood, the endocrine system, and social behaviors (McGann, 2017; Schaal & Porter, 1991; Shepherd, 2004).

II. How does olfactory performance compare between humans and other mammals?

Many of the animals that were once considered microsmatic exhibit hegemony of another sensory system, such as vision in primates (for review see, Schaal & Porter, 1991). Historically, investigations of olfactory systems followed a repetitive and predictable sequence. First, anatomists compared olfactory structures across species and then, based on these findings, inferred a species' olfactory acuity. For example, olfaction was considered unimportant in most bird species following comparative anatomical studies (e.g., Cobb, 1968). However, later electrophysiological (Tucker, 1965; Wenzel & Sieck, 1972) and behavioral (e.g., L. Clark & Mason, 1987; K. M. Goldsmith & Goldsmith, 1982; Papi, 1986; Wallraff, 1986) studies proved this conclusion premature.

Similarly, primates were initially categorized as microsmatic because of neuroanatomical findings showing primates possess comparatively smaller nasal annexes, olfactory epithelium, and olfactory bulb volume relative to total brain volume (e.g., Bauchot, 1981; Broca, 1879; Stephan, 1970). However, the brain regions that process olfactory inputs and provide the basis for smell perception are the olfactory tubercle, entorhinal cortex, mediodorsal thalamus, medial and lateral orbitofrontal cortex, and parts of the amygdala, hypothalamus, and insula (e.g., Neville & Haberly, 2004). As tasks become more complex and involve memory (e.g., comparing different odors), the temporal and frontal lobes are also recruited (e.g., Dade et al., 2002). Thus, one could argue that the well-developed neocortex and sophisticated neural pathways of humans compared to rodents and other mammals offer humans the potential for greater olfactory perception (Keverne, 1983).

Early evolutionary models of primate olfaction inferred two reductions in olfactory acuity. First a reduction occurred in all primates, and a later reduction occurred in

haplorrhines (i.e., tarsiers and anthropoids) (for review see, Heritage, 2014). These reductions were hypothesized to reflect tradeoffs between smell and the elaboration (e.g., enhanced binocularity; Martin, 1991; trichromacy; Surridge et al., 2003) of the visual system (for review see, Smith et al., 2007). Recently, these models have been supported by genetic findings demonstrating a progressive reduction in the proportion of functional olfactory receptor genes from rodents through the primate order to humans (Gilad et al., 2004; Rouquier et al., 2000). However, an account of anthropoid evolution can also explain this decrease in functional olfactory receptor genes without necessitating a decrease in olfactory acuity. As the eyes migrated towards the center of the face for more effective stereoscopic vision, the snout of anthropoids became progressively smaller (Jones, 1992). Snouts filter inhaled air so that pathogens and toxic fumes do not reach an organism's nasal cavity, but this filtration also reduces the number of odor molecules reaching olfactory sensory receptors. Thus, mammals with large snouts may compensate for less odor molecules reaching their olfactory sensory receptors by expressing a greater network of olfactory receptor cells. If true, then a reduction in human olfactory receptor cells and functional olfactory receptor genes does not necessarily imply a weakening of the olfactory sense. By evolving a reduced air filtration system (i.e., snout), more odor molecules are able to reach olfactory sensory receptors and fewer olfactory receptor cells may be necessary for odor detection (Shepherd, 2004).

Tests of olfactory acuity also challenge the view that humans have an inferior sense of smell compared to other mammals (e.g., Laska, 2017; Laska et al., 2005; Laska & Teubner, 1998). Olfactory sensitivity is assessed by determining detection thresholds for given odorants. As of 2017, approximately 3,300 odorant thresholds had been investigated in humans and of those odorants, 138 had also been examined in

other mammals. When comparing olfactory detection thresholds for these odorants, humans were discovered to have lower thresholds (i.e., higher sensitivity) than most other species tested, including species purported to possess highly developed olfactory systems like mice, rats, hedgehogs, shrews, pigs, and rabbits (for review see, Laska, 2017). Although dogs are considered the super-nose of the animal kingdom, humans are more sensitive than dogs to 5 of the 15 odorants investigated in both species.

Interestingly, humans outperformed dogs with plant odorants³, whereas dogs outperformed humans with odorants emitted from their prey species (Laska, 2004; Laska & Seibt, 2002; for review see, Laska, 2017). In fact, the overall consensus of comparative research is that the most important predictor of olfactory performance is the species-specific behavioral relevance of the stimuli used during testing (Laska, 2017; Shepherd, 2004).

Lastly, qualitative comparisons of olfactory capabilities between species demonstrate that humans use smell to guide their decision-making in the same behavioral contexts where smell is known to play an important role for other animals. In most animals, the chemical senses are used to detect hazardous molecules in the environment, and detection often results in an adaptive behavioral response. Humans display several adaptive behaviors when exposed to toxic volatile chemicals such as head turning, eye closing, suspension of breath (i.e., apnea), sneezing, and coughing. Indeed, humans that lack a functional sense of smell are at greater risk of gas poisoning

³ For 99% of our evolutionary history, humans lived as hunter-gatherers. Plants were an essential part of this lifestyle. They were a primary food source, used to construct tools and shelters, and their chemicals were used in hunting, fishing, and medicine. Yet, plants can be dangerous because many contain a variety of chemical and mechanical defenses designed for protection. Thus, humans faced the adaptive problem of figuring out which plants were useful, and which could be fatal (for review see, Wertz, 2019).

(e.g., Cain et al., 1987; Chalke & Dewhurst, 1955; Miwa et al., 2001) and harm by fire (Santos et al., 2004).

Many animal species also use smell to find and select food. While most humans do not currently hunt and forage for foods, they are able to follow food scent trails when challenged (J. Porter et al., 2007). Moreover, humans that lack a functional sense of smell are at greater risk of suffering from food poisoning (Croy et al., 2012) and malnutrition (Aschenbrenner et al., 2008). Finally, animals often use olfactory cues to learn about their environment. Humans are no exception and tend to quickly form long-lasting associations between odors and positive or negative experiences with foods (Brunstrom, 2005) and visual stimuli (Gottfried et al., 2002). In fact, long-term memory for odors often outperforms long-term memory for information presented in other sensory modalities (Engen & Ross, 1973; Goldman & Seamon, 1992; Wilson & Stevenson, 2006). Taken together, comparative research suggests humans do not have a diminished sense of smell. Instead, humans seem to have a robust olfactory system that plays a role in many different behavioral and situational contexts.

III. How does olfactory performance compare between human populations?

The olfactory system develops via both biological and environmental (e.g., culture, atmosphere, ecology) inputs (Olofsson & Wilson, 2018). Yet, most research on human olfactory acuity has been conducted with individuals living in Western, urban environments (see Box 1), an environment that is markedly different than the environment that humans lived in for the majority of their evolution. For instance, events such as the industrial revolution, and changing hygiene and sanitation practices and ideologies have dramatically altered the olfactory landscape (Sorokowska et al., 2013). Consequently, this raises an important question. Is olfactory performance deemed healthy or normal specific to Westerners or is it invariant to ecology and culture?

Comparisons of olfactory performance between the Tsimane', foraging horticulturalists residing in the Bolivian rainforest, and participants living in an industrialized German city suggest that olfactory acuity may vary between people living in industrialized and non-industrialized societies. While air pollution has a significant and negative impact on olfactory acuity (Guarneros et al., 2009), pollution cannot fully explain the difference in olfactory performance reported between these populations because the Tsimane' engage in slash-and-burn agriculture and cook with burning foliage (Goldsmith, 1998). Both activities expose the Tsimane' to comparable levels of pollutants that irritate the respiratory tract and affect olfaction (Guarneros et al., 2009). Instead, greater training of the olfactory system in the Tsimane', due partly to foraging activities within a tropical rainforest ecological environment, may explain their superior olfactory performance. Other research evaluating the psycholinguistic codability of odors suggests that odors are more easily named and that there is greater naming agreement for odors in a foraging society occupying the Malay Peninsula compared to a genetically and linguistically similar horticulturalist population occupying the same environment (Majid & Kruspe, 2018). Sustenance strategy and presumably greater olfactory training are again suggested to account for these differences in olfactory language and, possibly, olfactory cognition between populations. However, the scarcity of data from non-Western and non-industrialized societies precludes definitive conclusions about how biology and environment interact to engender differences in olfactory acuity between human populations.

Box 1. How WEIRD is human olfaction?

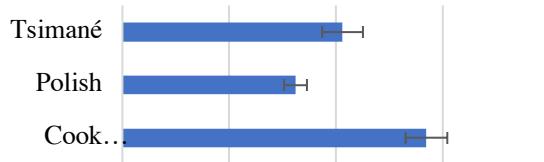
Research on human olfaction has typically been restricted to WEIRD (Western, Education, Industrialized, Rich) populations. Thus, the standard patterns and generalizations about how humans perceive, think about, and use odors may be limited or inaccurate (for review see, Roberts, Havlíček, & Schaal, 2020). In fact, recent cross-cultural investigations have uncovered differences in olfactory acuity between industrialized and non-industrialized societies (e.g., Sorokowska et al., 2013, 2015). Moreover, comparisons of odor lexicons also suggest marked differences in how odors are described among groups with different subsistence strategies (Burenhult & Majid, 2011; Majid & Burenhult, 2014; Majid & Kruspe, 2018). Three broad classes of explanation may account for population-level differences in human olfaction:

Ecology. Air pollution negatively affects odor detection, discrimination, identification, and perception (e.g., Hudson et al., 2006). Accordingly, populations living in less polluted environments have been found to perform better on measures of olfactory acuity (Sorokowska et al., 2013, 2015). For example, inhabitants of Cook Islands, one of the least polluted regions in the world, have lower thresholds of odor detection than European city dwellers (Sorokowska et al., 2015). In addition, temperature, humidity, barometric pressure, and air currents all affect the movement of odor molecules causing some environments to be more odorous (Goldsmith, 1998; Muller-Schwarze, 2006). Subsequently, people living in these environments will have more exposure to odors, which, in turn, also influences olfactory performance.

Experience. Sanitation, hygiene, and other modern innovations have contributed to the “deodorization” of Western societies. The deodorization hypothesis suggests that removal of odors from the environment has weakened olfactory abilities in people living in westernized and industrialized societies. That is, lack of experience with odors is thought to reduce sensitivity to odors (Jenner, 2011). This hypothesis is supported by evidence of a significantly enhanced odor-naming ability in a population of hunter-gatherers who use odors daily when foraging for foods and medicinal plants, compared to their horticulturalist neighbors, who share the same environment and a similar language (Majid & Kruspe, 2018). Moreover, laboratory experiments show that practice (i.e., experience) with odors leads to improved olfactory performance (e.g., Sorokowska et al., 2017). In fact, recently there has been renewed interest in olfactory training due to its efficacy in treating smell loss in COVID-19 patients (Whitcroft & Hummel, 2020).

Genetic Makeup. There is large interindividual variation within and between populations with regards to number and expression of olfactory receptor genes (for review see, Hoover, 2010). Moreover, studies have linked genotypic variants of odor receptors to the perception of specific odors. For example, variants of the OR7D4 receptor cause some people to perceive androstenone as “extremely unpleasant” or “sickening” and others to label it “vanilla” (Keller et al., 2007). Yet how population-level differences in olfactory receptor genes translate to olfactory acuity and perception, is unknown.

Comparison of odor detection thresholds (OT) between
3 ecologically distinct populations.



IV. How does human olfaction work?

In humans, air containing volatile chemical molecules (i.e., odorants) enters the nose and stimulates the cilia of olfactory receptor neurons located in the olfactory neuroepithelium lining the posterior nasal cavity (see Figure 2). Each olfactory receptor neuron only binds with a specific subset of chemical molecules and most of these ligands remain unknown. Neurons expressing the same type of olfactory receptor project axons to the same glomeruli, which are structures within the olfactory bulb containing axon terminals of olfactory sensory neurons and dendrites of mitral, periglomerular and tufted cells (for review see, Rawson & Yee, 2006). Odors usually contain mixtures of many different chemical molecules, which bind to different olfactory receptor neurons and create a pattern of activity in the glomeruli. Odor perception and discrimination is the result of down-stream brain areas decoding this ensemble activity pattern (for reviews see, Gottfried, 2006; D. E. Hornung, 2006). Therefore, animals with more neocortical support, and hence processing power (e.g., humans), are better equipped to recognize and decode odor information (Keverne, 1983). The axons of mitral and tufted cells coalesce and form the lateral olfactory tracts which project to several brain regions, including the amygdala, piriform cortex, and the entorhinal cortex. These brain regions then forward olfactory information to other areas; for example, the amygdala sends olfactory information to the hypothalamus. Thus, an elaborate network of neural connections supporting odor-guided behaviors exists in humans (for review see, Gottfried, 2006).

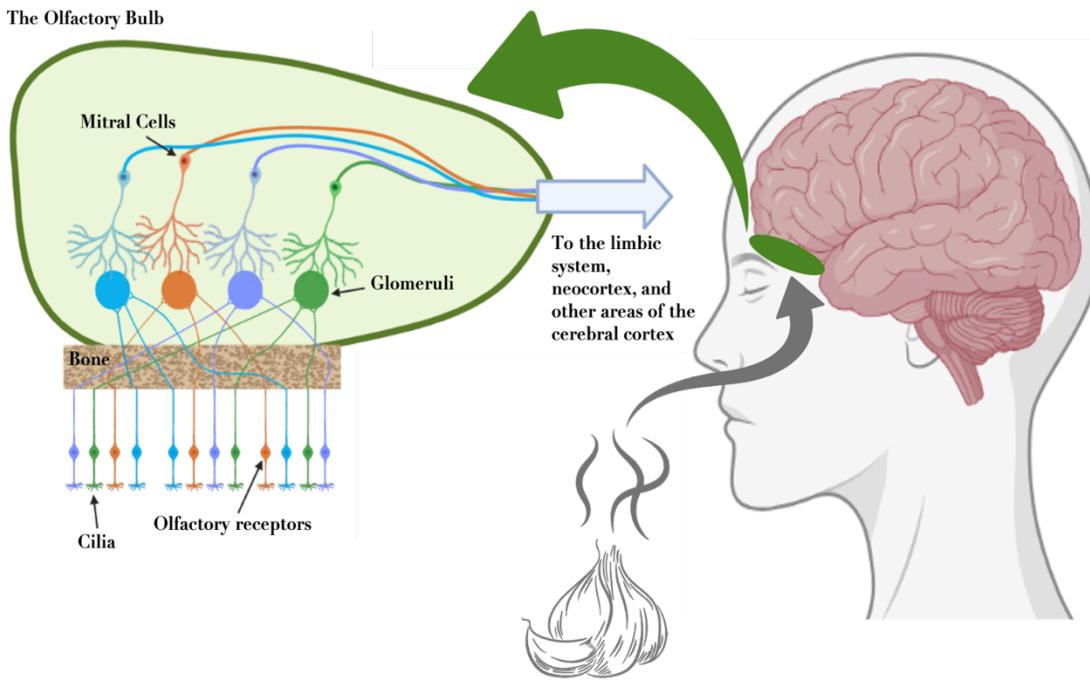


Figure 2. Basic anatomy of the human olfactory system.
Created with BioRender.com

Odor-Based Communication in Humans

The chemical senses are ancient and ubiquitous among living organisms, including bacteria. Unsurprisingly, the chemical exchange of information between organisms is the most prevalent mode of communication on our planet - every environmental niche on Earth is occupied by organisms communicating chemically (for review see, Wyatt, 2012).

When two animals encounter each other, a wealth of information, such as biological sex, sexual maturity, and health status, is transferred chemically. Animals produce hundreds of volatile chemical molecules, which are referred to collectively as their chemical profile. Chemical profiles vary highly between organisms. Chemicals that evolved as signals for communication between organisms of the same species (i.e., conspecifics) are known as pheromones. Other chemicals in an organism's chemical

profile, for example, odorous molecules caused by infections, are not pheromones but may be exploited as cues (Wyatt, 2009, 2010, 2012, 2017, 2020). Signature mixtures are subsets of molecules within an animal's chemical profile that are learned by others and allow for individual recognition. Moreover, signature mixtures can be used to identify group membership, reproductive status, emotional affectivity, and more. For example, family members likely share similar chemical profiles and others may learn a signature mixture specific to a family. Similarly, males may learn signature mixtures for when females are ovulating (for review see, Wyatt, 2010).

Evidence suggests that in mammalian chemical communication, most information is encoded by mixtures of chemicals that vary in combinations and proportions, and are learned by conspecifics (for reviews see, Apps, 2013; Burger, 2005). The manifold chemical mixtures represented in body odors likely convey diverse information about an organism, information that often informs mating behavior (for review see, Johnston, 1983). While research on human chemical communication has largely focused on olfaction and mating psychology, the answer to whether body odor and smell influence human mating remains inconclusive, partly due to methodologically flawed studies, failures to replicate (for review see, R.L. Doty, 2010), and persistent false beliefs about primate olfaction (for review see, McGann, 2017). Yet, the clear role of olfaction in the sexual behavior of other mammals, in particular non-human primates, suggests that odor likely influences human mating as well.

I. What evidence is there of chemical communication in non-human primates?

The prevalent view that primates rely little on olfaction in social interactions because of their poor sense of smell is changing in light of research demonstrating that several primate species exhibit high olfactory acuity, and body odors frequently influence primate social and sexual behaviors (for reviews see, Drea, 2015, 2020). For example,

studies reveal that various primate families (e.g., Lemuridae, Indridae, Callitrichidae, and Cebidae) use body odors for territorial marking, individual and kin recognition, and mate selection (for reviews see, Drea & Scordato, 2007; Epple, 1986, 1993; Kappeler, 1998). In fact, body odors from many primate species have been shown to convey information about the genetic and phenotypic quality of potential mates (Boulet et al., 2009; Charpentier et al., 2008, 2010; Setchell et al., 2011).

For example, in numerous primate species female body odor conveys information about reproductive status. Body odors (e.g., genital) from non-cycling females or females in non-fertile stages of their reproductive cycle smell differently than body odors from estrous or peri-ovulatory females. Exposure to odor from estrous and peri-ovulatory females increases male sexual attention, investigation (e.g., sniffing, licking, tongue flicking), and copulation attempts (*Macaca*: Cerda-Molina, Hernández-López, et al., 2006a; Cerda-Molina, Hernández-López, et al., 2006b; *Galago*: Clark, 1982; *Papio*: Clarke et al., 2009; Rigaill et al., 2013; *Cebuella*: Converse et al., 1995; *Catta*: Crawford et al., 2011; *Propithecus*: Mass et al., 2009; *Callithrix*: Smith & Abbott, 1998; *Saguinus*: Washabaugh & Snowdon, 1998; Ziegler et al., 1993). (*Catta*: Crawford et al., 2011) Moreover, exposure to odors from females near ovulation results in elevated and sustained testosterone concentrations (*Microcebus*: Perret, 1992; *Callithrix*: Ziegler et al., 2005), and activation of brain areas involved in male sexual arousal (*Callithrix*: Snowdon et al., 2006).

Other research indicates male primates communicate social status through scent. This research has predominately investigated scent marking in strepsirrhine primates; however, in most primate suborders social status is an important indicator of mate quality, particularly for males. Dominate males have greater resources (e.g., food, territory) and offer better protection for females and their offspring (for review see,

Zuckerman, 1932). In sifakas, male dominance rank is advertised both visually and olfactorily via chest staining caused by scent marking with the sternal glands. Higher ranked males scent mark more frequently than lesser ranked males, and thus have stained chests while subordinate males have clean chests (Lewis & Schaik, 2007). Additionally, chemical analyses indicate rank-related differences in sternal secretions. Dominant males express chemical compounds that are lacking in the chemical profiles of non-dominant males (Greene et al., 2011). Moreover, these visual and chemical indicators of social status change with fluctuations in rank (Lewis & Schaik, 2007). Similarly, the communication of social rank via smell is highly evident in ring-tailed lemurs. Males rub secretions from their glands into their tail fur creating an odor mixture that they waft at opponents or potential mates during “stink-fighting” (Evans & Goy, 1968; Jolly, 1966) or “stink-flirting”, (Walker-Bolton & Parga, 2017) respectively.

Finally, still more research reveals that primate body odors convey information about genetic diversity, immunity, kinship, health, and breeding history (for review see, Drea, 2020). So, while accounts of microsmia and sensory tradeoffs between vision and olfaction have contributed to the view that chemical communication is unimportant in primates, ample evidence exists of odor-reliant social communication. If historical classifications and commonly held beliefs about infra-human primate olfaction have diminished the significant role smell plays in their social and sexual interactions, then these views may also conceal the importance of chemical communication in the social and sexual lives of humans.

II. How is human body odor formed?

Odor constantly emanates from the human body via multiple sources, including the axillae, genitals, and breath. Body odor is largely produced by interactions between an individual’s microbiome and bodily exudates (for review see, James et al., 2013).

Skin is a large odor producing organ in humans because it contains numerous glands and is home to diverse microorganisms (for review see, Montagna, 1965). The high density of skin glands, particularly apocrine, in the axillae coupled with the conducive environment (e.g., occluded, moist, hairy) for microflora proliferation, has led many researchers to consider axillae specialized human scent organs (see Box 2) (for review see, Stoddart, 1990).

Axillary odor is produced when skin microorganisms, generally bacteria and yeast, metabolize precursor molecules secreted from apocrine, eccrine, apoecrine, and sebaceous glands (for review see, Natsch & Emter, 2020). The predominate odor-producing bacteria in the axillae are *Corynebacterium*, *Staphylococcus*, *Streptococcus*, *Micococcaceae*, and *b-Proteobacteria* (Grice & Segre, 2011; James et al., 2013; Leyden et al., 1981). Of all the glands present in the axillae, apocrine glands likely contribute the most to body odor and are often referred to as scent glands (Montagna, 1965). They are inactive prior to puberty, but hormonal changes cause activation and enlargement. After puberty, apocrine glands secrete approximately 1-10 microliters per gland each day in response to emotions (e.g., fear, anxiety), stress, and sexual arousal (for reviews see, Shelley & Hurley, 1953; Stoddart, 1990; Woppard, 1930). These secretions are milky and primarily consist of electrolytes, steroids, proteins, vitamins, and lipid compounds (Labows et al., 1979). Similarly, eccrine glands secrete in response to thermal stress and strong emotions (Wilke et al., 2007). Eccrine glands secrete up to 12 liters per day, dependent on environmental conditions (e.g., heat), of a thin solution that contains mostly water and electrolytes derived from blood plasma, as well as urea, lactate, free amino acids, proteins, albumin, globulins, prostaglandins, histamines, and esterases (Hurley, 2001; Sato, 1977). Apocrine glands are the most numerous comprising approximately 45% of all axillary glands. They secrete highly aqueous solutions, and in

greater quantities than both apocrine and eccrine glands (Sato et al., 1987). Sebaceous glands secrete a waxy substance called sebum. Sebum waterproofs and lubricates the skin, helping to create the axillae's ideal environment for microflora to flourish (Wheatley, 1986).

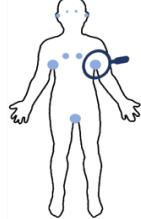
Human axillae are often considered analogous to scent glands found in other primates. Interactions between cutaneous microorganisms and axillary secretions produce over 200 volatile compounds, on average, per individual (Drea, 2015). Axillary sweat contains more volatiles and semi-volatiles than saliva or urine (Penn et al., 2007). Axillary odor is partially determined by the composition of cutaneous microflora (Leyden et al., 1981), which is idiosyncratic, but also varies systematically with age and sex (Marples, 1982; Somerville, 1969). For example, after the onset of puberty men have significantly more cutaneous microorganisms than women (Marples, 1982). Additionally, axillary odor is strongly influenced by genetic factors, such as an individual's endocrine system, immune system, and metabolic processes, as well as environmental factors, such as diet and climate. Thus, most studies of human body odor and social preferences, specifically mate choice, have used axillary body odor.

Box 2. Where does body odor come from?

1. APOCRINE GLANDS

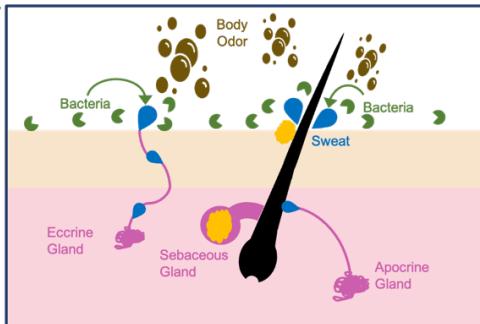
Several gland systems secrete molecules to the skin's surface, including apocrine, eccrine, apoeccrine, and sebaceous glands. However, the apocrine glands are the most important for body odor production and are distributed primarily around the areolae, axillae, genital and perineum regions, eyelids, and external ear canals.

Apocrine glands are so densely distributed within the axillae that they have been referred to as human's odor producing organ. They secrete over 200 odorless precursors, commonly including steroids, aldehydes, carboxylic acids, ketones, alcohols, hydrocarbons, and sulfur compounds.



2. CUTANEOUS MICROFLORA

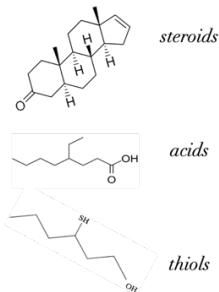
The skin's commensal microflora, predominantly bacteria and yeast, metabolize gland secretions. The most common axillary microbes include *Staphylococci* and *Corynebacteria*.



3. VOLATILE ORGANIC COMPOUNDS

Body odor is a unique chemical "fingerprint" that reflects complex interactions between our internal physiological and metabolic states, microbiome, and environment (e.g., diet and climate). Our bodies are shrouded in hundreds,

if not thousands, of different volatile compounds, however the characteristic armpit odor of 80% of the world's population is attributed mainly to steroids, such as androstenone and androstanol, carboxylic acids, particularly "goat-acid" or 4-ethyloctanoic acid, and thiol alcohols.



III. Do human pheromones exist?

Since the 1960s, researchers interested in human olfaction and its role in mating have focused principally on two broad questions: 1) do human pheromones exist (see Box 3), and 2) what information about an individual can be learned from their natural body odor? Yet, results from this literature are largely inconclusive and whether smell influences human social lives remains among the 125 most compelling multidisciplinary scientific challenges of this century (*Science*: Kennedy & Norman, 2005).

Box 3. The search for an elusive human pheromone

What are pheromones?

No standard definition of ‘pheromone’ exists. However, the earliest definition, which is based on insect research, states that a pheromone is a molecule(s) that evolved as a signal between members of the same species that elicits a species-specific reaction (Karlson et al., 1959; Karlson & Lüscher, 1959). For example, the first identified pheromone, bombykol, released by the female silk moth (*Bombyx mori*) initiates full mating behavior in male moths.

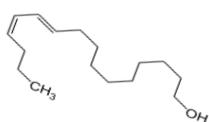
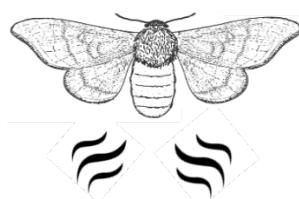
Do human pheromones exist?

Isolating bombykol as the female silk moth’s sex attractant pheromone took twenty years (Butenandt et al., 1959). While this initial discovery sparked a deep interest among researchers in identifying human pheromones, to date, there are no known human pheromones. Unlike insects, humans, and mammals in general, secrete and excrete hundreds of volatile and non-volatile molecules, making the isolation of a single pheromone a herculean feat. Moreover, human behavior is complex and rarely invariant. Instead, it involves a dynamic interplay between multiple molecular processes and the environment. Thus, the original concept of pheromone based on insect communication, is unlikely to exist in humans.

What now?

Starting in the late 1960s, a plethora of researchers began claiming to have identified human pheromones or demonstrated their effects, however most of this research is suspected of reporting false positives, partly stemming from small sample sizes and overestimated effect sizes (for reviews see, Doty, 2010, 2014; Wyatt, 2015, 2020). To identify human pheromones, researchers must employ more rigorous techniques that have been effective with other organisms, such as bioassays. Bioassays are repeatable experiments that allow for tracking activity while samples are collected and analyzed. Once a candidate molecule(s) is identified and synthesized, researchers then confirm that the molecule(s) at natural concentrations are both necessary and sufficient to produce the response recorded in initial bioassays (Wyatt, 2014). However, instead of searching for an elusive human pheromone, our time and resources may be better spent *first* meticulously investigating to what extent smell, including overall body odor, influences human social behavior and decision making, more generally.

Bombyx mori



Bombykol is released by females and the scent travels through the air as they flutter their wings. Males detect the scent from great distances of up to several miles and use it to locate females.

Are androstenone, androstenol, and androstadienone human sex pheromones?

The search for human male sex pheromones has primarily focused on testosterone derivatives (i.e., androstenone, androstenol, and androstadienone) because of their association with reproductive behaviors in other mammals, specifically pigs (e.g., Prelog & Ruzicka, 1944; Reed et al., 1974). Testosterone derivatives were first identified as sex pheromones in boars. They are synthesized in boar testes and conveyed to conspecifics through saliva. Exposure to boar pheromones elicits a stereotyped mating posture (i.e., lordosis) in sows (Claus et al., 1971; Prelog & Ruzicka, 1944). Testosterone derivatives are present in sexually dimorphic quantities (i.e., greater concentrations in men) in human urine (Brooksbank et al., 1972; Brooksbank & Haslewood, 1961) and axillary sweat (Bird & Gower, 1981; Brooksbank et al., 1974; Claus & Alsing, 1976; Gower et al., 1985), leading investigators to believe that these steroids could also be sex pheromones in humans.

Starting in the late 1970s, researchers began investigating experimentally whether androgen steroids present in axillary sweat functioned as pheromones in humans. Androstenone, androstenol, and later androstadienone were extensively studied in regard to whether olfactory exposure affects others' hormone levels (Cutler et al., 1986; Grammer, 1993; Lübke & Pause, 2014; Shinohara et al., 2000; Wyart et al., 2007), mood (Bensafi et al., 2003; Bensafi, Brown, et al., 2004; Bensafi, Tsutsui, et al., 2004; Benton, 1982; Cowley et al., 1980; Filsinger et al., 1984; Grosser et al., 2000; J. Hornung et al., 2018; Jacob et al., 2002; Jacob & McClintock, 2000; Kirk-Smith et al., 1978; Lundström & Olsson, 2005; Preti et al., 2003), social judgments (e.g., Banner et al., 2018; Banner & Shamay-Tsoory, 2018; Cowley et al., 1977; Frey et al., 2012; J. Hornung et al., 2017; Hummer & McClintock, 2009; Huoviala & Rantala, 2013; Kovács et

al., 2004; Parma et al., 2012), attractiveness preferences (e.g., Black & Biron, 1982; Cornwell et al., 2004; Cowley & Brooksbank, 1991; Ferenzi et al., 2016; Filsinger et al., 1985; Hare et al., 2017; Jacob et al., 2002; Kirk-Smith et al., 1978; Lundström & Olsson, 2005; Saxton et al., 2008; Thorne et al., 2002), and brain activity (e.g., Berglund et al., 2006; Burke et al., 2012; Chung et al., 2016; Gulyás et al., 2004; Hummer et al., 2017; Jacob et al., 2001; Savic et al., 2001, 2005). The vast majority of these studies reported positive results leading researchers to conclude that some testosterone derivatives are pheromones in humans. For example, studies find that near ovulation, women like the odor of testosterone derivatives more (Grammer, 1993; Hummel et al., 1991; Thornhill et al., 2013), and rate men more attractively while exposed (e.g., Ferenzi et al., 2016; Saxton et al., 2008; Thorne et al., 2002). One study used a speed dating paradigm and revealed men were rated significantly more attractive by women exposed to androstadienone masked by clove oil, than by women exposed to only clove oil or water (Saxton et al., 2008). However, other frequently overlooked studies dispute these findings (e.g. Black & Biron, 1982; Hare et al., 2017). For instance, a recent study found exposure to androstadienone had no effect on attractiveness ratings (Hare et al., 2017).

In recent decades, this literature on androstenone, androstenol, and androstadienone has met with criticism. First, while androgen steroids have been found to exert psychological and behavioral effects, these occur in both men and women (Ferenzi et al., 2016; Filsinger et al., 1985). Yet, sex pheromones are expected to exhibit sex-specific effects. Second, many studies have used questionable methodologies (for review see, R.L. Doty, 2010; Wyatt, 2015). For example, experiments frequently expose participants to concentrations of androgen steroids 1,000X above endogenous levels (e.g., Jacob & McClintock, 2000; Savic et al., 2005; Shinohara et al., 2000). Likewise, experiments rarely test with comparison odors. Although testosterone

derivatives have been found to alter mood, so too have many other odors. Lemon essential oil, for instance, reliably boosts positive moods and alertness (e.g., Kiecolt-Glaser et al., 2008; Lehrner et al., 2000; for review see, Herz, 2009). If putative pheromone studies do not use control or comparison odors, how can we be sure that any demonstrated effects are pheromonal rather than caused by, say, odor valence? In addition, another common problem includes underpowered experiments stemming from small sample sizes and overestimated effect sizes. Moreover, full replication studies are rare (for review see, Wyatt, 2020). Finally, the reasoning for which androgen steroids are expected to be human pheromones is flawed. There is no peer-reviewed, bioassay evidence that androstenone, androstenol, or androstadienone are human pheromones (for review see, Wyatt, 2015). While these molecules are pheromones in pigs, there is no reason to expect that, rather than the hundreds of other molecules secreted in the axillae, they specifically would be pheromones in humans especially since a large percentage of the human population expresses anosmia to these odorant molecules or find them ‘repellant’ (e.g., Androstenol: 90% anosmia in women, 45% anosmia in men; Androstenone: 9-20% anosmia in both men and women, of those that could smell, 70% women find odor ‘repellant’) (Gower et al., 1985). Taken together, there seems to be little to no basis for concluding that androstenone, androstenol, or androstadienone are human pheromones.

Is estratetraenol a human sex pheromone?

There have been two widely researched putative female pheromones. One is estratetraenol (EST), an endogenous steroid related to estrogen sex hormones. EST is found in women’s late-pregnancy urine (Breuer & Pangels, 1959; Thysen et al., 1968), but not on the skin or in axillary sweat (R.L. Doty, 2010). Monti-Bloch & Grosser (1991) were the first to identify EST as a putative pheromone, but their methodology was

obscure and their research was supported by EROX Corporation, which had a commercial interest in pheromones. In their paper, Monti-Bloch & Grosser (1991) demonstrated that EST affects the electrical potential of vomeronasal cells in men, but not women. However, subsequent research has shown humans and other great apes do not possess a functioning vomeronasal organ (Smith et al., 2014).

Ignoring dubious origins, countless experimental studies of EST have been conducted in the last 30 years (for review see, Wyatt, 2020). For example, exposure to EST has been reported to increase men's positive moods (Olsson et al., 2006), sexual arousal within a sexually arousing context (Bensafi, Brown, et al., 2004), and cooperation (Oren & Shamay-Tsoory, 2019). In addition, imagining studies have reported differential effects of exposure to EST between heterosexual men and women (Savic et al., 2001). Interestingly, homosexual women exhibit brain activation patterns in response to EST similar to that of heterosexual men (Berglund et al., 2006). Moreover, EST has been found to bias men towards perceiving walking light point displays as more feminine (Zhou et al., 2014), happy, and relaxed (Ye et al., 2019). Yet, there are reasons to doubt many of these findings. Again, problems include small sample sizes, overestimated effect sizes, and a lack of bioassay evidence (for reviews see, R.L. Doty, 2010; Wyatt, 2015). Moreover, many findings are not sex-specific (Bensafi, Brown, et al., 2004; Hare et al., 2017), nor are they specific to EST. For instance, the percentage of male participants that exhibit brain activation in areas of sexual arousal following exposure to EST (Sobel et al., 1999) is similar to percentages found with other odorants, including Chanel No. 5 perfume (Huh et al., 2008). As with androstenone, androstenol, and androstadienone, there is little convincing evidence that estratetraenol is a human sex pheromone.

Is copulin a human sex pheromone?

The other commonly cited female pheromone is copulin, a mixture of short-chain aliphatic acids (i.e., acetic, propionic, isobutyric, butyric, isovaleric, and isocaproic) produced by fermentation of vaginal flora (Bonsall & Michael, 1971). Copulin was first identified in the rhesus monkey (*Macaca mulatta*) and suggested to be a pheromone because exposure to natural and synthetic copulin increased frequency of ejaculation and mounting behavior in males (Curtis et al., 1971; Michael et al., 1971; Michael & Keverne, 1970). This discovery prompted investigations of vaginal secretions in other primate species, and copulin was found in several (Michael et al., 1972, 1975), including chimpanzees (Fox, 1982; Matsumoto-Oda, 2002) and humans (Michael et al., 1975; Preti & Huggins, 1975).

Michael and colleagues (1975) revealed the presence of copulin in humans using gas chromatography in a sample of $n = 50$ young women. The amount of copulin in their vaginal secretions fluctuated cyclically, increasing during the follicular phase of the menstrual cycle when likelihood of conception is highest. Additionally, the overall amount of copulin in women using hormonal contraception was significantly lower than naturally cycling women, and exhibited no fluctuations associated with the menstrual cycle.

Another lab likewise found that women produced copulin, noting only 30% of naturally cycling women (i.e., 3 out of the 9 women examined) consistently produced all aliphatic acids in the copulin mixture (Preti & Huggins, 1975). Based on these findings and behavioral findings with infra-human primates, researchers hypothesized that copulin communicated reproductive status in women, and thus men exposed to copulin would find women more attractive. Testing this hypothesis, Grammer and Jütte (1997) exposed men to copulin and found copulin increased testosterone levels and inhibited men's ability to discriminate women's attractiveness, meaning men's attractiveness ratings of

women's faces were high and showed little variation. A follow-up study failed to replicate these findings, but reported men's self-rated sexual desirability increased while exposed to copulin (Williams & Jacobson, 2016). In addition, another study employing a placebo-controlled, odor-masking design with a large sample of men ($n = 243$) to empirically test whether copulin affects men's sexual behavior and whether sexual experience mediated responses to copulin (Williams & Apicella, 2018; see Chapter 2). This study found no evidence that copulin affects men's perceptions of female attractiveness or their sexual motivation and decision making. Moreover, no mediation effects of prior sexual experience were found. Thus, copulin is also unlikely to be a human pheromone.

To date, no human pheromones have been confirmed. Proposed human pheromones lack systematic bioassay evidence, which is typically the first step in identifying a molecule(s) as a pheromone in other animals. Researchers start by demonstrating quantifiable behavioral and/or psychological responses to a synthesized version of the proposed pheromone in a repeatable experiment (i.e., bioassay). Then researchers confirm that natural concentrations of the proposed pheromone are necessary and sufficient to elicit the same responses recorded in the original bioassay (Wyatt, 2014, 2015). In future searches for human pheromones, researchers should investigate other molecules common to most human chemical profiles and examine candidate molecules with the same rigorous techniques used with other species.

IV. What information is conveyed through body odor that may influence mate choice?

Humans secrete hundreds of volatile chemical molecules that vary highly between individuals based on genetic makeup and environmental factors, including diet (for review see, Havlíček et al., 2017). Isolating a specific molecule(s) as a pheromone among the hundreds of molecules in an individual's chemical profile is difficult and,

instead, many researchers investigate natural body odor secretions as a whole. Although studies of body odor cannot identify specific molecules that cause observed effects, they can reveal whether smell is used in social communication and what information is communicated. Indeed, a growing literature suggests body odor conveys social information to others about both immutable characteristics (e.g., biological sex, age, kinship, and immunity) and transient characteristics (e.g., social status, reproductive status, health status, diet, and hygiene), all of which may influence mate choice (for review see, Havlíček et al., 2017).

Immutable characteristics

1. Sex and Age

Early studies investigating odor-based communication in humans demonstrated biological sex is discriminable via body odor (Russell, 1976; Schleidt & Hold, 1982). In a pioneering study, Russell (1976) showed that 9 of 13 women, and 13 of 16 men, could accurately determine which t-shirts were worn by men versus women by smelling the axillary region of the shirts. A later study employing a similarly small sample size revealed that while sex was largely discriminable through smell, the underlying mechanism influencing participant choices was intensity-matching. More intense body odors were likely to be accurately attributed to males, however the most intense female samples were also frequently inaccurately labeled male (e.g., Doty, Orndorff, Leyden, & Kligman, 1978). Male body odors may be more intense because the concentration of androgen steroids in their excretions are up to twenty times higher than concentrations found in women (Trotier, 2011), and the predominate microflora differs between the sexes (Jackman & Noble, 1983).

Similarly, body odor changes throughout the life span because of age-dependent differences in secretions and microflora. The sebaceous and apocrine glands become

active during puberty, and then activity sharply declines during the seventh decade (Gower & Ruparelia, 1993; Pochi et al., 1979). As a result of glandular changes, the fatty acid compositions of prepubertal children and elderly individuals are similar (Nazzaro-Porro et al., 1979). Moreover, prepubertal children (Cleveland & Savard, 1964), elderly men, and post-menopausal women (Brooksbank & Haslewood, 1961) excrete considerably less odorous precursor testosterone metabolites than adults of reproductive years (Brooksbank, 1962). Thus, age may smell the most distinct during reproductive years. In fact, Mitro (2012) revealed odors from different age categories are distinguishable, but only those odors originating from old-age donors (i.e., 75-95 years) could be correctly labeled. Yet, the other age groups tested (i.e., 20-30 years, and 45-55 years) were not distinct enough to mirror the age-dependent differences in glandular activity. We are unaware of other studies assessing the ability to determine age from body odor in humans; thus, more research should be conducted before conclusions can be made about whether age, as an indicator of reproductive potential, is detectable solely via body odor.

2. Kinship and Immunocompatibility

Other work suggests body odor communicates information about the Human Leukocyte Antigen (HLA) system that is believed to mediate kin detection and mate choice (for review see, Penn & Potts, 1999). HLA genes encode proteins that regulate the immune system. They are highly polymorphic and both alleles at a locus are expressed (Hedrick, 1994; Janeway, 1993; Klein, 1986; for review see, Knapp, 2005). Great inter-individual variation exists in HLA systems, but close genetic relatives are more likely to share similar compositions. Consequently, genetic relatedness is presumed detectable through body odor, in part, because of HLA similarity (Porter & Moore, 1981). In fact, strangers accurately pair t-shirts worn by mothers and their

children, but not t-shirts worn by spouses. This finding suggests shared environment, in the absence of overlapping genotypes, is not sufficient to produce detectable odor resemblance (Porter et al., 1985). Furthermore, Porter et al. (1986) demonstrated that siblings reliably discriminate each other's body odor from strangers, even when separated for 30 months, highlighting the possibility of odor-mediated incest avoidance.

In addition, odor resemblance derived from HLA similarity may influence mate choice because HLA heterozygosity (i.e., diversity) enhances resistance to a broader range of pathogens (for reviews see, Milinski, 2006; Penn et al., 2002; Potts & Wakeland, 1993). Pathogens have exerted strong selection pressure throughout evolution (Fumagalli et al., 2011), and researchers hypothesize new combinations of HLA genes must be adopted each generation to combat prevailing diseases (Van & Valen, 1973). HLA genes are expressed co-dominantly, therefore, to maximize offspring heterozygosity, individuals may prefer mates with the most dissimilar HLA genes to themselves (i.e., HLA-disassortative mating) (Wedekind et al., 1995). Alternatively, mates that are HLA-heterozygous may be more desirable. While mating with someone that is HLA-heterozygous will not ensure maximally heterozygous offspring, offspring will be more heterozygous on average, and this strategy is less complex than determining the mate with the most complementary HLA genes to oneself (Allendorf, 1986).

Early studies found women rated body odors from HLA-dissimilar men more pleasant and sexier than those from HLA-similar men (Wedekind et al., 1995; Wedekind & Furi, 1997). Yet, recent meta-analyses reveal that evidence for HLA-disassortative mating is non-significant (Havlíček et al., 2020; Winternitz et al., 2017). Instead, results indicate HLA-heterozygous individuals are preferred as mates (Winternitz et al., 2017). Moreover, studies frequently find that men's ratings of women's body odors are not influenced by HLA (Lobmaier, Fischbacher, Probst, et al., 2018; Lobmaier, Fischbacher,

Wirthmüller, et al., 2018; Santos et al., 2005; but see, Kromer et al., 2016; Wedekind & Furi, 1997). Researchers speculate that women might be more sensitive than men to information about genetic relatedness and immunocompatibility because women invest more heavily in each offspring and, compared to men, their lifetime reproductive potential is lower (Trivers, 1972).

In general, the literature on HLA and mate choice is filled with findings that often fail to replicate consistently, likely due in part to low power, which ranges from 24% to 57% in most studies (Winternitz et al., 2017). A recent genome-wide study that used a large sample, including data from 833 couples throughout Europe and the Middle East, found evidence of HLA-disassortative mating in several, but not all, populations (Dandine-Roulland et al., 2019). However, diverse cultural factors including socioeconomic status, family arrangements, and religion, greatly influence partner choice; thus, studies investigating actual couples may be less informative than those allowing subjects to choose the odor samples they find most attractive. Therefore, future work should employ similarly large and diverse samples, but investigate relationships between odor preferences and HLA instead.

Transient characteristics

1. Dominance and Social Status

Testosterone levels have frequently been associated with male dominance and women's mate preferences (for review see, Gangestad & Scheyd, 2005). Some researchers posit that dominance-associated traits (e.g., masculine facial features) are correlated with testosterone levels and therefore honest indicators of male genetic quality (e.g., Muller & Mazur, 1997). The immunocompetence handicap hypothesis (ICHH) predicts that men's attractiveness positively correlates with testosterone production because only men with high immunocompetence can tolerate the costs

associated with greater concentrations of immunosuppressive testosterone (Folstad & Karter, 1992). While this relationship is tenuous in humans (e.g., Nowak et al., 2018), testosterone has been found to suppress immune function in other mammals (for review, Grossman, 1985; Miller & Hunt, 1996; Muehlenbein & Bribiescas, 2005; Roberts, Buchanan, & Evans, 2004).

Other researchers suggest dominant men are judged to be attractive because they tend to achieve high socioeconomic status and can invest more resources in their mate and offspring (e.g., Buss, 1998). According to The Challenge Hypothesis, men with higher testosterone levels display more dominance behaviors, including aggression and status seeking (Archer, 2006; Wingfield et al., 2015). In fact, measurements of endogenous testosterone at a single-time point have been positively correlated with dominance (Carré et al., 2009; Grant & France, 2001), leading some researchers to infer that baseline testosterone levels reflect a dominance personality trait (Mehrabian, 1996; Sellers et al., 2007). Another prediction of The Challenge Hypothesis is that testosterone increases and encourages dominance behaviors in context where there is competition for resources and mating opportunities (Archer, 2006; Wingfield et al., 2015). Similarly, the Biosocial Model of Status suggests testosterone increases status seeking and competitive behaviors, and changes in status alter testosterone levels in such a way that winners of competitions exhibit a relative increase in testosterone compared to losers. This elevation in testosterone may reinforce successful status seeking and competitive behaviors in winners, whereas declining testosterone levels in competition losers may promote withdrawal from similar competitions in the future (Mazur & Booth, 1997). Indeed, empirical findings demonstrate that testosterone levels rise in anticipation of competitive events (for review see, Salvador, 2005), and react to competitive outcomes (e.g., Mehta & Josephs, 2006; Oliveira et al., 2009).

Little work has explored the relationships between testosterone, dominance and body odor attractiveness, however available evidence demonstrates that near ovulation, women judge the odor of testosterone (Thornhill et al., 2013; but see, Rantala et al., 2006) as well as a testosterone precursor, androstenone, more favorably (Grammer, 1993; Hummel et al., 1991). In addition, Havlíček et al. (2005) found that non-single women in the follicular phase of their menstrual cycle prefer body odor from men that score highly on psychological dominance, but not single women or women in other phases of their menstrual cycle. The authors suggest their findings are in accordance with the theory of mixed mating strategies because women's preferences for body odors of dominant men vary with women's relationship status and reproductive status. According to this theory, women prefer men of high genotypic quality as short-term or extra-pair copulation partners, but high parentally investing men as long-term partners (for review see, Gangestad & Simpson, 2000). Although a mixed mating strategy could explain why partnered women's body odor preferences vary across the menstrual cycle, why single women in the follicular phase did not show the same preference for dominant male body odors is unclear. Moreover, menstrual cycle effects are heavily debated with common criticisms including, unspecific measures of relationship status (e.g., relationship length and relationship type), lack of precise hormonal measurements of ovulation and cycle phase, and publication bias (Gildersleeve et al., 2014; Harris, 2011, 2013; Harris et al., 2013, 2014; Wood et al., 2014; Wood & Carden, 2014). In Havlíček et al. (2005), the method for measuring cycle phase was not reported, and relationship status was not defined in regard to length of relationship or type of relationship. In addition, the sample sizes for women in the follicular phase ($n = 30$) and other cycle phases ($n = 35$) were not reported disaggregated by relationship status, though clearly, they were small. Thus, because of the lack of studies and limitations within the existing

study, whether dominance, conveyed via body odor, influences women's mate preferences remains uncertain.

Finally, another study investigated whether personality traits were detectable through smell and discovered individuals could predict other's self-rated dominance solely through body odor assessments. Moreover, self-other agreement in odor-based dominance assessments were particularly accurate for assessments of the opposite sex, which may indicate odor-based assessments of dominance influence mate choice (Sorokowska et al., 2012). Although an intriguing finding, to our knowledge there have not been follow-up or replication studies. Future research should consider evaluating body odor attractiveness ratings as well as the accuracy of odor-based dominance judgments to better elucidate the role of body odor and dominance in mate choice.

Odor-based communication of dominance, or social status, seems probable because dominance behaviors and status seeking have been correlated with an individual's hormonal profile. Moreover, testosterone affects the functioning of apocrine sweat glands and testosterone metabolites are present as odorous precursors in axillary sweat. However, only two studies (i.e., Havliček et al., 2005; Sorokowska et al., 2012) have investigated the relationship between dominance and body odor, so more empirical research is required before we can determine whether dominance and social status conveyed via body odor influence mate choice.

2. Reproductive Status

Female sex hormones fluctuate with reproductive status and fecundity. Oestradiol levels are high and progesterone levels are low near ovulation, but this pattern reverses as the likelihood of conception decreases (Lipson & Ellison, 1996). Research reveals men can discriminate between women's body odor based on reproductive status, and prefer the body odor of women in the follicular phase of their

menstrual cycle (Cerda-Molina et al., 2013; Gildersleeve et al., 2012; Havliček et al., 2006; Kuukasjarvi et al., 2004; Singh & Bronstad, 2001). In fact, men's odor preferences are positively correlated with women's oestradiol levels and negatively correlated with progesterone levels (Lobmaier, Fischbacher, Wirthmüller, et al., 2018). However, several studies on men's odor preferences and women's reproductive status are limited by small sample sizes (e.g., $n = 4$, Doty et al., 1975; $n = 12$, Havliček et al., 2006; $n = 17$ in Study 1 and $n = 4$ in Study 2, Singh & Bronstad, 2001), and the method of retrospectively recalled day of last menstruation for estimation of cycle phase. Yet, Gildersleeve et al. (2012) employed a relatively large sample size ($n = 41$) and hormonally verified women's menstrual cycle phase, and nevertheless found men exhibited greater attraction to body odors collected from women near ovulation. In addition, other research shows men exposed to body odor from women in the follicular phase exhibit increased testosterone and sexual arousal. They also perceive greater sexual interest by women, and make riskier decisions (Miller & Maner, 2010; Miller & Maner, 2011). Thus, there is significant evidence to suggest men respond behaviorally and physiologically to shifts in women's body odor near ovulation, but replication studies using even larger samples of female donors are still needed.

3. Health Status

Many of the volatile chemical molecules emitted from the body reflect metabolic processes (for review see, Shirasu & Touhara, 2011). Consequently, possessing an infectious or metabolic disease (e.g., pneumonia or diabetes, respectively) commonly alters body odor. Historically, body odor was used for medical diagnoses because many diseases produce characteristic odors. For example, typhoid fever causes body odor that smells similar to musty or baked bread, whereas tuberculosis results in a stale-beer smell (for review see, Shirasu & Touhara, 2011). In humans, most research on the

detection of sickness through odor is anecdotal, however animal studies reveal sick odors initiate an avoidance response in conspecifics (e.g., Arakawa et al., 2011; Ehman & Scott, 2001).

One study with humans found exposure to body odor that is associated with a pathogenic threat (i.e., feces) increased intentions to use condoms, indicating humans also use odor as a pathogen-avoidance mechanism (Tybur et al., 2011). Although few studies have experimentally investigated the effects of disease on body odor preferences, evidence indicates that body odor collected from donors undergoing an acute immune response is judged to be more aversive and less attractive (Olsson et al., 2014; Sarolidou et al., 2020; but see, Schwambergová et al., 2021). Moreover, the body odor of patients with gonorrhea is rated less pleasant than body odor from patients that have recently recovered from gonorrhea and healthy controls. In fact, women considered axillary odors from men infected with gonorrhea ‘putrid’ (Moshkin et al., 2012), highlighting the link between olfaction, disgust, and mate selection. Disgust is an emotion that evolved for harm avoidance. Humans feel disgust when in contact with disease causing agents, such as spoiled food, dead organisms, feces, sweat, and sexual fluids. Thus, some researchers suggest pathogen disgust was co-opted by the sexual motivation system to decrease the likelihood of sexual relationships with mates that could harm an individual’s reproductive success (e.g., some sexually transmitted infections cause infertility) (Tybur et al., 2013). Although an intriguing hypothesis, more work investigating the relationships between disgust, sexual motivation, and body odors is required. Future research should investigate how sexually preferred and non-preferred body odors mediate the motivational systems, sexual disgust and sexual arousal.

4. Diet

Humans eat many aromatic foods, including meat and spices, that qualitatively change body odor because dietary chemical components or their metabolites are excreted in urine, feces, and from skin glands (for review see, Havlíček et al., 2019). Diet is widely considered the most impactful environmental influence on body odor. Indeed, women and trained tracking dogs cannot discriminate between the body odors of monozygotic twins with the same diets, but can when their diets vary (Hepper, 1988; Kalmus, 1955; Wallace, 1977). For example, Wallace (1977) demonstrated that ten female raters could discriminate between one set of twins that consumed different diets (bland versus spicy) for three days, but not a set of twins that ate the same meals for three days. However, the small sample size used ($n = 2$ twin pairs, $n = 10$ female raters) limits the strength of these findings, and we are unaware of replication studies or other studies investigating a similar question in humans using a large sample.

Limited evidence also indicates body odor communicates information about diet quality that affects mating preferences. For instance, consuming garlic, a bulbous flowering plant known to be good for health because of high antioxidant quantities, increases pleasantness ratings of axillary body odors (Fialová et al., 2016). Some researchers hypothesize the body odor of individuals that consume difficult to obtain foods may be preferred because consumption of these foods indicates the condition of a potential mate and/or their territory (for review see, Fialová et al., 2013). For instance, meat has not been readily available to humans for the majority of evolutionary history. Therefore, meat consumption may suggest high mate quality and food availability. Accordingly, Zuniga (2017) found meat consumption correlated positively with body odor attractiveness. However, Havlicek and Lenochova (2006) reported that when individuals were fed a diet rich in red meat, their body odor was rated less attractive than when they

refrained from eating meat. One possible explanation for these conflicting findings is that meat consumption has a curvilinear effect on body odor preferences. Meat consumption in Havliček and Lenochova (2006) was comparatively higher, which may have resulted in adverse effects on body odor (Havlíček et al., 2019). In fact, consuming too much meat affects body odor similarly to metabolic disorders, implying high meat consumption could cause an individual to smell sickly (Havlíček & Lenochova, 2006).

There are few studies of odor-based mate preferences and diet in humans. Although some dietary components have been investigated, only one or two studies have investigated the same components causing the research area to be fragmental. Thus, more empirical work is necessary before we can conclude that diet alters odor-based mate preferences in humans. Future research should also explore general nutritional status, which has been shown to olfactorily affect perceptions of mates in other animals (see, Fialová et al., 2019).

5. Hygiene and Artificial Fragrances

Modern hygiene practices (e.g., showering, axillae shaving, and deodorant) have transient effects on body odor because they reduce odor-producing microflora and suppress the secretion of odorous precursor compounds (Selwyn, 1982). However, exudates and microflora are often quickly restored (Shelley et al., 1953). For example, after cleansing, unshaved axillae take 6 hours to emit odor, but axillae shaving increases that length of time to between 24-48 hours (Kohoutová et al., 2011; Shelley et al., 1953). Moreover, some odor-suppressive activities, including washing, actually increase the rate of bacterial multiplication on the skin causing the elimination of odor to be short-lived (Selwyn, 1982).

Yet, more curious than the desire to reduce natural body odor, is the act of replacing natural body odor with different smells, often artificial fragrances containing

sexual secretions from other organisms. Historically, human perfumes have commonly included bodily secretions, such as musk produced from the Himalayan musk deer, anal gland secretions from sexually active civet cats and beavers, and ambergris from sperm whales. In fact, the ingredients of most perfumes consist of synthetic (or real) insect pheromones as top notes (e.g., floral scents), resinous materials that smell of odorous sex steroids (e.g., androstenone) as middle notes, and synthetic (or real) mammalian pheromones as base notes, which have a urinous or fecal odor at high concentrations (for review see, Stoddart, 1990).

A common explanation for the use of artificial fragrances is that they mask natural body odor with socially acceptable pleasant smells (i.e., odors of other organism's sexual secretions). While masking body odor seems at odds with the hypothesis that information conveyed by natural body odor influences mate preferences, the application of artificial fragrances indicates olfaction remains a salient form of social communication. For example, fragrances may be used to convey cleanliness, social status, personality, or openness to sexual encounters (for reviews see, Allen et al., 2019; Largey & Watson, 1972). Moreover, artificial fragrances may interact with underlying body odor and form a mixture that is suggested to enhance the availability of information about an individual's genotype (Milinski & Wedekind, 2001). For example, individuals with the same perfume preferences also share HLA alleles (Hämmerli et al., 2012; Milinski & Wedekind, 2001). In addition, one study demonstrated that individuals learn which fragrances blend best with their own body odor and select those fragrances which produce the most pleasurable mixtures (Lenochová et al., 2012). Thus, regardless of whether artificial fragrances are used to mask natural body odor or blend with natural body odor, these findings clearly necessitate further research on individual fragrance preferences and odor-based sexual communication.

Summary Conclusion

Although the findings presented in this section are promising, research on odor-based communication and mate choice in humans is limited and fragmental. In general, scant original research has been conducted, and almost no replication studies.

Moreover, most experiments have been limited by small sample sizes and overestimated effect sizes, similar to studies of putative human pheromones. Moving forward, researchers should consider the strength of evidence and quality of prior experiments before continuing to build on unstable foundations, and prioritize rigorous methods and replication studies over novel findings.

V. The future of research on human olfaction and mate preferences

In most mammals, mate preferences are strongly influenced by smell. Since the 1960s, a mountain of evidence has accumulated suggesting humans also use odor-based communication to guide mate choice, but much of this work has been severely criticized. Common criticisms include small sample sizes, overestimated effect sizes, publication bias, and a lack of replication studies. In addition, several studies possess design flaws, such as the use of unnaturally high concentrations of putative pheromones and inappropriate controls (for reviews see, R.L. Doty, 2010, 2014; Wyatt, 2020). Finally, highly publicized papers, for example, McClintock's (1971) *Nature* article proposing human pheromones regulate the menstrual cycle, have been challenged on statistical grounds (e.g., Strassmann, 1997, 1999; for reviews see, Doty, 2010, 2014). Thus, currently there is no conclusive evidence to support the existence of human pheromones, and little compelling research demonstrating smell influences mate preferences. This dissertation seeks to rebuild the foundation for research on odor-based communication and mate preferences in humans. Specifically, I focus on first

principles and use rigorous protocols to investigate whether smell even plays a role in attraction.

Chapter 2, originally published in 2018 in the journal *Adaptive Human Behavior and Physiology*, investigates the putative female pheromone, copulin, addressing limitations in prior studies of copulin, and human pheromone research more generally. Copulin, a mixture of fatty acids, is secreted vaginally in several primate species. In humans, exposure to copulin is reported to increase men's testosterone levels, alter men's perceptions of women's attractiveness (Grammer & Jütte, 1997), increase men's cooperative behaviors (Steinbach et al., 2012) and increase men's perceptions of their own mate value (Williams & Jacobson, 2016). However, using the largest sample size to date ($n = 243$ men), a placebo-controlled masking design, and sexual experience as a mediator variable, Chapter 2 reports no evidence that copulin affects men's perceptions of women's attractiveness, preferences for short- versus long-term mating, sexual motivation, self-reported willingness to take sexual risks, or perceptions of own mate value. Moreover, prior sexual experience does not mediate the effect of copulin on any dependent measures. Finally, chemoreceptors in genital skin were explored as a possible chemosensory pathway along with the pathway traditionally tested, the main olfactory system. The pathway used for copulin exposure was not significant. These findings challenge the conclusion that copulin is a human pheromone.

Chapter 3 was inspired by early studies of physical and vocal attractiveness. The study of mate preferences from an evolutionary perspective often begins by examining whether individuals of one sex share similar preferences for mates, and evidence of shared preferences is often interpreted as support for the hypothesis that these preferences are adaptations that have evolved to select high-quality mates. A large literature exists demonstrating shared preferences for physical and vocal attractiveness

(e.g., Collins, 2000; Feinberg et al., 2005; Grammer & Thornhill, 1994; Langlois & Roggman, 1990; Mealey et al., 1999; Perrett et al., 1999; Puts et al., 2013; Rhodes et al., 1998, 1999; Rhodes & Tremewan, 1996; Singh, 1993; Singh et al., 2010; Singh & Young, 1995), however research on smell and mate preferences has largely overlooked this fundamental question. Thus, Chapter 3 investigates how consistently individuals of one sex rated the attractiveness of body odors of members of the opposite sex. Moreover, using a uniform methodology to facilitate cross-modality comparisons, individuals also rated the attractiveness of faces and voices of members of the opposite sex. The primary finding was that level of agreement does not significantly differ between modalities. Therefore, to the extent that evidence exists for shared facial and vocal attractiveness preferences, there is also evidence of shared attractiveness preferences for body odors.

Chapter 4 examines the relationships between independent multisensory judgements of attractiveness (i.e., face, voice, and body odor). Some researchers argue that attractiveness judgments made across different sensory modalities reflect a common underlying variable related to fitness (i.e., the information is redundant), such as fecundity or disease resistance. Others posit attractiveness judgments made in different modalities reflect distinct fitness correlates (i.e., the information is unique). The primary goal of Chapter 4 was to estimate the strength of the relationships between an individual's facial, vocal, and odor attractiveness, and to explore the source of these relationships. The findings suggest within-person attractiveness correlations across the three modalities tested are larger when men rate women than vice versa. In fact, there was no evidence of covariance between modalities of attractiveness when women rate men, suggesting men's attractiveness in each modality reflects distinct information. In contrast, a latent general attractiveness factor (i.e., common fitness correlate) modestly

contributes to observed covariances between modality-specific attractiveness judgments of women, providing limited support for the redundancy hypothesis.

In conclusion, smell undoubtedly influences human social behavior. However, most prior research investigating the role of odor in human mate choice is unreliable. Thus, we should proceed from the starting line and focus on rebuilding this field with well-designed experiments employing methods that have proven to be successful with other animals, and in combating the replication crisis in psychology. The data from this dissertation is a first step in the right direction and demonstrates that human odor-based communication is a worthy avenue of future study.

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CHAPTER 2: SYNTHETIC COPULIN DOES NOT AFFECT MEN'S SEXUAL BEHAVIOR

Chemical communication plays an important role in the social interactions and mating behavior of diverse animal taxa; yet its role in humans remains equivocal. Using a randomized, placebo-controlled experiment involving 243 male participants, we test whether exposure to synthetic copulin – a mixture of volatile fatty acids secreted vaginally in primates, increases 1) men's sexual motivation using an incentivized behavioral task, 2) self-reported willingness to take sexual risks, 3) preference for short-term mating, 4) perceptions of female attractiveness and 5) self-reported mate value. Because chemical receptors are found throughout the body and human chemosensory pathways have yet to be definitively identified, we also manipulate the location of copulin exposure (i.e., olfactory epithelium versus epidermal keratinocytes in the genital region). Finally, we examine whether prior sexual experience mediate any behavioral effects. Unlike previous reports, we fail to find any effects of copulin exposure on measures of men's sexual behavior.

Introduction

Chemical communication is the most ubiquitous form of communication among organisms (Wyatt 2014). It is used to track prey, detect predators, recognize in-group conspecifics, and identify mates (Engen 1983; for review, Carlson 2013). Historically, the relevance of chemical communication in primates, including humans, has been criticized due to selection for trichromacy and regression of the olfactory bulb (Barton et al. 1995). Instead, primates have been classified as microsmatic because, compared to other mammals like rodents, primates have proportionally smaller olfactory bulbs, less surface area in the nasal cavity dedicated to the olfactory epithelium and more pseudogenized olfactory receptor genes (Smith and Bhatnagar 2004). Recently, however, these views have been challenged. First, there is no correlation between the size of the olfactory cortex, the olfactory epithelium or the number of olfactory receptors and olfactory function (Laska and Freyer 1997; Laska and Teubner 1998, 1999a, b; Laska et al. 2005) – the most important factor in odor discrimination tasks is the species-specific ecological validity of the stimuli tested (Laska et al. 2005). Second, research with Lemuridae, Indridae, Callitrichidae, and Cebidae suggest that chemical signals are involved in diverse behaviors, such as territorial marking, self- and kin-recognition as well as reproductive behaviors (Kaplan et al. 1977; Rogel 1978; Epple 1986; Epple et al. 1986; Millhollen 1986). Third, humans are capable of recognizing at least one trillion olfactory stimuli (Bushdid et al. 2014) and perform similarly to canines on scent-tracking tasks (Porter et al. 2007). Together, these findings suggest that we may have radically underestimated the role of olfaction in human behavior.

Humans use olfaction to avoid spoiled foods and to detect the presence of harmful environmental pollutants (Engen 1983). Odors also affect mood and memories. Exposure to pleasant odorants can improve mood (for review, Maddocks-Jennings and

Wilkinson 2004; Trotier 2011) and odor-elicited memories are often more emotional and sometimes more accurate than other sensory-elicited memories, due to the olfactory bulb's direct projection to the limbic system (Herz et al. 2004). In fact, olfactory loss is an important diagnostic indicator in medicine as it is often the first symptom of neurodegenerative diseases within the brain, including those associated with Alzheimer's and Parkinson's (Rawson et al. 2012). In short, olfaction is important in humans.

Chemical Signals

While there is little debate as to what constitutes an odor, research on pheromones is more contentious because an agreed upon definition for pheromone is lacking. Traditionally, scientists have defined pheromones in mammals as non-volatile chemicals transduced by the vomeronasal organ (VNO) and transmitted to the accessory olfactory bulb (AOB) (Savic et al. 2001; Witta and Wozniak 2006; Trotier 2011). Since humans lack an AOB and a functional VNO, it follows that, according to this definition, pheromone signaling cannot exist. Yet this type of communication is unquestioned in many species, like dogs and elephants, which also lack a functional VNO (Grus et al. 2005). Moreover, a number of studies show that the VNO is unnecessary for the detection of chemical signals (Hudson and Distel 1986; Savic et al. 2001; Barton 2006; Witta and Wozniak 2006; Trotier 2011). For instance, sexual behavior in female pigs is influenced by androstenone even after their VNO has been blocked (Dorries et al. 1997). In ewes with a removed VNO, ovulation is still induced upon smelling a ram (Signoret 1991). These, and other findings, suggest that the pathway for mammals to communicate via chemicals is not limited to the VNO. Many researchers now prefer the term chemical signal instead of pheromone due to the

confusion and conflict surrounding pheromone's definition. Thus, in this paper, we also employ this terminology and define a chemical signal as any chemical emitted by one individual that alters either the behavior or physiology of another organism (Luscher and Karlson 1959; Wyatt 2014).

Recent studies have found that chemoreceptors are not unique to the olfactory and gustatory systems; they exist in tissues throughout the human body.

Chemoreceptors have been discovered in spermatogenic cells (Spehr et al. 2003), epidermal keratinocytes (Busse et al. 2014), muscle tissue (Griffin et al. 2009), the kidneys (Pluznick et al. 2009), and pulmonary neuroendocrine cells (Gu et al. 2014). The chemo-attractants for many of these receptors have not been isolated, but in the examples that have, the results are remarkable. For example, synthetic sandalwood binds to chemical receptors in epidermal keratinocytes and causes an increase in rapidity of wound healing (Busse et al. 2014). It is currently unknown whether biological odorants could act as chemo-attractants, binding to chemical receptors in various tissues, including the olfactory epithelium or epidermal keratinocytes in the genital region, and influence sexual arousal, ejaculate volume, or even sexual behaviors. The current study undertakes the first exploration of an alternative pathway for chemical communication. Although a long shot, we test if copulin affects men's behavior through a genital epidermal keratinocyte pathway, in addition, to testing the conventional olfactory pathway.

Odors and Attraction

The most prolific work examining the role of olfaction in mate selection involves human leukocyte antigen (HLA); more commonly referred to by its rodent counterpart – the major histocompatibility complex (MHC). HLA is an immunologically important group of genes implicated in self versus other recognition. Research demonstrates that

humans use HLA-mediated odors to inform mate assessment (for review, Havlicek and Roberts 2009). HLA-disassortative mating may have been selected for in order to increase offspring pathogen resistance by the avoidance of inbreeding (Wedekind et al. 1995; Wedekind and Füri 1997; Jacob et al. 2002; Thornhill et al. 2003; Santos et al. 2005; Roberts et al. 2008).

Similar work focuses on axillary secretion exposure, with most studies reporting behavioral and physiological effects (Brooksbank and Haslewood 1961; Cleveland and Savard 1964; Schleidt and Hold 1982; Cutler et al. 1998; McCoy and Pitino 2002; Grammer et al. 2003; Witta and Wozniak 2006; Saxton et al. 2008; Savic and Berglund 2010). For instance, Black and Biron (1982) demonstrated female participants rated male confederates wearing a 3 α androstenol exaltolide (synthetic androstenol) perfume more attractive. Androstenol is a testosterone derivative found in high concentrations in post-pubescent male axillary secretions (Parma et al. 2017).

While much work has examined effects of male axillary secretions, there has been less attention given to female odors. The empirical work that exists concentrates on shifts in women's odor corresponding with shifts in their menstrual cycle (for review, Haselton and Gildersleeve 2011). These studies find that 1) men prefer the body odor of ovulating women (Doty et al. 1975; Singh and Bronstad 2001) and 2) odor samples taken from women at high conception risk increase men's testosterone (Jütte and Grammer 1997; Miller and Maner 2010, 2011), sexual arousal (Miller and Maner 2010, 2011) and risk-taking (Miller and Maner 2011; also see Cerdá-Molina et al. 2013).

Copulin

In this paper, we assess the effects of copulin – a mixture of 5 aliphatic acids reported to fluctuate with the menstrual cycle – on men's behavior (Michael et al. 1975; Preti and Huggins 1975). The behavioral and psychological effects of copulin have been

documented in studies with non-human primates (Michael and Keverne 1968; Michael et al. 1971; Michael and Zumpe 1982; Cerdá-Molina et al. 2006; Matsumoto-Oda et al. 2003; but see Goldfoot et al. 1976). Yet, only a few human copulin behavioral studies have been published and their results are conflicting.

Michael et al. (1975), as well as Preti and Huggins (1975), used gas chromatography to analyze the chemical content of human vaginal secretions. They found women produce copulin at greater concentrations during the follicular phase and these concentrations drop after ovulation (Michael et al. 1975). The authors also report that hormonal contraceptives reduced the overall content of copulin in vaginal secretions and eliminated the fluctuations in amount across the cycle. All women sampled ($N = 50$) produced acetic acid, however, only one-third of women produced the other copulin components en bloc (Michael et al. 1975; Preti and Huggins 1975). Note, a follow-up study by Huggins and Preti (1981) did not find fluctuations in copulin concentrations corresponding with non-pill using women's reproductive cycle. Thus, the function of copulin, as well as whether individual differences exist in copulin production, is unknown. It has been speculated that copulins are a leaky cue to women's mate quality and reproductive status and men who are better at detecting concentration fluctuations may have a mating advantage (Williams and Jacobson 2016).

We know of only two published behavioral studies directly testing the effects of synthetic copulin on men's behavior (i.e., Jütte and Grammer 1997; Williams and Jacobson 2016). Jütte and Grammer (1997) found that men exposed to synthetic copulin exhibited an increase in testosterone levels and were inhibited in their ability to discriminate female attractiveness, meaning their assessments of the attractiveness of female faces were higher on a scaled rating system and less varied, which may be due to a ceiling effect. In a follow-up study, Williams and Jacobson (2016) failed to replicate

the attractiveness finding, though their results trended towards significance. The researchers did, however, find that men rated themselves more sexually desirable when exposed to copulin (Williams and Jacobson 2016). Steinbach et al. (2012) exposed men to liquid synthetic copulin while playing a tragedy of the commons game and found they were significantly more likely to cooperate. These mixed findings could be due to methodological limitation such as differences in exposure technique, small sample sizes and sampling variation.

Previous copulin studies have failed to acknowledge associative learning as a potential mechanism. The pleasurable sensation of sexual arousal could become associated with copulin odor such that future copulin exposure could prime past sexual experiences and affect behavior and physiology (Trotier 2011). This does not preclude the hypothesis that copulin detection has been selected for in men. Men may have a biological predisposition to learn via sexual experience the association between copulin concentration and ovulatory status. For example, Knaapila et al. (2012) found that only sexually experienced women rated androstenone as pleasant and suggested the odor of androstenone acquired a hedonic value from the past sexual context in which it was encountered. Cerdá-Molina et al. (2013) conjectured that because the chemicals found in vaginal secretions are also found in vinegar, fruits, etc., it is only via its association with sexual experience that vaginal secretion could influence men's sexual arousal.

The current study is the first to empirically test the effects of synthetic copulin on men's sexual behavior whilst exploring prior sexual experience as a possible mediator. In addition to examining the role of past sexual experience and varying the location of copulin exposure (e.g., olfactory epithelium versus epidermal keratinocytes in the genital region), we address some of the limitations of past research. Specifically, we employ a placebo-controlled, odor masking design using a large sample of men. Odor masking

was used to blind the experimenter to the condition and to increase ecological validity as many scented products, like perfumes, are used in modern settings. Also, to better approximate real-world settings, participants were asked to rate female faces for attractiveness during the exposure phase of the study, such that they smell copulin whilst in a mating mindset. We seek not only to replicate previous findings, but also to extend upon this research by examining additional behavioral outcomes including sexual risk-taking, sexual motivation, preference for short-term versus long-term mating and self-perceived mate value.

Methods

Participants

We recruited 243 male participants from a large, Ivy League university in an urban setting. Eligibility requirements included heterosexual orientation, no use of psychotropic medication or steroids, no cigarette smoking, and no nasal congestion or other known olfactory conditions that may impede the ability to smell. However, $n = 12$ participants that completed the study self-identified as non-heterosexual and were excluded prior to performing any analyses. Of the recruited participants, $n=168$ received research credits and the remaining $n = 75$ were paid \$10. Excluding the latter group from analysis did not change results. We analyzed a sample of 231 out of the recruited 243 participants. The sample has a mean age of 20.92 ($SD = 3.90$). Participants identified as White ($n = 135$), Black ($n = 22$), Asian ($n = 66$) and other ($n = 10$). Approximately three quarters (71.3%) of participants identified as single, while the rest reported being in a relationship. The university's Office of Regulatory Affairs approved all procedures.

Procedures

The experiment was conducted in a non-deception lab; thus, participants were told the research objective was to examine the role of a potential female pheromone in sexual attraction and that they may or may not be exposed to a potential pheromone. Each session consisted of 1–5 participants and the same female graduate student oversaw each session. We initially employed a double-blind design by having a graduate student not affiliated with the study assign labels A and B to the containers containing the mixtures and asked that he keep the code locked away until after analysis. However, the mixtures smelled differently and the graduate student running the sessions correctly guessed which container held the copulin mixture and began to discriminate the two odors, thus double-blinding was unable to be maintained throughout the study. Using a random number generator, participants were assigned to one of four conditions: nasal exposure, genital exposure, both genital and nasal exposure, neither genital nor nasal exposure/control. In all conditions, a facemask was worn over the nose and gauze was placed over the genitals. After consenting to the study, participants were first given a facemask to wear over their nose; this not only tested the nasal pathway but also kept participants from being nasally exposed to the genital gauze odor. They were then given gauze to place inside their pants but over their underwear in the genital region. They were specifically advised to not allow the gauze to make direct contact with their skin.

The facemask and gauze were treated with 5 ml of mixture via pipetting. Facemask and genital gauze were treated according to participant condition (e.g., nasal exposure, genital exposure, both genital and nasal exposure and neither genital nor nasal exposure/control), see Table 1). Participants were blind to their condition.

After participants put on their facemask and placed the gauze in their pants, they completed a survey that included basic demographic questions. Participants also

provided attractiveness assessments for thirty photographed women's faces. Together, these tasks took approximately 15 min. Following this, participants removed their facemasks and gauze pad. Participants then completed surveys to measure self-perceived mate value, preference for long versus short-term mating, sexual risk-taking, sexual history and completed a task to measure sexual motivation by choosing whether to view sexually explicit images. Finally, participants watched a 5-min video clip about plants to eliminate any potential embarrassment in the event that they were aroused during the study. Participants were debriefed and thanked.

Table 1

Conditions by area of exposure and mixture to which exposed.

<u>Area of Exposure</u>		<u>Conditions</u>		
		Nasal	Genital	Both
Nasal		Copulin	Control	Copulin
Genital		Control	Copulin	Copulin

Measures

Synthetic Copulin

100 mL of synthetic copulin was produced according to the concentration at ovulation recorded by Michael et al. (1975; see Appendix A, Table 5). This solution was diluted to 0.08 mL of copulins per 1 mL of distilled water. This is the concentration of copulin used in previous studies (Jütte and Grammer 1997; Williams and Jacobson 2016; Steinbach et al. 2012). The method of production was obtained via personal communication with Oberzaucher (October 7, 2013) and Steinbach (November 15, 2013). To mask the scent of copulin, 12.5 g of vanillin were added to the mixture (Sigma-Aldrich, St. Louis). Vanillin was chosen because it is often used in women's perfumes. The control solution

consisted of 12.5 g of vanillin mixed with 1.25 L of distilled water. Both mixtures were refrigerated and stored in scientific-glass containers labeled with A or B. 5 mL of experimental or control solution was applied using a glass pipette to a gauze pad for genital exposure and a gauze pad safety pinned inside a facemask for nasal exposure.

Attractiveness Assessment

Participants were presented with 30 photographs of Caucasian women baring neutral expressions taken from the Karolinska Directed Emotional Faces (KDEF) set and asked to rate their attractiveness on a 5-point scale, with 1 indicating very unattractive and 5 indicating very attractive.

Mate Value Participants

Participants used a 7-point scale to rate their own mate quality using the Mate Value Scale (MVS). This is a 4-item measure taken from Edlund and Sagarin (2014, see Appendix B, Table 6). A higher score indicates higher self-perceived mate value.

Preference for Short-Term Versus Long-Term Mating

Participants preferences for short-term versus long-term mating strategies were assessed using the revised Socio- sexual Orientation Inventory (SOI-R 5-pt. response scale) (Penke and Asendorpf 2008, see Appendix C, Table 7). Higher scores indicate a preference for short-term mating.

Sexual Risk-Taking

Participants were asked eight questions on their willingness to engage in risky sexual practices taken from Ariely and Loewenstein (2006). Responses were made on a sliding scale that stretched between “no” (0) to “possibly” (50) to “yes” (100). An example

question is as follows: Would you trust a woman you've just met who says she is using birth control?

Sexual Motivation

Participants completed 10 sessions of a sorting task that required them to categorize a series of numbers as either odd or even. Before each session they were given a choice to view either a sexually explicit photograph or a nature scene photograph. When making the choice, participants were told that selecting the sexually explicit photograph would result in having to sort 8 numbers as odd or even in that session, whereas choosing the nature scene would only result in sorting 5 numbers. The number of times a participant chose to view sexually explicit photographs was summed and used as a measure of sexual motivation. Sexual photos were scored as one and nature photos were scored as two giving a range of scores from 10 to 20. Stimuli were selected from the International Affective Picture System (IAPS).

Sexual Experience

We collected binary measures of virginity. Participants were asked whether they have ever had vaginal sex or oral sex.

Probe

For the final measure, participants were asked whether or not they thought they were exposed to a female pheromone during the experiment.

Results

All statistical tests were two-tailed. Table 2 reports descriptive statistics for the entire sample and disaggregated by condition. Preliminary analyses were conducted to determine equivalence across the four conditions on demographic characteristics (race,

age, relationship status and virginity). A Chi-Square Test of Independence was used to assess whether the proportion of different race categories varied across conditions. The finding was not significant $\chi^2 = (9, 230) = 5.40, p = .80$. No differences in the number of virgins $\chi^2 = (3, 229) = 3.07, p = .38$ or relationship status $\chi^2 = (3, 230) = 3.81, p = .28$ between the conditions were found. A one-way ANOVA revealed that age $F(3, 225) = .61, p = .61$ also did not vary between conditions.

There was no indication that participants correctly identified whether or not they were exposed to copulin $\chi^2 = (3, 227) = 2.42, p = .49$. Participant responses to the probe question were also equally distributed across the four conditions, $\chi^2 = (3, 229) = 2.22, p = .53$. Furthermore, virgins and non-virgins did not vary in answer accuracy to the probe question $\chi^2 = (1, 229) = .97, p = .32$. In addition, exploratory analysis revealed that there was not a placebo effect of participants thinking they were exposed to copulin on any of the dependent variables. That is, t-tests revealed mean ratings of the attractiveness of the face stimuli $t(224) = -0.16, p = .87$, variance in participant ratings of the face stimuli's attractiveness $t(227) = -1.05, p = .29$, self-reported mate value $t(227) = .65, p = .51$, preference for short-term versus long-term mating $t(227) = .61, p = .55$, sexual risk-taking $t(227) = -0.46, p = .65$ and sexual motivation $t(227) = -1.56, p = .12$ did not vary between those who thought that they were exposed to copulin and those who did not.

A Shapiro-Wilk test was used to test for normality on the main dependent variables mean attractiveness ratings, variance in within participant ratings of the face stimuli's attractiveness, self-reported mate value, preference for short-term versus long-term mating, sexual risk-taking, and sexual motivation; variance in within participant ratings of the face stimuli's attractiveness, self-reported mate value, preference for short-term versus long-term mating and sexual motivation were non-normal ($p > .05$).

Levene's test for equality of variance was not violated for attractiveness ratings $F(3, 224) = .77, p = .51$, variance in attractiveness ratings $F(3, 228) = 1.68, p = .17$, self-reported mate value $F(3, 227) = 1.16, p = .33$, preference for short-term vs. long-term mating $F(3, 227) = 1.24, p = .30$, sexual risk-taking $F(3, 227) = .32, p = .81$, or sexual motivation $F(3, 227) = .30 p = .83$.

Table 2

Descriptive statistics for the full sample and by condition.

	Neither	Genital	Nasal	Both	Total
<i>N</i>	57	60	57	56	230
Age	21.32 (4.60)	21.20 (5.26)	20.54 (2.01)	20.59 (2.69)	20.92 (3.90)
White	56.1	56.7	63.2	58.9	58.7
Black	10.5	6.7	14.0	7.1	9.6
Asian	29.8	30.0	21.1	28.6	27.4
Other	3.5	6.7	1.8	5.4	4.3
Relationship Status (Single)	64.9	78.3	75.4	66.1	71.3
Sexual Experience (Virgin)	24.6	26.7	15.8	28.6	24.0

Note. Standard deviations are in parentheses. Proportions are reported for ethnicity, relationship status and virginity for the full sample and by condition.

Table 3 provides means and standard deviations of each dependent variable by condition. Five separate one-way ANOVAs were computed to test the effects of copulin exposure on our six main dependent variables. While we report results from ANOVAs, the non-parametric Kruskal-Wallis test did not yield meaningfully different results. Mean attractiveness ratings significantly varied between groups $F(3, N = 222) = 3.25, p = .02$, but in the opposite direction predicted. Post hoc comparisons using Tukey HSD indicated that the mean score for the condition with copulin exposure in both locations (nasal and genital) was borderline significantly lower on average than the condition of

exposure to control mixture in both locations $p = .05$. Variance in within-participant attractiveness ratings across faces $F(3, 226) = 2.23, p = .09$, self-perceived mate value $F(3, 225) = .40, p = .75$, preference for short-term versus long-term mating $F(3, 225) = .13, p = .94$, sexual risk-taking $F(3, 225) = .55, p = .65$ and sexual motivation $F(3, 225) = 1.03, p = .38$ did not vary by condition.

Separate 2×4 ANOVAs were also conducted to examine the effect of virginity (Factor A) and treatment type (Factor 5) on our dependent variables. A Phi-Coefficient test was used to assess the correlation between oral and vaginal sex virginity. Oral sex virginity was highly correlated with vaginal virginity, $\phi = .71, p < .001$ and thus no separate analyses were run to examine the effect of oral sex exposure. Only one of the models was significant (see Table 4). There was no interaction with virginity $F(3, 218) = .07, p = .98$ or main effect of virginity $F(1, 218) = .38, p = .54$ on mean levels of attractiveness. When examining variance in attractiveness ratings of the face stimuli, there was a main effect of virginity $F(1, 221) = 5.54, p = .02$, no main effect of treatment type $F(3, 221) = .91, p = .44$, and an interaction $F(3, 221) = 2.95, p = .03$. A separate ANOVA for virgins and non-virgin was run with post-hoc comparisons using Tukey HSD revealing that when non-virgins were exposed to copulin nasally and genitally, they became significantly less discerning on average (exhibited reduced variance in within participant ratings of the face stimuli) than participants exposed to control in both locations $p = .05$. We also found a main effect of virginity $F(1, 221) = 17.31, p < .001$ on self-reported mate value – with virgins reporting lower mate value, but no main effect of treatment type $F(3, 221) = .96, p = .41$ or their interaction $F(3, 221) = 1.21, p = .31$ was found. Similarly, when examining short-term vs. long-term mating, we found a main effect of virginity $F(1, 221) = 50.67, p < .001$, where virgins reported greater preferences for long-term mating, but no main effect of treatment type $F(3, 221) = .07, p = .98$ or their

interaction $F(3, 221) = .42, p = .74$ was found. When looking at variance in sexual risk-taking, a main effect of virginity $F(1, 221) = 10.84, p < .001$ was found, where virgins reported less willingness to take risks, but no main effect of treatment type $F(3, 221) = .82, p = .48$ or their interaction $F(3, 221) = 1.10, p = .35$ was found. Finally, when examining sexual motivation, no main effect of virginity $F(1, 221) = .35, p = .55$ or treatment type $F(3, 221) = .76, p = .52$ or their interaction $F(3, 221) = .55, p = .65$ was found.

Table 3

Mean scores and standard deviations for each measure.

Measure	Neither	Genital	Nasal	Both
Attractiveness Mean	2.29 (0.61)	2.17 (0.49)	2.19 (0.55)	1.98 (0.49)
Attractiveness Variance	0.82 (0.40)	0.76 (0.32)	0.75 (0.31)	0.66 (0.30)
Mate Value Score	5.12 (0.93)	5.31 (0.88)	5.16 (1.00)	5.19 (1.16)
Sociosexual Orientation Inventory	9.18 (2.67)	9.36 (2.52)	9.40 (2.35)	9.16 (2.79)
Sexual Risk-Taking	67.00 (13.53)	65.15 (13.51)	68.19 (15.04)	67.78 (13.21)
Sexual Motivation	13.14 (2.86)	14.00 (3.11)	13.91 (3.04)	13.43 (3.13)

Note. Standard deviations in parentheses.

Table 4

Means and standard deviations for dependent variables by condition and disaggregated by sexual experience.

Measure	Sexual Experience	Neither	Genital	Nasal	Both
Attractiveness Mean	Virgin	2.30(0.84)	2.13(0.49)	2.13(0.63)	1.92(0.57)
	Non-Virgin	2.29(0.52)	2.18(0.49)	2.21(0.54)	2.01(0.46)
Attractiveness Variance	Virgin	0.54(0.32)	0.69(0.28)	0.78(0.22)	0.63(0.35)
	Non-Virgin	0.92(0.38)	0.79(0.34)	0.74(0.33)	0.68(0.28)
Mate Value Score	Virgin	4.48(1.27)	5.06(0.95)	4.86(1.28)	4.50(1.38)
	Non-Virgin	5.33(0.69)	5.41(0.85)	5.22(0.95)	5.47(0.94)
Sociosexual Orientation Inventory	Virgin	7.48(1.82)	7.25(1.82)	7.56(1.57)	6.90(1.88)
	Non-Virgin	9.74(2.69)	10.14(2.30)	9.75(2.33)	10.07(2.59)
Sexual Risk-Taking	Virgin	66.32(18.03)	57.28(14.96)	60.26(21.24)	62.72(10.11)
	Non-Virgin	67.22(11.97)	68.08(11.84)	69.67(13.34)	69.80(13.85)
Sexual Motivation	Virgin	12.79(3.09)	14.00(3.61)	12.89(3.26)	13.81(4.13)
	Non-Virgin	13.26(2.81)	14.00(2.95)	14.10(2.99)	13.28(2.67)

Note. Standard deviations in parentheses.

Discussion

Previous studies have reported an effect of copulin exposure on men's testosterone levels, perception of women's attractiveness (Jütte and Grammer 1997), cooperation (Steinbach et al. 2012) and self-reported mate value (Williams and Jacobson 2016). In the largest study on copulin to date, utilizing two different routes of exposure, we found no evidence that copulin affect men's sexual motivation, self-reported willingness to take sexual risks, preference for short-term mating over long-term mating, perceptions of female attractiveness or self-reported mate value. We also found no mediation effects of prior sexual experience on any of our dependent measures.

While the current study deviated from the methodology of Jütte and Grammer (1997) in

that they used gaseous synthetic copulin, it was consistent with Steinbach et al. (2012) and Williams and Jacobson (2016), who both used liquid copulin produced in the same manner as the current study.

Based on the current results, we argue that copulin should stop being termed a putative human pheromone or even a chemical signal. To achieve this status, the following criteria would need to be demonstrated (see Wyatt 2014): 1) synthesized copulin should produce the same behavioral and physiological reactions in conspecifics as naturally produced copulin and at equivalent concentrations as naturally produced copulin 2) that each constituent acid of the copulin mixture should be necessary and sufficient to cause said reaction(s) 3) that only the proposed mixture of chemicals should elicit these reactions 4) that a credible pathway evolved to facilitate copulin communication and 5) that the quantities of copulin may vary between individuals of different, for example, mate quality or status, but individuals themselves cannot be recognized by the copulin they produce. Our study demonstrates the failure of the very first criteria.

There are a number of potential limitations with the current study. First, we implemented a masking technique to increase ecological validity since perfume and other fragranced products (e.g., soap) are used regularly. Copulin without any masking, as used in previous designs, was not assessed; therefore, we cannot conclude whether unmasked copulin would have yielded significant findings. However, olfactory processing, unlike other sensory systems, is not additive, meaning there is no mixing of molecules (Carlson 2013). Consequently, masking techniques are not expected to impact the olfactory systems unconscious processing of odors – only the conscious perception of the smell. Whereas other sensory systems project directly to the thalamus, the brain region that integrates sensory information and is suggested to be where

conscious perception comes online, the olfactory system first projects to the olfactory cortex, then the amygdala, insular cortex, hypothalamus (or hippocampus) and then finally to the thalamus. Thus, odorant molecules can affect physiology and behavior before conscious awareness of an odor (Carlson 2013; Wyatt 2014; Parma et al. 2017).

A second limitation may have to do with the use of vanillin as the masking agent and control. Vanillin is used as a base note in many perfumes; therefore, men may associate vanillin with a pleasant feminine scent. Any scent men associate with women could increase sexual arousal and result in higher scores for all participants. However, this was not likely to be a significant limitation as participant scores were low on average. Future work could examine the role of copulin without masking or use different masking odorants. A third limitation is the possibility of “leaky” odors. Because all participants were run in the same laboratory space it is possible that everyone was exposed to the copulin odor upon entering the lab. We minimized this potential problem by having participants don surgical face masks over their noses and mouths prior to data collection. However, future research could benefit from running participants in the different conditions on different days or in different rooms in order to eliminate or reduce the possibility of odor “leakage”. A final limitation of our design stems from informing participants of their possible exposure to a “putative female pheromone” which could have inadvertently primed sexual behavior. We think this unlikely however, because we found no effect of whether participants thought they were exposed to copulin on any of our dependent measures.

While we failed to find an effect of copulin, this does not mean human olfaction is poor, or that chemosensory communication does not exist in humans. Recent work suggests body odors constitute a special subclass of ecologically relevant odors that influence mate preference (for review, Grammer et al. 2005) and have implications for

health (Whittle et al. 2007; Prugnolle et al. 2009; Moshkin et al. 2012; Olsson et al. 2014). Humans are able to discriminate body odors from sick and healthy individuals (Olsson et al. 2014). PET and fMRI studies demonstrate separate olfactory processing for common odors (e.g., lavender) and body odors. This may suggest, similar to faces, body odors contain evolutionarily significant information and thus utilize a special processing region akin to the fusiform face area (Parma et al. 2017). Heterosexual women and homosexual men exhibit activation of the anterior hypothalamus in addition to primary olfactory cortex when exposed to androstenol, a testosterone derivative found in post-pubertal male axillary secretions. In contrast, exposure to non- body odors resulted only in activation of primary olfactory cortex (Savic and Berglund 2010). Homosexual women and heterosexual men process androstenol in primary olfactory cortex and estra-1, 3, 5 (10), 16-tetraen-3-ol, found in female urinary secretions, in the anterior hypothalamus (Berglund et al. 2006). Brain imaging evidence, as a whole, suggests the potential for body odors to strongly influence human social behaviors.

There are no definitive human pheromones to date. The quest continues, but we argue that in the future, researchers should focus on individual's chemical profiles instead of trying to identify a specific human pheromone. To identify a specific molecule or mixture of molecules as a pheromone, researchers would need to satisfy points one through five mentioned above and show the proposed pheromone is a species-wide signal and results in universal stereotyped physiological and/or behavioral reactions in a conspecific (Wyatt 2014). For now, it may be more worthwhile to devote efforts on determining what internal and external components construct an individual's chemical profile, how the secretory environment (e.g., hair) impacts odor production and how these inputs affect social assessments, like mate choice, and behavioral outputs. Once we have a strong theoretical framework for what evolutionarily significant information

may be present in body odors, only then can we perform meaningful empirical studies. Identifying a specific molecule(s) that occur within the backdrop of all human's chemical profiles and results in stereotyped reactions in conspecifics will require rigorous bioassay testing, behavioral studies and, we predict, many decades of research.

Conclusion

Odors permeate all aspects of human life and yet, skepticism surrounding the relevance of odors in human social behavior remains. Some of the reluctance to acknowledge the importance of smell in humans may be partly due to older conceptual and largely erroneous views of how chemical signaling works. While we find no evidence that copulin is involved in men's sexual behavior, we advocate for more research examining the effects of human body odor on social behavior.

Chapter 2 References

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CHAPTER 3: HUMANS EXHIBIT SHARED PREFERENCES FOR BODY ODORS EQUIVALENT TO EVIDENCE OF SHARED PREFERENCES FOR FACES AND VOICES

Studies of mate choice from an evolutionary perspective often begin by investigating whether individuals of one sex share similar preferences for mates. Evidence for shared preferences is often interpreted as support for the hypothesis that preferences are adaptations that have evolved to select high-quality mates. To date, the importance of body odor in human mate choice is uncertain because fundamental questions, such as whether preferences for body odor are shared, have not yet been systematically explored. Here, we asked groups of heterosexual men and women to rate the attractiveness of the body odors, faces, and voices of opposite-sex individuals ($N = 1,284$). We used our data to produce quantitative estimates of the amount of rater agreement for each of the three modalities of attractiveness, applying a uniform methodology that facilitates cross-modality comparisons. Overall, we found evidence of agreement within all three modalities. Yet, our data also suggest a larger component of attractiveness judgments that can be attributed to personal preferences and idiosyncratic noise. Furthermore, our results provide no evidence that agreement regarding odor attractiveness is substantially quantitatively different from the amount of agreement found in other modalities that have been the focus of most previous work. Thus, to the extent that evidence exists of shared preferences for faces and voices, our results reveal evidence of shared preferences for body odors.

Introduction

An abundance of research indicates that humans, like other animals, discriminate between potential mates based on physical appearance (for review see, Fink & Penton-Voak, 2002; Grammer, Fink, Miller, & Thornhill, 2003; Rhodes, 2006; Thornhill & Gangestad, 1999). Evolutionary theorists suggest that shared attractiveness judgments are adaptations that have evolved to facilitate selection of high-quality mates (for review see, Etcoff, 2011; Fink & Penton-Voak, 2002; Grammer et al., 2003; Møller & Thornhill, 1998; Symons, 1979; Thornhill & Gangestad, 1993). Some evidence for this adaptationist perspective stems from studies demonstrating widespread agreement in features considered attractive (e.g., averageness, symmetry) in others, as well as studies showing agreement between individuals on judgments of overall attractiveness in others (e.g., Grammer & Thornhill, 1994; Langlois & Roggman, 1990; Mealey, Bridgstock, & Townsend, 1999; Perrett et al., 1999; Rhodes, Proffitt, Grady, & Sumich, 1998; Rhodes, Sumich, & Byatt, 1999; Rhodes & Tremewan, 1996). Though olfaction is important for mate selection in many mammals (for reviews see, R. E. Brown, 1979; Eisenberg & Kleiman, 1972), the role of smell in human mate choice remains unclear. To date, little work has examined agreement in attractiveness judgments of body odors. This lack of research is surprising because, historically, estimating agreement has been the starting point for research on attractiveness preferences in other domains such as faces, voices, and bodies. Here, we add to the understanding of olfaction's role in human mate choice by examining agreement in preferences for body odor and comparing that level of agreement with agreement in preferences for faces and voices.

Human olfactory acuity

Little is known about the role of olfaction in human social behaviors, particularly mate choice, in part, because of persistent, erroneous beliefs about human olfaction. Since the early 1800s, humans have been classified as “microsmatic” (i.e., poor smellers) and, to date, non-specialists whose research touches on olfaction often mistakenly propagate this myth (for review see, McGann, 2017). The microsmatic conclusion was drawn partly from comparative research indicating that in humans, the amount of brain devoted to olfaction is relatively small (e.g., Turner, 1890), as is the number of functional olfactory receptor genes (e.g., Glusman, Yanai, Rubin, & Lancet, 2001; Zozulya, Echeverri, & Nguyen, 2001; for review see, Nei, Niimura, & Nozawa, 2008). Yet, it is now known that the human olfactory system is capable of detecting practically all volatile chemicals larger than one or two atoms and discriminating between more than 1 trillion odors (Bushdid et al., 2014). While the relative amount of brain devoted to olfaction is smaller in humans than in other mammals, the absolute size of the human olfactory bulb is larger. Moreover, the human brain possesses an intricate network of cortical regions that interpret olfactory inputs, such as the orbitofrontal cortex which is much larger in humans and extensively connected to other neocortical regions (for review see, Gottfried & Zelano, 2011; Zelano & Sobel, 2005). Although humans have fewer genes that code for olfactory receptor proteins than other mammals, humans have more than double the amount of olfactory receptor noncoding pseudogenes (Glusman et al., 2001; Young et al., 2002; Zhang & Firestein, 2002; for review see, Nei et al., 2008). The role of pseudogenes in olfaction is under debate, and the relationship between pseudogenes and olfactory acuity remains unclear. Finally, researchers have also doubted whether odor-based communication is possible because the vomeronasal organ, thought to be specialized for pheromone detection, is vestigial in humans.

However, we now know that odor-based communication also occurs through the main olfactory system in most mammals, including humans (Spehr, Kelliher, et al., 2006; for reviews see, Baum & Cherry, 2015; Baxi et al., 2006; Spehr, Spehr, et al., 2006).

Olfaction and mate choice

While experts in the field of olfaction now widely consider humans to be excellent smellers, debate continues regarding the importance of smell in mate selection. In primates, particularly humans, the visual system is thought to play the leading role in mate selection, and thus the study of smell has been neglected. Additionally, studies of olfaction and mate selection in humans, have been marred by methodological and theoretical limitations (e.g., lack of blinding, lack of appropriate control conditions, no theoretical basis, failure to test a clear hypothesis, statistical errors, etc.) (for review see, Doty, 2010).

One of the earliest studies examining odor-based communication indicated that humans could identify a person's biological sex from smell (Russell, 1976). Follow-up studies suggested the underlying mechanism was that more intense odors are likely to be accurately attributed to males (e.g., Doty, Orndorff, Leyden, & Kligman, 1978). However, many researchers believed that hormone derivatives in axillary sweat were responsible and studied these as putative sex pheromones (e.g., Benton, 1982; Cowley & Brooksbank, 1991; Filsinger, Braun, & Monte, 1985; Gustavson, Dawson, & Bonett, 1987; Jacob, Hayreh, & McClintock, 2001; Jacob & McClintock, 2000; Kirk-Smith & Booth, 1980; Nixon, Mallet, & Gower, 1988). For example, one controversial study reported that women were significantly *more* likely to elect to sit in chairs sprayed with a testosterone derivative (i.e., androstenone), whereas the *opposite* was true for men (Kirk-Smith & Booth, 1980).

Another body of research has examined how immunological compatibility affects mate selection, specifically by examining how human leukocyte antigen (HLA) genotypes affect body odor attractiveness judgments. Since genetically related individuals are more likely to have similar HLA genotypes, researchers hypothesize that greater allelic HLA-similarity of relatives enables people to identify kin through smell (for review see, Havlíček & Roberts, 2009; Penn, 2002; Penn & Potts, 1999). Moreover, HLA heterozygosity is thought to enhance resistance to a broader range of pathogens; thus, researchers hypothesize that mating with HLA-dissimilar (i.e., different from oneself) and HLA-heterozygous individuals is beneficial for offspring (e.g., McClelland et al., 2003). The first empirical study on HLA-dissimilarity and mate selection indeed found humans are attracted to HLA-dissimilar mates (Wedekind et al., 1995). However, subsequent work (e.g., Croy et al., 2020) and meta-analyses have failed to replicate this finding (Havlíček et al., 2020; Winternitz et al., 2017). One study (Winternitz et al., 2017) instead reported a preference for mates with greater HLA genetic diversity (as measured by HLA-heterozygosity). In general, the literature on HLA and mate choice is filled with claims of positive findings that often fail to replicate consistently. The reasons for the poor replication record are complex, but low power is probably an important contributing factor. The average power of studies on HLA and mate choice is low, ranging from 24% to 57% (Winternitz et al., 2017).

Finally, another body of work has studied the relationship between body odor attractiveness and other putative fitness cues such as facial symmetry (e.g., Gangestad & Thornhill, 1998; Thornhill & Gangestad, 1999), diet (Fialová, Hoffmann, Roberts, & Havlíček, 2019; Fialová, Roberts, & Havlíček, 2016; Havlicek & Lenochova, 2006; for review see, Fialová, Roberts, & Havlíček, 2013), and health (Moshkin et al., 2012; Olsson et al., 2014). Although significant relationships were reported, many of these

studies have also relied on small sample sizes and have not yet been replicated (e.g., Moshkin et al., 2012). So, while the literature on smell and mate selection in humans seems to be vast and promising, consensus on the importance of olfaction in mate choice remains low. Moreover, answers to fundamental questions are uncertain, such as to what extent people agree on attractiveness judgments of others' body odors.

Attractiveness preferences as adaptations

In the early 1990s, many researchers, influenced by Symons (1979), began examining the hypothesis that attractiveness judgments are evolved adaptations for the selection of optimal mates. Adaptations are solutions to problems affecting the reproductive success of individuals within a species, such as obtaining ideal mates for successful sexual reproduction. Selection should have favored psychological adaptations for evaluating traits that vary with mate quality, such as health and fecundity, and finding those traits attractive (e.g., symmetry, voice-pitch, waist-to-hip ratio, and body odor) that indicate high genotypic and reproductive quality. If attractiveness judgments are not arbitrary or idiosyncratic, but rather shared, then shared attractiveness preferences provides some evidence that these judgments are adaptations that have evolved to solve the problem of mate choice (Gangestad & Scheyd, 2005).

In fact, evolutionary researchers studying attractiveness judgments within certain modalities—such as faces, bodies, and voices—have typically started by assessing the amount of agreement between people in features considered attractive and also, in their judgments of others' overall attractiveness (e.g., Collins, 2000; Feinberg, Jones, Little, et al., 2005; Grammer & Thornhill, 1994; Langlois & Roggman, 1990; Mealey et al., 1999; Perrett et al., 1999; Puts et al., 2013; Rhodes et al., 1998, 1999; Rhodes & Tremewan, 1996; Singh, 1993; Singh et al., 2010; Singh & Young, 1995). Past research on body

odor attractiveness has largely overlooked this fundamental question. We know of only two studies that have sought to examine consistency in judgments of opposite-sex body odors (Lobmaier, Fischbacher, Wirthmüller, et al., 2018; Thornhill et al., 2003). First, Thornhill and Gangestad (1999) reported high internal consistencies for male ($n = 61$) and female ($n = 48$) ratings of opposite-sex body odors ($\alpha = 0.66$, high-fertility female raters; $\alpha = 0.90$, low-fertility female raters; $\alpha = 0.90$, male raters). Second, Lobmaier et al. (2018) examined men's ($n = 55$) preferences for women's ($n = 28$) body odors and reported high concordance in judgments using the average-agreement intraclass correlation coefficient (ICC = 0.983).

The present study builds on prior research by examining how consistently individuals of one sex rate the attractiveness of body odors of members of the opposite sex. We define and estimate two distinct parameters measuring agreement in judgments of attractiveness. The first is the individual-agreement ICC and the second is the average-agreement ICC, where the average is calculated across four raters - which of these two parameters is most appropriate depends on the research question. Intuitively, the individual-agreement ICC is appropriate if the goal is to estimate the similarity between the judgments of two individual raters. The average-agreement ICC instead reveals the agreement between two ratings obtained by averaging the individual ratings of k individuals from different groups (in our analyses, we set $k = 4$). The average-agreement ICC is relevant when variability across raters, due to measurement error or individual preference heterogeneity, is not of interest. For example, a researcher may want to know the level of agreement in ratings that have been purged of variance due to measurement error and idiosyncratic individual taste parameters. If so, using an average-agreement ICC with a high value of k is generally preferable. When the unit of analysis is the average rating of a team of experts, the average-agreement ICC is also

appropriate. For example, we may wish to measure agreement between the average ratings of two independent teams of k experts who evaluated the same donor.

The fact that our two parameters have a simple definition and a clear interpretation makes relating our estimates to those in other studies easier, such as a recent examination of agreement in attractiveness judgments of faces that accounted for variance attributed to shared preferences and personal preferences (e.g., Hehman et al., 2017). We also use a common and transparent methodology to conduct all of our analyses in the same estimation sample and using the same scales, which facilitates comparability of measured agreement across modalities since any observed differences cannot be attributed to methodological differences or differences in the composition of the estimation samples. Evidence of agreement, in the form of strong statistical evidence against the null that an ICC parameter is zero, would provide support for the hypothesis that body odor judgments are not arbitrary and may, instead, reflect adaptations for mate choice, perhaps related to underlying fitness markers, such as reproductive hormones or HLA-heterozygosity. Of course, shared preferences within a single society may also be culturally-derived. Thus, further research would be necessary to fully evaluate evolutionary explanations for the role of olfaction in mate choice. If we find no agreement within sexes in attractiveness judgments of body odors for opposite-sex individuals (i.e., a null result), further exploration of the variability within rater's judgments would help determine whether odor preferences are person specific or whether smell is simply unimportant in human mate choice.

Methods

Preregistration

We preregistered our research questions, methods, and plan for analysis on Open Science Framework (OSF; <https://osf.io/xybp3>) prior to data collection. While our research questions and methods remain unchanged, the analyses reported in this paper depart from those originally planned; the new analyses were planned after a statistical consultation with an independent advisor. The preliminary and main analyses discussed here are the only analyses we have attempted on these data.

Moreover, we initially planned to analyze hormone data and included exclusion criteria in our preregistration that were specific to saliva assays. We have not assayed any of the collected saliva samples due to laboratory and labor disruptions associated with the COVID-19 pandemic. Therefore, we also depart from initially preregistered exclusion criteria (i.e., anabolic steroid usage). We further depart from initially preregistered exclusion criteria by including data from participants who reported using psychotropic medications, smoking, having nasal congestion the day of odor ratings, and having experienced unspecified smell loss in their lifetime. Dropping these participants would have resulted in a substantial loss of power. We decided to include these participants before data analysis began. We assessed whether these variables affected odor attractiveness and intensity ratings and found no evidence that they did (see Table 8); thus, we felt justified in our decision to include these participants.

Participants

We recruited $n = 102$ men and $n = 96$ women from a large urban university campus using a web-based subject pool (SONA system) to take part in this study. The study consisted of two parts that took place on different days. In the first part, we refer to participants as “donors” because they provided an odor and voice sample, and had their

photograph taken. In the second part, we refer to participants as “raters” because they rated the attractiveness of a subset of opposite-sex participants’ odors, voices, and photographs. Participation in part 2 occurred in same-sex groups of between one and nine participants (*Med.* = 4). Men and women visited the laboratory separately to minimize social exposure that could influence their attractiveness judgments. We conducted an average of five study sessions every Monday, Wednesday, and Friday from October 14, 2019 to December 9, 2019. Part 2 contained 22 for men and 21 sessions for women, in which 1,284 opposite-sex attractiveness ratings were made. The current study investigates attractiveness preferences for the opposite sex; therefore, 11 men and 5 women were excluded from analyses because they either identified as non-heterosexual or chose not to identify their sexuality. Participants received course credit for participation.

Compliance

In research involving the collection of body odor, providing dietary, behavioral, and hygiene guidelines is standard procedure to control for extraneous variables that may affect the purity of samples and perceptions of body odor pleasantness. Although compliance measures may reduce ecological validity, they are necessary if we wish to discuss putative components of body odor attractiveness. Moreover, these measures also reduce the likelihood that attractiveness preferences are caused by cultural influences, such as diet, hygiene, and fragrance use. These procedures are similar to studies of facial attractiveness that exclude makeup use. In a preliminary analysis, we assessed whether diet (i.e., aromatic foods, e.g., garlic and cabbage), certain behaviors (i.e., strenuous exercise and sexual activity), fragranced hygiene products, and showering affected ratings. Compliance was generally high. Comparative analyses revealed fragrance use led to significantly higher odor attractiveness ratings for both

men and women, meaning men and women wearing fragrances were reported to smell better. Other compliance measures did not significantly affect odor attractiveness and intensity ratings when each sex was analyzed separately (see Table 9), which is how we report results. However, when we pooled male and female ratings, noncompliance with behavior and shower guidelines were also associated with significantly higher odor attractiveness ratings.

Table 8

Comparison of odor attractiveness and intensity ratings between raters who did comply (i.e., C) or did not comply (i.e., NC) with smoking (i.e., nonsmoker), nasal congestion (i.e., no nasal congestion), lifetime smell loss (i.e., none), and medication usage (i.e., none) guidelines. Results are presented in full and disaggregated by sex.

	Smoker		Nasal Congestion		Smell Loss		Medication									
	C	NC	C	NC	C	NC	C	NC								
Female Raters																
Odor Attractiveness Ratings																
Mean	11.89	10.93	11.71	12.61	11.88	10.67	11.72	13.97								
SD	3.52	4.16	3.55	3.54	3.50	5.20	3.53	3.35								
N	78	5	72	11	80	3	83	2								
t-statistic	0.59		-0.78		0.58		-0.89									
p	0.56		0.44		0.56		0.38									
Female Raters																
Odor Intensity Ratings																
Mean	3.84	3.76	3.80	3.95	3.83	4.07	3.83	3.47								
SD	1.04	0.80	1.05	0.88	1.02	1.29	1.04	0.19								
N	78	5	72	11	80	3	83	2								
t-statistic	0.17		-0.37		-0.39		0.49									
p	0.86		0.71		0.70		0.63									
Male Raters																

Odor Attractiveness Ratings																
Mean	11.79	11.28	11.65	12.08	11.70	12.22	11.69	12.02								
SD	3.24	2.23	3.30	2.74	3.12	3.80	3.19	3.00								
N	72	7	60	19	71	8	72	8								
t-statistic	0.41		-0.52		-0.44		-0.28									
p	0.68		0.61		0.66		0.78									
Male Raters																
Odor Intensity Ratings																
Mean	3.56	3.70	3.54	3.68	3.55	3.76	3.56	3.69								
SD	0.98	0.93	0.93	1.09	0.93	1.31	0.99	0.64								
N	72	7	60	19	71	8	72	8								
t-statistic	-0.36		-0.58		-0.59		-0.36									
p	0.72		0.57		0.56		0.72									
All Raters																
Odor Attractiveness Ratings																
Mean	11.84	11.13	11.68	12.27	11.79	11.79	11.70	12.41								
SD	3.38	3.01	3.42	3.01	3.31	4.00	3.36	2.96								
N	150	12	132	30	151	11	155	10								
t-statistic	0.71		-0.87		-0.00		-0.65									
p	0.48		0.38		1.00		0.52									
All Raters																
Odor Intensity Ratings																
Mean	3.71	3.73	3.69	3.78	3.69	3.85	3.70	3.64								
SD	1.02	0.84	1.00	1.01	0.99	1.25	1.03	0.58								
N	150	12	132	30	151	11	155	10								
t-statistic	0.06		0.43		-0.47		0.18									
p	0.95		0.67		0.64		0.86									

Note. Raters made four attractiveness ratings on 7-point Likert scales. These ratings were summed to create an overall attractiveness score; thus, overall attractiveness ratings range from 4 to 28. Raters made one intensity rating on a 7-point Likert scale; thus, intensity ratings range from 1 to 7.

* p < .05, **p < .01, ***p < .001

Table 9

Comparisons of odor attractiveness and intensity ratings of samples from women and men donors who did comply (i.e., C) or did not comply (i.e., NC) with dietary, behavioral, fragrance, and shower guidelines. Results are presented in full and disaggregated by sex.

	Diet		Behavior		Fragrance		Shower									
	C	NC	C	NC	C	NC	C	NC								
Female Donors																
Odor Attractiveness Ratings																
Mean	11.92	11.80	11.72	14.16	11.57	18.28	11.83	14.74								
SD	2.94	3.29	2.86	4.29	2.69	1.93	2.94	2.66								
N	62	22	78	6	80	4	78	4								
t-statistic	0.16		-1.94		-4.90		-1.94									
p	0.87		0.06		< 0.001***		0.06									
Female Donors																
Odor Intensity Ratings																
Mean	3.59	3.41	3.57	3.21	3.49	4.56	3.52	3.61								
SD	0.83	0.94	0.81	1.42	0.84	0.53	0.87	0.54								
N	62	22	78	6	80	4	78	4								
t-statistic	0.84		0.98		-2.53		-0.22									
p	0.40		0.33		0.01*		0.83									
Male Donors																
Odor Attractiveness Ratings																
Mean	11.63	12.24	11.58	13.08	11.38	16.18	11.54	13.97								
SD	3.77	4.14	3.86	3.56	3.71	2.11	3.82	3.44								
N	68	19	76	11	80	7	79	8								
t-statistic	-0.60		-1.21		-3.36		-1.72									
p	0.55		0.23		0.001**		0.09									

Male Donors

Odor Intensity Ratings								
Mean	3.88	3.95	3.97	3.35	3.86	4.31	3.90	3.85
SD	1.24	1.30	1.28	0.86	1.27	0.82	1.28	0.85
N	68	19	76	11	80	7	79	8
t-statistic	-0.22		1.55		-0.91		0.10	
p	0.83		0.12		0.36		0.92	

All Donors

Odor Attractiveness Ratings								
Mean	11.77	12.00	11.65	13.46	11.48	16.95	11.69	14.22
SD	3.39	3.67	3.38	3.74	3.24	2.22	3.40	3.10
N	130	41	154	17	160	11	157	12
t-statistic	-0.37		-2.07		-5.51		-2.50	
p	0.71		0.04*		<0.001***		0.01*	

All Donors

Odor Intensity Ratings								
Mean	3.74	3.66	3.77	3.30	3.67	4.40	3.71	3.77
SD	1.07	1.14	1.08	1.05	1.09	0.71	1.11	0.74
N	130	41	154	17	160	11	157	12
t-statistic	0.41		1.69		-2.18		-0.19	
p	0.68		0.09		0.03*		0.85	

Note. Raters made four attractiveness ratings on 7-point Likert scales. These ratings were summed to create an overall attractiveness score; thus, overall attractiveness ratings range from 4 to 28. Raters made one intensity rating on a 7-point Likert scale; thus, intensity ratings range from 1 to 7.

* p < .05, **p < .01, ***p < .001

Procedures

Odor collection

Participants visited the lab twice, on separate days, for 75-minute sessions.

During the first visit, participants provided an odor sample. Starting two days prior to the

first visit, participants were asked to follow strict dietary and behavioral inclusion criteria based on previous research (e.g., Kamiloglu et al., 2018; Zhou & Chen, 2009) to limit contamination of their odor samples (e.g., sexual activity and the consumption of pungent spices were prohibited). Participants were also asked to refrain from (1) showering, (2) using deodorant, and (3) using any fragranced products, such as lotions and perfumes, the day of body odor collection. We administered a compliance survey. Body odor was collected on 4x4-inch sterile absorbent compresses (Johnson & Johnson) that were secured to participants' axillae with skin safe (Nexcare) tape for one hour. Compresses were frozen at -20° Celsius, and later thawed 30 minutes before use in rating sessions. Samples were thawed once and discarded after the final rating session.

Photographing

During the first part of the study, we used an instant camera (60mm f/12.7 lens) to take portraits (62mm X 42mm photographs) of participants' faces. Participants were asked to remove any makeup, eyewear, and jewelry, and to pull long hair back. All participants were photographed in a black T-shirt with a neutral expression against a white background.

Voice recording

During the first part of the study, we recorded participants' voices as they read the "Rainbow Passage" (Fairbanks, 1960) into a cardioid condenser microphone (*Blue, Snowball*) for studio-quality recordings, using the application software, Audacity. We saved the recordings on a private SoundCloud account.

Attractiveness ratings

Three rating stations were set up in the laboratory: an odor station, a photograph station, and a voice station. A separate experimenter managed each rating station. Each participant was randomly assigned an order to cycle through the stations and only one participant at a time made ratings at a given station. All the samples (i.e., body odor samples, photographs, and voice recordings) of participants scheduled to be rated in the second part of the study were removed from storage and placed at the appropriate station 30 minutes before the first session of that day. Men participating in the second part of the study on a specific date rated women also participating in the second part of the study on that date. Raters did not know they were rating the same donors at each station. A donor's face, odor, and voice sample were uniquely labeled such that a rater could not match their samples between stations.

At the odor station, an experimenter presented samples in wide-mouth, amber, polypropylene jars. The order that samples were presented was randomized for each participant. Odor jars contained compresses from both axillae of a single donor. An experimenter, wearing odorless cotton gloves, removed lids from jars one at a time and held the jars while a participant smelled the jar's headspace. After the participant smelled the jar's headspace, the experimenter replaced the jar's lid while the participant made a series of judgments about the sample's odor. Participants were asked to rate the intensity of the odor on a 7-point Likert scale, with 7 representing "very intense". Then, participants made four judgments related to attractiveness (i.e., how pleasant, how attractive, how sexy, how much they liked...) using 7-point Likert scales, with 7

representing the highest score (e.g., very attractive). We summed the ratings to create an overall attractiveness score for each odor sample (see Table 10).⁴

At the photograph station, an experimenter handed participants portraits of faces in a randomized order for each participant. Participants made four judgments using the same scale described for odor, but wording changed to reflect faces. Additionally, participants were asked, “Do you know the person in this photograph?”. Observations in which at least one member of a rating dyad recognized the other member’s photograph were excluded (i.e., 37 observations) from all (i.e., face, odor, and voice) analyses.

At the voice recording station, participants wore large, over-the-ear, closed-back, noise-cancelling headphones and listened to audio files of voices. An experimenter played each audio file once in a randomized order for each participant. Participants made four judgments using the same scale described for odor, but wording changed to reflect voices.

⁴ Using a correlation matrix, we present the relationships between each of the summed attractiveness ratings in each modality as well as the relationship between each rating and the total attractiveness score in each modality. Questions within a given modality were highly correlated; thus, we felt justified in summing each to create an overall attractiveness score within each modality.

Table 10

Correlation matrix of attractiveness-rating-scale items.

		Face			
		Pleasant	Attractive	Sexy	Like...
Face	Attractiveness Score	0.868	0.944	0.909	0.927
	Pleasant	1.000	0.741	0.651	0.773
	Attractive	0.741	1.000	0.878	0.823
	Sexy	0.651	0.878	1.000	0.785
	Like...	0.773	0.823	0.785	1.000
		Odor			
		Pleasant	Attractive	Sexy	Like...
Odor	Attractiveness Score	0.934	0.951	0.915	0.940
	Pleasant	1.000	0.855	0.768	0.869
	Attractive	0.855	1.000	0.855	0.847
	Sexy	0.768	0.855	1.000	0.798
	Like...	0.869	0.847	0.798	1.000
		Voice			
		Pleasant	Attractive	Sexy	Like...
Voice	Attractiveness Score	0.886	0.937	0.889	0.929
	Pleasant	1.000	0.749	0.643	0.832
	Attractive	0.749	1.000	0.853	0.809
	Sexy	0.643	0.853	1.000	0.740
	Like...	0.832	0.809	0.740	1.000

Analysis

In this section, we describe the construction of the core estimation sample that we use in our primary analyses of agreement or interrater reliability. Most statistical methods developed for analyses of dyadic data were developed for at least one of three major data structures (see chapter 1 in Kenny et al., 2020). In a standard design, each subject is a member of exactly one dyad. In a social-relations model (SRM) design, each subject is paired with multiple others. For example, in a round-robin SRM design, each of the n subjects rates the remaining $n - 1$ subjects on some dimension. Finally, in a one-with-many design, each subject is paired with multiple others, but these others are not necessarily paired with the subject. In the design phase of our study, we opted for a

data structure that does not map cleanly onto any of these three common structures. Instead, our data were gathered in a way that allows us to generate subsamples that conform to each of the three structures. In effect, our strategy therefore enabled us to retain substantial versatility in the range of analyses possible, though often at the cost of limiting some of these analyses to a suitably selected subsample with the appropriate structure. For example, analyses developed for round-robin data are necessarily limited to a subset of data with groups of individuals who all rated each other.

In our analyses of interrater reliability, our goal was to evaluate how consistently raters assess each of three modalities of attractiveness: face, odor and voice. In the literature, quantifying the amount of consistency by reporting a parameter from the family of intraclass correlation coefficients is common. Besides facilitating comparability with the prior literature, we also chose a methodology that would retain as much of the data as possible and allow us to compare the consistency of rater evaluations across modalities (i.e., Is rater agreement similar for evaluations of faces and odor?) and across sexes (i.e., Are female and male rater agreements for a specific modality similar in magnitude?).

Shrout and Fleiss (1979) and McGraw and Wong (1996) describe 10 different versions of the ICC. Each parameter is defined within a general framework in which each of n targets (or in this context, donors) is evaluated by k raters. Targets are indexed by $i = 1, \dots, n$ and raters are indexed by $j = 1, \dots, k$. When the k raters rating each target are the same, common practice is to rely on a model in which rater j 's evaluation of donor i 's sample is assumed to be determined by:

$$y_{ij} = \mu + d_i + r_j + u_{ij},$$

where μ is the population mean, d_i is a donor random effect, r_j is a rater random variable, and u_{ij} is a random disturbance. We make the conventional assumption that

the random effects are mutually independent and that each random effect is normally distributed with mean 0.

Our first measure of consistency is then the individual-agreement ICC parameter, $\rho_{A,1}$, defined as the correlation between two individual ratings of the same donor. Under the assumptions of the two-way random effects model, it can be shown that:

$$\rho_{A,1} = \text{Corr}(y_{ij}, y_{ij'}) = \frac{\sigma_d^2}{\sigma_d^2 + \sigma_r^2 + \sigma_u^2}$$

where σ_d^2 , σ_r^2 , and σ_u^2 are, respectively, the variances of random variables d_i , r_j and u_{ij} .

Some texts refer to the parameter as the individual AA-ICC or the ICC(1) (e.g. McGraw & Wong, 1996).

Our second measure of consistency is the correlation between two average measurements of size k taken on the same donor, $\rho_{A,k}$. Again, under the assumptions of our model, this average-agreement ICC can be written as:

$$\rho_{A,k} = \text{Corr}(\bar{y}_{ij}, \bar{y}_{ij'}) = \frac{\sigma_d^2}{\sigma_d^2 + (\sigma_r^2 + \sigma_u^2)/k}$$

Some texts refer to this parameter as the average AA-ICC or the ICC(k) (e.g., McGraw & Wong, 1996).

The two parameters we estimate in our empirical analyses below are known as measures of so-called absolute agreement, meaning the variance from systematic differences across raters, σ_c^2 , is included in the denominator.⁵ When the same k raters evaluate each donor, the two ICCs defined above can be estimated consistently by replacing each of the three parameters in the formulae above by an unbiased estimate

⁵ In preliminary analyses not shown here, we found that rater effects account for a non-negligible account for variance, implying that it would be inappropriate to rely on a model that assumes that systematic differences across raters do not contribute to outcome variance.

of the variance component in question. Given this data structure, these variance component estimators are easily derived using standard analysis of variance (ANOVA) procedures.

Estimation Sample

To construct our estimation sample estimate, we partitioned our original dataset into several subgroups, each of which can be thought of as a small round-robin study with a fixed number of men and women rating each other (see Table 11 for descriptive statistics). Each of the four women in a subgroup rated each of the four men, and vice versa. We chose the subgroups to maximize the overall sample size, subject to two constraints. First, we did not allow any overlap across subgroups and second, we required all ratings within a subgroup to be non-missing. We were able to identify nine independent 4×4 subgroups from which we can define a total of 288 dyads with non-missing data. To probe the robustness of our findings to alternative sample inclusion criteria, we also reran our analyses in a sample of individuals who complied with the behavioral, fragrance and showering guidelines analyzed in Table 9. These analyses were conducted in a smaller sample of six independent 4×4 subgroups due to the more restrictive inclusion criteria.

Table 11

Descriptive statistics for the estimation sample.

	Men	Women
<i>N</i>	36	36
Age	20.50 ± 1.45	19.56 ± 1.04
Single (%)	52.8	69.4
White %	61.1	52.7
Black (%)	8.3	5.5
Hispanic (%)	5.5	8.3
Asian (%)	25.0	30.5

Estimation

For each modality, our empirical approach is to estimate, separately for men and women, the parameter of interest in each of the subgroups, $b = 1, \dots, n$. If we denote this parameter vector,

$$\hat{\boldsymbol{\theta}} = \{\hat{\theta}^1, \hat{\theta}^2, \dots, \hat{\theta}^{n-1}, \hat{\theta}^n\},$$

our estimator is simply the unweighted average across subgroups:

$$\hat{\theta} = \frac{1}{n} \sum_{b=1}^n \hat{\theta}^b = f(\hat{\boldsymbol{\theta}}).$$

To generate approximately valid standard errors for hypothesis tests and confidence intervals, we rely on a block jackknife procedure that exploits the independence across subgroups. The procedure takes the data vector with n estimates and generates nine unique delete-1 Jackknife samples, where the b th delete-1 Jackknife sample is simply $\hat{\boldsymbol{\theta}}_b = \hat{\boldsymbol{\theta}} \setminus \hat{\theta}^b$. The b th jackknife replication of $\hat{\theta}$ is defined as $\hat{\theta}_b = f(\hat{\boldsymbol{\theta}}_b)$ and the jackknife standard error is defined by:

$$SE(\hat{\theta}) = \sqrt{\left(\left(\frac{n-1}{n} \right) \sum_{b=1}^n \left(f(\hat{\theta}_b) - \bar{f}(\hat{\theta}) \right)^2 \right)}$$

where $\bar{f}(\hat{\theta}) = \frac{1}{n} \sum_{b=1}^n f(\hat{\theta}_b)$. In our empirical applications, we use this procedure to estimate the ICCs for each of the three modalities, separately by sex, and to compare male and female interrater agreement on a specific modality. For each sex separately and each modality, we estimate $\rho_{A,1}$ and $\rho_{A,4}$. Within each sex and for each ICC, we also estimate the difference in agreement across all three pairwise combinations of attractiveness modalities. Finally, we estimate, for each modality of attractiveness, the difference between the male agreement parameter and the female agreement parameter.

Results

First, we examined whether the body odor of some men and women are consistently judged as more or less attractive by the opposite sex, as well as consistency in judgments of face- and voice-attractiveness ratings. This approach allowed us to compare evidence of shared attractiveness preferences across modalities. Table 12 reports the individual-agreement ICC (Panel A) and the average-agreement ICC (Panel B) for male and female ratings of opposite-sex donors in each modality (i.e., face, odor, and voice), as well as differences between male and female estimates. The individual-agreement ICC estimates indicate low (< 0.4; Cicchetti, 1994) consistency for female attractiveness ratings of male faces ($\hat{\rho}_{A,1}^F = 0.30$), body odors ($\hat{\rho}_{A,1}^F = 0.27$) and voices ($\hat{\rho}_{A,1}^F = 0.36$). Likewise, the individual-agreement estimates indicate low consistency for male attractiveness ratings of female faces ($\hat{\rho}_{A,1}^M = 0.21$), body odors ($\hat{\rho}_{A,1}^M = 0.24$) and voices ($\hat{\rho}_{A,1}^M = 0.23$). The estimated average-agreement parameter estimates indicate fair to good (0.5 – 0.75; Cicchetti, 1994) consistency for female

attractiveness ratings of male faces ($\hat{\rho}_{A,4}^F = 0.55$), body odors ($\hat{\rho}_{A,4}^F = 0.53$), and voices ($\hat{\rho}_{A,4}^F = 0.66$). For male attractiveness ratings of females, consistency is low to fair for faces ($\hat{\rho}_{A,4}^M = 0.38$), body odors ($\hat{\rho}_{A,4}^M = 0.44$), and voices ($\hat{\rho}_{A,4}^M = 0.44$) (see also Figure 3)

Columns (8) through (10) of Table 12 show the estimated magnitude of the difference between the male and the female rater agreement for each modality. The estimated female *individual* rater agreement is always greater than the estimated male agreement. However, the standard error of each estimated sex difference is too large to allow us to draw any strong conclusions from this observation. For the average-agreement parameters, the sex differences follow a qualitatively similar pattern. But again, the standard errors are too large to provide any meaningful information about the phenomenon of interest. For a graphical illustration, the estimates and the associated 95% CI are depicted in Figure 4. Despite a sample size that compares favorably to those in most studies in this literature, even larger samples are needed for well-powered and informative analyses of sex differences in rater agreement. For example, consider the sex difference in average-agreement ICC with the smallest standard error: 0.14 (voice). Assuming the sampling distribution of $\hat{\Delta}$ is normal with mean Δ and standard deviation 0.14, our study's power to detect a true effect size of Δ at the 5% significance level is approximately (Gelman & Carlin, 2014):

$$1 - \Phi(1.96 - \Delta/0.14) + \Phi(-1.96 - \Delta/0.14)$$

where Φ denotes the normal cumulative distribution function. Figure 3 shows how the statistical power varies depending on the true effect size. Our study was clearly underpowered to detect even true effect sizes as large as 0.20 in absolute value. Since we believe that the true effect sizes are smaller than 0.20 (in absolute magnitude), we

emphasize that our study's estimates, considered in isolation, only contribute modestly to meaningfully reducing uncertainty about the range of true effect sizes that should be considered plausible.

Table 12

Individual-agreement (Panel A) and average-agreement (Panel B) intraclass correlations for male and female ratings of opposite-sex donors' faces, odors, and voices

Female Raters			Male Raters			Sex Differences			
$\hat{\rho}_{A,K}^F$			$\hat{\rho}_{A,K}^M$			$\Delta = \hat{\rho}_{A,K}^F - \hat{\rho}_{A,K}^M$			
(1)	(2)	(3)	(5)	(6)	(7)	(8)	(9)	(10)	
Face	Odor	Voice	Face	Odor	Voice	Face	Odor	Voice	
Panel A. Individual Agreement ($K=1$)									
Estimate	0.301	0.274	0.364	0.211	0.240	0.230	0.091	0.034	0.134
Jackknife SE	[0.079]	[0.060]	[0.059]	[0.081]	[0.082]	[0.077]	[0.131]	[0.098]	[0.113]
<i>P</i>	1x10 ⁻⁴	5x10 ⁻⁶	7x10 ⁻¹⁰	0.009	0.003	0.003	0.488	0.729	0.237
Panel B. Average Agreement ($K=4$)									
Estimate	0.546	0.533	0.660	0.384	0.440	0.440	0.163	0.093	0.219
Jackknife SE	[0.088]	[0.090]	[0.055]	[0.116]	[0.110]	[0.103]	[0.173]	[0.150]	[0.136]
<i>P</i>	7x10 ⁻¹⁰	4x10 ⁻⁹	0x10 ⁰	0.001	6x10 ⁻⁵	0.000	0.347	0.535	0.106

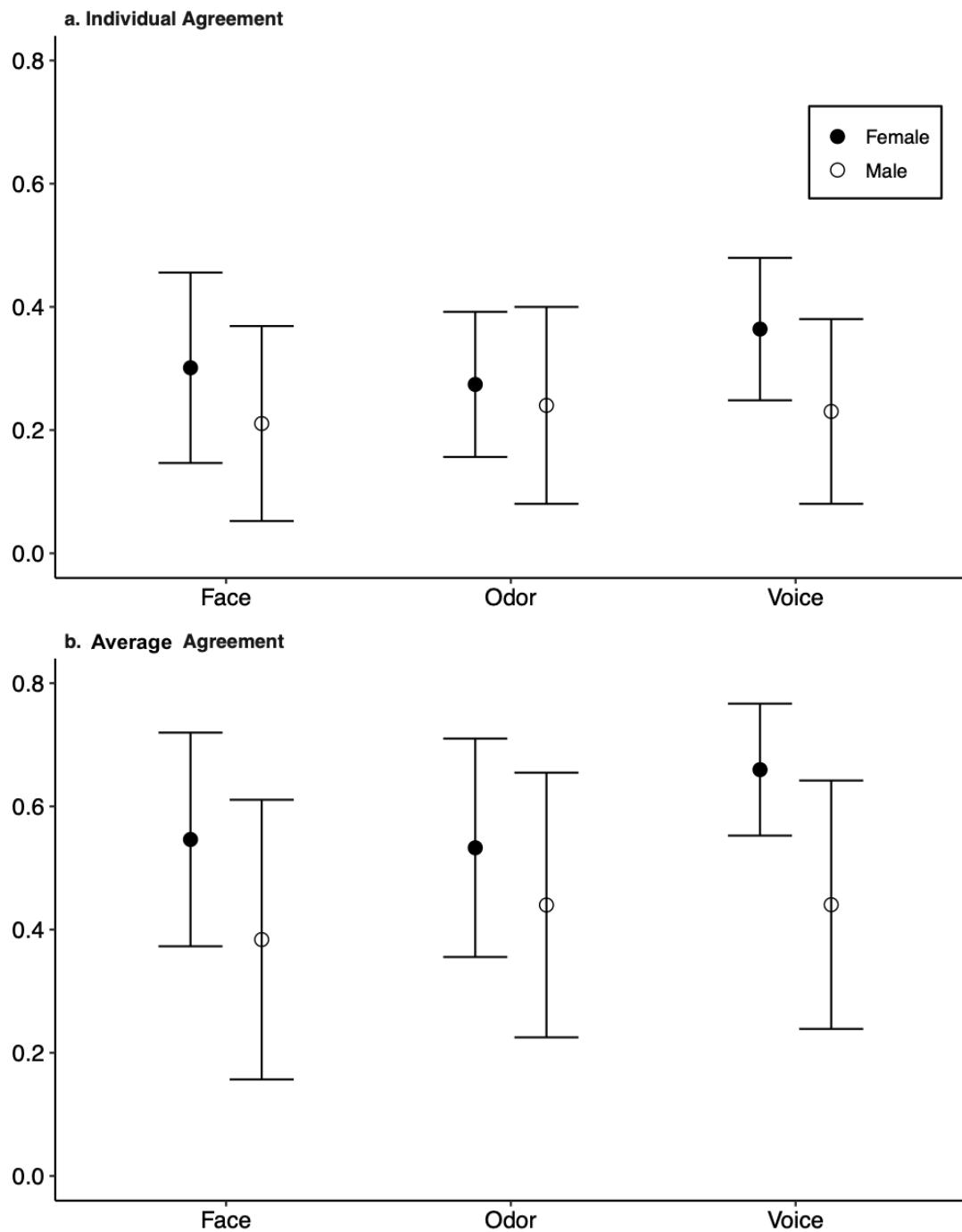


Figure 3. Intraclass Correlation Coefficients: Individual Agreement & Agreement between Average Measurements of Size $k = 4$. This figure displays estimates of the $\rho_{A,1}$ parameter (a) and estimates of the $\rho_{A,k}$ parameter (b) for the three modalities of attractiveness: face, odor and voice. Estimates are based on the two-way random effects model defined in the main text and are reported separately by sex (female raters on the left and male raters on the right). The 95% confidence intervals are constructed from jackknife standard errors, using procedures described in the main text.

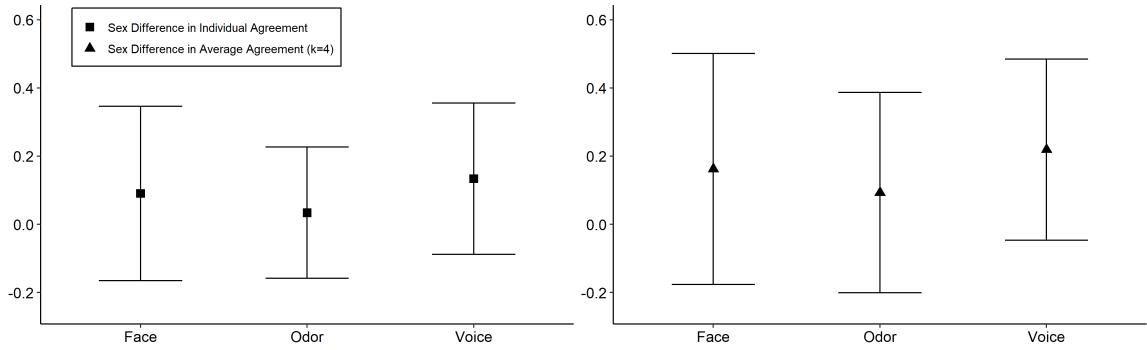


Figure 4. Sex Differences in Interrater Agreement. This figure shows the estimated sex difference ($\hat{\rho}_{A,k}^F - \hat{\rho}_{A,k}^M$) in interrater agreement for each of the three modalities of attractiveness. The left panel reports the difference in individual agreement ($\hat{\rho}_{A,1}^F - \hat{\rho}_{A,1}^M$) and the right panel shows results for agreement between measurements of size $k = 4$. The 95% confidence intervals are constructed from jackknife standard errors, using procedures described in the main text.

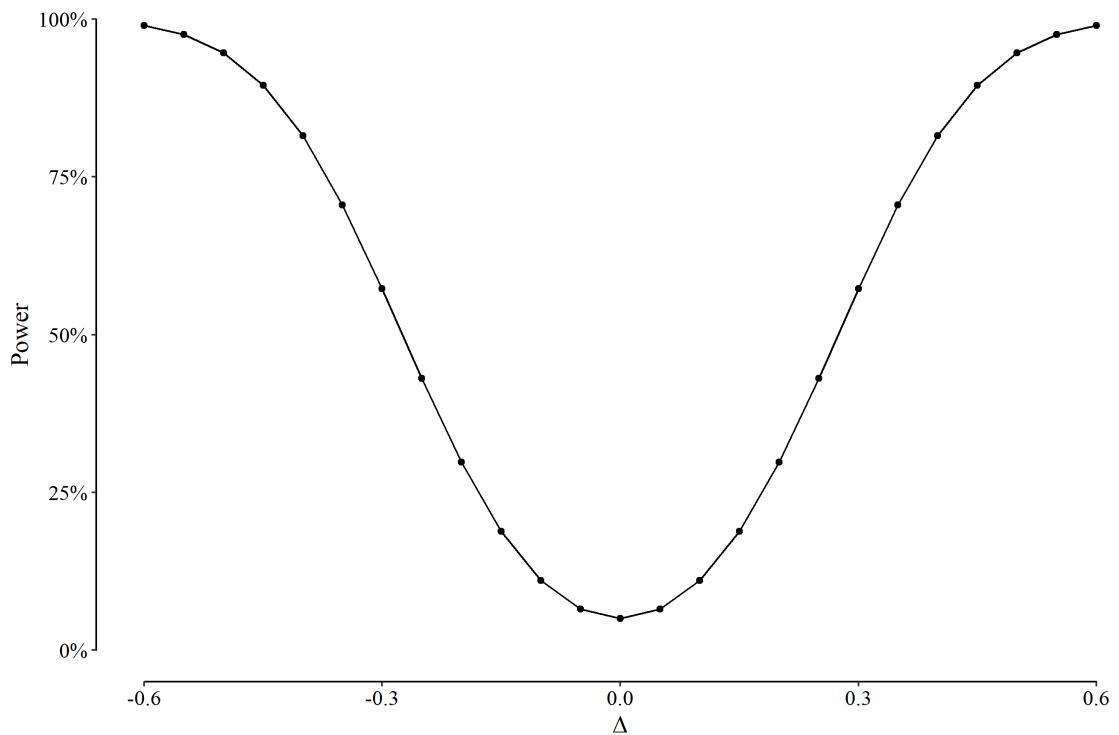


Figure 5. The Power to Detect Sex Differences in Rater Agreement. This figure shows how statistical power varies dependent on true effect size. Our study is underpowered to detect a true effect size as large as 0.20 in absolute value.

Next, we compared levels of consistency in attractiveness judgments across modalities. The results are summarized in Figure 6. See Table 13 for the underlying data. No statistically significant differences exist, and the point estimates in Table 13 are roughly similar in magnitude across the modalities. The results are consistent with interrater agreements that are very similar in magnitude across modalities, across both men and women.

Finally, to probe the robustness of the results reported in Table 12, we reran the analyses in a sample of subjects who complied with behavioral, diet and fragrance guidelines. The results of these analyses are shown in Table 14. As expected, the estimates are not as statistically precise as those from our preferred, larger, estimation sample. However, the overall pattern of results is qualitatively similar, with a tendency for consistency to be slightly higher than in the main analyses. Again, the individual-agreement ICC estimates indicate low (< 0.4 ; Cicchetti, 1994) consistency for female attractiveness ratings of male faces ($\hat{\rho}_{A,1}^F = 0.36$), body odors ($\hat{\rho}_{A,1}^F = 0.35$) and voices ($\hat{\rho}_{A,1}^F = 0.35$). Likewise, the individual-agreement estimates indicate low consistency for male attractiveness ratings of female faces ($\hat{\rho}_{A,1}^M = 0.25$), body odors ($\hat{\rho}_{A,1}^M = 0.11$) and voices ($\hat{\rho}_{A,1}^M = 0.16$). The estimated average-agreement parameter estimates indicate fair to good (0.5 – 0.75; Cicchetti, 1994) consistency for female attractiveness ratings of male faces ($\hat{\rho}_{A,4}^F = 0.63$), body odors ($\hat{\rho}_{A,4}^F = 0.60$), and voices ($\hat{\rho}_{A,4}^F = 0.56$). For male attractiveness ratings of females, consistency is low for faces ($\hat{\rho}_{A,4}^M = 0.36$), body odors ($\hat{\rho}_{A,4}^M = 0.27$), and voices ($\hat{\rho}_{A,4}^M = 0.32$)

Table 13

Comparisons of agreement across pairwise combinations of attractiveness modalities reveal no differences.

	Female Raters			Male Raters		
	(1)	(2)	(3)	(4)	(5)	(6)
	Δ Face-Odor	Δ Face-Voice	Δ Odor-Voice	Δ Face-Odor	Δ Face-Voice	Δ Odor-Voice
Panel A. Individual Agreement (K=1)						
Estimate	0.027	-0.063	-0.090	-0.029	-0.020	0.010
Jackknife SE	[0.072]	[0.090]	[0.053]	[0.079]	[0.125]	[0.112]
<i>P</i>	0.707	0.487	0.089	0.708	0.875	0.930
Panel B. Average Agreement (K=4)						
Estimate	0.014	-0.113	-0.127	-0.056	-0.057	0.000
Jackknife SE	[0.079]	[0.095]	[0.076]	[0.109]	[0.166]	[0.157]
<i>P</i>	0.864	0.231	0.094	0.608	0.734	0.998

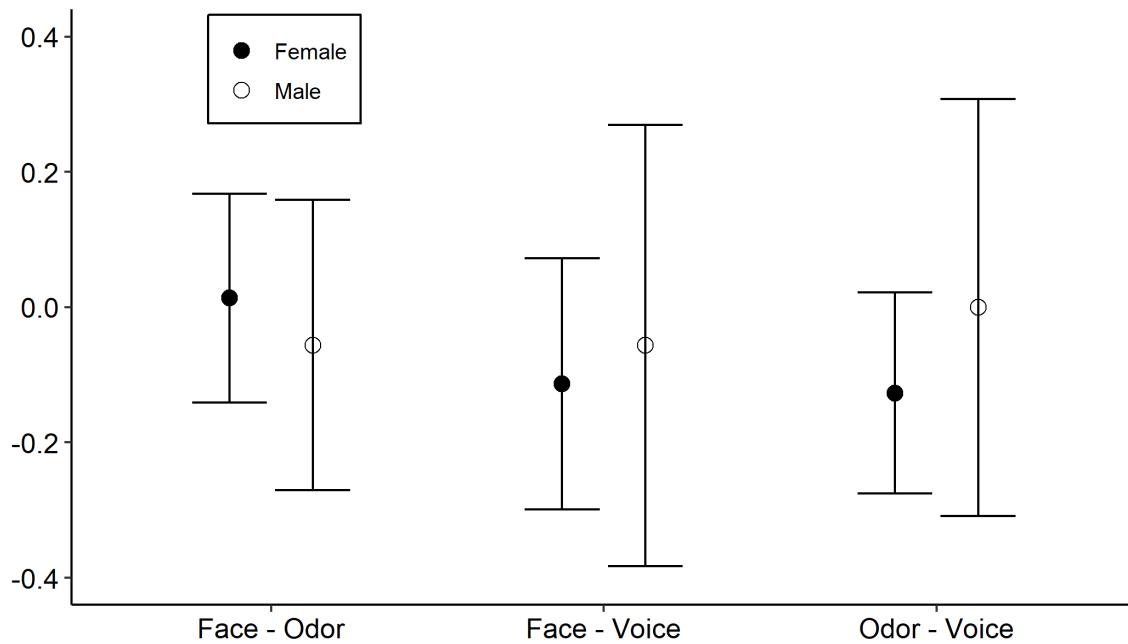


Figure 6. Cross-Modality Similarity in Rater Agreement. The figure shows, separately for each sex, the estimated differences in interrater agreement across the three pairwise combinations of modalities: face vs. odor, face vs. voice, and odor vs. voice. All results shown are for agreement between measurements of size $k = 4$ ($\rho_{A,k=4}$). The upper panel shows results for men and the lower panel shows results for women. The 95% confidence intervals are constructed from jackknife standard errors, using procedures described in the main text.

Table 14

Robustness analyses excluding any subject who did not comply with behavioral, fragrance, or showering guidelines. Individual-agreement (Panel A) and average-agreement (Panel B) intraclass correlations for male and female ratings of opposite-sex donors' faces, odors, and voices.

Female Raters				Male Raters				Sex Differences			
$\hat{\rho}_{A,K}^F$				$\hat{\rho}_{A,K}^M$				$\Delta = \hat{\rho}_{A,K}^F - \hat{\rho}_{A,K}^M$			
(1)	(2)	(3)	(5)	(6)	(7)	(8)	(9)	(10)			
Face		Odor		Voice		Face		Odor		Voice	
Panel A. Individual Agreement ($K=1$)											
Estimate	0.358	0.352	0.351	0.249	0.109	0.159	0.109	0.243	0.192		
Jackknife SE	[0.085]	[0.090]	[0.113]	[0.140]	[0.048]	[0.085]	[0.195]	[0.085]	[0.140]		
<i>P</i>	2.5x10 ⁻⁵	9.4x10 ⁻⁵	1.9x10 ⁻³	0.075	0.024	0.060	0.575	0.004	0.172		
Panel B. Average Agreement ($K=4$)											
Estimate	0.634	0.603	0.556	0.364	0.272	0.318	0.270	0.331	0.238		
Jackknife SE	[0.094]	[0.130]	[0.158]	[0.173]	[0.104]	[0.136]	[0.230]	[0.125]	[0.193]		
<i>P</i>	1.7x10 ⁻¹¹	3.6x10 ⁻⁶	4.3x10 ⁻⁴	0.035	0.009	0.020	0.242	0.008	0.216		

Discussion

Possibly the most conclusive and replicable finding in social psychology is that attractiveness is an important factor in social interactions (for review see, Grammer et al., 2003). Symons (1979) suggested shared attractiveness preferences are evolved adaptations for choosing fitness-enhancing mates, and since the 1990s, evidence has accumulated demonstrating shared attractiveness preferences for others' faces (e.g., Grammer & Thornhill, 1994; Langlois & Roggman, 1990; Mealey et al., 1999; Perrett et al., 1999; Rhodes et al., 1998, 1999; Rhodes & Tremewan, 1996), bodies (e.g., Singh, 1993; Singh et al., 2010; Singh & Young, 1995), and voices (Collins, 2000; Feinberg,

Jones, Little, et al., 2005; Puts et al., 2013). Research into whether similar patterns exist for body odor preferences has largely been neglected.

We investigated whether some men and women generally smell more or less attractive to the opposite sex. Moreover, to provide a benchmark from which we could assess evidence for agreement in judgments of body odors, we used the same methodology and analysis to also examine whether some men and women generally look and sound more or less attractive to the opposite sex. We found little agreement in female ratings of men's attractiveness for faces, voices, and body odors using the individual-agreement ICC. However, we found fair to good agreement in all attractiveness modalities using the mean-agreement ICC ($k = 4$). For male ratings of women's attractiveness, we found that agreement in the attractiveness modalities was statistically distinguishable from zero but low. Yet, encouragingly, we report statistically equivalent levels of agreement in judgments of attractiveness for each modality of attractiveness within both sexes.

Although our estimated agreement for within-sex judgments of opposite-sex attractiveness in each modality (i.e., face, voice, and odor) seems lower than estimates reported in earlier studies, the parameters we used were different and not readily comparable to prior literature. For example, Thornhill and Gangestad (1999) measured consistencies for male ($n = 61$) and female ($n = 48$) ratings of opposite-sex body odors using Cronbach's alpha ($\alpha = 0.66$, high-fertility female raters; $\alpha = 0.90$, low-fertility female raters; $\alpha = 0.90$, male raters). Similarly, Lobmaier and colleagues (2018) reported an ICC of 0.983 for male ($n = 55$) ratings of women's ($n = 28$) body odors. As discussed at length elsewhere (Flake, Pek, & Hehman, 2017; Hönekopp, 2006), high alphas and ICC estimates do not necessarily provide evidence of strong interrater agreement. The fundamental difficulty is that these parameters are strongly influenced by the number of

items (here, raters), which often varies across studies, hampering comparability. Likewise, an ICC near one is very hard to interpret unless which of the many possible ICCs have been estimated is made explicit (McGraw & Wong, 1996). Through personal correspondence (June 8, 2020), we were able to determine that the parameter estimated by Lobmaier et al. (2018) was the average-agreement ICC for their $n = 55$ male raters. Because their study estimated a different parameter than the present study, the lower estimates we have reported are not at odds with what they found. On the contrary, the value of $\rho_{A,1}$ implied by Lobmaier et al.'s (2018) estimate of $\rho_{A,55}$ is around 0.5 and hence, in the same ballpark as the estimates of individual agreement reported in the present study, see Bliese (2000) for the formulae needed to rescale parameter estimates for comparability.

Misinterpretations of Cronbach's alpha and the average-agreement ICC can cause overestimations of the strength of evidence for shared attractiveness preferences because the contribution of personal preference is typically unreported or defined as random noise (Hönekopp, 2006). Our analysis not only reported the average-agreement ICC ($k = 4$), which filters out some of the idiosyncratic component of any individual's ratings, but also the individual-agreement ICC, which reports the correlation between the individual judgments of two raters assigned to the same donor. The individual-agreement ICC parameters reported here show that there is some agreement between raters' ratings in each attractiveness modality that can be attributed to a shared preference, but a larger component also exists that can be attributed to personal preference and noise. Our ICC estimates are in line with recent research using statistical methods accounting for variance attributed to both donor (i.e., shared preference) and rater (i.e., personal preference) characteristics to investigate agreement in attractiveness judgments of faces (e.g., Hehman et al., 2017). Moreover, because we used a uniform

methodology and analysis across attractiveness modalities, we were able to directly compare the amount of variance explained by agreement in ratings of faces, voices, and body odors. Thus, any differences in variance attributable to agreement between modalities could not be caused by differences in the sample or analysis. We found no significant differences in levels of agreement in attractiveness ratings between modalities. So, although we cannot make a strong claim for evidence of evolved attractiveness preferences, especially because we are unsure of how much agreement would constitute evidence, our data do demonstrate that to the degree that shared preferences exist for faces and voices, they also exist for body odors.

What underlying variables related to mate quality may be involved in shared body odor preferences? One possible contributor is reproductive hormones that convey information about fecundity and social dominance. Lobmaier et al. (2018) found men's judgments of women's body odor were positively correlated with women's oestradiol and negatively correlated with their progesterone. Endogenous levels of oestradiol and progesterone, within the normal range, are significant indicators of fecundity (Baird et al., 1999; Lipson & Ellison, 1996b) and thus of female fitness. Similarly, the immunocompetence handicap hypothesis of sexual selection predicts men's testosterone levels will positively correlate with secondary sexual characteristics because only men in prime condition can develop and maintain those costly traits (Folstad & Karter, 1992; Zahavi, 1975; but see, Nowak et al., 2018). Suggestively, studies find that near ovulation, women judge the odor of testosterone (Thornhill et al., 2013; but see, Rantala et al., 2006) as well as a testosterone precursor, androstenone, more favorably (Grammer, 1993; Hummel et al., 1991). Moreover, women prefer the body odor of socially dominant men, whose levels of testosterone are believed to be higher than less socially dominant men (Havliček et al., 2005; Sorokowska et al., 2012).

The association between reproductive hormones and judgments of body odor attractiveness may be explained by varying ratios of hormone metabolites between and within the sexes. While hormone metabolites are initially odorless, interactions with microorganisms present in the axillae cause the release of odors (for review see, Natsch & Emter, 2020). Thus, the amount and/or ratio of hormone metabolites present as odor-precursors in axillary sweat may cause a relationship between circulating hormones and body odor judgments.

Another possibility is that donor HLA genes influence raters' perceptions of body odor. The HLA gene family is divided into three classes with class I and class II coding for proteins primarily involved in the functioning of the immune system (Hedrick, 1994; Janeway, 1993; J. Klein, 1986; for review see, Knapp, 2005). HLA genes are the most polymorphic in the human genome and because both alleles at each HLA locus are expressed, researchers hypothesize that heterozygous individuals exhibit a selective advantage (for reviews see, Penn et al., 2002; Penn & Potts, 1999). Mate choice may be influenced by HLA allelic diversity because pathogens have exerted a strong selection pressure throughout human evolution (Fumagalli et al., 2011). In fact, studies reveal correlations between HLA alleles and an individual's susceptibility to various infectious diseases, such as HIV (Trachtenberg et al., 2003), tuberculosis (Sveinbjornsson et al., 2016), leprosy (Krause-Kyora et al., 2018), and malaria (Hill et al., 1991). Researchers speculate that a population's epidemic and demographic history can explain the high variance in the frequency of HLA alleles across populations (Prugnolle et al., 2005). Whereas earlier studies found that, across vertebrates, including humans, individuals prefer HLA- (i.e., MHC in non-human vertebrates) dissimilar mates (e.g., Egid & Brown, 1989; Potts et al., 1991; Santos et al., 2005; Thornhill et al., 2003; Wedekind et al., 1995; Wedekind & Furi, 1997; Yamazaki et al., 1976; for reviews see, Boyse et al., 1987;

Jordan & Bruford, 1998; Potts & Wakeland, 1993), recent meta-analyses reveal this preference is weak in non-human primates (Kamiya et al., 2014) and non-significant in humans (Havlíček et al., 2020; Winternitz et al., 2017). If anything, results suggest that humans prefer HLA-diverse (i.e., heterozygous) individuals (Winternitz et al., 2017). Thus, agreement in body odor attractiveness ratings could indicate a shared preference for mates expressing HLA-heterozygosity. Some men and women may generally smell better or worse to others because of high or low HLA allelic diversity; however, the mechanism through which HLA haplotype is communicated via body odor is unknown.

Other possibilities include health status and diet because both have been shown to alter body odor. While there are few studies investigating disease and odor preferences, evidence suggests that body odors from unhealthy and healthy donors are perceptually distinguishable and that body odor from unhealthy donors is more aversive (Olsson et al., 2014; Sarolidou et al., 2020). In fact, Moshkin (2012) found body odor from patients infected with gonorrhea is rated less pleasant than body odor from recently recovered and healthy patients. Dietary influences on body odor preferences are similarly understudied, but humans consume a variety of aromatic foods (e.g., garlic, cabbage, red meat, and spices) that can modify body odor (for review see, Havlíček et al., 2019). Body odor samples from monozygotic twins are often indistinguishable unless their diets vary (Wallace, 1977). Donors who maintain a vegetarian diet have been shown to produce less intense and more attractive body odors than donors who consume at least one red meat dish daily (Havlíček & Lenochova, 2006). Interestingly, some species exhibit assortative mating according to diet. For example, fruit flies fed a starch diet prefer to mate with other fruit flies also fed a starch diet, whereas fruit flies fed a sugar diet prefer to mate with other fruit flies fed a sugar diet (Ma et al., 2015). While further research is required, body odor might communicate cultural and environmental

information about an individual via the foods that they consume. Moreover, body odor may be used to assess the quantity and quality of foods eaten by potential mates (for review see, Fialová et al., 2013).

Though our findings support the hypothesis that shared preferences for body odors exist to the extent that shared preferences for faces and voices exist, convenience sampling limits the strength of our interpretation. The current study cannot fully distinguish between attractiveness preferences shaped by evolution and preferences transmitted culturally, because we investigated preferences in a single society. In general, cross-cultural research on odor perception is scant, particularly for mate choice. However, evidence shows that in traditional societies where odor is more significant to daily activities, such as food foraging, olfactory performance and cognition are superior to those of individuals living in industrialized cities (Burenhult & Majid, 2011; Majid & Burenhult, 2014; Majid & Kruspe, 2018; Sorokowska et al., 2013; Wnuk & Majid, 2012). Future research should investigate body odor preferences cross-culturally. Facial averageness and symmetry are generally accepted as cues of mate quality, in part because both predict attractiveness judgments in many different societies (e.g., Apicella et al., 2007; Cunningham et al., 1995; D. Jones & Hill, 1993; Little et al., 2007; Rhodes et al., 2001). Although demonstrating that, to a degree, some men and women generally smell better than others is a promising first step, additional steps must be taken before we can conclude body odor preferences are adaptations for optimal mate selection.

Furthermore, outside of a controlled laboratory setting, humans often wear fragrances, shower, and choose to eat food regardless of their aromatic properties. While controlling for these variables by instituting a two-day washout period before odor sampling is standard procedure in this literature, we are unaware of studies demonstrating that two days are adequate to return a donor's "natural" body odor. Thus,

these methods could result in evidence that raters agree on odors but not necessarily "natural" body odors.

The human olfactory system is highly sensitive and discriminating. Moreover, a growing body of research suggests olfaction influences attractiveness and mate selection. The current study adds to our understanding of the role of body odor in attraction, by finding agreement in attractiveness judgments of others' body odors comparable to the agreement found with faces and voices. Therefore, olfactory attractiveness, similar to physical and vocal attractiveness, should be considered a research area worth more rigorous investigation.

Chapter 3 References

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CHAPTER 4: JUDGMENTS OF WOMEN'S ODOR, FACE, AND VOICE

ATTRACTIVENESS COVARY, BUT NOT MEN'S

Human mate value is thought to be assessed on numerous variables including, reproductive potential and disease resistance. Many of these variables have been correlated with judgments of physical, vocal, and odor attractiveness. Some researchers posit that attractiveness judgments made across different sensory modalities reflect the same underlying variable(s) (i.e., the information is redundant); others suggest that judgments made in different modalities reflect different variables. Studies of human attractiveness indicate that attractiveness judgments of others' faces, bodies, and voices are intercorrelated, which is suggested to support the redundancy hypothesis. Less is known about body odor attractiveness because only a single study has simultaneously investigated the relationships between judgments of body odor, face, and voice attractiveness. Here, men and women independently rated the attractiveness of opposite-sex participants' body odors, faces, and voices, comprising the largest number of observations to date ($n = 1,284$ ratings). For men, we found no evidence of covariance between modalities of attractiveness. However, our findings suggest that for women there is weak covariance between odor, face, and voice attractiveness and, moreover, that a general attractiveness factor (i.e., a common underlying variable) modestly contributes to the observed covariances between modality-specific attractiveness judgments, providing some evidence for the redundancy hypothesis.

Introduction

Person perception often entails rapid and spontaneous judgments, including judgments of attractiveness (e.g., Willis & Todorov, 2006). Attractive individuals fare better on diverse measures of economic, health, and social outcomes (Hamermesh, 2011; Hosoda et al., 2003). Predictably, a voluminous research literature has considered the factors underlying attractiveness judgments, with most attention paid to visual inputs (e.g., faces) and, to a lesser extent, auditory inputs (i.e., voices). Even less work has considered the role of odor in attractiveness judgments, in part, because humans have been inaccurately labeled as poor smellers (Laska, 2011; McGann, 2017; Schaal & Porter, 1991; Shepherd, 2004). However, most consequential social interactions, including those involving courtship and mating, usually occur in-person where information about individuals can be readily extracted from how a person looks, sounds, and smells. Yet, few studies have examined these inputs simultaneously, despite scientific consensus that person perception (e.g., Zuckerman, Kunitate, & Elkin, 1995; Zuckerman, Miyake, & Hodgins, 1991; Zuckerman & Sinicropi, 2011), and specifically attractiveness judgements (for review see, Groyecka et al., 2017), involve multisensory inputs. Such data is important for assessing the extent to which each of these sensory modalities provide unique, rather than redundant information.

Attractiveness preferences are thought to be evolved species-typical adaptations for choosing high quality mates (Symons, 1979); that is, mates who are able to successfully interact with their social and physical environments to acquire resources and reproduce (Andersson, 1994; Darwin, 1874; Fisher, 1915). Human attractiveness judgments are multimodal, such that they involve more than one sensory input. The reason for this multimodality is debated, with arguments stemming from research on the evolution of animal signaling and sexual selection for multiple ornaments. One

hypothesis, the redundancy (or ‘back up’) hypothesis, states that multiple traits provide redundant or overlapping information about mate quality (Møller & Pomiankowski, 1993). Redundancy can work to amplify messages, thus making them more detectable and memorable (for review see, Wiley, 1983). Redundancy is also beneficial in situations where messages are unreliable and communication channels are prone to disruption. Having multiple channels through which to communicate information helps to ensure the message is received (for reviews see, Johnstone, 1997; Wiley, 1983). Moreover, redundancy can reduce dishonesty in signaling⁶ because only individuals of high quality would have the resources necessary to produce multiple traits communicating the same information (Møller & Pomiankowski, 1993; for reviews see, Candolin, 2003; Johnstone, 1997; Johnstone, 1996). In contrast, the multiple messages hypothesis states that each trait broadcasts unique information regarding an individual’s mate quality (Johnstone, 1995, 1996; for reviews see, Candolin, 2003; Johnstone, 1997). Multiple messages may be evaluated together and indicate an individual’s overall mate quality, or different receivers may attend to different components in accordance with their own condition and genetic makeup (for review see, Candolin, 2003).

To assess whether redundant or unique information is being conveyed by different traits, human attractiveness researchers have typically started by examining 1) whether multiple sensory modalities independently affect global assessments of attractiveness and, 2) correlations between attractiveness judgments in different modalities.

⁶ There is debate in human olfaction literature whether the term “signal” or “cue” is appropriate. I do not enter this debate here. By definition, a signal evolved for communication between a sender and a perceiver, and a cue is any feature of the world that can be used to guide behavior (Smith, Harper, & Harper, 1995). For example, the release of CO₂ by an organism guides mosquitoes to its location. In this context, CO₂ is a cue as its release by the organism was not evolutionarily selected to convey location to mosquitoes.

Relatively few studies have compared the contributions of different sensory modalities to overall (i.e., global) judgments of attractiveness. In fact, this literature has largely been limited to how different visual inputs contribute to overall judgements of physical attractiveness. Findings suggest that both faces and bodies (e.g., T. A. Brown et al., 1986; Mueser et al., 1984; Peters et al., 2007) independently contribute to overall perceptions of attractiveness. For example, Peter, Rhodes, & Simmons (2007) found that when photographs of women were examined, facial attractiveness accounted for 47% of variance in overall attractiveness, while body attractiveness accounted for 32%. For men's photographs, face and body accounted for 52% and 24%, respectively, of the variance in overall attractiveness. The remaining unexplained variance was not caused by an interaction between the modalities of attractiveness, but rather likely due to discrepancies in methodology between conditions. Less work has examined voices, but there is some evidence that voices independently contribute to global judgments of attractiveness as well (e.g., Oguchi & Kikuchi, 1997; Saxton et al., 2009; Wells et al., 2013; M. Zuckerman et al., 1991). These findings are often interpreted as evidence of multiple messages (i.e., unique information is conveyed by each modality of attractiveness). We are unaware of research that has explored the contribution of body odor to global judgments of attractiveness.

More commonly, researchers measure how attractiveness judgments across modalities correlate. This assessment has usually been restricted to faces and voices. Numerous studies report that women's facial and vocal attractiveness positively correlate, with the strength of the association ranging from weak ($r = 0.2$; Wells et al., 2013) to medium ($r = 0.5$; Abend et al., 2015) (Abend et al., 2015; Collins & Missing, 2003; Feinberg et al., 2005; Lander, 2008; Valentova et al., 2017; Wells et al., 2013; Zuckerman et al., 1995; but see, Zäske et al., 2018), however the same relationship is

generally not found in men (Lander, 2008; Valentova et al., 2017; Wells et al., 2013; Zäske et al., 2018; Zuckerman et al., 1995; but see, Saxton et al., 2006). In contrast to research demonstrating that sensory inputs independently contribute to measures of overall attractiveness, concordance between judgments of attractiveness is usually suggested to support the redundancy hypothesis (e.g., Feinberg, Jones, DeBruine, et al., 2005) because concordance is thought to indicate that a common trait, such as reproductive potential, is being communicated by each attractiveness modality. Thus, many researchers suggest that different attractiveness modalities in women convey redundant information, whereas in men they convey multiple, unique messages (e.g., Valentova et al., 2017; Wells et al., 2013).

Yet, neither research paradigm fully distinguishes between the redundancy and multiple messages hypotheses because the information being conveyed by different sensory modalities could be both concordant and unique. For example, a woman's face may indicate that she is highly immunocompetent while her voice may indicate that she has high reproductive potential. Both messages separately indicate high mate quality and judgments of her facial and vocal attractiveness may positively covary, but not necessarily because they reflect a common variable. Thus, once a correlation is established the next step is usually to determine the relationship between judgments of attractiveness and variables of mate quality, such as immunocompetency and reproductive potential (e.g., Wheatley et al., 2014). The present study also examines covariance between attractiveness modalities. However, unlike previous research in this field, the present study additionally estimates the relationship between each modality of attractiveness and a latent general factor of attractiveness. Consequently, our analysis will indicate how much a common trait contributes to the observed correlations between

modality-specific attractiveness judgments allowing us to better distinguish between the redundancy and multiple messages hypotheses.

While few studies have compared judgments of body odor attractiveness with other modalities of attractiveness, there is some evidence that judgments of odor and facial attractiveness are positively correlated in women (Rikowski & Grammer, 1999; Thornhill et al., 2003; Thornhill & Gangestad, 1999). For example, Rikowski & Grammer (1999) reported a strong correlation ($r = 0.70$), with a small sample of women ($n = 19$). Studies using somewhat larger samples, ($n = 65$) report weaker correlations $r \sim 0.25$ (Thornhill et al., 2003; Thornhill & Gangestad, 1999). Significant positive relationship between judgments of men's facial and odor attractiveness were only found when restricted to female raters between days 5 and 14 of their menstrual cycles (i.e., "high-fertility women"), however sample sizes were minuscule ($n = 14$ Rikowski & Grammer, 1999; $n = 13$; Thornhill & Gangestad, 1999). Finally, a recent study, using a speed dating setup, assessed the relationship between pre-date multimodal (i.e., visual, auditory, and olfactory) attractiveness ratings and post-date propensity to meet again, finding that only visual attractiveness ratings significantly positively correlated with post-date decisions. Moreover, results revealed weak positive correlations between ratings of visual and auditory, as well as visual and olfactory attractiveness, in both sexes. However, olfactory and auditory attractiveness ratings were not correlated (Roth et al., 2021).

Odor has likely received less attention partly because of the prevalent belief in both scientific and popular culture that humans have a poor sense of smell. This belief can be traced back to 19th century neuroanatomical work proposing that primates' comparatively smaller nasal annexes, olfactory epithelium, and olfactory bulb volume relative to total brain volume (e.g., Bauchot, 1981; Broca, 1879; Stephan, 1970; Turner,

1890) were evidence that primates, particularly humans, have a diminished olfactory system compared to other mammals. However, we now know that areas of the neocortex are involved in processing and perceiving olfactory inputs (e.g., Dade et al., 2002; Keverne, 1983; K. Neville & Haberly, 2004), which may suggest that the highly developed neocortex and neural pathways of the human brain are evidence of olfactory expertise. Furthermore, when olfactory acuity is tested, humans often have lower detection thresholds (i.e., greater sensitivity) to odorants than mammals that are known for their olfactory prowess, such as various species of rodents (for review see, Laska, 2017). Thus, the consensus on human olfactory abilities is now beginning to shift with many researchers even recognizing the importance of olfaction in humans, as with other mammals, for choosing mates (for review see, Pause, 2017).

In the current study, we simultaneously investigate the relationship between judgments of body odor, face, and voice attractiveness by having groups of men and women rate the attractiveness of opposite-sex participants independently for each modality (i.e., face, odor, and voice). If judgments of attractiveness do not covary between modalities, then this may suggest that each modality conveys unique information (i.e., multiple messages). On the other hand, evidence of concordance between modalities of attractiveness could indicate that overlapping (i.e., redundant) information is being conveyed. However, information conveyed by different modalities of attractiveness could be both concordant and unique. Thus, unlike previous research that has only investigated correlations between modalities, here we also estimate the relationship between each modality of attractiveness and a latent general factor of attractiveness. If we find evidence of concordance between ratings of odor, face, and voice attractiveness, then this analysis will help us differentiate between the redundancy and multiple messages hypotheses

Methods

Participants

We recruited $n = 102$ men and $n = 96$ women attending a large urban university using a web-based subject pool (SONA system) to take part in this study. Participants received course credit for participation. The study entailed 2 laboratory sessions that took place on different days. In the first session, participants were called “donors” because they provided an odor and voice sample, and had their photograph taken. In the second session, participants were called “raters” because they rated the attractiveness of a subset of opposite-sex participants’ odors, voices, and photographs. Participation in the second session occurred in same-sex groups of 1 to 9 participants (*Med.* = 4). An average of 5 study sessions were conducted 3 days per week from October 14, 2019 to December 9, 2019. There were 22 different second sessions with all male participants and 21 different seconds sessions with all female participants, in which a total of 1,284 opposite-sex attractiveness ratings were made.

Compliance

There are several variables that may affect olfactory performance, including smoking, nasal congestion, the inability to smell (i.e., smell loss), and medications. Thus, during the second study session, raters completed a survey pertaining to these variables prior to making any ratings. We assessed whether the variables affected their odor attractiveness and intensity ratings and found no evidence ratings were significantly affected (see Table 15); therefore, we felt justified including participants regardless of their responses to these questions.

Body odor may be modified by several variables, including diet, hygiene, and

contamination by other odor sources (e.g., other humans). Consequently, researchers interested in investigating “natural” body odor commonly initiate a two day washout period during which donors follow a set of dietary, behavioral, and hygiene guidelines meant to diminish the effects of extraneous variables (e.g., Zhou & Chen, 2009). While compliance measures may reduce ecological validity, they are necessary precautions to facilitate discussion of what underlying variables of mate quality may be conveyed via “natural” body odor. In addition, these measures reduce the likelihood that attractiveness preferences reflect cultural influences, such as diet, hygiene, and fragrance use. Odor compliance measures are similar to controlling for makeup, jewelry, and hair in studies of facial attractiveness. During the first study session, donors completed a compliance survey prior to body odor sampling. Compliance was generally high. However, we assessed whether diet (i.e., aromatic foods, such as spices and red meat), certain behaviors (i.e., strenuous exercise and sexual activity), fragranced products (e.g., lotion, perfume, deodorant), and showering affected odor attractiveness and intensity ratings and found that fragrance use led to significantly higher odor attractiveness ratings for both men and women, meaning that men and women wearing fragrances or deodorant were reported to smell better. Other compliance measures did not significantly affect odor attractiveness and intensity ratings when disaggregated by sex, which is how results are reported. However, when male and female ratings were pooled, noncompliance with behavior and shower guidelines were also associated with significantly higher odor attractiveness ratings (see Table 16).

Table 15

Comparison of odor attractiveness and intensity ratings between raters who did comply (i.e., C) or did not comply (i.e., NC) with smoking (i.e., nonsmoker), nasal congestion (i.e., no nasal congestion), lifetime smell loss (i.e., none), and medication usage (i.e., none) guidelines. Results are presented in full and disaggregated by sex.

	Smoker		Nasal Congestion		Smell Loss		Medication									
	C	NC	C	NC	C	NC	C	NC								
Female Raters																
Odor Attractiveness Ratings																
Mean	11.89	10.93	11.71	12.61	11.88	10.67	11.72	13.97								
SD	3.52	4.16	3.55	3.54	3.50	5.20	3.53	3.35								
N	78	5	72	11	80	3	83	2								
t-statistic	0.59		-0.78		0.58		-0.89									
p	0.56		0.44		0.56		0.38									
Female Raters																
Odor Intensity Ratings																
Mean	3.84	3.76	3.80	3.95	3.83	4.07	3.83	3.47								
SD	1.04	0.80	1.05	0.88	1.02	1.29	1.04	0.19								
N	78	5	72	11	80	3	83	2								
t-statistic	0.17		-0.37		-0.39		0.49									
p	0.86		0.71		0.70		0.63									
Male Raters																
Odor Attractiveness Ratings																
Mean	11.79	11.28	11.65	12.08	11.70	12.22	11.69	12.02								
SD	3.24	2.23	3.30	2.74	3.12	3.80	3.19	3.00								
N	72	7	60	19	71	8	72	8								
t-statistic	0.41		-0.52		-0.44		-0.28									
p	0.68		0.61		0.66		0.78									
Male Raters																

Odor Intensity Ratings

Mean	3.56	3.70	3.54	3.68	3.55	3.76	3.56	3.69
SD	0.98	0.93	0.93	1.09	0.93	1.31	0.99	0.64
N	72	7	60	19	71	8	72	8
t-statistic	-0.36		-0.58		-0.59		-0.36	
p	0.72		0.57		0.56		0.72	

All Raters

Odor Attractiveness Ratings

Mean	11.84	11.13	11.68	12.27	11.79	11.79	11.70	12.41
SD	3.38	3.01	3.42	3.01	3.31	4.00	3.36	2.96
N	150	12	132	30	151	11	155	10
t-statistic	0.71		-0.87		-0.00		-0.65	
p	0.48		0.38		1.00		0.52	

All Raters

Odor Intensity Ratings

Mean	3.71	3.73	3.69	3.78	3.69	3.85	3.70	3.64
SD	1.02	0.84	1.00	1.01	0.99	1.25	1.03	0.58
N	150	12	132	30	151	11	155	10
t-statistic	0.06		0.43		-0.47		0.18	
p	0.95		0.67		0.64		0.86	

Note. Raters made four attractiveness ratings on 7-point Likert scales. These ratings were summed to create an overall attractiveness score; thus, overall attractiveness ratings range from 4 to 28. Raters made one intensity rating on a 7-point Likert scale; thus, intensity ratings range from 1 to 7.

* p < .05, **p < .01, ***p < .001

Table 16

Comparisons of odor attractiveness and intensity ratings of samples from women and men donors who did comply (i.e., C) or did not comply (i.e., NC) with dietary, behavioral, fragrance, and shower guidelines. Results are presented in full and disaggregated by sex.

	Diet		Behavior		Fragrance		Shower									
	C	NC	C	NC	C	NC	C	NC								
Female Donors																
Odor Attractiveness Ratings																
Mean	11.92	11.80	11.72	14.16	11.57	18.28	11.83	14.74								
SD	2.94	3.29	2.86	4.29	2.69	1.93	2.94	2.66								
N	62	22	78	6	80	4	78	4								
t-statistic	0.16		-1.94		-4.90		-1.94									
p	0.87		0.06		< 0.001***		0.06									
Female Donors																
Odor Intensity Ratings																
Mean	3.59	3.41	3.57	3.21	3.49	4.56	3.52	3.61								
SD	0.83	0.94	0.81	1.42	0.84	0.53	0.87	0.54								
N	62	22	78	6	80	4	78	4								
t-statistic	0.84		0.98		-2.53		-0.22									
p	0.40		0.33		0.01*		0.83									
Male Donors																
Odor Attractiveness Ratings																
Mean	11.63	12.24	11.58	13.08	11.38	16.18	11.54	13.97								
SD	3.77	4.14	3.86	3.56	3.71	2.11	3.82	3.44								
N	68	19	76	11	80	7	79	8								
t-statistic	-0.60		-1.21		-3.36		-1.72									
p	0.55		0.23		0.001**		0.09									
Male Donors																
Odor Intensity Ratings																
Mean	3.88	3.95	3.97	3.35	3.86	4.31	3.90	3.85								

SD	1.24	1.30	1.28	0.86	1.27	0.82	1.28	0.85
N	68	19	76	11	80	7	79	8
t-statistic	-0.22		1.55		-0.91		0.10	
p	0.83		0.12		0.36		0.92	
All Donors								
Odor Attractiveness Ratings								
Mean	11.77	12.00	11.65	13.46	11.48	16.95	11.69	14.22
SD	3.39	3.67	3.38	3.74	3.24	2.22	3.40	3.10
N	130	41	154	17	160	11	157	12
t-statistic	-0.37		-2.07		-5.51		-2.50	
p	0.71		0.04*		<0.001***		0.01*	
All Donors								
Odor Intensity Ratings								
Mean	3.74	3.66	3.77	3.30	3.67	4.40	3.71	3.77
SD	1.07	1.14	1.08	1.05	1.09	0.71	1.11	0.74
N	130	41	154	17	160	11	157	12
t-statistic	0.41		1.69		-2.18		-0.19	
p	0.68		0.09		0.03*		0.85	

Note. Raters made four attractiveness ratings on 7-point Likert scales. These ratings were summed to create an overall attractiveness score; thus, overall attractiveness ratings range from 4 to 28. Raters made one intensity rating on a 7-point Likert scale; thus, intensity ratings range from 1 to 7.

* p < .05, **p < .01, ***p < .001

Procedures

Odor collection

Participants visited the lab twice, first as donors and then as raters. Each session was 75 minutes and occurred on different days. Starting two days before the first session, donors were asked to follow a set of dietary, behavioral, and hygiene inclusion guidelines that are standard procedures for limiting contamination of “natural” body odor (e.g., Kamiloğlu et al., 2018; Zhou & Chen, 2009). Moreover, donors were asked to

refrain from (1) showering, (2) using deodorant, and (3) using any fragranced products, such as lotions and perfumes, the day of body odor collection. A compliance survey was administered prior to body odor sampling.

Body odor was collected on 4x4-inch sterile absorbent compresses (Johnson & Johnson) that were secured to participants' axillae with skin safe (Nexcare) tape for 1 hour. Compresses were frozen at -20° Celsius and thawed once, 30 minutes prior to use in rating sessions

Photographing

During the first session, we used an instant camera (60mm f/12.7 lens) to take photographs (62mm X 42mm photographs) of participants' faces. Donors were asked to remove makeup, eyewear, and jewelry, and to pull long hair back. All donors were photographed in a black T-shirt with a neutral expression against a white background.

Voice recording

During the first session, donors' voices were recorded using a cardioid condenser microphone (*Blue, Snowball*) for studio-quality recordings. Donors were instructed to read the "Rainbow Passage" (Fairbanks, 1960) while their voices were recorded in the audio recording application software, Audacity, and saved on a private SoundCloud account.

Attractiveness ratings

During the second sessions, an odor rating station, a photograph rating station, and a voice rating station were setup, and each was managed by a separate experimenter. Samples (i.e., body odor, photographs, and voice recordings) from the same donors were placed at the appropriate rating stations 30 minutes before a rating session began. Raters made independent odor, voice, and face ratings. Each donor

sample had a unique code so that raters could not match samples from the same donor across rating stations. Raters were randomly assigned an order to filter through rating stations with only a single rater at a rating station at a time.

Odor samples were contained in wide-mouth, amber, polypropylene jars. Jars contained compresses from both axillae of a single donor. An experimenter, wearing odorless cotton gloves, removed lids from jars one at a time and held the jars while a rater smelled the headspace. The order that odor samples were presented was randomized for each rater using a random number generator. After the rater smelled the jar's headspace, the experimenter replaced the jar's lid while the rater made a series of judgments about the sample's odor. Raters were asked to rate the intensity of the odor on a 7-point Likert scale, with 7 representing very intense. Then, raters made four judgments related to attractiveness (i.e., how pleasant, how attractive, how sexy, how much they liked...) using 7-point Likert scales, with 7 representing the highest score (e.g., very attractive). The scores for each of the four judgments were summed to create an overall attractiveness score (see Table 17)⁷.

Photographs of donor faces were presented by an experimenter in a randomized order for each rater. Raters made four judgments using the same scale described for odor, but wording changed to reflect faces. Additionally, raters were asked, "Do you know the person in this photograph?". Observations where a rater knew the donor were excluded (i.e., 37 observations) from all (i.e., face, odor, and voice) analyses.

Voice recordings were played by an experimenter in a randomized order for each rater. Raters wore large, over-the-ear, closed-back, noise-cancelling headphones while

⁷ Using a correlation matrix, we present the relationships between each of the summed attractiveness ratings in each modality as well as the relationship between each rating and the total attractiveness score in each modality. Questions within a given modality were highly correlated, thus we felt justified in summing each to create an overall attractiveness score within each modality.

at the voice rating station. Raters made four judgments using the same scale described for odor, but wording changed to reflect voices.

Table 17

Correlation matrix of attractiveness-rating-scale items.

		Face			
		Pleasant	Attractive	Sexy	Like...
Face	Attractiveness Score	0.868	0.944	0.909	0.927
	Pleasant	1.000	0.741	0.651	0.773
	Attractive	0.741	1.000	0.878	0.823
	Sexy	0.651	0.878	1.000	0.785
	Like...	0.773	0.823	0.785	1.000
		Odor			
		Pleasant	Attractive	Sexy	Like...
Odor	Attractiveness Score	0.934	0.951	0.915	0.940
	Pleasant	1.000	0.855	0.768	0.869
	Attractive	0.855	1.000	0.855	0.847
	Sexy	0.768	0.855	1.000	0.798
	Like...	0.869	0.847	0.798	1.000
		Voice			
		Pleasant	Attractive	Sexy	Like...
Voice	Attractiveness Score	0.886	0.937	0.889	0.929
	Pleasant	1.000	0.749	0.643	0.832
	Attractive	0.749	1.000	0.853	0.809
	Sexy	0.643	0.853	1.000	0.740
	Like...	0.832	0.809	0.740	1.000

Analysis

Estimation Sample

In this section, we describe the construction of the core estimation sample used in our primary analyses of the sources of covariation between different modalities of attractiveness. We begin with an original data set in which each observation contains information about how a rater evaluated an opposite-sex donor's facial attractiveness, odor attractiveness and vocal attractiveness. Since no rater was asked to evaluate the same donor more than once, each row in the data set contains information about a

unique (ordered) donor-rater observation. Next, we excluded from our original sample 1) observations where either the donor or rater identified as non-heterosexual, 2) observations where the rater recognized the donor from the facial photograph, and 3) observations with missing or incomplete data about some basic rater and donor characteristics (including demographic characteristics and compliance measures). Applying these restrictions, and removing observations with incomplete data, leaves $N = 949$ observations. In a final step, we dropped observations if the donor indicated that they did not comply with the request to abstain from the use of any fragranced products or deodorant on the day that their body odor sample was collected. Applying the fragrance restriction leaves $N = 881$ observations, 437 of which correspond to pairs where a female rater evaluated an opposite-sex donor (and 444 to pairs with a male rater and female donor). For each donor, we defined the rater's judgment in a modality by taking the sum of the four attractiveness questions about the modality in question.

Table 18 provides summary statistics for each of the three aggregated modality variables, both for the overall sample and by rater's sex.

Table 18

Summary statistics for face, odor, and voice attractiveness for overall sample and by rater's sex.

		All Ratings (N = 881)	Male Ratings (N = 444)	Female Ratings (N = 437)
Face	Mean	12.633	13.124	12.135
	SD	5.334	5.504	5.114
Odor	Mean	11.344	11.282	11.407
	SD	5.383	4.963	5.783
Voice	Mean	15.070	15.126	15.014
	SD	5.488	5.212	5.761

Note. Raters made four attractiveness ratings on 7-point Likert scales. These ratings were summed to create an overall attractiveness score; thus, a donor's overall attractiveness score ranged from 4 to 28. The statistics above reflect the average attractiveness score within a given modality.

Two-Factor Model

The primary goal of our empirical analyses is to estimate the strength of the relationship between a person's attractiveness across three modalities – face, odor, and voice – and to explore the sources of these relationships. We fit a simple model which assumes attractiveness in modality j is determined as follows:

$$m_j = \mu_j + \beta_j A + u_j,$$

where $j \in \{F, O, V\}$ denotes facial, odor, and voice attractiveness, and A is a latent general attractiveness factor and u_j is a mean-zero modality-specific disturbance that is assumed to satisfy, for any pair of modalities $j \neq k$, $\mathbb{E}[u_j u_k]$ and, for any individual modality, $\mathbb{E}[u_j A]$. The assumption that $\mathbb{E}[u_j u_k]$ for any $j \neq k$ is substantively important and means that the specific factors that influence one modality (vocal attractiveness, say) are unrelated to the specific factors that influence the other (facial attractiveness, say). Thus, any within-person correlation between attractiveness in modalities j and k

arises through A . For example, if A and the three measured m are normalized to have mean zero and variance one, we have:

$$\begin{aligned}
\mathbb{E}[m_j m_k] &= \mathbb{E}[(\beta_j G + u_j)(\beta_k G + u_k)] \\
&= \mathbb{E}[(\beta_j \beta_k G^2 + \beta_j G u_k + \beta_k u_j G + u_j u_k)] \\
&= \beta_j \beta_k \mathbb{E}(G^2) + \beta_j \mathbb{E}(Gu_k) + \beta_k \mathbb{E}(u_j G) + \mathbb{E}(u_j u_k) \\
&= \beta_j \beta_k
\end{aligned}$$

Figure 7 shows a path representation of our two-factor model. In this model, the variables $\mathbf{m} = (m_F, m_O, m_V)$ are observed, with m_F defined as the average of the four evaluations of the donor's facial attractiveness, and m_O and m_V defined analogously. Prior to model fitting, we residualize each of the attractiveness judgments on rater fixed-effects. We take this step to address concerns that within-person correlations in attractiveness judgments may otherwise reflect differences in how raters use the response scale (with some potentially being systematically more generous raters than others, in which case the correlations found could be spurious). Table 19 reports the variance-covariance and correlation matrices for the original and residualized variables, both for the overall sample and separately by the sex of the rater.

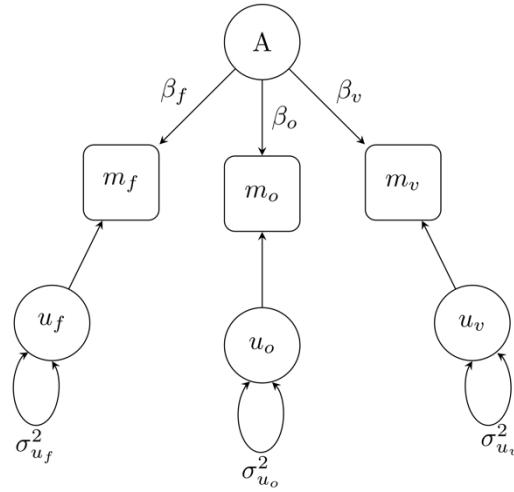


Figure 7. Path Diagram Underlying Baseline Two-Factor Model of Attractiveness. The figure displays a path diagram which assumes that attractiveness in a single modality (face, odor, or voice) is determined by a latent general attractiveness factor, A, and factors unique to a given modality (u). Modality specific factors influence one modality (odor attractiveness, say), and are unrelated to the factors influencing another (facial attractiveness, say). Therefore, any within-person correlation between attractiveness in different modalities arises through the latent general attractiveness factor, A.

Estimation

Prior to estimation, we normalize the latent variable A so its mean is zero and its variance is one. This normalization is not substantively important since it does not impact the standardized coefficient estimates numerically. That is, under any arbitrary rescaling of A , the standardized path coefficients we focus on in our discussion of the results are the same. We estimate the model parameters by maximum likelihood, clustering errors by the rater to take potential independence across observations into account. Since we do not demean or rescale any of the observed variables prior to estimation, the core of the model consists of nine parameters:

- Three intercepts: $\tilde{\mu} = (\tilde{\mu}_F, \tilde{\mu}_o, \tilde{\mu}_V)$
- Three disturbance variances: $\tilde{\sigma}_u^2 = (\tilde{\sigma}_{u,F}^2, \tilde{\sigma}_{u,o}^2, \tilde{\sigma}_{u,V}^2)$
- Three unstandardized path coefficients, $\tilde{\beta} = (\tilde{\beta}_F, \tilde{\beta}_o, \tilde{\beta}_V)$.

In practice, we follow the prior literature in estimating separate coefficients for male and female raters, doubling the number of parameters in the final model to 18. Where necessary, we use superscript $s \in \{m, f\}$ to denote male and female coefficients, respectively. For some intuition on the identification, the model is just identified since we use 18 moments in the data to recover 18 parameters. For each sex, the nine moments are three means, three variances and three covariances (see Table 16). Procedurally, we estimate the model using the individual-level, untransformed, variables and then convert the unstandardized, original parameter estimates into standardized coefficients with more straightforward interpretations. For example, the standardized path coefficient for modality j can be calculated from the original coefficient estimates as follows:

$$\beta_V = \frac{\tilde{\beta}_j}{\sqrt{\tilde{\beta}_j^2 + \tilde{\sigma}_{u,j}^2}}$$

And the proportion of variance in m_V explained by the general attractiveness factor is given by β_V^2 .

Table 19

Variance-covariance and correlation matrix of attractiveness modalities.

<u>All Raters</u>						
Original Variable	Face		Odor		Voice	
	COV	COR	COV	COR	COV	COR
Face	28.45	1	2.33	0.081	4.43	0.151
Odor	2.33	0.081	28.98	1	2.74	0.092
Voice	4.43	0.151	2.74	0.093	30.12	1

<u>All Raters</u>						
Adjusted for Rater Fixed Effects	Face		Odor		Voice	
	COV	COR	COV	COR	COV	COR
Face	18.04	1	-0.02	-0.001	1.61	0.081
Odor	-0.02	-0.001	18.26	1	0.44	0.022
Voice	1.61	0.081	0.44	0.022	22.11	1

<u>Male Raters</u>						
Original Variable	Face		Odor		Voice	
	COV	COR	COV	COR	COV	COR
Face	30.29	1	3.00	0.110	6.39	0.222
Odor	3.00	0.110	24.64	1	5.08	0.197
Voice	6.39	0.222	5.08	0.197	27.16	1

<u>Male Raters</u>						
Adjusted for Rater Fixed Effects	Face		Odor		Voice	
	COV	COR	COV	COR	COV	COR
Face	17.70	1	1.29	0.079	2.73	0.144
Odor	1.29	0.079	15.12	1	2.32	0.133

Voice	2.73	0.144	2.32	0.133	20.32	1
<u>Female Raters</u>						
Original Variable						
	Face		Odor		Voice	
	COV	COR	COV	COR	COV	COR
Face	26.15	1	1.72	5.8×10^{-2}	2.39	8.10×10^{-2}
Odor	1.72	5.8×10^{-2}	33.45	1	0.36	1.09×10^{-2}
Voice	2.39	8.10×10^{-2}	0.36	1.09×10^{-2}	33.19	1
<u>Female Raters</u>						
Adjusted for Rater Fixed Effects						
	Face		Odor		Voice	
	COV	COR	COV	COR	COV	COR
Face	17.93	1	-1.30	-0.066	0.42	0.020
Odor	-1.30	-0.066	21.49	1	-1.46	-0.064
Voice	0.42	0.020	-1.46	-0.064	23.97	1

Results

Table 20 reports the maximum-likelihood estimates of the untransformed model parameters. The standardized estimates derived from these estimates are shown in Table 21. For female donors (male raters), we estimate that a one-standard deviation-unit (SD unit) increase in general attractiveness, A , increases (i) facial attractiveness (m_F) by 0.29 SD units (SE = 0.13, P<0.011), (ii) odor attractiveness (m_O) by 0.27 SD units (SE = 0.13, P<0.040), and (iii) vocal attractiveness (m_V) by 0.49 SD units (SE = 0.19, P<0.008). According to the point estimates, the common attractiveness factor A is thus estimated to explain $\hat{\beta}_F^2 = 0.29^2 \sim 8.6\%$ of the variance in facial attractiveness, (m_F), $\hat{\beta}_O^2 = 0.27^2 \sim 7.3\%$ of the variance in odor attractiveness (m_O), and $\hat{\beta}_V^2 = 0.49^2 \sim 24.2\%$ of the variance in vocal attractiveness (m_V). Since a joint test of the null

hypothesis that the three standardized path coefficients are identical – $\beta_F^m = \beta_O^m = \beta_V^m$ – fails to reject ($\chi^2(2) = 0.63, P = 0.730$), these findings do not provide strong evidence that the general attractiveness factor A is a better predictor of attractiveness in some modalities than others. But overall, our results provide evidence consistent with the hypothesis that a general attractiveness factor A contributes modestly to the observed correlations between modality-specific attractiveness judgments male raters make of female donors.

For male donors (female raters), our results are qualitatively different and generally less informative. We estimate that in this group, a one-standard deviation-unit (SD unit) increase in general attractiveness, A , (i) increases facial attractiveness (m_F) by 0.14 SD units (SE = 0.26, P=0.584), (ii) *decreases* odor attractiveness (m_O) by -0.46 SD units (SE = 0.89, P<0.606), and (iii) increases vocal attractiveness (m_V) by 0.14 SD units (SE = 0.28, P<0.610). We emphasize that due to the low precision of these estimates, they do not provide much evidence that the standardized path coefficients are heterogeneous across domains. A joint test of the null hypothesis that the three standardized path coefficients are identical – $\beta_F^f = \beta_O^f = \beta_V^f$ – again fails to reject ($\chi^2(2) = 0.85, P = 0.265$).

Table 20

Unstandardized coefficients from two-factor model.

	Male Ratings ($N = 444$)			Female Ratings ($N=437$)		
	Coef	SE	P	Coef	SE	P
<u>Face</u>						
Path ($\tilde{\beta}_F$)	1.230	0.493	0.013	0.611	1.112	0.582
Intercept ($\tilde{\mu}_F$)	13.124	0.000	0.000	12.135	0.000	0.000
Variance ($\tilde{\sigma}_{u,F}^2$)	16.143	1.856	0.000	17.516	2.207	0.000
<u>Odor</u>						
Path ($\tilde{\beta}_o$)	1.048	0.527	0.047	-2.115	4.097	0.606
Intercept ($\tilde{\mu}_o$)	11.282	0.000	0.000	11.407	0.000	0.000
Variance ($\tilde{\sigma}_{u,o}^2$)	13.990	1.575	0.000	16.965	17.461	0.331
<u>Voice</u>						
Path ($\tilde{\beta}_v$)	2.213	0.841	0.009	0.688	1.346	0.609
Intercept ($\tilde{\mu}_v$)	15.126	0.000	0.000	15.014	0.000	0.000
Variance ($\tilde{\sigma}_{u,v}^2$)	15.374	3.888	0.000	23.443	3.031	0.000
log pseudolikelihood	-7640.416					

Table 21

Standardized coefficients from two-factor model.

	Male Raters ($N = 444$)				Female Raters ($N=437$)			
	Estimate	SE	P	$R^2(\beta_j^2)$	Estimate	SE	P	$R^2(\beta_j^2)$
<u>Standardized Path Coefs</u>								
Face β_F	0.293	0.115	0.011	8.6%	0.145	0.264	0.584	2.1%
Odor β_O	0.270	0.131	0.040	7.3%	-0.457	0.885	0.606	20.9%
Voice β_V	0.492	0.186	0.008	24.2%	0.141	0.276	0.610	2.0%

Our findings that within-person correlations across modalities are larger when women are rated by men than vice versa is consistent with most previous literature, which finds that female attractiveness tends to be more highly correlated across modalities than male attractiveness. To examine if the male-female differences in parameters are statistically significant, we conducted several formal hypothesis tests, the results of which are shown in Table 22. The upper panel reports from three tests, each of which examines if one of the standardized path coefficients (corresponding to face, odor, or voice) can be equated across the two groups. None of the three individual tests rejects the null of equal parameters across the group. In the bottom panel, we report analogous tests for unstandardized path coefficients. We again fail to reject the null in all three cases. The bottom panel shows that a joint test of the three individual hypotheses also fails to reject ($\chi^2(3) = 0.945, P = 0.18$).

Table 22

Tests of equal path coefficients across sexes.

		Z	P> Z
Standardized Path Coefficients			
1	$\beta_F^M = \beta_F^F$	-0.51	0.607
2	$\beta_O^M = \beta_O^F$	-0.81	0.417
3	$\beta_V^M = \beta_V^F$	-1.06	0.291
Unstandardized Path Coefficients			
		$\Delta\chi^2$	df
4	$\tilde{\beta}_F^f = \tilde{\beta}_F^m$	0.259	1
5	$\tilde{\beta}_O^f = \tilde{\beta}_O^m$	0.586	1
6	$\tilde{\beta}_V^f = \tilde{\beta}_V^m$	0.924	1
Joint Test of (4)-(6)		0.945	3.000
			0.184

In summary, our first objective was to estimate the strength of the relationship between a donor's attractiveness across three modalities – face, odor, and voice. For female attractiveness, we find weak covariance between all attractiveness modalities. For males, on the other hand, we find no evidence of covariance between their face, odor, and voice attractiveness. We cannot reject the null hypothesis that the male and female estimates are statistically similar. Thus, there could be no relationships between the modalities of attractiveness tested when women rate men, or the relationship could be comparable to what is reported for men rating women. For an unknown reason, the female ratings of men were imprecise. This imprecision could suggest that for men, our sample size was too small to detect relationships between their face, odor, and voice attractiveness. Our final objective was to investigate potential sources of relationships between attractiveness modalities, to distinguish between the redundancy and multiple

messages hypotheses. We find that a latent general attractiveness factor (i.e., common variable) contributes modestly to the correlations between women's face, odor, and voice attractiveness.

Discussion

For most of human evolutionary history courtship and mating has occurred in-person, where social information about an individual can be obtained from how they look, sound, and smell. Thus, sensory perceptions of other's attractiveness likely evolved in the context of being experienced together. Yet, little work has investigated how independent multisensory attractiveness ratings are related. While some studies have examined the contributions of face and body to overall attractiveness (e.g., Brown et al., 1986; Mueser et al., 1984; Peters et al., 2007), and others have correlated facial and vocal attractiveness (Abend et al., 2015; Collins & Missing, 2003; Feinberg, Jones, DeBruine, et al., 2005; Lander, 2008; Valentova et al., 2017; Wells et al., 2013; M. Zuckerman et al., 1995), scant research has considered body odor attractiveness. Our study simultaneously investigates the relationships between judgments of body odor, face, and voice attractiveness. In the current study, men and women rated the attractiveness of opposite-sex participants' body odors, faces, and voices ($n = 1,284$ ratings). For women, we observed a weak covariance between odor, face, and voice attractiveness. However, for men, we found no evidence of covariance between modalities of attractiveness. Our findings are consistent with most prior studies, which also report with-in person attractiveness correlations across sensory modalities in women (Abend et al., 2015; Collins & Missing, 2003; Feinberg, Jones, DeBruine, et al., 2005; Lander, 2008; Rikowski & Grammer, 1999; Thornhill & Gangestad, 1999; Valentova et al., 2017; Wells et al., 2013; M. Zuckerman et al., 1995), but not men (Lander, 2008; Valentova et al., 2017; Wells et al., 2013; Zäske et al., 2018; Zuckerman

et al., 1995). In contrast, Roth et al. (2021) found weak, but significantly positive correlations between both male and female face and voice, as well as face and body odor attractiveness. However, the authors suggest that their effect sizes were too small and larger studies would be necessary to detect nuances between male and female judgments. In the current study, we more than doubled their number of participants. Yet, we cannot reject the null hypothesis that there are no sex differences in our estimates because, for an unknown reason, women's ratings of men were less precise. This imprecision may indicate that for men, even our larger sample size was too small to detect relationships between face, odor, and voice attractiveness.

In addition, we estimated the relationship between face, voice, and body odor attractiveness, and a latent general factor of attractiveness, to better discriminate between the redundancy (Møller & Pomiankowski, 1993) and multiple messages hypotheses of multimodal signaling (Johnstone, 1995, 1996). This analysis indicated how much a common trait (i.e., redundant information) contributed to the observed correlations between modality-specific attractiveness judgments. Some theorists argue that multimodal information reflects a common trait because redundancy diminishes error in the perception of mate quality since no single indicator of mate quality is likely to correlate perfectly with an underlying variable (e.g., fecundity) (for review see, Candolin, 2003). Redundant indicators are also suggested to make dishonesty easier to detect because only individuals of superb quality can spare the resources necessary to produce multiple indicators of the same information (Møller & Pomiankowski, 1993; for reviews see, Candolin, 2003; Johnstone, 1997; Johnstone, 1996). Other researchers argue that attractiveness judgments made in different sensory modalities reflect different variables of mate quality (i.e., multiple unique messages) (Johnstone, 1995, 1996; for reviews see, Candolin, 2003; Johnstone, 1997). Multiple messages might be evaluated

together to determine overall mate value, or individuals may attend to different messages dependent on their own condition and genotype (for review see, Candolin, 2003). Our results revealed that a latent general attractiveness factor (i.e., common underlying variable) modestly contributed to the observed covariances between modality-specific attractiveness judgments in women.

The contribution of a general attractiveness factor to modality-specific attractiveness to women's face, voice, and odor attractiveness provides some support for the hypothesis female attractiveness in different modalities reflects a common trait (i.e., is redundant). However, because male attractiveness across domains is not significantly correlated, their face, voice, and odor may reflect several unique traits (i.e., multiple messages). Indeed, researchers posit levels of female reproductive hormones, an indicator of fecundity and reproductive status (Baird et al., 1999; Lipson & Ellison, 1996a), underlie perceptions of women's modality-specific attractiveness (Feinberg et al., 2008), and evidence exists supporting hormonally influenced attractiveness in each modality we tested. For example, women with relatively high estrogen levels have more feminine faces, a quality judged to be attractive (M. J. Smith et al., 2005). In addition, women's voices are judged to be most attractive near ovulation, when estrogen levels are high (e.g., Pipitone & Gallup, 2008). Finally, women with relatively high levels of oestradiol emit body odor judged to be most attractive (Lobmaier, Fischbacher, Wirthmüller, et al., 2018). In contrast, men's attractiveness in different modalities may convey distinct information, such as developmental stability, absence of harmful mutations, health status, and testosterone levels. For instance, perceptions of men's facial attractiveness may reflect health and immunity (e.g., Rhodes et al., 2003; Roberts et al., 2005), whereas their vocal attractiveness may relate to trait or context-dependent dominance (e.g., Hodges-Simeon et al., 2010; Puts et al., 2006). However, there is little

research on the precise fitness correlates of attractiveness preferences. In this study, we are similarly limited because we too cannot determine the fitness correlates to attractiveness in the modalities tested. Thus, what variable(s) associated with mate value is conveyed by modality-specific attractiveness in both men and women remains uncertain (for review see, Gangestad & Scheyd, 2005).

The current study did not control for menstrual cycle effects and other context-dependent variables, such as perceivers own attractiveness (Little et al., 2001), demonstrated to affect facial attractiveness ratings. In the future, studies should determine whether context-dependent variables differentially affect modality-specific attractiveness to determine how context manipulates correlations between odor, face, and voice attractiveness judgments. In addition, our choice of vocal stimuli could have altered the strength of correlations between vocal and attractiveness ratings in other modalities. Zäske et al. (2018) reported face and voice attractiveness were uncorrelated when naturalistic speech was used, but a small significantly positive correlation was discovered between facial and vocal attractiveness when simple vowels were used instead. We used naturalistic speech (i.e., the rainbow passage) for voice samples, which cannot control for speaker characteristics, including dialect and speech patterns. Therefore, vocal attractiveness ratings could, in part, reflect socio-cultural preferences instead of preferences for vocal features. Finally, although our findings provide some evidence that, in women, modality-specific attractiveness conveys information about a common trait, we only report weak correlations between independent multisensory attractiveness judgments. Thus, our results also indicate female body odors, faces, and voices provide unique information. In fact, the redundancy and multiple messages hypotheses are not mutually exclusive, and humans likely evolved multiple methods of communicating and perceiving information about mate value.

The next step to determine whether modality-specific attractiveness conveys redundant or unique messages is to determine the fitness correlates for each feature judged to be attractive. In addition, future research should investigate whether an individual's attractiveness in different modalities reflects disparate or concordant information, and how disparate/concordant information affects overall judgments of attractiveness. Moreover, future studies should examine whether sensory environment alters the importance of different sources of information. For example, perhaps vision and audition are most important for mate choice at a distance, but smell becomes more important as proximity between individuals increases.

Mate preferences are based on numerous, often interacting, indicators of mate value. Yet, multisensory inputs to mate choice have received little attention, particularly olfaction. More studies are necessary to understand the contribution of body odor to mate selection, however the current study is a first step and adds to our knowledge of the relationships between body odor attractiveness and attractiveness in other sensory modalities.

Chapter 4 References

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Appendix A

Table 5

Concentrations of fatty acids found in vaginal secretions from three separate phases of the menstrual cycle (Michael et al., 1975). Synthetic copulin were produced according to menstrual day 14 data. Meaning, the percentages of each acid per 100 mL are as followed: 78.38% acetic acid, 13.21% propanoic acid, 4.94% butanoic acid, 0.76% methylpropanoic acid, and 2.14% methylbutanoic acid (Sigma-Aldrich, St. Louis).

	Volume-percent of acids in vaginal secretions.		
	Menstruation (day 2)	Ovulation (day 14)	Pre-menstruation (day 29)
Acetic acid	95.2	78.38	97.54
Propanoic acid	2.32	13.21	1.45
Butanoic acid	1.20	4.94	0.50
Methylpropanoic acid	0.32	0.76	0.30
Methylbutanoic acid	0.97	2.14	0.21

Appendix B

Table 6

Edlund and Sagarin (2014) Mate Value Scale.

Mate Value Scale								
Overall, how would you rate your level of desirability as a partner?	(Extremely undesirable)	1	2	3	4	5	6	7 (Extremely desirable)
Overall, how would members of the opposite sex rate your level of desirability as a partner?	(Extremely undesirable)	1	2	3	4	5	6	7 (Extremely desirable)
Overall, how do you believe you compare to other people in desirability as a partner?	(Very much lower than average)	1	2	3	4	5	6	7 (Very much higher than average)
Overall, how good of a catch are you?	(Very bad catch)	1	2	3	4	5	6	7 (Very good catch)

Appendix C

Table 7

Question Used from Penske and Asendorpf's (2008) SOI-R (Our measure of short-term vs. long-term mating preference)

Revised Sociosexual Orientation Inventory	
1.	With how many different partners have you had sex within the past 12 months?
2.	With how many different partners have you had sexual intercourse on one and only one occasion?
3.	With how many different partners have you had sexual intercourse without having an interest in a long-term committed relationship with this person?
4.	Sex without love is okay.
5.	I do not want to have sex with a person until I am sure that we will have a long-term, serious relationship.
6.	I can imagine myself being comfortable and enjoying casual sex with different partners.
7.	How often do you have fantasies about having sex with someone you're not in committed relationship with?
8.	How often do you experience sexual arousal when you are in contact with someone you are not in a committed romantic relationship with?
9.	In everyday life, how often do you have spontaneous fantasies about having sex with someone you have just met?