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FAKTORY PŘISPÍVAJÍCÍ K INTERINDIVIDUÁLNÍM ROZDÍLŮM V ČICHOVÝCH SCHOPNOSTECH A VŠÍMAVOSTI VŮČI PACHŮM

FACTORS CONTRIBUTING TO INTERINDIVIDUAL DIFFERENCES IN OLFACTORY ABILITIES AND ODOUR AWARENESS

Disertační práce

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ABSTRAKT

Hlavní náplní disertační práce je výzkum zaměřený na vybrané faktory, které přispívají k rozdílům mezi jedinci v čichových schopnostech a ve všímavosti vůči pachům a využívání čichu při každodenních činnostech u dětí, dospívajících a mladých dospělých. Práce sestává ze dvou částí. **Kapitola 1** nejprve obecně shrnuje okolnosti, které v posledních několika málo desetiletích vedly k oživení vědeckého zájmu o lidský čich a přispěly tak i k markantnímu nárůstu počtu psychofyzických studií čichového vnímání. Dále jsou nastíněna vybraná psychofyzická měření čichu, která byla provedena ve studiích zahrnutých v této práci, a k nim vztahující se čichové schopnosti. Poté jsou představeny vybrané faktory, jež, jak ukázal předchozí výzkum, přispívají k interindividuálním rozdílům v psychofyzických testech schopnosti identifikace a diskriminace pachů a čichové senzitivity a jimiž se autorka zabývala ve vlastním výzkumu. Jedná se o vliv pohlaví (jenž je zasazen do rámce vývoje lidského čichu), dětské genderové nonkonformity (či sexuální orientace) a osobnostních rysů. Nakonec jsou krátce zmíněny také intraindividuální rozdíly v čichových schopnostech. Posléze se pozornost přesouvá ke všímavosti vůči pachům. Nejprve jsou představeny možné přístupy, jak lze výzkum lidského čichu přiblížit kontextu každodenního života, z nichž jedním je posouzení všímavosti vůči pachům. Dále je uvedena definice všímavosti vůči pachům a je představen dotazník COBEL a škála OAS, s jejichž použitím byla všímavost vůči pachům v našich studiích konkrétně hodnocena. Poté jsou popsány faktory přispívající k rozdílům ve všímavosti vůči pachům, které byly jejich pomocí doposud identifikovány, tedy vliv věku a pohlaví. Po shrnutí úvodní kapitoly následuje část druhá, která je sestavena ze sedmi studií, jež byly publikovány nebo podány do mezinárodních impaktovaných časopisů a které se vybraným faktorům blíže věnují. Markantní jsou rozdíly vyskytující se mezi jedinci *normosmickými,* vykazujícími

normální čichové schopnosti v rámci své věkové skupiny, a jedinci, u nichž byla diagnostikována *izolovaná kongenitální anosmie* a kteří od narození postrádají čich, zatímco v ostatních ohledech jsou zdrávi. Studie uvedená v **Kapitole 2** ukazuje, že tato porucha čichu je spojena se zvýšenou nejistotou ve vztazích s druhými lidmi, vyšším rizikem výskytu depresivních symptomů a rovněž s vyšším rizikem úrazů v domácnosti. Explorativní studie v **Kapitole 3** se pak dále zabývala možným odlišným průběhem *smyslově specifického nasycení (sensory-specific satiation)* při konzumaci potraviny u těchto jedinců. Z těchto studií tedy zároveň vyplývá, ve kterých oblastech lidského chování a každodenních činnostech se čich výraznou měrou uplatňuje. Během ontogeneze je stále patrnější vliv významného demografického faktoru, pohlaví, jenž se dlouhodobě těší neutuchajícímu zájmu výzkumníků i širší veřejnosti. Mezipohlavní rozdíly ve prospěch dívek se projevují nejen v čichových schopnostech, ale též v tom, nakolik jsou si děti vědomy přítomnosti různých vůní a pachů ve svém okolí a jak čich v běžných situacích každodenního života využívají. Studie uskutečněné v České republice a Namibii s dětmi mladšího a středního školního věku, uvedené v **Kapitole 4,** dokládají, že je tomu tak i napříč kulturami. V období mladšího školního věku rovněž pravděpodobně nadále probíhá utváření čichových preferencí; ve studii v **Kapitole 5** ukazujeme vztah předchozí zkušenosti s čichovými podněty, jež byla hodnocena pomocí testu schopnosti identifikace pachů, s vnímanou příjemností těchto stimulů. Ve dvou studiích v **Kapitole 6** se věnujeme souvislosti některých osobnostních rysů, zejména úzkostnosti, s čichovými schopnostmi adolescentů a mladých dospělých. V **Kapitole 7** uvádíme výzkum s mladými dospělými dokládající, že značná variabilita v čichových schopnostech u dospělých existuje nejen *mezi* pohlavími, ale rovněž *v rámci* obou pohlaví a že se vztahuje k *dětské genderové nonkonformitě,* jež se užívá jako měřítko pohlavní typičnosti či atypičnosti. **Kapitola 8** propojuje stěžejní témata,

jimž byly věnovány předchozí kapitoly, tedy téma mezi- a vnitro-pohlavních rozdílů v čichu, vlivu zkušenosti i všímavosti vůči pachům, a na totožném vzorku ukazuje souvislost mezi zpětně hodnocenou mírou zkušeností s vůněmi a pachy, nabytých za delší časový úsek (od raného dětství do dospělosti) skrze určité činnosti bohaté na čichové podněty, a schopností identifikace pachů a všímavostí vůči čichovým podnětům.

KLÍČOVÁ SLOVA

Čichové schopnosti, činnosti bohaté na čichové podněty; genderová nonkonformita; mezipohlavní rozdíly; osobnost; příjemnost; sexuální orientace; všímavost vůči pachům; vývoj

ABSTRACT

The main body of the thesis deals with selected factors underlying the considerable variability in human olfactory abilities and some odour awareness-related measures, addressed in samples ranging in age from middle childhood to young adulthood. The thesis consists of two parts. The first part **(Chapter 1),** first presents the major advances and developments that brought about something of a renaissance of scientific interest in the human sense of smell, including the recent proliferation of psychophysical studies, both basic research and clinical. Next, an outline of olfactory psychophysical measures and related olfactory abilities that are of relevance to the studies presented in this thesis is provided. Subsequently, the selected factors contributing to interindividual differences in olfactory abilities, that have been addressed by this thesis, are reviewed, namely the effect of sex (or gender), which is approached from a developmental perspective, childhood gender nonconformity, and personality. Finally, *intra*individual fluctuations in olfactory performance are also mentioned in brief. Next, the focus shifts to odour awareness by first introducing the various approaches that can be adopted to get closer to the real-life context as opposed to laboratory setting (where most olfactory studies continue to be carried out), of which assessing odour awareness is one option. After that, a definition of odour awareness is given and the two particular tools which have been used in our studies are briefly introduced. Finally, the factors contributing to differences in odour awareness which have been identified thus far using these two tools, namely age and sex/gender, are reviewed. The second part is comprised of seven studies, published or submitted to peer-reviewed academic journals that address the effects of the selected factors. These include, firstly, the level of intactness of olfactory function, with a focus on a phenomenon known as *isolated congenital anosmia*,

characterised by a lack of the sense of smell since birth in otherwise healthy individuals. The study given in **Chapter 2** shows increased social insecurity, risk of depressive symptoms, and of household accidents, while the study in **Chapter 3** explores potentially different patterns of food appreciation (in relation to *sensory-specific satiation*) in individuals with congenital anosmia, thus highlighting some of the domains in which the sense of smell seems to play a major role. Over the course of ontogeny, the effects of a major demographic factor, sex (or gender), become increasingly evident not only in olfactory abilities, but also in odour awareness, which has attracted considerable attention from both researchers and the general public. We show the cross-cultural consistency of this sex (gender) difference in a sample of pre-pubertal and pubescent Czech and Namibian children in **Chapter 4.** Also, the formation of olfactory preferences and affective responses to odours is likely still in progress in prepubertal children, and in **Chapter 5** we show the relation of olfactory experience, assessed in terms of a degree of the ability of odour identification, and perceived odour pleasantness. In **Chapter 6,** we turn to the population of adolescents and young adults, showing an association between specific olfactory abilities and personality traits, particularly neuroticism and its facet, anxiety. Finally, in young adults, we demonstrate that significant variability in olfactory abilities is not limited to that *between* the sexes, but exists *within* the sexes as well, and relates to sex-atypicality, assessed here in terms of *childhood gender nonconformity* **(Chapter 7).** The study given in **Chapter 8,** carried out on the identical sample, brings together all the major topics addressed in the previous chapters, namely those of both inter- and intra-sexual differences in olfaction, the effect of experience, and odour awareness, establishing a link between self-reported, retrospectively assessed long-term olfactory experience via engagement in specific olfaction-related activities since early childhood, odour identification, and odour awareness exhibited at present.

KEYWORDS

Development; gender nonconformity; hedonics; odour awareness; olfaction-related activities; olfactory abilities; personality; sex differences; sexual orientation

PREFACE

The old strange fragrance filled the air,
A fragrance like the garden pink,
But tinged with vague medicinal stink
Of camphor, soap, new sponges, blent
With chloroform and violet scent.

'Miss Thompson Goes Shopping'
She visits the Chemist
Martin Armstrong (1882 – 1974)

Long before I even thought of putting an effort into a PhD, my interest in olfaction had been sparked by seemingly ordinary, yet nonetheless intriguing observation: how is it that some people come across as „olfactory connoisseurs" and enjoy life in its many fragrant and aromatic forms, whilst others seem largely untouched by its multi-faceted olfactory splendour, remaining indifferent and emotionally sterile even when face to face with the most glorious scent? Conversely, how come that some withdraw in disgust at the slightest hint of anything less than pleasant smelling, feeling great discomfort, while it barely registers with others? Needless to say, I consider myself as belonging to the former group. This work may thus also be viewed as a personal voyage of self-discovery as well as an explorative step towards understanding those who just feel otherwise about this aspect of themselves.

The topic of this thesis overlaps and brings together several disciplines, namely anthropology of olfaction (or senses in general), psychophysics[1], an interdisciplinary field occupying the intersection between cognitive psychology and experimental psychology, and

[1] Psychophysics is the scientific study of relationships between physical stimuli and perceptual phenomena. In a typical psychophysical study, individuals are tested in a laboratory setting intended to maximise the control of stimulus variation, stimuli often vary along only a single or a few physical dimensions, such as intensity, and individuals' responses are constrained to, for example, forced choice or scale ratings (Teller & Palmer, 2001).

differential psychology. Olfactory anthropology, as defined by Candau (2004), explores four lines of research: firstly, the variability of olfactory perception, secondly, olfactory abilities and "know-how", thirdly, odour use, and, fourthly, odour representations. The first three are central to the topic of this thesis, which addresses *interindividual variability* (1) in *olfactory abilities* and *odour awareness*[2] (2) in relation to dealing with diverse odours, particularly within the context of *olfaction-related activities* (3). There are several recurring themes in this thesis: the subjective importance attached to the sense of smell, in health and disease, its use (or inability to do so) within the context of everyday life, the olfactory experience thus acquired, and, in turn, how this experience finds expression in our capacity to process olfactory stimuli and in knowledge of our sense of smell and the olfactory environment that surrounds us. The topic also draws on the rich history of differential psychology, which has recently been enjoying a revival of interest (for review see Revelle, Wilt, & Condon, 2011), and follows the legacy of psychophysics, whose interest in differences between individuals in the sense of smell, particularly those between men and women, is as old as the field itself. Indeed, substantial interindividual variability in perception is the hallmark of olfaction and, by extension, of olfactory research and has been, therefore, in the focus of researchers since the very first pioneering studies.

The purpose of the following paragraphs is to outline the aims and scope of the thesis, its structure and the key topics explored herein. The thesis consists of an introductory chapter **(Chapter 1)** and seven chapters comprised of original research papers published in

[2] The term "odour awareness" was coined by Smeets, Schifferstein, Boelema, and Lensvelt-Mulders (2008) to account for marked interindividual differences in the degree to which individuals tend to pick up olfactory cues and rely on them to guide their selective attitudes and actions. While for some individuals, odours simply "stand out" from the olfactory background and they are always spontaneously commenting on odours present in the surrounding environment, body odour of self and others, food aroma or disturbing malodours, others only notice these odours after they have been pointed out to them (assuming, of course, they are able to detect and discriminate them). An olfaction-oriented individual, that is, one exhibiting a high degree of odour awareness, readily notices the presence of odour cues in the surrounding environment, relies on them in directing his or her attitudes and actions, and, tapping his or her previous experience, actively seeks desirable, pleasant olfactory stimulation and avoids unwanted, potentially disturbing odour stimuli.

international peer-reviewed journals or submitted manuscripts, of which two are under revision and another two are currently under review. The introductory chapter first presents the major advances and developments that, after an "era of chemosensory darkness", to use Shepherd's (2003) words, brought about something of a renaissance of scientific interest in the human sense of smell, including the recent proliferation of psychophysical studies, both basic research and clinical. Next, a brief outline of selected olfactory psychophysical measures and related olfactory abilities that are of relevance to the studies presented in this thesis is provided. Subsequently, the selected factors contributing to interindividual differences in olfactory abilities, that have been addressed by this thesis, are reviewed, namely the effect of sex (or gender),[3] which is approached from a developmental perspective, *childhood gender nonconformity*[4] (or sexual orientation), and personality. Finally, *intra*individual fluctuations in olfactory performance are also mentioned in brief. Next, the focus shifts to odour awareness by first introducing the various approaches that can be adopted to get closer to the real-life context as opposed to laboratory setting (where most olfactory studies continue to be carried out), of which assessing odour awareness is one option. After that, a definition of odour awareness is given and the two particular tools which have been used in our studies are briefly introduced. Finally, the factors contributing to differences in odour awareness which have been identified thus far using these two tools, namely age and sex/gender, are reviewed.

[3] Although we fully acknowledge the sex/gender distinction and its relevance, particularly in some areas of research (e.g. Prince, 2005), we use these terms interchangeably throughout the text, as most researchers in the field do. This is mainly because the differences discussed here are assumed to cover both biological predispositions attributable to sex, i.e. "the sum of those differences in the structure and function of the reproductive organs on the ground of which beings are distinguished as male and female, and of the other physiological differences consequent on these", as defined by The Oxford English Dictionary, and gender differences, i.e. "behavioural, cultural, or psychological traits typically associated with one sex" (ibid).

[4] Homosexual men tend to recall sex-atypical interests, behaviour, and self-concepts during childhood, such as disliking stereotypic male activities (e.g. competitive sports) and participating in stereotypic female activities (e.g. cross-dressing, preferring girls over boys as playmates). Referred to as childhood gender nonconformity (Bailey, Finkel, Blackwelder, & Bailey, 1996), it is a strong but not perfect correlate of adult sexual orientation, especially in men (Bailey & Zucker, 1995).

In the following chapters, seven original research papers are presented, of which three have already been published in international peer-reviewed journals (**Chapters 2, 3,** and **6**) and others are in the form of submitted manuscripts that were under revision or review at the time of the submission of the thesis. Editorial decision had already been issued for the studies in **Chapter 5** (revision) and **Chapter 7** (minor revision). The papers are ordered so as to first address the issue of the long underestimated significance of the sense of smell, which, somewhat paradoxically, becomes particularly evident in its absence, hence highlighting the interindividual differences between *congenitally anosmic*[5] individuals and individuals with an intact sense of smell (**Chapters 2** and **3**). Since age is a major demographic factor affecting olfactory performance as well as odour awareness, a developmental perspective was taken in ordering the following papers. Furthermore, it also respects the fact that some of the studies were carried out on identical samples. In children, this was the case with studies presented in **Chapters 4** (the Czech sample) and **5.** In adults, the sample was identical in **Chapters 6** (Study 2), **7,** and **8.** Over the course of ontogeny, the effects of another major factor, sex (or gender), become increasingly evident and in **Chapter 4** we show the cross-cultural consistency of this sex (gender) difference in a sample of pre-pubertal/pubescent Czech and Namibian children, as well as an association between odour identification and odour awareness in the former, which is interpreted in terms of olfactory experience. Also, in prepubertal children, the formation of olfactory preferences and affective responses to odours is likely still in progress, and in **Chapter 5** we show the relation of olfactory experience, assessed in terms of a degree of the ability of odour identification, and perceived odour pleasantness. In **Chapter 6,** we turn to the population of adolescents (Study 1) and young

[5] Congenital anosmia is characterised by lack of smell function from the time of birth. It may accompany certain congenital endocrine disorders, defects in head or facial shape, and hearing or visual disabilities. Two endocrine abnormalities often associated with congenital anosmia are, firstly, failure to respond to parathyroid hormone (pseudohypoparathyroidism) and abnormally decreased activity of the gonads (hypogonadotropic hypogonadism) (Wynbrandt & Ludman, 2009:35). The most common form of congenital anosmia is Kallmann's syndrome or olfactory dysplasia, characterized by hypogonadotropic hypogonadism and anosmia (Li, Doty, & Kennedy, 2003:603).

adults (Study 2), showing an association between specific olfactory abilities and personality traits, particularly neuroticism and its facet, anxiety. In **Chapter 7,** we introduce the idea that significant variability in olfactory abilities is not limited to that *between* the sexes, but exists *within* the sexes as well, and relates to sex-atypicality, assessed here in terms of *childhood gender nonconformity*. The study given in **Chapter 8,** carried out on the identical sample, brings together all the major topics addressed in the previous chapters, namely those of both inter- and intra-sexual differences in olfaction, the effect of experience, and odour awareness, establishing a link between self-reported, retrospectively assessed long-term olfactory experience via engagement in specific olfaction-related activities since early childhood, olfactory abilities, and odour awareness exhibited at present. The individual studies are introduced in more detail below.

As noted above, the sense of smell has long been neglected by scientists since it was believed to be only of minor importance to humans. Times have, however, changed and olfaction has been acknowledged as equally deserving of scientific attention as, for instance, vision. Not an insignificant role in its reinstatement have played studies illuminating the adaptive significance of the sense of smell in humans, including those which approach the subject from the perspective of its absence rather than its presence. Two such studies are presented in **Chapters 2** and **3.** The aim of the former was to investigate the lifestyle of congenital anosmics, that is, people born without a sense of smell. Specifically, we were interested to find out whether congenital anosmia affected dietary habits of these people, whether they felt more vulnerable to environmental hazards, and if they exhibited insecurity in social interactions or experienced any distress in their relationships. In so doing, this study brings into attention the self-reported lower perceived quality of life[6] and specific olfaction-

[6] Although the concept of quality of life covers multiple related ideas such as well-being, level of living, standard of living, and livability and, in the broadest sense, refers to the overall nature of an individual or group's lived environmental experience, that is, the satisfaction of desires associated with human needs and

related complaints of congenitally anosmic individuals. The latter aimed to explore one of the possible consequences of this olfactory disorder related to eating behaviour, namely a differential pattern of food appreciation of a simple food during consumption, by tracking the changes in its pleasantness over the course of a single serving and comparing them to data from individuals with an intact sense of smell.

There is a substantial body of evidence showing that across the lifespan, females exhibit better olfactory abilities than males, particularly as regards the ability of odour identification. Aptly depicted as lying "between evidence and enigma" by Brand and Millot (2001), sex differences in olfaction are an attractive research topic that continues to be pursued with undiminished enthusiasm, yet findings pointing towards the female olfactory superiority remain largely unexplained. Various interpretations have been proposed, including those relating to anatomical or physiological differences directly involved in the processing of olfactory information, differences in cerebral asymmetry, hormonal status, more complex differences in higher levels of brain organisation and function or differences in cognitive style. While we appreciate the relevance of these interpretations as well as the fact that they may not necessarily be mutually exclusive, but quite the opposite, in the studies included in this thesis that address this conundrum, we propose that long-term olfactory experience might, to a considerable extent, account for some of the differences. In professionals, the role of extensive chemosensory training in achieving expertise is widely acknowledged – but how about lay individuals? The answer might possibly lie in the varying degree of engagement in various common, everyday activities over the long term: at least in our socio-cultural context, women's greater odour exposure in specific functional contexts such as use of cosmetic products, cooking, household chores or child care over the long term seems indisputable

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wants (Byrne, 2007), in this text it is used in the strict sense of health-related quality of life, i.e. degree of mental and physical well-being. It is evaluated by means of various self-report measures (for review see Bullinger, 2002), including those addressing specifically nasal or olfactory dysfunction (Anderson, Murphy, & Weymuller, 1999; Frasnelli & Hummel, 2005; Nordin, Bramerson, Murphy, & Bende, 2003).

(Bianchi, Milkie, Sayer, & Robinson, 2000; Coltrane, 2000; Fuwa & Cohen, 2007). In children, the fact that gender stereotyping of activities is encouraged from very early in ontogeny is reflected in the knowledge of gender stereotyping of household activities demonstrated by girls (but not boys) as young as 2 years of age (Poulin-Dubois, Serbin, Eichstedt, & Sen, 2002). We aimed to explore this possibility in **Chapter 4** (in Namibian and Czech children), as well as in **Chapter 8** (in Czech young adults), offering evidence for an association between odour identification and odour awareness, which are assumed to reflect olfactory experience, in Czech children, and a relationship between self-reported long-term engagement in olfaction-related activities, olfactory abilities, and odour awareness in Czech adults. The absence of an association between self-reports of involvement in such activities and olfactory measures or odour awareness in Namibian children (who were only asked three questions to assess their olfactory environment) highlights, amongst other things, the need to develop and employ more sensitive measures, such as those we employed in the aforementioned study with young adults. On the other hand, this study extends the evidence that sex differences in olfaction have cross-cultural validity and, addressing a very recent and promising research topic of odour awareness, it demonstrates girls‘ greater proficiency in use of odour cues in the context of everyday life across two very different cultures.

Speaking of children, the formation of olfactory preferences, that is, relatively stable evaluative judgments in the sense of liking or disliking a stimulus, or preferring it or not over other stimuli (Scherer, 2005), is likely still in progress in middle childhood. The one major factor that is well-known to affect odour pleasantness is familiarity or, if you like, previous experience with an odour object/source, such that familiar odours are perceived as more pleasant (for review see Rouby, Pouliot, & Bensafi, 2009). However, does knowledge of an odour's identity affect the perceived pleasantness of all odours alike? In **Chapter 5** we argue that this shouldn't be the case: the hypothesised relationship between odour pleasantness and knowledge of an odour’s identity should primarily make sense for those exhibiting malodour-like properties. This is because from an evolutionary perspective, chemosensory perception was probably largely involved in helping our ancestors avoid digesting rotten, mould-ridden, poisonous, or otherwise inedible foodstuffs. Therefore, it is for such malodours that the knowledge that their source, despite what chemosensation may suggest, is harmless and even perfectly edible, should make any major difference. Thus, in this study we aimed to investigate whether individual knowledge of an odour’s identity, assessed by means of a cued odour identification test, would predict its perceived pleasantness and whether this effect would only (or predominantly) pertain to odours rated on average as rather unpleasant. We found a positive effect of prior experience for two of the most unpleasant odours (garlic and fish) but not for any pleasant odours: relatively higher pleasantness ratings were exhibited by those participants who correctly identified these odours compared to those who failed to correctly identify them, which might suggest that knowledge of an odour’s identity should matter primarily for malodours.

In **Chapter 6,** we turn to the population of adolescents (Study 1) and young adults (Study 2), aiming to investigate possible associations between specific olfactory abilities and personality traits. Starting as early as in 1890’s and throughout the entire history of modern olfactory psychophysics, researchers have been preoccupied with measuring and comparing absolute detection thresholds in men and women. The more mixed and sometimes contrasting results these efforts yielded over the decades, the more fervour was put into pursuing this quest. Part of this grand endeavour was determining which personality traits might underlie the greater olfactory sensitivity of some individuals. As postulated by Eysenck (1967), for nearly 50 years, extraversion/introversion and neuroticism have been the prime candidates. In particular, as regards neuroticism, or, more specifically, its facet (trait) anxiety, its possible association with olfactory processing is founded on the evidence of a close relationship between the olfactory and limbic systems: the "olfactory brain" includes the limbic structures of amygdala and hippocampus, which are also involved in emotional processing and regulation. Since both the amygdala and hippocampus have been found to be structurally and (or) functionally altered in highly anxious individuals, implications for processing of olfactory information might also be expected. Recent studies, including ours, indeed show that trait anxiety levels are associated with various aspects of sensory processing. Namely, we report that individuals exhibiting higher levels of (trait) anxiety showed a lower olfactory detection threshold (i.e. greater sensitivity) and better odour discrimination abilities. However, perhaps a yet more intriguing question is which personality traits (or temperamental ones, for that matter) show a relationship with the greater tendency of some individuals to orient towards the sometimes subtle olfactory stimuli and pick up olfactory cues more readily than others? This definitely seems a promising new research avenue worthy of pursuit.

Thus far we have only considered intersexual differences. Nonetheless, it has been suggested that similar mechanisms which are supposed to influence the average differences between men and women also give rise to intrasexual variation in such traits. Thus, both men and women vary in the level of development of traits which are typical of their own or the opposite sex and, consequently, both men and women can show rather sex-typical or sex-atypical psychological characteristics and exhibit varying degrees of gender nonconformity. Hence, given the robustness of intersexual differences in olfaction, intrasexual variation might also be expected with respect to sex-atypicality, assessed in terms of childhood gender nonconformity. We aimed to explore this possibility of intrasexual variation in olfactory performance in **Chapter 7,** where we show that men who had been *less* gender-conforming in childhood indeed exhibit a better ability of odour identification and, moreover, a better ability of odour discrimination than the more gender-conforming ones. Furthermore, in women, childhood gender nonconformity scores were negatively associated with the olfactory threshold: those who had been *more* gender-conforming in childhood exhibited greater olfactory sensitivity. Thus, both men and women exhibited significant intrasexual variability in olfactory performance related to childhood gender nonconformity.

What specific mechanisms underlie this intrasexual variability is up to future studies to identify. Nevertheless, in the aforementioned study in **Chapter 8,** we also aimed to investigate whether individuals with varying degrees of childhood gender nonconformity might also be expected to differ in the extent to which they engage in various olfaction-related everyday activities and hence in the level of long-term olfactory experience (as well as olfactory abilities). This hypothesis was based on the observation that gender-nonconforming boys frequently appear to be interested in activities which would be considered typical of the opposite sex, such as doing hair, makeup, dressing-up, cooking or cleaning, as can be gleaned from reports of men who were gender-nonconforming boys (Hockenberry & Billingham, 1987). Although we did find associations between childhood gender nonconformity and self-reports of engagement in certain olfaction-related activities, childhood gender nonconformity did not seem to affect the relationship between these self reports of involvement in such activities and participants' odour awareness and odour identification ability. In other words, the observed relationship was not driven solely by childhood gender nonconformity, suggesting its more general relevance.

This preface has presented an outline of the aims and scope of the thesis, its structure and the key topics explored herein. However, before proceeding to the introductory chapter, just in case you happen to be wondering about the fate of poor Miss Thompson, still trapped, as we pondered these weighty matters, in the midst of so many fragrant allurements at the chemist‘s, let the poet finish:

Undoubting bought of Mr. Wren,
Being free from modern scepticism,
A bottle for her rheumatism;
Also some peppermints to take
In case of wind; an oval cake
Of scented soap; a penny square
Of pungent naphthaline to scare
The moth. And after Wren had wrapped
And sealed the lot, Miss Thompson clapped
Them in beside the fish and shoes;
'Good day,' she says, and off she goes.
...

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CONTENTS

PART I

PART II

1. INTRODUCTION

The past three decades have witnessed a surge of interest in the study of the sense of smell, which has long been neglected, partly due to the belief that it was only of minor importance to humans, and partly because of methodological difficulties. Historically, based predominantly on between-species comparisons of neuroanatomical features such as the relative size of the olfactory brain or the absolute size of olfactory epithelia (Brown, 2001), there has been a strong tendency to view primates, including humans, as "poor smellers" (microsmats; Negus & Straatsma, 1960; Turner, 1890) with an increased emphasis on visual perception (King & Fobes, 1974; Walker & Jennings, 1991; Zhang & Webb, 2003). This view has been strengthened by the evidence that the size of the intact olfactory receptor repertoire has undergone a substantial decrease in primates, including humans, relative to other mammals (Gilad, Man, Paabo, & Lancet, 2003; Rouquier, Blancher, & Giorgi, 2000) with concomitant acquisition of full trichromatic vision (Gilad, Wiebel, Przeworski, Lancet, & Paabo, 2004). However, in a long series of assessments of olfactory performance in multiple nonhuman primate species, employing a large variety of odour stimuli and novel psychophysical methods (Hubener & Laska, 2001; Laska & Hudson, 1993), Laska and colleagues have challenged this view, demonstrating that between-species comparisons of neuroanatomical features or the number of functional olfactory receptor genes are poor predictors of olfactory performance, and strictly rejected the use of labels such as "microsmatic" or "macrosmatic" as overgeneralisation (Laska, Bautista, & Salazar, 2006; Laska, Genzel, & Wieser, 2005; Laska, Hofmann, & Simon, 2003; Laska & Seibt, 2002; Laska, Seibt, & Weber, 2000; Laska, Wieser, Bautista, & Salazar, 2004; Lotvedt, Murali, Salazar, & Laska, 2012). Comparative morphological studies have corroborated this position (Smith & Bhatnagar, 2004; Smith, Bhatnagar, Tuladhar, & Burrows, 2004), demonstrating that the “microsmatic/macrosmatic” divide lacks a basis in the morphology of the nasal chambers and that nasal cavity morphology must be reconsidered in terms of functions (olfaction versus air conditioning) traditionally assigned to various cavity structures. Comparisons of olfactory threshold values of squirrel monkeys, humans, and other mammalian species have shown that not only were the threshold values of humans comparable to those of squirrel monkeys, that is, in the same order of magnitude, for most odorants tested, but also comparable to those of dogs on longer chain compounds and even lower than those of rats on shorter chain compounds (Laska et al., 2000). Even though these data must be interpreted with caution, as different testing methodologies have been employed, which may lead to widely differing results, they lend further support to the view that the long-held dichotomy of „microsmatic“ and „macrosmatic“ vertebrates is no longer tenable. The finding that species conceived of as „microsmatic“ surpass the so-called „macrosmats“ in detection of specific odours seems to be indicative of the involvement of natural selection in determining olfactory sensitivity for various odours in a given species. As Laska et al. (2000) have shown, carnivorous, insectivorous, or sanguivorous species such as the dog, the hedgehog, or the vampire exhibited greater sensitivity to short-chain carboxylic acids, components of body-borne prey odours, than the squirrel monkey. In contrast, the frugivorous squirrel monkey exhibited significant olfactory superiority over the other species for amyl acetate and 1,8-cineole, which are components of fruit odours (Knudsen, Tollsten, & Bergstrom, 1993).

Thus, in humans, to reconcile the findings of relatively high olfactory sensitivity (Devos, 1990) with the fact that it must be achieved with a relatively low number of olfactory receptors, several hypotheses have been offered, which are yet to be tested. Firstly, humans have been proposed to receive richer retronasal smells. Shepherd (2004) speculates that the advent of fire and, much later, animal domestication, plant cultivation, use of spices and herbs, and invention of procedures such as fermentation made it more odorous. Nevertheless, from an evolutionary perspective, a more plausible suggestion regarding potential links between diet and "tuning" of chemosensory perception would be that diet diversification placed demands on human chemosensation to more efficiently process a broader repertoire of chemosensory cues so as to avoid rotten, toxic, or otherwise inedible foodstuffs. Secondly, it has been hypothesised that the reduced repertoire of olfactory receptor genes in humans is offset by the greater processing capacity of the human brain, afforded by the relatively more extensive brain regions dedicated to olfaction, memory, and the specifically human higher association areas (Shepherd, 2004). Thirdly, Porter et al. (2007) have suggested that the long-standing tradition of viewing human olfaction as inferior to that of other species may partly reflect behavioural demands rather than abilities, as evidenced by their finding that humans are capable of the demanding "macrosmatic" behaviour of scent-tracking, that they spontaneously mimic the tracking patterns of the so-called "macrosmats", and that they improve with practice.

Numerous studies have recently reinstated the long underestimated adaptive significance of the sense of smell in humans in the context of mate choice (for review see Havlicek & Roberts, 2009) as well as its importance for human safety and well-being (Stevenson, 2010), including those reporting a decline in perceived quality of life in olfactory loss (Hummel & Nordin, 2005). As Critchley (1986) put it, the olfactory system may be viewed as the "sentinel of the brain", whose most critical function is that of a warning system that may alert individuals to such hazards as fire, leaking gas, or spoilt food. Thus, it is no wonder that major complaints of individuals who have lost their sense of smell relate, in the first place, to reduced ability to detect gas leaks or smoke (Miwa et al., 2001; Varga, Breslin, & Cowart, 2000), difficulties with cooking and burning food, and consumption of rotten food (Miwa et al., 2001; Temmel et al., 2002), leaving these individuals with a 'sense of vulnerability' (Tennen, Affleck, & Mendola, 1991). In accordance with the functions of the sense of smell delineated above, these individuals also tend to report problems potentially negatively affecting the social aspect of everyday life, such as insecurity about one's own body odour, mood changes (Temmel et al., 2002), and depression (Nordin, Bramerson, & Blomqvist, 2000; Temmel et al., 2002; Tennen et al., 1991; Varga et al., 2000). Our study (**Chapter 2**) with individuals who were born without a sense of smell (a condition called *isolated congenital anosmia*, ICA) has revealed that these people tend to differ from normosmics[1] in terms of greater social insecurity, that they suffer from an increased risk of depressive symptoms, and are more subject to household accidents. Hence, in line with previous findings, we show that absence of olfactory input seems to negatively affect our sense of security and well-being with regard to control of potential environmental hazards and in social interactions, particularly with people we do not have a close relationship with. Although no differences in personal hygiene routines were found between ICA patients and normosmics, potentially reflecting adoption of coping strategies by the former group, this might possibly be a telling sign of their preoccupation with control of body odour, which, within the Western "deodorised" sociocultural context at least, is only tolerable in close relationships, particularly with sexual partners (Hyde, 2006; MacPhee, 1992; Molotch & Norén, 2010:40).

[1] Normosmia is the subjectively perceived normal olfactory function, usually defined as the ability to detect the great majority of tested odours in a given olfactory test (Landis, Briner, Lacroix, & Simmen, 2013). It is not an inherent characteristic of a given individual but depends on population averages. Specifically, in the Sniffin' Sticks test (Hummel, Sekinger, Wolf, Pauli, & Kobal, 1997), sum of the three constituent subtests is expressed as reliable heuristic "TDI" index, also referred to as the composite score (Wolfensberger, Schnieper, & Welge-Lussen, 2000). Normative data are available for this index based on samples of several thousand healthy European, American, and Australian men and women of all ages (Hummel, Kobal, Gudziol, & Mackay-Sim, 2007; Kobal et al., 2000). The following age-related levels with regard to the intactness of olfactory function have been defined: intact sense of smell (normosmia), indicated by the TDI score of more than 30; reduced ability to smell (hyposmia) for the score range of 30 to 15, which can be further subdivided into mild hyposmia (30-25), moderate hyposmia (25-20), and severe hyposmia (20-15) and, finally, functional anosmia (if score is less than 15), a condition in which some spurious olfactory sensations are still present but, nonetheless, cannot be made any effective use of in everyday life, given their fragmentary nature.

Further, although the problems with food evaluation may not necessarily lead to them eating less food than individuals with an intact sense of smell (Aschenbrenner, Scholze, Joraschky, & Hummel, 2008; Mattes et al., 1990), people affected by olfactory loss do report numerous changes in dietary habits (Aschenbrenner, Hummel, et al., 2008), driven most likely by reduced food appreciation (Ferris & Duffy, 1989; Miwa et al., 2001; Nordin et al., 2000; Temmel et al., 2002). Although it is beyond doubt that such self-reports greatly contribute to a better-informed, more complex understanding of the impact of olfactory loss in the context of everyday life and highlight the specific needs of patients that would otherwise go unnoticed, empirical studies are needed that would help identify the particular processes underlying this complex pattern of changes. Thus, in an explorative study in **Chapter 3**, we show that over the course of consumption of a simple food, congenitally anosmic individuals might experience a less pronounced decline in hedonic valence of a stimulus than healthy controls. Further research is needed to replicate these findings with a wide variety of different foods and to determine whether olfactory loss early in life might interfere with the development or expression of *sensory-specific satiation*, a phenomenon whereby the reward value of a particular food decreases during consumption because of repeated exposure to a particular sensory signal. Alternatively, this differential pattern of food appreciation in congenitally anosmic individuals might reflect a learned compensatory strategy.

The other reason why the sense of smell had long been treated with neglect by researchers, only to emerge as a burgeoning field at the turn of the century, were the manifold methodological conundrums involved in the control and presentation of chemosensory stimuli. Contemporaneous advances in other fields of science have stimulated major progress in the field of chemosensory research (for review see Doty, 2003a) and olfactory psychophysics has not lagged behind. Psychophysics[2], the study of the quantitative relation

[2] Traditional psychophysics sought to formulate mathematical functions relating physical magnitudes of stimuli and magnitudes of psychological sensations (or changes thereof), such as the Weber's Law (Weber, 1834). In the

between environmental stimulation, the physical dimension, and sensory-perceptual experience, the psychological dimension (Schiffman, 2008:441), has a long and enduring tradition in chemosensory research. Established by German scientist and philosopher Gustav Theodor Fechner (Fechner, 1860), who was among the first to develop procedural and mathematical concepts on which many psychophysical tests of olfactory performance have been modelled (Fechner, 1860; Thurstone, 1927a, 1927b; Weber, 1834), traditional olfactory psychophysics concerned itself with absolute detection thresholds[3], differential thresholds[4], and various indices of suprathreshold sensation magnitude. Developed within the theoretical framework of mathematical laws which govern build-up of suprathreshold sensation relative to intensity of a stimulus, first applications of these tests to measuring absolute (detection) odour thresholds were attempted, for instance, by Fischer and Penzoldt (1887). Among other topics that occupied the minds of researchers were explorations of interindividual variability or, more specifically, sex differences in olfactory sensitivity, perception, and discrimination abilities (Toulouse & Vaschide, 1899b, 1899c), or quantitative assessment of lateralisation of olfactory function in humans (Toulouse & Vaschide, 1899a, 1900; Washburn, 1901). Many of these applications required that olfactory stimuli be tightly controlled in terms of chemical purity and precise presentation, which called for development of devices that would allow presentation of odorants in known concentrations and well-defined quantities for various durations. Starting with the pioneering work of Zwaardemaker (1889) in the field of

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present day, any procedure that provides a quantitative measure of sensory function and requires a verbal or conscious overt response is referred to as psychophysical (Doty & Laing, 2003:204).

[3] The absolute or detection threshold is the lowest odorant concentration where presence of an odour is reliably detected. It should be discerned from the recognition threshold, which is the lowest concentration at which odour *quality* can be reliably discerned. In this case, the procedure is similar, only the individual is asked to indicate which of the stimuli has the target quality (Doty & Laing, 2003:206).

[4] The differential threshold (also referred to as difference threshold, „just noticeable difference“ (JND) or, simply, difference) is the smallest difference in concentration of a given odorant that can be perceived. In other words, it seeks to establish the smallest amount by which a stimulus must be changed in order to make it perceptibly stronger or weaker. The above-mentioned Weber’s Law (Weber, 1834) states that the increment in odorant concentration (ΔI) required to produce a JND increases as the comparison concentration (I) increases, with the ratio approximating a constant: $\Delta I/I = K$ (Doty & Laing, 2003:208).

olfactometry[5], most notably his draw-tube olfactometer (Zwaardemaker, 1925, 1927), numerous such devices have been devised since (for review see Brattoli et al., 2011).

Although a number of methods of odour stimulus control and presentation exist (for review see Hawkes & Doty, 2009b:64-66), in paradigms in which it is not necessary to control the precise amount of volatile molecules reaching the olfactory epithelium, including quantitative assessment of interindividual differences in olfactory performance, commercially available psychophysical tests[6] appear to be gaining in popularity, fuelling the recent proliferation of both basic research and clinical studies. Major advantages afforded by these tests include presentation of odour stimuli in a standardised manner, availability of norms for the specified age range, as well as direct comparability of findings across studies. This, however, comes at the price of not being able to expand the test by adding more stimuli to the set, modify stimulus concentration, or not being able to evaluate performance on tasks for which the particular test was not designed. A drawback common to all procedures considered psychophysical, whether performed using commercially available tests or not, is that they require a verbal or conscious overt response on the part of the individual, thus providing no

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[5] The term ‚olfactometry' refers to a technique which allows presentation of olfactory stimuli in a precise manner by controlling stimulus concentration, its change over the course of presentation, or concentration stability over repeated measures (Hummel, 2010). In static olfactometry, each concentration step in a series is prepared from successive dilutions of a single chemical compound. The nominal stimulus is the gaseous headspace, which is actively sniffed from a single container, e.g. a bottle equipped with a nosepiece. On the other hand, in dynamic olfactometry, continuous, well-regulated flow of gas is delivered, which contains odorised air (such as field-collected air sample) mixed in varying proportions with the carrier gas (typically odourless air or nitrogen) (Smeets et al., 2007:12).

[6] These include, for instance, (cued) odour identification tests such as the new 40-item Monell Extended Sniffin' Sticks Identification Test (MONEX-40; Freiherr et al., 2012), University of Pennsylvania Smell Identification Test (UPSIT; Doty, Shaman, & Dann, 1984) and its many variations (Brief/Cross-Cultural Smell Identification Test, B-SIT/CC-SIT; Doty, Marcus, & Lee, 1996; Quick Smell Identification Test, Q-SIT; Jackman & Doty, 2005; Picture Identification Test, PIT; Vollmecke & Doty, 1985), Smell Diskettes Olfaction Test (Simmen, Briner, & Hess, 1999) or Odourized Marker Test (OMT; Vodicka, Pellant, & Chrobok, 2007). Commercial tests of odour discrimination are also available, such as the Odor Discrimination/Memory Test (OMT; Doty, 2003b) or Düsseldorf Odour Discrimination Test (Weierstall & Pause, 2012). Odour detection threshold can be assessed, for example, by means of the Smell Threshold Test (STT; Doty, 2000). Other tests provide a set of measures, such as the Lyon Clinical Olfactory Test, which includes threshold detection, supra-threshold detection, and identification (LCOT; Rouby et al., 2011) or the Sniffin' Sticks test, which consists of tests of odour identification, discrimination, and (detection) threshold (Hummel et al., 1997). Finally, pediatric tests of olfactory function are also available, such as the Pediatric Smell Wheel (Cameron & Doty, 2013) or the retronasal Candy Smell Test (Renner et al., 2009).

information about, for instance, autonomic nervous system responses to odours or odour-exposure related changes in brain activity, and inviting potentially confounding variables, such as verbal fluency (Larsson, Nilsson, Olofsson, & Nordin, 2004; Larsson, Oberg, & Backman, 2005). However, these are vastly outweighed by convenience of use, particularly outside the laboratory setting or with large samples of individuals, particularly children, as was often the case with studies that comprise this thesis.

Having addressed the major advances and developments which have had a bearing on the field of olfactory psychophysics and led to the recent proliferation of psychophysical studies, both basic research and clinical, in the following paragraphs I will give a brief outline of olfactory psychophysical measures that are of relevance to the studies presented in this thesis.

1.1. OLFACTORY PSYCHOPHYSICS: SELECTED MEASURES

The human olfactory system is capable of detection and discrimination among thousands of airborne chemicals, both single chemicals and odorant mixtures, at concentrations that were even found to be below the detection limit of sophisticated analytical instruments, such as the gas chromatograph[7] (Takagi, 1989). Psychophysics, which has traditionally sought to formulate mathematical functions relating physical magnitudes of stimuli and magnitudes of psychological sensations (or changes thereof), must operate within this framework of complexity. It has not always been successful, in part, as Amoore (1965) notes, because of the lack of a simple physical dimension analogous, for instance, to wavelength for colour or frequency for pitch that correlates with olfactory quality. Also, it is well-known that different odorant mixtures produce different psychophysical results: for instance, odour type (the so-called "poor blenders", i.e. odorants that blend poorly in mixtures, vs. "good blenders") largely determines which odorants will be perceived in a mixture (Livermore & Laing, 1998). Numerous studies have sought the link between physicochemical properties of odorants and odour perception (Amoore, 1963; Dravnieks, 1982; Dravnieks, Masurat, & Lamm, 1984; Laffort & Dravniek.A, 1973; Schiffman, 1974; Schiffman, Robinson, & Erickson, 1977), for instance by varying stimuli along a single dimension such as carbon chain length (Laska & Teubner, 1999) or single perceptual descriptor (Rossiter, 1996). Nevertheless, mathematical models employing various physicochemical properties have largely fallen short of explaining the psychological dimensions of odour quality or intensity. The various complicating factors include the fact that whilst some odorants with similar structure may smell similar, others may smell different, such as vanillin and isovanillin, which differ only in the position of their substituents on the

[7] Gas chromatography is an analytical technique used to separate volatile organic compounds. In the most generic form, chromatography is based on the separation of compounds (or ions) present in a sample matrix (Carlin & Dean, 2013).

benzene group. Vanillin has a rich vanilla odour, whereas isovanillin has a weaker, very different, somewhat phenolic odour (Turin, 1996:11). Another example is the fairly extensive class of enantiomers[8] with six-membered ring flexibility, which do not smell the same (Brookes, Horsfield, & Stoneham, 2009). On the other hand, chemical compounds with different structures may produce similar odours, such as benzaldehyde and cyanide, which smell of bitter almonds. Further, some odour characteristics, such as perceived quality (Grossisseroff & Lancet, 1988) or pleasantness (Doty, 1975), may be influenced by stimulus concentration. Finally, as we shall see in the section on sex differences in olfactory abilities (**1.2.1**), repeated testing or olfactory training may result in lower detection thresholds, i.e. greater sensitivity to them (Haehner et al., 2013; Wysocki, Dorries, & Beauchamp, 1989; Yee & Wysocki, 2001) and in changes in perceived quality (Jacob, Wang, Jaffer, & McPhee, 2006).

Hence, psychophysics has afforded limited understanding of the mechanisms underlying the perception of odour quality. However, quantitative psychophysical measures have substantially furthered our knowledge regarding the influence of various factors on human olfactory function, and hence both inter- and intra-individual variability therein. In the following paragraphs the measures that are of relevance to the studies included in this thesis will be introduced, without going into detail in terms of their mathematical foundations (for review see Kingdom & Prins, 2010), which is beyond the scope of this thesis.

[8] Structures of organic molecules that are not identical, but mirror images of each other are called enantiomers (from Greek εχθρός, "enemy". The old term is *optical antipode*). Enantiomers belong to the group of isomers called stereoisomers. In contrast to constitutional isomers, stereoisomers are identical in the connectivity of the atoms, but differ in the overall shape of the molecules. The prefix stereo- (Greek στερεό, "solid") refers to the fact that stereoisomerism involves structures that must be regarded as three-dimensional (Meierhenrich, 2008:18).

1.1.1. Detection threshold

Modelled on mathematical concepts developed by Weber (1834) and Fechner (1860) (as well as others in the twentieth century), the detection threshold has historically been the most common and popular index of olfactory acuity in humans, first investigated as early as in late nineteenth century (e.g. Fischer & Penzoldt, 1887). It has considerable appeal to researchers as it measures performance in physical units of concentration, hence appearing less subjective than the majority of other psychophysical measures. However, given the high degree of variability, both within and across individuals, as well as within a given stimulus, a word of caution should be sounded against excessive reliance on a measure which may be interpreted as a single concentration value, above which a given substance can be perceived and below which it cannot. This is because even when it is conceived of as an arbitrary point on a function that plots probability of detection against stimulus concentration, the function is still likely to exhibit reversals, "notches", or "dips" for most odorants (Doty, 1991), suggesting that it is far from being a straightforward measurement. Further, odour detection values are known to depend on many factors such as method of stimulus dilution (Doty, 1992:106), headspace volume that is sniffed (i.e. the gaseous space over the liquid or the odour source in the vessel in which the stimulus is presented) (Doty, Gregor, & Settle, 1986), number of trials (Pierce, Doty, & Amoore, 1996) or hydrophobicity or hydrophilicity (Sobel, Khan, Saltman, Sullivan, & Gabrieli, 1999). Besides exhibiting considerable interindividual variability, as will be discussed in section **1.2.1,** detection threshold values are not "fixed" even for a given individual. As an extreme example, Stevens, Cain, and Burke (1988) measured detection threshold values of three individuals for three chemical compounds over the course of 30 days and found that intraindividual variability across the testing period was comparable to interindividual variability on a given test day, which highlights the need to employ procedures with more trials that yield more stable results (Doty, McKeown, Lee, &

Shaman, 1995; Jones, 1955). This concern also relates to the reliability[9] of commercially available psychophysical tests of olfactory performance. However, as Doty et al. (1995) points out, repeated estimates of the detection threshold yield respectable reliability coefficients and particularly for the test employed in all our studies, the Sniffin' Sticks test (Hummel et al., 1997), it has been reported to range between .43 and .85 (Albrecht et al., 2008). However, it should be noted that intraindividual variation is still to be expected (for details see section **1.3** on intraindividual variability), for instance, across the menstrual cycle (e.g. Doty, Snyder, Huggins, & Lowry, 1981) or as a result of olfactory training (Haehner et al., 2013), whose effects may transfer between odorants (Engen, 1960; Rabin & Cain, 1986).

Defined as the lowest odorant concentration which can be perceived or discerned from a blank sample, as noted above, detection threshold values are not fixed but vary on a trial-to-trial basis even within one testing session and are thus somewhat elusive to measure. Therefore, the average threshold value needs to be estimated mathematically. There are three methods which have become most popular for measuring odour detection thresholds (for review see Doty, 1992), of which the first two were formally developed by Fechner (1860), although not in relation to the olfactory modality.

1.1.1.1. The method of constant stimuli

Also referred to as the method of right and wrong cases or the constant method, it consists in presentation of a series of concentrations of a given odorant, ranging from imperceptible to clearly perceptible. Typically, there are hundreds of trials and the order of presentation of the individual concentrations is randomised in an effort to obtain a reliable result. In its two-alternative forced-choice (2-AFC) variant, the individual is always presented

[9] The utility of an olfactory test reflects the degree to which it is reliable (consistent, dependable, or stable) and valid (accurately measures what it declares to measure). Although a test cannot be valid without being reliable, the reverse is not the case; i.e., a test can be reliable but not valid (Doty & Laing, 2003:214). Specifically, for the Sniffin' Sticks test, reliability of .61 has been reported for the olfactory threshold component, .54 for the test of odour discrimination, and .73 for odour identification (Hummel et al., 1997).

with a pair of stimuli (odorant versus blank sample) at each concentration level in a counterbalanced order. The individual is repeatedly asked to indicate which of the two stimuli elicited a stronger sensation, regardless of whether he or she was able to discern any difference. The proportion of correct responses is then plotted as a function of concentration of the odorant, and the threshold value is defined as the concentration which corresponds to the 75% correct performance level, that is, as a point located halfway between chance (50%) and perfect (100%) performance. There is also a 3-AFC variant of this method there, in which two blanks are presented along with the target stimulus. In this case, the threshold is defined at the concentration of the odorant corresponding to the 66.67% correct performance level, that is, a point located halfway between chance (33.33%) and perfect (100%) performance.

As noted above, the resulting function is not monotonic but tends to show reversals, “notches”, or “dips”, which have been observed in human (Doty, Laing, Doty, & Breipohl, 1992) as well as animal data (Marshall, Blumer, & Moulton, 1981; Marshall, Doty, Lucero, & Slotnick, 1981). However, Doty (1992) states that there is variability across odorants in their tendency to yield such reversals in the function and recommends ignoring them to obtain olfactory threshold estimates of any practical value.

Despite the fact that the method of constant stimuli is considered a quintessential psychophysical measurement procedure (Gescheider, 1997), in human olfactory research it has been of limited use. This is because it requires hundreds of trials to yield a meaningful estimate of the olfactory threshold, introducing the unwanted effects of olfactory adaptation (Dalton, 2000), also known as olfactory/odour fatigue[10], as well as general boredom on the part of the tested individual.

[10] Odorant exposure, if recent and relatively continuous, may lead to a temporary decline in its perceived intensity and increase in detection threshold (for review see Cometto-Muñiz & Cain, 1995). Further, some chemical compounds lead to a decrease in the perception of other chemicals, which is referred to as cross-adaptation. Doty and Laing (2003:217) enumerate the general rules that have been identified regarding olfactory adaptation: (1) The magnitude of adaptation has been found to be a function of exposure duration and stimulus concentration. (2) It is further known to be influenced by an individual’s attention level. (3) The rate and degree

1.1.1.2. The method of limits

Also referred to as the method of minimal changes, this is a widely used method of estimating the olfactory threshold. In its classical version, the tested individual is presented with alternating series of ascending and descending odorant concentrations. In an ascending series, starting from an initially imperceptible level, the odorant is presented in an incrementally increasing concentration until its detection is reported by the individual. During a descending series, starting from an initially perceptible level, the stimulus is presented in an incrementally decreasing concentration until its detection can no longer be reported. The estimate of the detection threshold is the average concentration of the transition points at which reports of detection and non-detection are given.

However, this classical procedure of testing was abandoned in reaction to concerns about olfactory adaptation resulting from the suprathreshold stimuli, expressed by some researchers (Pangborn, Berg, Roessler, & Webb, 1964). A more common approach is to present one or more ascending series only, which is referred to as the ascending method of limits (AML). Nevertheless, as Doty (1992) notes, the major drawback to this variant is that it yields higher threshold estimates, indicative of lower sensitivity, compared to those obtained from multiple ascending series.

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of recovery from adaptation depend on the magnitude and duration of the stimulus which has caused it. (4) Cross-adaptation occurs, in the majority of cases, asymmetrically, i.e. whilst exposure to A decreases the perceived intensity of B, exposure to B may not decrease the perceived intensity of A. (5) Sensitivity to a given odorant is typically reduced more by exposure to that odorant than to any other odorant. (6) In rare instances, an odorant may have a larger adapting effect on the sensitivity to another odorant than it does on itself. (7) Sensitivity to an odorant that self-adapts strongly is usually also reduced strongly by other odorants. (8) Adaptation of one side of the nose leads to adaptation, albeit to a lesser degree, on the other side of the nose as well. (9) Adaptation to odorants comprised of several chemicals tends to be less pronounced than adaptation to single-component odorants. (10) Adaptation can be relatively rapid. For instance, exposure to vapours of lemon or orange oil results in complete loss of olfactory sensations, on average, in three minutes.

1.1.1.3. The staircase (up-down) method

This is a widely used variant of the aforementioned method of limits (Cornsweet, 1962), which yields a reliable estimate of odour threshold with a minimum number of trials. According to Doty et al. (1995), threshold estimates thus obtained are more reliable than those based on a single-series ascending method of limits because it is less dependent on early trials during which the individual is getting used to the procedure and may thus respond differently than on later trials. Also, because the procedure of the single-staircase (SS) method consists in increasing stimulus concentration following a trial on which an individual fails to detect the stimulus and decreasing the concentration following those on which he or she succeeds, the presented concentrations tend to fluctuate around the perithreshold level, yielding a more accurate threshold estimate. It should, however, be noted that the estimate is not directly comparable to those obtained by means of the method of constant stimuli or the classical method of limits. This is because, as shown in the following example, two correct trials are needed for a downward reversal and only one incorrect trial triggers an upward reversal. Hence, the threshold concentration thus determined is the value selected correctly by the tested individual 71% of the time (Wetherill & Levitt, 1965).

A single-staircase procedure is employed in testing the detection threshold with the odour threshold component of the Sniffin' Sticks test (Hummel et al., 1997), which has been used in the studies included in this thesis. It consists of 16 dilution steps of the odorant (2-phenylethanol or n-butanol), each of which forms a triplet with two blanks. Given the fact that it was originally devised for clinical evaluation, for ease of use the individual dilution steps are not given in units of concentration but as a dimensionless quantity. Thus, a single-staircase, three-alternative forced-choice (3-AFC) method is used, in which, starting with the lowest concentration (dilution number 16), an ascending (low to high concentration) series of even-numbered triplets is presented, with successful trials prompting another presentation of the same triplet in a random order. Two successful trials in a row mark a turning point; starting with the nearest lower concentration, a descending series of triplets is presented until the individual fails to detect the target. This marks a reversal towards the higher concentrations and, starting with the next higher concentration, an ascending series of triplets is presented until two correct trials occur, marking another reversal. The testing is finished after the total of 7 reversals is reached. The threshold score is computed as the arithmetic mean of the dilution number at the last four reversals. Ranging from 1 to 16, higher scores indicate greater olfactory sensitivity (i.e. lower threshold).

To sum up, currently it is preferred to employ forced-choice procedures due to their greater reliability (Doty et al., 1995). In a forced-choice procedure, the individual is required to indicate, on a given trial, which of the two (or more) stimuli smells the strongest, rather than to report whether an odour has been perceived or not. The forced-choice paradigm thus answers some of the concerns of signal detection theory (Green & Swets, 1966; see below) that individuals may rely on their own set of criteria for reporting detection or non-detection and hence threshold measures reflect not only their sensitivity to the given chemical compound, but also these internal criteria or biases. Further, as we have seen, the two most widely used methods of odour detection threshold estimation are the ascending method of limits (AML; in combination with a forced-choice paradigm also termed ASTM) and the single staircase (SS) method, with the latter yielding more reliable estimates (Doty et al., 1995). Obviously, different methods yield different threshold estimates, as will any alterations to the number of alternatives (blanks plus the target stimulus) presented at each concentration level, rendering the task easier or harder. A more difficult procedure with a lower probability of being correct by mere guessing will naturally produce higher detection threshold estimates, indicative of individuals' lower olfactory sensitivity.

As a final note, an alternative to the notion of absolute threshold measurement, that will be only briefly mentioned here, is provided by the signal detection theory (Green & Swets, 1966). In short, signal detection theory recognises that stimulus perceivability emerges gradually as the level of the stimulus is increased above the background as well as the fact that both the neural system and the background are "noisy", which results in some responding to the background noise alone. It also takes into account the individual's response criterion/bias (Tanner & Swets, 1954), which, according to Doty and Laing (2003:208), can be viewed as an internal rule that a given individual uses to decide whether or not to report that he or she has detected a stimulus, that is, the liberalism or conservatism in reporting detection under specific circumstances. For instance, if two individuals can detect the same weak stimulus but one reports not having detected it whilst the other gives an affirmative response, the difference lies not in the individuals' respective abilities of odour detection but in their response criteria for reporting detection. In a non-forced-choice detection threshold paradigm, the conclusion would, however, be that the individuals exhibited different olfactory sensitivity to the given compound.

1.1.2. Odour quality discrimination

Tests of odour quality discrimination establish the degree to which an individual can differentiate between different odours. Hence, the forced-choice olfactory detection threshold may, in fact, be viewed as a specific case of odour discrimination, namely one in which an individual is required to compare the alternatives, i.e. blanks(s) and the target stimulus, and report which is different, that is, which smells stronger.

Odour discrimination tests count among the tasks that are the least demanding in that the individual is only asked to discern between the stimuli without any further need to identify them. That is not to say, though, that tests of odour discrimination may not vary in terms of their difficulty level, which relates to the similarity of the presented stimuli, their number as well as the number of trials. Regarding the stimuli, as this is an odour *quality* discrimination task (as opposed to *intensity* discrimination), the stimuli, presented in suprathreshold concentrations, should be matched for perceived intensity. There are three procedures to quantitatively assess odour discrimination (for review see Doty & Laing, 2003). In the most basic version of this test, the individual is presented with a number of same- and different-odorant pairs and asked to indicate whether the two olfactory stimuli have the same or different quality. The proportion of pairs that have been correctly reported as being the same or different is then used as the measure of discrimination (e.g. De Wijk & Cain, 1994; Luzzi et al., 2007; Zatorre & Jones Gotman, 1991).

A widely adopted approach is asking the individual to select the odd stimulus from a set from which only the odd stimulus differs. The proportion of correct trials is taken as a measure of odour discrimination. According to some authors (Frijters, 1980; Frijters, Kooistra, & Vereijken, 1980), its three-alternative version with two identical stimuli and one odd stimulus, with both types of stimuli occurring on half the trials as the odd one, should be referred to as the triangle test. When only one stimulus type serves as the odd one, the task should be termed a three-alternative forced-choice test (Frijters et al., 1980). The Sniffin' Sticks (Hummel et al., 1997) odour discrimination test also falls into this category. It is comprised of 16 triplets of stimuli, with two stimuli in a given triplet being identical, and the individual is asked to indicate the odd one. The score is the total of correct trials (0-16), with higher scores indicating a better ability of odour discrimination.

Yet another approach is based on multidimensional scaling (MDS), which provides spatial representation of the stimuli. All possible pairs of stimuli (or selected subsets thereof) are rated on a line scale anchored with descriptors such as “completely different” or “exactly the same” and correlation matrix among these ratings is produced, to which an algorithm is applied that places the stimuli in a two- or more dimensional space relative to perceived similarity (e.g. Carrasco & Ridout, 1993). However, being time-consuming and computationally rather complex, it is not used routinely.

Surprisingly, cognitive factors involved in odour discrimination tasks have been addressed only recently (Hedner, Larsson, Arnold, Zucco, & Hummel, 2010). As the task involves detecting similarities and differences between odorants, it places demands on processes which draw on executive functions. Specifically, a transient representation of the target odour must be formed and used for comparison and subsequent selection of this target odour. Indeed, Hedner et al. (2010) reported that individuals who performed well in executive functioning (measured by means of digit span backward) also exhibited superiority in odour discrimination (and identification). Besides, they also found an association between proficiency in semantic tasks with a strong verbal component (letter fluency, general knowledge, and vocabulary) and odour discrimination. This was in line with the previous finding that prior verbal processing or labelling leads to enhanced discrimination of the stimuli. As Jönsson and Olsson (2012:121) put it, before an odour is identified (correctly or not), the perception of it is unclear, fuzzy, as evidenced by the finding that it is more difficult to discriminate between unidentified odours than between ones that have been identified (De Wijk & Cain, 1994; Jonsson, Moller, & Olsson, 2011).

1.1.3. Odour quality identification

Odour identification refers to verbal labelling of a given olfactory stimulus, either by naming or by selecting a proper alternative from a list of descriptors (comprised of one target and several distractors). Alternatively, a set of pictures may be used instead of verbal labels. It is a semantic memory task in that it places demands on an individual's knowledge of an odour's identity (for review see Richardson & Zucco, 1989). Indeed, Larsson et al. (2000, 2004) have demonstrated a positive association between general semantic knowledge, verbal fluency, and proficiency in odour identification. Importantly, the semantic influence has been shown to be independent of variability in demographic factors, such as age and sex, odour sensitivity, and perceptual speed (Larsson et al., 2005), indicating that odour identification and semantic memory draw on similar cognitive abilities.

Tests of odour quality identification or, shortly, odour identification, are probably the most widely used type of test of olfactory performance. A Web of Science search of "odor identification", which currently yields around 900 results as well as the wide availability of commercial odour identification tests attest to their popularity. This is largely due to their considerable predictive value in the context of clinical research with respect to neurodegenerative diseases (for review see Doty, 2003c), for instance in terms of conversion from mild cognitive impairment to dementia in Alzheimer's disease (Conti et al., 2013) or differentiation among clinical subtypes of Parkinson's disease (Iijima et al., 2011). There is also a robust body of evidence that odour identification is impaired in "normal" aging (e.g. Larsson, Finkel, & Pedersen, 2000), which is, of the known factors, attributable to age-related deficits in odour sensitivity, quality discrimination, and perceptual speed. This decline in odour identification in old age relates to the observed concomitant impairment of odour memory in the elderly. Episodic odour memories are mediated by semantic factors, such as odour identification, and the difficulties of older individuals concerning odour identification underlie the age-related deficits in episodic odour memory (Larsson & Backman, 1997; Lehrner, Gluck, & Laska, 1999).

There are three categories of odour identification tests, namely naming tests, yes/no identification tests, and multiple-choice identification. In an odour naming test (also termed "free odour identification test"), the individual is asked to provide a name for the stimulus, whilst in a yes/no odour identification test the requirement is to indicate whether the stimulus smells like an object named by the researcher. Finally, multiple-choice, cued odour identification tests consist in providing the individual with a set of labels or pictures, comprised of a target and distractors, and asking him or her, on a given trial, to select one that best describes the stimulus. This was employed in the studies included in this thesis (along with free odour identification in **Chapter 4**). The 16-item Sniffin' Sticks test (Hummel et al., 1997) of cued odour identification involves a 4-AFC task in which the individual is required to choose a label from a list of four, which he or she thinks best describes the odour's source. The score is the total of correct trials.

Although such a testing procedure may seem straightforward and trouble-free or, at least, less complicated than measurements of detection thresholds, multiple conundrums, discussed at length in **Chapter 5,** are involved even in the most usable form of the test, the cued odour identification test. Since it has been repeatedly shown that spontaneous, free (uncued) odour identification is difficult (e.g. De Wijk & Cain, 1994), odour naming tests which give no response alternatives have been of limited value. Yes/no odour identification tests fare somewhat better, even though they are less sensitive than cued odour identification tests (Serby, Larson, & Kalkstein, 1990) because chance performance on this type of test is

50% compared to 33% on a 3-AFC and 25% on a 4-AFC cued odour identification test. Therefore, more trials must be carried out to obtain the same statistical power as the latter.

Nevertheless, use of cued odour identification tests raises its own concerns. These relate, as is the case for the other two types of odour identification tests, to perceptual properties of the stimuli, e.g. their detectability and to how realistically the target items (“veridical” labels) are physically represented by the odour stimuli. Further, there is also the issue of whether the given odour possesses any real-life significance, that is, whether it is at all important for an individual to know what it is or what it signifies, i.e. the item’s cultural relevance. Besides, the issues of how perceptually close the representations of the target and the distractors are within some of the human odour spaces, as well as the level of semantic similarity between the labels, also come into play. For instance, Gudziol and Hummel (2009) have demonstrated that use of more contrasted distractors, such as lilac, peanut, honey for the target odour of turpentine (instead of the usual triplet of mustard, rubber, and menthol) significantly affects performance on the Sniffin’ Sticks test. In a similar vein, increasing the number of distractors from three to six will render the task more difficult and yield lower identification scores in older participants (Negoias, Troeger, Rombaux, Halewyck, & Hummel, 2010).

In the following text, performance on the above-mentioned measures will be referred to as olfactory threshold/sensitivity, the ability of odour discrimination, and (cued) identification, respectively. In general, olfactory abilities can be defined as the abilities to detect and process meaningful information in odours (Flanagan & Harrison, 2012:132). To recapitulate briefly, the absolute (detection) olfactory threshold refers to the minimum concentration of a tested odorant that an individual is able to reliably differentiate from a blank sample. The test of odour discrimination ability establishes the degree to which an individual can differentiate between odours in suprathreshold concentrations. Finally, the ability of cued odour identification consists in correct verbal labelling of a given olfactory stimulus by selecting a proper alternative from a list of descriptors. Next, I will focus on selected factors affecting these olfactory abilities that are of relevance to the studies presented in this thesis.

1.2. INTERINDIVIDUAL DIFFERENCES IN OLFACTORY ABILITIES

As noted above, standardised psychophysical tests of olfactory abilities afford a quantitative measure of various aspects of olfactory performance, reflecting, firstly, the degree of intactness of olfactory function, which is indicative of the state of both the peripheral and central olfactory system, and, secondly, individual level of olfactory acuity within the age-related normosmic range. To address the first point, factors which contribute to reduced olfactory function include genetic predispositions (Grossisseroff, Ophir, Bartana, Voet, & Lancet, 1992; Karstensen & Tommerup, 2012; Weiss et al., 2011), neurodegenerative diseases (for review see Doty, 2003c), head injury (for review see Costanzo, DiNardo, & Reiter, 2003), infections (for review see Welge-Lüssen & Wolfensberger, 2006), and exposure to environmental toxicants (for review see Hastings & Miller, 2003). However, these will not be considered here. The focus will be on selected factors contributing to differences in normal olfactory function which are of relevance to the studies presented in the following chapters.

1.2.1. The effect of sex/gender from a developmental perspective

Sex differences in human olfaction, or, more precisely, the female olfactory superiority across virtually all age groups and cultures studied is a well-established yet poorly understood phenomenon (for review see Brand & Millot, 2001), whose robustness has led some to refer to it as an inborn sexually dimorphic trait (e.g. Doty, 1992). In the following paragraphs, evidence on sex differences in olfactory abilities of children and adults will be reviewed, leaving, however, the differential effects of aging in either sex aside, as it is beyond the scope of the studies presented in the thesis.

Although the manifold methodological conundrums and potential biases involved in the research of olfactory perception in infants and children have been hindering our more complex understanding of the development of human olfactory abilities, studies show that at least from a certain age up and on some psychophysical tests, girls outperform boys. In newborns, however, the evidence is mixed at best, because, for instance, 2-week-old, exclusively bottle-fed girls but not boys spent more time oriented towards the breast odour of an unfamiliar lactating female than to either the same female's axillary odour or the breast odour of a nonparturient female (Makin & Porter, 1989). However, their responses to the lactating female's axillary odour and a clean pad did not differ. This might reflect the female infants' better ability to discriminate between some of the odours or, possibly, the greater salience of a biologically relevant odour such as that of human breast milk for newborn girls than boys. Nevertheless, in a later study with bottle-fed newborns of the same age by Porter, Makin, Davis, and Christensen (1991), both infant girls and boys exhibited preferential orientation towards the breast odour of their mother over a clean pad and when the former was paired with the odour of their familiar formula, girls showed no preference whereas boys spent more time oriented towards the formula odour. Finally, when exposed to the breast odour of an unfamiliar lactating female versus the odour of their formula, both girls and boys oriented preferentially towards the odour of human breast milk, despite minimum, if any, experience therewith. Preferential orientation towards lactating females' breast odours in girls and boys alike was demonstrated in breast-fed infants of the same age as well (Porter, Makin, Davis, & Christensen, 1992). This, in the first place, suggests the supreme importance of recognizing biologically relevant odours such as that of human breast milk for individual survival of human newborns, irrespective of sex, but any evidence of a better ability of olfactory discrimination in newborn girls is tentative at best. Nevertheless, the female superiority, particularly in the ability of odour identification and odour awareness, is present at least by preschool age (Ferdenzi, Coureaud, Camos, & Schaal, 2008; Ferdenzi, Mustonen, Tuorila, & Schaal, 2008; Richman, Post, Sheehe, & Wright, 1992), with girls also exhibiting higher composite scores of olfactory threshold, discrimination, and identification (TDI) and an earlier age-related increase thereof (Renner et al., 2009). The authors however note that this differential increase in the TDI scores was mainly due to differences in odour identification, which has a cognitive verbal component (Larsson et al., 2004; Larsson et al., 2005). There was only a slight contribution of the discrimination score and none of the olfactory threshold score. In another study, no sex difference in the scores of odour discrimination was observed at all in children aged 2-18 years (Richman, Sheehe, Wallace, Hyde, & Coplan, 1995). That the girls' higher scores of odour identification indeed can be accounted for by their superior verbal abilities (both verbal age and olfactory verbal fluency) has been demonstrated by Monnery-Patris, Rouby, Nicklaus, and Issanchou (2009). What is more, they also report a significant effect of verbal age on threshold detection scores for tetrahydrothiophene.

Thus, the female superiority in odour identification seems to be established relatively early in ontogeny, hold across the lifespan, and exhibit a later decline with aging (Doty, Shaman, Applebaum, et al., 1984; Larsson et al., 2004; Ship, Pearson, Cruise, Brant, & Metter, 1996). In the case of olfactory sensitivity to various odours, measured by detection thresholds, the evidence in preschool and prepubertal children is mixed (Hummel, Bensafi, et al., 2007; Monnery-Patris et al., 2009; Solbu, Jellestad, & Straetkvern, 1990; Toulouse & Vaschide, 1899c), but sex differences may appear during puberty, when boys become less sensitive to some biologically relevant odours such as androstenone (Dorries, Schmidt, Beauchamp, & Wysocki, 1989) and androstadienone (Hummel, Krone, Lundstrom, & Bartsch, 2005; Chopra, Baur, & Hummel, 2008), whereas girls either retain the same threshold levels or become even more sensitive. Chopra et al. (2008) further reported pubescent girls' greater olfactory sensitivity for other body-related odours such as 2-methyl,3-mercapto-butanol (2M3M; a malodorous component of human sweat) and carbon disulfide/hydrogen sulfide (H2S; sulphur compounds being present in oral malodour and intestinal gases). Adult women, while also appearing to be more sensitive to androstadienone than men (Koelega & Köster, 1974; Lundstrom, Hummel, & Olsson, 2003), however, do not seem to reliably extend their olfactory superiority to odour thresholds in general (Hedner et al., 2010; Hummel, Kobal, et al., 2007; Kobal et al., 2000; Kobal et al., 2001; Lundstrom et al., 2003). Sex differences in detection thresholds between men and women have been an attractive research topic since the dawn of olfactory psychophysics. Perhaps the most well-known of those early studies are those carried out by Toulouse and Vaschide (1899b, 1899c). Based on a sample of 237 men and women of all ages, tested for sensitivity, discrimination, and perception with camphor and floral odours, they found female superiority in olfactory sensitivity to the odour of camphor, which was in stark contrast to the findings of Bailey and co-workers, who concluded that men were more sensitive (Bailey & Nichols, 1884; Bailey & Powell, 1883). Other early authors to report greater olfactory sensitivity in women were Le Magnen (1952), who employed pentadecanolide (Exaltolide) and found that adult women were highly sensitive to its odour and perceived it as very intense, whereas adult men and young children were hardly able to detect it, and Schneider and Wolf (1955), who noted women's lower thresholds for citral. In the following decades, however, general claims about women's lower olfactory thresholds have been abandoned. This is because sex differences in olfactory sensitivity to a number of odorants in favour of women do not appear to be particularly robust, as they were not seen by all authors (Amoore & Venstrom, 1966; Griffiths & Patterson, 1970; Kloek, 1961; Matzker, 1965; Mesolella, 1934; Punter, 1983; Venstrom & Amoore, 1968) and, in some cases, seem to require relatively large sample sizes to be observed. Rather, olfactory sensitivity appears to be strictly odour-specific (Lundstrom, McClintock, & Olsson, 2006). Perhaps the most extensively investigated over the past decades have been the sex differences in sensitivity to the 16-androstenes, the putative human sex pheromones (for review see Havlicek, Murray, Saxton, & Roberts, 2010). For 5α-androst-16-en-3-one (androstenone), it was found that 26.8% to 44.3% of men showed specific anosmia[11] to its odour, whereas only 7.6% to 25% of women were unable to detect it (Baydar, Petrzilka, & Schott, 1993; Dorries et al., 1989; Griffiths & Patterson, 1970). Women are also seem less likely than men to exhibit specific anosmias for 5α-androst-16-en-3α-ol (androstenol) (Kloek, 1961) and have been reported to show greater sensitivity to its odour (Koelega & Köster, 1974). Studies in which other musk-like compounds were employed yielded similar results: besides the above-mentioned study by Le Magnen (1952) with Exaltolide, sex differences in olfactory sensitivity in favour of women were found in the studies by Koelega and Köster (1974) and Koelega (1994b) with oxohexadecanolide, and in the National Geographic Smell Survey with Galaxolide (Wysocki & Gilbert, 1989).

On the other hand, for odours which bear no biological relevance, olfactory thresholds of men and women do not appear to differ to any significant degree, as evidenced by results obtained with n-butanol (Koelega, 1970), safrol (Koelega & Köster, 1974), pyridine (Dorries et al., 1989), phenyl ethyl alcohol (Segal, Topolski, Wilson, Brown, & Araki, 1995; D. A. Stevens & O'Connell, 1991; Zatorre & Jones Gotman, 1990). What is more, an instance of *men's* superiority in olfactory sensitivity has recently been reported (Olsson & Laska, 2010). Men were found to detect the sperm attractant bourgeonal at significantly lower concentrations than women, whereas no such sex differences were observed for helional, a structural analogue of bourgeonal, or for n-pentyl acetate, an aliphatic ester.

[11] Specific anosmia, also known as “odour blindness” (Amoore, 1968; Whissell & Amoore, 1973), refers to markedly increased absolute (detection) thresholds (hence reduced sensitivity) for one or a few related odorants in an otherwise normosmic individual. First noted by Blakeslee (1918) for the scent of verbena flowers, numerous specific anosmias have been identified since, such as that for musk (Whissell & Amoore, 1973), androstenone (Amoore, Pelosi, & Forrester, 1977; Wysocki & Beauchamp, 1984), isobutyric and isovaleric acid (Amoore, 1967), isobutyraldehyde (Amoore, Forrester, & Pelosi, 1976), or even cyanide (Sayek, 1970); for review see Wysocki and Beauchamp (1991) and Takagi (1989). Suggested to have a genetic basis (Whissell & Amoore, 1973; Wysocki & Beauchamp, 1984), many specific anosmias are nonetheless alleviated by repeated exposure and olfactory training in a significant proportion of individuals (Doty et al., 1981; Jacob et al., 2006; Mainland et al., 2002; Wysocki et al., 1989; Yee & Wysocki, 2001).

Hence, to sum up, whilst the body of evidence for differences in odour identification between men and women across the lifespan seems fairly robust, comparisons of odour detection thresholds have produced mixed results. In the following paragraphs, we turn to the various competing, though not necessarily mutually exclusive, interpretations that have been proposed thus far to account for these intriguing findings.

1.2.1.1. Possible explanations for sex differences in olfactory performance

As can be seen, for over a century, the phenomenon of sex differences in olfactory sensitivity (and other olfactory abilities) has been, due to its "enigmatic" nature (Brand & Millot, 2001), one of the most extensively researched topics, and it continues to hold the undiminished interest of researchers until the present day. Interpretations of these sex differences remain, however, rather incomplete (for review see Brand & Jacquot, 2007; Brand & Millot, 2001). They include, firstly, a suggestion that anatomical or physiological differences directly involved in olfactory processing might play a role, such as the size and shape of nasal airways (Etoz, Etoz, & Ercan, 2008; Lopez, Toro, Schilling, & Galdames, 2012; Springer et al., 2008). Although this has not been extensively researched, in a study by Leopold (1988), the volume of the space between the mid-portion of the septum and the middle turbinate was strongly associated with olfactory acuity. However, a more recent study did not seem to corroborate this finding (Soler, Hwang, Mace, & Smith, 2010). Hornung and Leopold (1999) found that increases in the size of compartments of the nasal cavity around the olfactory cleft generally increased olfactory abilities and concluded that sex differences in the anatomy of the nasal cavity might contribute to sex differences in olfactory abilities. On a similar note, Damm et al. (2002) reported significant correlations between odour thresholds and volumes of the anterior part of the lower and upper meatus of the right nasal cavity and argued that two nasal segments have a bearing on interindividual differences in odour thresholds in healthy individuals, namely the segment in the upper meatus below the cribriform plate and the anterior segment of the inferior meatus. Most recently, Jun et al. (2010) also demonstrated that the volume around the turbinates was correlated with the olfactory threshold (but not odour identification). Finally, somewhat peculiarly, it has been even suggested that oral hygiene habits might play a role (Griep et al., 1996).

Sexual dimorphism of the cerebral hemispheres (Goldstein et al., 2001; for review see Zaidi, 2010) and cerebral asymmetry (Gilmore et al., 2007) have also been proposed by Brand and Millot (2001) to influence olfactory processing, based on correlations of anatomical asymmetry with behavioural asymmetry. In their study, Millot and Brand (2000) videotaped the smelling behaviour of dextrals,[12] which involved odour identification and recognition, and found that compared to women, men more often used the right nostril than the left one regardless of the odour. These results were taken to indicate a more pronounced cerebral asymmetry in men than in women and a predominant involvement of the right cerebral hemisphere in olfactory processing in (right-handed) men. Nevertheless, as they note, the correspondence with specific functional aspects of olfactory processing is currently not known.

Many sex differences are known to arise from the action of gonadal hormones on the central nervous system during early (prenatal and perinatal) periods of brain development

[12] The topic of lateralised differences in olfactory sensitivity in relation to the individuals' handedness is another one that has had a century-long history of research. The pioneers in the field of research on sex differences in olfaction, Toulouse and Vaschide (1899a, 1900), were also the first to report differential sensitivity to various monorhinally presented odours in dextrals and sinistrals. They reported that 56 out of 64 right-handed individuals (including men, women, and also several children) exhibited increased sensitivity to the odour of camphor on the left side of the nose, whereas in 5 left-handed or ambidextrous individuals the right side was more sensitive. However, a follow-up study with 15 right-handed women revealed higher sensitivity to ammonia on the right side. Taken together, their early observations suggested that for camphor, the side of greater nasal sensitivity was contralateral to hand dominance, whereas for ammonia it was ipsilateral. Although (or, perhaps, because) contrasting and mutually conflicting results have been reported since (Koelega, 1979; Lubke, Gottschlich, Gerber, Pause, & Hummel, 2012; Zatorre & Jones Gotman, 1990), their early observations have laid the groundwork for an area of research that is still very much alive today. For instance, lateralised differences in olfactory performance on tests of olfactory sensitivity (Frye, Doty, & Shaman, 1992; Youngentob, Kurtz, Leopold, Mozell, & Hornung, 1982) and odour discrimination (Hummel, Mohammadian, & Kobal, 1998), hedonic judgments (Dijksterhuis, Moller, Bredie, Rasmussen, & Martens, 2002), as well as emotional responses to odours (Royet, Plailly, Delon-Martin, Kareken, & Segebarth, 2003) as a function of handedness have been found.

(Hines, 2011; Lenz & McCarthy, 2010; McCarthy, 2010). This also provides a substrate affected by hormonal influences later in life, such as during puberty. In their review, Doty and Cameron (2009) mention three types of sexually dimorphic behavioural traits: firstly, those that require, for full expression, relevant hormones both during an early critical stage (i.e. prenatal and early perinatal) and later in life, secondly, those that require relevant hormones only at a later stage in life, and, thirdly, those that require only relevant hormones during an early critical period. In olfaction, differences in hormonal status have also been proposed to contribute to sex differences, namely that androgens depress and estrogens enhance olfactory performance, more specifically sensitivity (Good, Geary, & Engen, 1976; Le Magnen, 1952; Schneider, Costiloe, Howard, & Wolf, 1958). With respect to the above-mentioned classification, these could be conceived of as the first or the second type. However, if this should be so, as Doty notes (Doty, 1986a; Doty & Cameron, 2009), four predictions should be true. Firstly, prepubertal children should be expected to show little sex difference in olfactory sensitivity because of the absence of clear-cut sex differences in circulating levels of the primary reproductive hormones at this time (Faiman, Reyes, & Winter, 1979; Winter & Faiman, 1972, 1973). Secondly, sex differences in olfactory sensitivity should become evident around puberty, supposedly driven by the underlying hormonal changes (August, Kaplan, & Grumbach, 1972; Burr, Sizonenk.Pc, Kaplan, & Grumbach, 1970; Jenner, Kelch, Kaplan, & Grumbach, 1972; Lenko, Lang, Aubert, Paunier, & Sizonenko, 1982; Root, 1980; Sizonenko, Burr, Kaplan, & Grumbach, 1970; Sizonenko & Paunier, 1975) and continue well into middle adulthood. Thirdly, if endocrine effects were sizeable enough to override the detrimental effects of aging, women at menopause should exhibit a marked decline in olfactory sensitivity because of the dramatic decrease of estrogen levels at that time (Davison, Bell, Donath, Montalto, & Davis, 2005; Nedergaard, Henriksen, Karsdal, & Christiansen, 2013). Fourthly and finally, older men should experience an increase in olfactory sensitivity due to reduction in circulating levels of testosterone and elevation of circulating levels of estrogen (Elmlinger, Dengler, Weinstock, & Kuehnel, 2003; Orwoll et al., 2006). Nonetheless, the data available thus far provide little support for these predictions. As far as detection thresholds are concerned, the evidence is mixed in both children and adults, as discussed above, with the specific cases of sex difference being, but for bourgeonal (Olsson & Laska, 2010), invariably in favour of females, regardless of age (e.g. Hummel, Kobal, et al., 2007). However, this does not rule out the possibility of the third type of sexually dimorphic traits, which only requires relevant hormones during an early critical period, and this would actually appear to be the most likely candidate for an endocrine-based explanation for (at least some of) the sex differences in human olfaction. Our finding concerning intrasexual variability in olfactory performance with respect to childhood gender nonconformity (or gender identity/sexual orientation) **(Chapter 7),** which relates to prenatal exposure to androgen steroids (for review see Savic, Garcia-Falgueras, & Swaab, 2010), seems to corroborate this view, albeit rather indirectly.

Furthermore, it has also been proposed that the female olfactory superiority is a marginal expression of complex differences in higher levels of brain organisation and function, specifically of sex differences in certain cognitive abilities, such as verbal recall (Maitland, Intrieri, Schaie, & Willis, 2000) and verbal fluency (Burton & Henninger, 2013; Halari et al., 2006; Soleman et al., 2013) in favour of women, but see Wallentin (2009) for a critical review. For instance, verbal (letter) fluency is known to be positively associated with performance on the tasks of odour identification (Larsson et al., 2004; Larsson et al., 2005) and discrimination (Hedner et al., 2010; Larsson et al., 2005). Further, Lorig (1999) advanced a hypothesis that olfactory processing shares some of the cortical resources employed in language processing and that their simultaneous processing brings about interference between them. Hence, an advantage in verbal tasks could be associated with an advantage in certain olfactory performance measures, such as odour identification.

Of the many explanations/interpretations, the one that is of particular interest in our studies included in **Chapters 4** and **8** is the long-term olfactory experience. In their review, Brand and Millot (2001) put forward the hypothesis that women may in general encounter olfactory stimuli more often than men and thus they can have greater experience with a wider variety of odours. At least in western industrialized societies, this might be due to women's long-term greater odour exposure within specific contexts, such as cooking, use of cosmetic products, or housework (Bianchi, Milkie, Sayer, & Robinson, 2000; Coltrane, 2000; Fuwa & Cohen, 2007), which starts as early as in infancy. In children, the fact that gender stereotyping of activities is encouraged from very early in ontogeny is reflected in the knowledge of gender stereotyping of household activities demonstrated by girls (but not boys) as young as 24 months of age (Poulin-Dubois, Serbin, Eichstedt, & Sen, 2002). Although most evidence for the effect of prior odour exposure on olfactory performance comes from laboratory studies (e.g. P. Dalton, Doolittle, & Breslin, 2002; Schab & Crowder, 1995), within the real-life context, the long-term effect of olfactory expertise has been demonstrated in perfumers, who show functional reorganisation of olfactory and memory brain regions (Delon-Martin, Plailly, Fonlupt, Veyrac, & Royet, 2013; Plailly, Delon-Martin, & Royet, 2012), and in other professionals, including chefs (Martin, Apena, Chaudry, Mulligan, & Nixon, 2001).

From an evolutionary viewpoint, women's better olfactory sensitivity could be argued to have been selected specifically in the context of mate choice. For instance, in a questionnaire study on the importance of the respective senses in various contexts, Havlicek et al. (2008) replicated the existing findings of women's greater reliance on olfactory cues compared to men, who were found to be more visually oriented, in the context of mate choice and during sexual arousal. However, women also attached greater importance to olfactory cues than men in contexts unrelated to sexual behaviour, which is perfectly in line with findings presented in section **1.4** of this thesis. A previous study by Herz and Cahill (1997) found that women rated olfactory cues as more important than all other sensory cues when choosing a potential lover. In a similar vein, Herz and Inzlicht (2002) asked their participants to select various characteristics related to social status, personality, and physical traits desirable in a potential lover. Both men and women rated the pleasantness of the potential lover as most important, but in terms of physical cues, women attached significantly more importance to body odour, whereas men seemed more interested in visual appearance. Another support for this hypothesis seems to come from the numerous studies demonstrating lower odour detection thresholds (i.e. greater olfactory sensitivity) and lower rates of specific anosmia to body odour-related compounds in women than in men. However, as we have seen, many specific anosmias can nonetheless be alleviated by repeated exposure and olfactory training in a significant proportion of individuals (Doty et al., 1981; Jacob et al., 2006; Mainland et al., 2002; Wysocki et al., 1989; Yee & Wysocki, 2001) and odour detection thresholds in general are amenable to training (Haehner et al., 2013), even though some have argued that this only pertains to adult women of reproductive age (Dalton et al., 2002; Diamond, Dalton, Doolittle, & Breslin, 2005). Further, as discussed at length above, the female olfactory superiority is not limited to adult women but emerges relatively early in ontogeny, when the context of mate choice is far from relevant.

Alternatively, it might also be hypothesised that the better olfactory abilities of women have resulted from various selection pressures, such as gathering and food preparation. Cross-cultural comparisons show that gathering has been dominated by women in most hunter-gatherer societies (e.g. Eibl-Eibesfeldt, 2007). Hence, for survival it was imperative that toxic, rotten, mould-ridden, or otherwise inedible foodstuffs be avoided. The vital importance of the sense of smell in food assessment has been highlighted by studies in anosmic individuals (e.g.

Miwa et al., 2001; Temmel et al., 2002). This is all the more important during pregnancy. Indeed, women tend to report increased olfactory sensitivity, particularly during the first trimester of pregnancy (Cameron, 2007; Nordin, Broman, Olofsson, & Wulff, 2004), although the evidence based on psychophysical measures seems substantially less consistent, as some authors have failed to observe any differences in olfactory sensitivity (Kolble, Hummel, von Mering, Huch, & Huch, 2001) or odour identification performance (Cameron, 2007). Thus, changes in olfactory perception in pregnancy rather seem to consist in altered hedonic ratings (Cameron, 2007; Kolble et al., 2001) and self-assessments of environmental odour intolerance (Nordin, Broman, & Wulff, 2005), which may, nevertheless, serve an adaptive prophylactic function with regard to the developing foetus, as has also been suggested in the case of nausea and vomiting (Pepper & Roberts, 2006).

Finally, yet another context in which the superior female olfactory abilities could have been selected is mother-infant bonding. Findings of several methodologically similar studies (Kaitz, Good, Rokem, & Eidelman, 1987; Porter, Cernoch, & McLaughlin, 1983; Russell, Mendelson, & Peeke, 1983; Schaal et al., 1980) seem to converge on a mother's ability to recognise the body odour of her newborn from a soiled t-shirt and scalp within several days postpartum (for review see Porter, 1998). What is more, extensive interaction with the newborn does not appear necessary for the mother to develop the capacity to recognise the body odour of her child (Kaitz et al., 1987; Porter et al., 1983).

In the preceding paragraphs, various interpretations of the sex differences in olfaction in favour of females have been given, which, however, should not be viewed as mutually exclusive but, rather, as mutually complementary. At present, none of them has received unequivocal support. Further research based on specific hypotheses relevant to the individual theories might provide us with a clearer understanding of this intriguing phenomenon. Some of these explanations have nonetheless set the stage for hypothesising about intrasexual variability in olfactory performance, which will be addressed below.

1.2.2. Gender nonconformity and/or sexual orientation

It has been suggested that similar mechanisms that are supposed to influence the average differences between men and women, e.g. prenatal or early perinatal exposure to androgen steroids, which affect gender differences in brain anatomy, and consequently gender differences in behaviour, cognition, personality factors, and others (Hines, 2011; Lenz & McCarthy, 2010; McCarthy, 2010), also give rise to a within-gender variation in such traits (Lippa, 2005; Savic et al., 2010). Thus, both men and women vary in the level of development of traits which are typical of their own or the opposite gender and, consequently, both men and women can show rather gender-typical or gender-atypical psychological characteristics (Lippa, 2005) and exhibit varying degrees of gender nonconformity. In **Chapter 7** we present, to the best of our knowledge, the first study to demonstrate intrasexual variability in olfactory performance with respect to gender nonconformity. Specifically, we report that in men, those who had been *less* gender-conforming in childhood exhibited a better ability of odour identification and, moreover, a better ability of odour discrimination than the more gender-conforming ones, irrespective of their sexual orientation. In women, the findings were less clear: there was a trend of a negative association of gender nonconformity and the olfactory threshold, i.e. those who had been *more* gender-conforming in childhood exhibited greater olfactory sensitivity.

How these findings should be understood in terms of the various interpretations given for the sex differences above is up to future studies to determine. For instance, verbal fluency seems a plausible candidate because, as we have seen, it affects performance on odour identification (Larsson et al., 2004; Larsson et al., 2005), in which there were pronounced differences between men exhibiting varying degrees of childhood gender nonconformity. Differences in verbal fluency related to sexual orientation, of which childhood gender nonconformity tends to be a strong predictor, especially in men (Bailey & Zucker, 1995),[13] have been demonstrated by Rahman, Abrahams, and Wilson (2003): gay men tended to score the highest or similarly to heterosexual women and lesbian women scored the lowest or similarly to heterosexual men. In a similar vein, Neave, Menaged, and Weightman (1999) reported that homosexual men outperformed their heterosexual counterparts in verbal associations, while the opposite pattern was found in spatial abilities, particularly in mental rotations. Nevertheless, in a follow-up study in **Chapter 8,** we focused specifically on another possible interpretation of the present pattern of findings, namely the potentially differential long-term olfactory experience of men who exhibit varying degrees of childhood gender nonconformity. It has been shown that gender-nonconforming boys appear to be interested in activities which would be considered typical of the opposite sex, such as doing hair, makeup, dressing-up, cooking, or cleaning, as can be gleaned from reports of men who were gender-nonconforming boys (Hockenberry & Billingham, 1987), whereas in women the findings are less clear. Besides, both non-heterosexual men and women prefer gender-nonconforming hobbies and occupations (Lippa, 2008) and they also exhibit different hobbies and occupational choices compared to their heterosexual counterparts (Lippa, 2000). Therefore, individuals with varying degrees of gender nonconformity, particularly men, might also be expected to differ in the extent to which they engage in various everyday activities and hence in the level of long-term olfactory experience. We found, amongst other things, positive associations between self-reports of more frequent exposure to a greater variety of potentially intense or novel food odours and flavours in childhood and at present and odour identification in women and men, respectively. However, despite the fact that gender non-conforming men

[13] It is worth pointing out that despite an association between sexual orientation and gender atypicality, which is often described in terms of greater gender nonconformity (Bailey, Finkel, Blackwelder, & Bailey, 1996), empirical evidence suggests that greater gender nonconformity is not a perfect correlate of non-heterosexual orientation since only a proportion of homosexual individuals show gender-atypical traits. For example, about a third of gay men recalled childhood gender-conforming behaviour similar to that of heterosexual men (Bailey & Zucker, 1995). Also, some studies have failed to replicate the previous results on the relationship between sexual orientation and gender-related traits such as 2D:4D (McFadden et al., 2005) or cognition (Gladue & Bailey, 1995).

and gender-conforming women tended to report greater engagement in some of these olfaction-related activities, both in childhood and at present, these associations were not affected by the participants' sexual orientation or gender nonconformity, but pertained to the entire sample. This, on one hand, indicates the non-selectiveness of the effect of long-term olfactory experience on odour identification performance but, on the other, signifies that other explanations must be sought to account for the observed olfactory superiority of gender-nonconforming men over gender-conforming ones, such as the aforementioned differences in verbal fluency. Future studies should therefore address the replicability of the findings reported in **Chapter 7** and employ various measures of cognitive performance to help identify the precise mechanisms underlying these differences.

1.2.3. Personality

The idea that personality traits might have a bearing on olfactory performance (specifically olfactory sensitivity) was first advanced by Koelega (1970). At that time, there had been a marked progress in the development of electrophysiological recording procedures and there was also considerable interest in applying psychophysiological recording techniques to the study of the individual-difference variable of trait anxiety, which was widely assumed to be characterised by high activation patterns (Duffy, 1972). Another major development was the publication of Eysenck's book *The biological bases of personality* (Eysenck, 1967), in which he attempted to explain interindividual differences in extraversion and neuroticism in terms of arousal, postulating cortico-reticular arousal for the former and limbic arousal for the latter. Despite the significant modifications to the theory introduced by Gray (1972), the arousal theory of extraversion and neuroticism has inspired a great many studies, and the field of olfactory research was not an exception. However, especially in terms of neuroticism, the results reported thus far have been inconsistent, as has often been the case with other studies in which psychophysical methods or psychological reports were used to explore differences in sensory sensitivity (sensory thresholds, pain thresholds) in individuals differing in neuroticism.

Thus, inspired by Eysenck's increasingly popular three-dimensional personality model of extraversion, neuroticism, and psychoticism, to investigate the potential association between extraversion, neuroticism, and olfactory sensitivity, Koelega (1970) ran three experiments with both men and women, employing a variety of odorants (amyl acetate, butanol, dupical, exaltolide, muscone, musk). While Eysenck's theory predicts that in introverts, their higher cortical excitability is linked to a facilitation of learning and perception and they should therefore exhibit higher sensory sensitivity (i.e. lower thresholds) than extraverts, (Koelega, 1970) nevertheless found several unexpected positive associations of olfactory sensitivity with extraversion, and none with neuroticism. In a later study, Koelega (1994b) found no relationship between olfactory thresholds for five odorants (amyl acetate, butanol, exaltolide, isovaleric acid, and musk) and extraversion/introversion. Another study (Filsinger, Fabes, & Hughston, 1987) focused on ratings of intensity, pleasantness, and familiarity of four odorants (androstenol, androstenone, exaltolide, and pyridine) and found no relationship with the degree of extraversion. More recently, employing the Freiburger Personality Inventory (Fahrenberg, Hampel, & Selg, 1989, 2010) and tests of olfactory thresholds to four odorants (androstenone, citral, isoamylacetate, and linalool), Pause, Ferstl, and Fehm-Wolfsdorf (1998) reported a positive correlation between olfactory sensitivity to linalool and isoamylacetate, respectively, and neuroticism in a sample of men. Moreover, neuroticism was found to be a stronger predictor of olfactory sensitivity than extraversion. This is in line with findings of two studies on the relationship between emotional (personality) styles and olfactory sensitivity. Rovee, Harris, and Yopp (1973) found that olfactory sensitivity for octanol was associated with levels of anxiety in women, assessed with Taylor Manifest Anxiety Scale. According to Eysenck's theory, anxiety correlates with emotionality and introversion, but might be associated with impaired performance as the attentional distractibility increases (Eysenck & Eysenck, 1985). It was indeed demonstrated that highly anxious women had reliably higher thresholds than women low in anxiety. In a similar vein, Herbener, Kagan, and Cohen (1989) carried out a meta-analysis of two studies and found a relationship between olfactory sensitivity to butanol and level of shyness in men, which was discussed as being strongly related to introversion: men high in shyness exhibited lower olfactory thresholds for butanol (i.e. higher sensitivity) than their counterparts with low shyness scores. Finally, most recently, Croy, Springborn, Lotsch, Johnston, and Hummel (2011) reported a negative association of the NEO-FFI Big Five (Costa & McCrae, 1992) dimension of Neuroticism with trigeminal chemosensory detection thresholds (tested with carbon dioxide), but not with olfactory detection thresholds (tested with phenyl ethyl alcohol).

Potential links between personality and the ability of odour identification have also been sought. Using a short form of the Eysenck Personality Inventory (Floderus, 1974) and a Swedish version of the *National Geographic Smell Survey* (Wysocki & Gilbert, 1989), consisting of six “scratch and sniff” microencapsulated odorants (androstenone, amyl acetate, eugenol, Galaxolide, mercaptan, and rose), Larsson et al. (2000) reported that neuroticism, impulsivity, and lack of assertiveness, respectively, were reliable predictors of odour identification, whereas extraversion and openness to experience were not. Specifically, individuals high in neuroticism, low in impulsivity, and low in lack of assertiveness exhibited superiority in odour identification.

As can be seen, there have been several separate efforts to link measures of olfactory performance, particularly detection (absolute) thresholds for various odorants, to extraversion, neuroticism, and other personality traits, yielding diverse and sometimes contrasting results. A major obstacle to comparing these findings is the great variety of odorants used to measure absolute (detection) thresholds, which are notoriously known to vary, especially with respect to trigeminal component (Cometto-Muñiz & Cain, 1990, 1991, 1993, 1994; Cometto-Muñiz, Cain, & Abraham, 1998; Doty & Cometto-Muñiz, 2003), as well as the diverse personality measures used in previous studies.

In **Chapter 6,** we present two studies on the association of olfactory perception and (trait) anxiety, a subscale of the Big Five dimension of Neuroticism, in adolescents (Study 1) and heterosexually and non-heterosexually oriented young adults (Study 2), in which we employed a widely established standardised psychophysical test of olfactory performance and an extensively used personality assessment tool. The possible association of olfactory performance with this particular personality characteristic is founded on the evidence of a close relationship between the olfactory and limbic systems: the “olfactory brain” includes the limbic structures of amygdala and hippocampus (for review see Hawkes & Doty, 2009a; Zald & Pardo, 2000), which are also involved in emotional processing and regulation (for review see Davis & Whalen, 2001; Dolcos, LaBar, & Cabeza, 2005; LeDoux, 2003; Phelps & LeDoux, 2005; Tottenham & Sheridan, 2010). Since both the amygdala and hippocampus have been found to be structurally and (or) functionally altered in highly anxious individuals (Bremner, 2004; Milad, Rauch, Pitman, & Quirk, 2006), implications for processing of olfactory information might also be expected. In line with these predictions, we found a positive association between olfactory performance on the test of odour discrimination and identification, and the Neuroticism subscale Anxiety**.** In a similar vein, the most recent study by La Buissonnière-Ariza, Lepore, Kojok, and Frasnelli (2013) demonstrates increased odour detection speed in highly anxious healthy adults. Thus, trait anxiety currently seems the direction to go when exploring links between personality traits and olfactory performance. However, to be able to make any conclusive statements about whether trait anxiety actually impairs or enhances olfactory performance, diverse tasks must be employed, since this depends on the difficulty and nature of the given task (Eysenck & Calvo, 1992), and large samples of participants should be recruited, because highly anxious individuals show a specific pattern of responding (Bresin, Robinson, Ode, & Leth-Steensen, 2011). In either case, in future studies, researchers may find it useful to control for the effect of anxiety on olfactory performance as well as for that of other personality traits, which may affect performance on cognitive tasks that have been shown to predict olfactory performance. For instance, most recently, Burton and Henninger (2013) reported that extraversion was correlated with verbal fluency in both men and women, which is known to predict odour identification (Larsson et al., 2004; Larsson et al., 2005). In addition, in men, verbal fluency was also positively associated with agreeableness whilst in women, verbal fluency was associated with openness to experience and conscientiousness. Finally, given the susceptibility of levels of olfactory performance to long-term olfactory experience, future studies should also focus on identification of those personality (or temperamental) traits associated with some individuals' greater tendency to actively seek olfactory stimulation and orient towards the sometimes subtle olfactory stimuli and hence to extend their olfactory knowledge.

1.3. INTRAINDIVIDUAL VARIABILITY IN OLFACTORY PERFORMANCE

Despite the focus of this thesis on interindividual variability in olfactory abilities, effects of olfactory training and long-term olfactory experience have been recurrently mentioned on several occasions, indicating that there is considerable potential for intraindividual variability as well. While a heritable component to certain aspects of olfactory perception certainly is conceivable (Knaapila et al., 2007; Pinto, Thanaviratananich, Hayes, Naclerio, & Ober, 2008), it is not yet fully understood which particular aspects of olfactory processing it affects. It seems to have a bearing on sensitivity to the odour of specific substances, such as androstenone and androstadienone (Keller, Zhuang, Chi, Vosshall, & Matsunami, 2007) or isovaleric acid (Menashe et al., 2007), and hence on the development of specific anosmia. Nevertheless, the sole fact that repeated exposure to the given odour results in sensitization in a significant proportion of individuals initially afflicted with specific anosmia (Mainland et al., 2002; Wysocki et al., 1989) and the unafflicted alike (Jacob et al., 2006; Wang, Chen, & Jacob, 2004), suggests a high degree of plasticity. Hence, many of the demographic and environmental factors, which have been shown to modify the activity of the olfactory system (for review see Hawkes & Doty, 2009a:37-47), give rise to variability both inter- and intra-individually. Some of these factors may be stable, such as the biological sex, and thus linked to specific variations in individual olfactory performance, such as those induced by changes in the levels of reproductive hormones (Caruso et al., 2001; Derntl, Schöpf, Kollndorfer, & Lanzenberger, 2013; Doty, 1986b; Doty & Cameron, 2009; Doty et al., 1981; Farage, Osborn, & MacLean, 2008; Gandelman, 1983; Good et al., 1976; Hummel, Gollisch, Wildt, & Kobal, 1991; Lundstrom et al., 2006; Mair, Bouffard, Engen, & Morton, 1978; Navarrete-Palacios, Hudson, Reyes-Guerrero, & Guevara-Guzmán, 2003; Parlee, 1983; Pause, Sojka, Krauel, Fehm Wolfsdorf, & Ferstl, 1996; Purdon, Klein, & Flor-Henry, 2001; Vierling & Rock, 1967; Watanabe, Umezu, & Kurahashi, 2002). Others affect the olfactory function of all humans in a non-selective manner. Of these, the most consequential is the role of development, both in terms of maturation (which has been addressed in the section on sex differences) and aging (Cain & Gent, 1991; Doty, Shaman, Applebaum, et al., 1984; Larsson et al., 2005; Wysocki & Gilbert, 1989). Of course, that is not to say that all human olfactory abilities deteriorate at the same rate (Hummel, Kobal, et al., 2007); for instance, in a given individual, the ability of odour identification appears to decrease as a function of certain odorant properties, which seem to manifest themselves in perceived odour pleasantness (Konstantinidis, Hummel, & Larsson, 2006). Smoking (for review see Hawkes & Doty, 2009a:44-45; Katotomichelakis et al., 2007; Vent et al., 2004) and exposure to environmental toxicants (for review see Hastings & Miller, 2003) are another two factors with deteriorating effects. However, optimistically, as Frye, Schwartz, and Doty (1990) report, previous smokers show gradual improvement depending on the amount and duration of previous smoking,[14] while the outlook is not so positive for individuals exposed to toxic chemicals (Altman et al., 2011; Dalton et al., 2010) or urban dwellers (Calderon-Garciduenas et al., 2010; Calderon-Garciduenas et al., 2007; Guarneros, Hummel, Martinez-Gomez, & Hudson, 2009).

An interesting phenomenon is that of an alternating pattern of left-right nasal congestion and decongestion, referred to as the nasal cycle (for review see Frye, 2003). Most people experience changes in the relative degree of engorgement of each side of the nose from time to time (Haight & Cole, 1984), but in some individuals such changes are coordinated, resulting in a pattern of periodic shifts in relative left-right nasal airflow. However, only about 10% - 15% individuals experience a true nasal cycle, while parallel cycles and one side-only engorgement fluctuations are more frequent (Gilbert & Rosenwasser, 1987; Mirza, Kroger, &

[14] Although smoking has been shown to damage olfactory cells, which causes hyposmia, it has been found that previous smokers do not suffer from elevated risk of olfactory dysfunction compared to persons who have never smoked (Frye et al., 1990). Thus, smoking-related damage is reversible. This is due to the unique properties of the olfactory epithelium, whose basal cells have the remarkable capacity to undergo continuous regeneration throughout life: following nerve injury, basal cells regenerate, differentiate into neurons, grow new axons back to the olfactory bulb, and re-establish functional connections (Costanzo, 2000; B. J. Goldstein, Fang, Youngentob, & Schwob, 1998; Graziadei, Karlan, Montigraziadei, & Bernstein, 1980; Yee & Costanzo, 1998).

Doty, 1997). Importantly, these left-right engorgement fluctuations have been suggested to be an overall index of autonomic nervous function (Werntz, Bickford, Bloom, & Shannahoff-Khalsa, 1983) and shown to correlate with such measures as the relative EEG activity of the two cerebral hemispheres (Werntz et al., 1983), verbal and spatial cognitive processing (Klein, Pilon, Prosser, & Shannahoff-Khalsa, 1986), and asymmetrical activity in paired body organs (Shannahoff-Khalsa, Kennedy, Yates, & Ziegler, 1996). Another interesting fact is that the different airflow on each side of the nose caused by the relative engorgement results in qualitatively different perception through the left and right nostril (Sobel et al., 1999).

Various sources of intraindividual variability have been mentioned in the preceding paragraphs. In the following text, we will elaborate upon the one source which is (often implicitly) assumed to exert substantial influence on olfactory perception in everyday life, yet has received surprisingly little attention out of the laboratory context thus far, namely the effect of long-term olfactory experience. Specifically, we will investigate its effect on individuals' differential propensity to pick up olfactory cues and rely on them in guiding their attitudes and actions, which is becoming an increasingly popular approach to get closer to the real-life context in olfactory research.

1.4. ODOUR AWARENESS AND USES OF ODOUR CUES IN EVERYDAY LIFE

Although psychophysical studies conducted in laboratory contexts have substantially enhanced our understanding of interindividual variability in olfactory abilities (Ayabe-Kanamura et al., 1998; Doty, Applebaum, Zusho, & Settle, 1985; Havlicek et al., 2012; Hedner et al., 2010; Wysocki & Gilbert, 1989; Wysocki, Pierce, & Gilbert, 1991) and their development (Cameron & Doty, 2013; Doty, Shaman, Applebaum, et al., 1984; Koelega, 1994a; Monnery-Patris et al., 2009; Renner et al., 2009; Richman et al., 1992; Richman et al., 1995; Stevenson, Mahmut, & Sundqvist, 2007; Stevenson, Sundqvist, & Mahmut, 2007), as well as contextual effects on chemosensory perception (Ayabe-Kanamura, Kikuchi, & Saito, 1997; Bensafi, Rinck, Schaal, & Rouby, 2007; Herz, 2003; Prescott, Burns, & Frank, 2010; Seo, Buschhuter, & Hummel, 2008), these findings can be far removed from how individuals use their sense of smell in more ecologically (externally) valid, real-life settings, as pointed out by Kirk-Smith and Booth (1987). One approach to remedying this problem is to employ social odours, such as samples of human body odour, and investigate, for instance, discrimination, recognition, pleasantness ratings, and sex categorisation (Mallet & Schaal, 1998; Schleidt, Hold, & Attili, 1981), identification (Weisfeld, Czilli, Phillips, Gall, & Lichtman, 2003) or personality judgements based on body odour perception (Sorokowska, Sorokowski, & Szmajke, 2012). Another option is to study the effects of odours perceived in ecologically valid contexts on choice of location in other people’s presence (Kirk-Smith & Booth, 1980), school-task performance (Rodionova & Minor, 2005), mood and perceived health (Knasko, 1992) or even compliance and willingness to volunteer (James, 2006), spontaneous helping (Gueguen, 2012b) or receptivity to courtship requests (Gueguen, 2012a). Conversely, individual behaviour and experiences in specific everyday contexts have been shown to induce changes in odour liking and quality perception through evaluative conditioning.[15] For example, Baeyens et al. (1996) demonstrated that the background odour of a faculty lavatory acquired the affective-evaluative tone of the situation with which it was associated. Namely, members of the staff who considered the time spent there an agreeable break from work later evaluated the toilet-paired conditioning odour they had been exposed to more positively than the control odour, whereas the opposite was true for those who considered it a necessary evil. Similarly, odours paired with a positive, relaxing therapeutic massage were later evaluated more positively than those the clients had been exposed to during a negative, painful one (Baeyens et al., 1996).

Finally, yet another approach is to assess the perceived olfactory ecology of individuals by means of various, self-report metacognitive[16] measures, which afford unique insights into how people interact with their daily olfactory environments, which may not be observable or reproducible within the laboratory settings. Such measures include "odour awareness" (Smeets, Schifferstein, Boelema, & Lensvelt-Mulders, 2008), "subjective significance of olfaction" (Croy, Buschhuter, Seo, Negoias, & Hummel, 2010), "attitudes towards the sense of smell" (Martin et al., 2001), "sensitivity to the cognitive and affective qualities of odours" (Cupchik, Phillips, & Truong, 2005), "affective impact of odours"

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[15] Two ways whereby odour hedonics can be acquired have been highlighted in the literature. Firstly, mere exposure effect can, although rather marginally, contribute to changes in odour hedonics (Balogh & Porter, 1986). However, the major source of human evaluative reactions towards odours are assumed to be associative processes (Engen, 1988), namely evaluative conditioning, which is the preferred term (De Houwer, Baeyens, & Field, 2005; also known as evaluative, affective or associative learning or conditioning), used to refer to associatively induced changes in liking that result from pairing of stimuli in a certain manner. To be specific, when an odour that is initially perceived as neutral (conditioned stimulus, CS) is paired with a positively or negatively valenced event or stimulus (unconditioned stimulus, US), the originally neutral odour (CS) itself takes on the positive or negative valence of that event or stimulus in one's perception (Levey & Martin, 1975, 1987, 1990). In odour-related studies within experimental settings, the US may be, for instance, a sweet or savoury tastant (sucrose or monosodium glutamate and NaCl solution) as in a study by Yeomans, Mobini, Elliman, Walker, and Stevenson (2006) or a visual stimulus, such as an image (Hvastja & Zanuttini, 1989). In a more real-life research setting, examples of US include toilet-room activities or therapeutic massages (Baeyens, Wrzesniewski, De Houwer, & Eelen, 1996).

[16] Metacognition refers to what people know about cognition in general, and about their own cognitive and memory processes in particular, and how they put that knowledge to use in regulating their information processing and behaviour (Koriat, 2007:290). According to Nelson and Narens (1990), it covers the processes of, firstly, monitoring, by which people self-reflect on their own cognitive and memory processes and, secondly, control, which relates to how they put their metaknowledge to use in regulating their information processing and behaviour.

(Wrzesniewski, McCauley, & Rozin, 1999) and, in children, "children's olfactory behaviours in everyday life" (Ferdenzi, Coureaud, et al., 2008).

The term "odour awareness" was coined by Smeets et al. (2008) to account for marked interindividual differences in the degree to which individuals tend to pick up olfactory cues and rely on them to guide their selective attitudes and actions. While for some individuals, odours simply "stand out" from the olfactory background and they are always spontaneously commenting on odours present in the surrounding environment, body odour of self and others, food aroma or disturbing malodours, others only notice these odours after they have been pointed out to them (assuming, of course, they are able to detect and discriminate them). An olfaction-oriented individual, that is, one exhibiting a high degree of odour awareness, readily notices the presence of odour cues in the surrounding environment, relies on them in directing his or her attitudes and actions, and, tapping his or her previous experience, actively seeks desirable, pleasant olfactory stimulation and avoids unwanted, potentially disturbing odour stimuli.

Defined as a "person's awareness of the olfactory sensations he or she perceives" (Smeets et al., 2008), odour awareness is conceived of as a stable trait, rather than as a state-like feature. In terms of the four degrees of awareness proposed by Sommerville and Broom (1998), which include perceptual awareness, cognitive awareness, assessment awareness, and executive awareness, the concept of odour awareness is stated to encompass the last three levels (Smeets et al., 2008). While in perceptual awareness, according to Sommerville and Broom (1998), a stimulus elicits activity in the brain but the individual may or may not be capable of modifying the response voluntarily, in cognitive awareness a flexible response is possible. In assessment awareness, the individual is able to assess and deduce the significance of a situation in relation to itself over a short time span, whilst in executive awareness, the individual is able to assess, deduce, and plan over the longer term.

In the literature, there is still an ongoing debate as to the distinction between the concepts of "awareness" and "attention", which seem to be intimately related. Whilst some have argued that there is a tight connection between the two concepts (O'Regan & Noe, 2001), others see them as different (Lamme, 2003). However, recently it has been shown that distinct neural processes might be involved in both functions (Wyart, Dehaene, & Tallon-Baudry, 2012; Wyart & Tallon-Baudry, 2008). Here, "awareness" and "attention" are used interchangeably, particularly because many of the items on the original Odor Awareness Scale (Smeets et al., 2008), which has been used in our study in **Chapter 8,** are worded in terms of paying attention to odours.

Given the relative recency of research on odour awareness, the evidence of interindividual differences is still rather modest, involving mainly differences between the sexes, and factors underlying this variability are largely unclear. Nevertheless, studies with professionals such as perfumers and wine tasters, who would fit the description of highly olfaction-oriented individuals, suggest that their expertise is not driven by lower sensory thresholds (Parr, Heatherbell, & White, 2002) but by extensive training (Bende & Nordin, 1997; Melcher & Schooler, 1996; Solomon, 1990). This view has recently been corroborated by Arshamian, Willander, and Larsson (2011), who found that individuals exhibiting a high degree of odour awareness, determined by self-reported presence of olfactory dreams, high olfactory imagery capacity,[17] and olfactory interests, did not show lower olfactory thresholds. Instead, they performed better than their lower-scoring counterparts on the test of odour identification, which is a semantic memory task, in that it relates to an individual's general

[17] Imagery refers to the percept-like representations of stimuli in the absence of stimulation of sensory receptors (Pylyshyn, 1973, 2003). Thus, olfactory imagery refers to the ability of an individual to experience the sensation of smell in the absence of an odour stimulus (for review see Stevenson & Case, 2005). The very existence of olfactory imagery is a highly controversial, hotly debated issue, with some claiming that there is no such thing (Crowder & Schab, 1995), whilst others argue that there is (Cain & Algom, 1997). Olfactory imagery can be investigated either directly through participants' self-reports of such experiences or indirectly, by observing whether imagining an odour and its actual perception lead to similar performance on a particular task. The body of evidence obtained employing the former approach is referred to as "phenomenal imagery", whereas the latter establishes evidence for "performance imagery" (Stevenson & Case, 2005).

olfactory knowledge or experience (Hedner et al., 2010; Larsson et al., 2004; Larsson et al., 2005).

Before proceeding to outline the body of evidence currently available, I will briefly mention the two measures of odour awareness with which these results have been obtained, namely Children's Olfactory Behaviors in Everyday Life questionnaire (Ferdenzi, Coureaud, et al., 2008) and the Odor Awareness Scale (Smeets et al., 2008).

1.4.1. Children's Olfactory Behaviors in Everyday Life Questionnaire

The 16-item COBEL questionnaire (Ferdenzi, 2007; Ferdenzi, Coureaud, et al., 2008) was developed in France with first- to fifth-graders (aged 6-12 years) to evaluate children's self-reported awareness of odours and use of olfactory cues in the context of everyday life. Children's active seeking of olfactory stimulation, awareness of odours present in their everyday living environment, and affective responses towards odours are assessed separately for the food, social, and environment-related olfactory context. The food-related context includes items on olfaction-related food dislikes (whether there any foods or drinks that the child dislikes because of their odour), response to unknown odour (what will the child do when faced with a dish he/she does not know), and food odour guessing (when the child smells a food odour, does he/she ever try to guess what it is). Items of the social olfactory context subset include those on the odour of self (whether the child ever happens to smell parts of his/her own body or clothes), the family (does the child notice that relatives have a specific body odour and how they feel about it), and of other people (does the child register people's natural body odour). Finally, the subset of environment-related olfactory context items includes, for instance, questions regarding smells remembered by the child from the previous day, odours sought when feeling sad, treasured odorous objects, whether the child ever happens to smell its school things, registers the presence of any odours in the car, bathroom, and outside, and how he/she feels about the smell of tobacco. The tool can be administered either as a questionnaire to literate children, or, with pre-literate children, as a structured interview. Due to the limited attention span of young children, various response formats are used (multiple-choice, yes/no questions, 3-point rating scales, as well as open-ended questions), to keep the process of completion/interview engaging. Each items is scored on a 3-point scale to rate the behaviour as poorly (0), moderately (0.5) or highly (1) olfaction-oriented. The individual scores are added up, with the total score ranging between 0 and 16.

1.4.2. The Odor Awareness Scale

The 32-item Odor Awareness Scale (Smeets et al., 2008) is a metacognitive measure to learn about adults' self-assessments of their tendency to notice, pay attention or attach importance to odours in certain everyday situations, and their knowledge of how olfactory experiences shape their everyday behaviours. The items are phrased as statements regarding noticing, paying attention or attaching importance to odours, both pleasant and unpleasant, encountered in everyday situations in the four contexts proposed by Schleidt, Neumann, and Morishita (1988), namely food and drink, man, nature, and civilisation. Most items are five-category response format (“always”, “often”, “sometimes”, “seldom”, and “never”), with greater frequency, degree or probability scoring more points. The total score is obtained by adding up the scores of the individual items and can range between 72 and 151, with higher scores indicating greater odour awareness.

1.4.3. Interindividual differences: the effect of sex and age

As noted above, research on interindividual differences in odour awareness is still in its beginnings. A major contribution has been made by Camille Ferdenzi (Ferdenzi, Coureaud, et al., 2008; Ferdenzi, Mustonen, et al., 2008), who has developed the COBEL questionnaire for assessing odour awareness in children and found higher odour awareness scores in girls than in boys across all age categories (6, 7, 8, 9, and 10 years of age). Notably, despite the fact that girls showed greater verbal fluency than boys, their reports of higher attention and reactivity to social odours of others and self, some environmental odours, and affective odours (but not food odours) were not driven solely by their better verbal skills. In a cross-cultural study with Finnish and French children (Ferdenzi, Mustonen, et al., 2008), in line with previous findings, girls reported greater attention and reactivity to odours in the context of everyday life than boys. Specifically, the significantly higher scores pertained to six items, of which four were predominantly related to social odours (body odour of relatives, seeking the odour of self on clothes and directly on the body, and odours sought when sad, which most of the time were odours of self or significant others). The other two were odours found in nature and, more generally, outdoors. In our samples of Namibian and Czech children (**Chapter 4**), despite substantial cultural differences, we reported largely identical results: girls declared themselves to be aware of social and environmental (but not food-related) odours to a greater degree than boys.

In adults, women’s superiority in odour awareness seems unchallenged in both young and older adults, although the evidence available thus far only pertains to European countries, namely the Czech Republic (**Chapter 8**), Germany (Sucker et al., 2010), Italy (Dematte et al., 2011), and Spain (Buron, Bulbena, Pailhez, & Cabre, 2011). In the study by Sucker et al. (2010), positive items (odours to be approached) and negative ones (odours to be avoided) were analysed separately, yielding higher scores of women on both the positive and negative subset. This is in agreement with the finding of Smeets et al. (2008), who report that individuals who tended to be aware of one type of odour were more likely to be aware of the other type as well, although not always to the same extent. In our study in **Chapter 8**, however, the sex difference marginally missed significance, which could be due to the higher ratio of sex-atypical to sex-typical individuals in the sample.

In terms of age, children's total scores on COBEL were found to increase with age (Ferdenzi, Coureaud, et al., 2008; Ferdenzi, Mustonen, et al., 2008), specifically as regards odour-related dislikes, remembering yesterday's odours, and appreciating people's natural body odour, which was ascribable to the children's progressively better memory and verbal fluency. Our study (**Chapter 4**) yielded results that are generally in line with these findings: older children scored higher and the increase pertained specifically to environmental and food-related odours, but not social ones. The positive effect of age on odour awareness has also been observed in young (**Chapter 8**) and older adults (Dematte et al., 2011), but this finding has not always been consistent (Buron et al., 2011).

Overall, the higher scores of females of all ages and of older adult participants have been interpreted in terms of greater exposure, and hence broader experience with odours (Dematte et al., 2011; Ferdenzi, Coureaud, et al., 2008; Ferdenzi, Mustonen, et al., 2008), potentially acquired through more frequent/longer-term engagement in olfaction-related activities. This possibility has been explored in our studies in **Chapters 4** (in Namibian children) and **8** (in Czech adults). Whilst in Namibian children, in whom odour experience through engagement in everyday activities was assessed by asking how many siblings and pets they had, and how frequently they helped to cook at home, no relationship with COBEL scores or performance on an odour naming task was found, in Czech young adults, there was a positive association of odour awareness scores, cued odour identification scores, and self-reports of involvement in such activities both in childhood and at present. This was assessed by means of an inventory developed specifically for the purposes of the study, which consisted of selected olfaction-related activities listed in the parent-report Olfactory Diversity Questionnaire (Ferdenzi, 2007) and reported to show a moderate to strong association with children's both free- (i.e. odour naming) and forced-choice odour identification scores. Thus, it might be that more sensitive measures of individual differences in olfactory experience than those used in **Chapter 4** are required to yield positive results, such as those observed in **Chapter 8**. Alternatively, the expected relationship may, indeed, only be observable in adult participants, whether because of the assumed relatively lower interindividual variability in children's olfaction-related activities compared to adults or because of the lower reliability of young children's self-reports (for review see Stone & Lemanek, 1990). For instance, as regards the reliability of clinical interviews, the age of the child is an important variable in that the reliability of children's self-reports has been shown to increase with age, while the reliability of parental reports exhibited a decrease with the age of the children (Edelbrock, Costello, Dulcan, Kalas, & Conover, 1985). This also seems to explain the positive association between parental reports of their children's olfaction-related activities and the children's both free (odour naming) and forced-choice odour identification scores reported by Ferdenzi (2007) in children aged 6 – 12 years. On the other hand, in adults the observed positive relationship may as well be, to a considerable degree, a mere by-product of a phenomenon known as the extreme response style (Greenleaf, 1992; Hamilton, 1968; Merrens, 1970), whereby up to 30% of all respondents tend to consistently favour or avoid extreme response categories, regardless of the specific item content (Austin, Deary, & Egan, 2006; Eid & Rauber, 2000).

Further, even though in Czech adults (**Chapter 8**), the frequency of engagement in some activities was associated with sexual orientation or gender nonconformity, the positive relationship between self-reports of engagement in such activities and odour awareness remained unaffected regardless. Besides, albeit this was only limited to either sex in this study, both of these self-report measures were associated with the ability of (cued) odour identification, which, as noted above, is thought to reflect prior olfactory experience (Schab & Crowder, 1995; Stevenson & Boakes, 2003; for review see Wilson & Stevenson, 2003). However, an association of odour awareness with odour identification seems the exception rather than the rule, as no such relationship was reported by Ferdenzi, Mustonen, et al. (2008) in children or Dematte et al. (2011) and Smeets et al. (2008) in adults. Semi-longitudinal and longitudinal developmental studies, employing both self- and parental reports of children's everyday olfactory behaviours as well as repeated psychophysical measurements, might provide us with answers as to whether children exposed more frequently to a greater variety of odours over the long term grow up to become individuals who exhibit greater awareness of odours and/or superiority in certain olfactory abilities, and whether these children more often than not tend to be girls.

1.5. CONCLUSION

One of the truisms of research on olfactory performace is that there are considerable differences among individuals in olfactory sensitivity, the ability of odour identification, and discrimination. Quantitative psychophysical measures have substantially furthered our knowledge regarding the influence of various factors, particularly those of sex and age, on human olfactory function and its development. Nevertheless, concerns are being voiced that such laboratory findings can be far removed from how people actually use their sense of smell in the context of everyday life. Thus, recently there has been a move towards approaches that acknowledge the context in which olfactory processing takes place most of the time. These include use of social odours as stimuli, observations of the effects of odours perceived in ecologically (externally) valid contexts or use of various self-report (or, in the case of young children, parental report) measures, which afford unique insights into how people interact with their olfactory environments. We have adopted the third approach in several studies included in this thesis. Despite the recency of research on olfactory behaviour (or olfaction-related activities), a number of intriguing findings have emerged that suggest that common, perhaps even routine everyday activities we choose to occupy ourselves with do matter, over the long term, olfactionwise. Now and then we hear the magic phrase of “olfactory experience” or “odour knowledge” being offered as an explanation for the better ability of odour identification, olfactory imagery or, generally, chemosensory expertise of the more olfactory proficient of us. Odour experience is, however, somewhat elusive to deal with out of laboratory and its well-designed olfactory training sessions. We believe that the questions worth asking – and answering – are: Where does this experience come from? Are there any meaningful differences between us in the amount of “olfactory training” we allow ourselves in our everyday lives over the long term and if so, what is it that makes us seek this sensory experience? How does this experience find expression in our olfactory abilities or the way we orient towards chemosensory stimuli and use olfactory cues to guide our attitudes and behaviour? We believe that the direction to go are (semi)longitudinal developmental studies, which might provide us with answers as to whether children who expose themselves more frequently (why is it so?) to a wider variety of odours (in which contexts?) grow up to become increasingly olfaction-oriented individuals, who also show superiority in certain olfactory abilities. Also, we ask, are these people more likely to be of the female sex? More than a decade ago, it was proposed that, because of what they (choose to) do, women may encounter olfactory stimuli more often than men, which, in turn, might partly account for their olfactory superiority. Since then, this idea seems to be recurrently appearing and disappearing in the form of speculations in the literature but other than that, it has received little attention from the scientific community. However, at the same time, we believe that in the realm of olfactory perception, as elsewhere, it is not all black and white, or women versus men. We have introduced the idea of intrasexual variability in olfactory performance in one of the studies presented in this thesis and found gender-nonconforming (i.e. sex-atypical) men to perform as well as gender-conforming women, as opposed to gender-conforming men. These are entirely uncharted waters and, to the best of our knowledge, our study was the first attempt at their (albeit cursory) exploration. In a follow-up study, we have addressed the idea that differential olfactory experience, assessed in terms of self-reported engagement in various olfaction-related activities, might be partly responsible for the olfactory superiority of gender-nonconforming men. We found that these self-reports were indeed associated with both odour identification and odour awareness, but that this relationship was not affected by the degree of participants' childhood gender nonconformity. This, on the one hand, supports our idea that the effect of odour experience should, albeit perhaps to a varying degree, apply to all of us without exception, but, on the other hand, it leaves open the question of what underlies the superior olfactory abilities of these men. With verbal fluency being the prime candidate, future studies will delve into this conundrum more thoroughly.

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CHAPTER 2

LEARNING ABOUT THE FUNCTIONS OF THE OLFACTORY SYSTEM FROM PEOPLE WITHOUT A SENSE OF SMELL

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Learning about the Functions of the Olfactory System from People without a Sense of Smell

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Abstract

The olfactory system provides numerous functions to humans, influencing ingestive behavior, awareness of environmental hazards and social communication. Approximately ⅕ of the general population exhibit an impaired sense of smell. However, in contrast to the many affected, only few patients complain of their impairment. So how important is it for humans to have an intact sense of smell? Or is it even dispensable, at least in the Western world? To investigate this, we compared 32 patients, who were born without a sense of smell (isolated congenital anosmia - ICA) with 36 age-matched controls. A broad questionnaire was used, containing domains relevant to olfaction in daily life, along with a questionnaire about social relationships and the BDI-questionnaire. ICA-patients differed only slightly from controls in functions of daily life related to olfaction. These differences included enhanced social insecurity, increased risk for depressive symptoms and increased risk for household accidents. In these domains the sense of olfaction seems to play a key role.

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Introduction

The olfactory system provides many functions for humans, influencing ingestive behavior, increasing awareness of environmental hazards and social communication (for overview see [1]). For example, the olfactory system is important for detecting food and providing good taste quality, for avoiding potential dangerous situations in long- and short distance, like fire and microbial threats. Additionally olfaction seems to play a key role in mate choice and helps to detect emotions in other people [2].

But does olfaction enrich information from other sensory systems, like the visual, tactile or auditory senses? Does it thus allow us to experience the world more deeply? Or does the olfactory sense possess functions of it own, which cannot be fulfilled by other systems? A number of extensive studies from various countries indicate that approximately 15–20% of the population exhibits some olfactory loss, and that 2.5–5% exhibit functional anosmia. However, one more recent study [3] indicated that 3.8% of the population exhibit severe olfactory loss. These differences in numbers seem to relate to differences in the interpretation of test results and differences in the study design [3,4,5,6,7,8]. Despite these differences, it appears that a relatively large portion of the general population exhibits olfactory loss. Unlike eyeglasses for visually impaired people, there is no compensation for an impaired sense of smell. But relative to the large portion of people who are affected, only few complain. So how important is it for humans to have an intact sense of smell? Is it even dispensable, at least in the Western world?

One approach to answer this question is to ask people with acquired olfactory disorders what they miss. Those patients typically complain about difficulties with cooking, a lack of appetite and low interest in eating [9,10]. In addition, they are subject to an increased risk for hazardous events [11,12]. Furthermore these patients report daily life problems associated with social situations [13] and concerns about their body odor [14]. About 17 to 30% of patients with olfactory disorders report decreased quality of life including symptoms of depression [14,15,16]. The loss of quality of life is most severely perceived by younger patients with poor olfaction [17,18] (for overview see [19]).

But studying people with an acquired olfactory disorder might lead to distorted results: it may be difficult to determine if their problems result from the loss of olfactory ability, rather than its absence.

Therefore, we aimed to study people who were born without a sense of smell. Among clinicians, this phenomenon is known as **Isolated congenital anosmia (ICA)**. ICA is characterized by the lack of the sense of smell since birth in otherwise healthy people [19]. In the Smell and Taste Clinic at the Department of Otorhinolaryngology of the University Medical School Dresden we see approximately 20 patients per year diagnosed with ICA. Diagnosis of ICA involves a detailed medical history and psychophysical examination, electrophysiological measurements and magnetic resonance imaging with special focus on the structure of the olfactory bulb [20]. Hypoplastic or aplastic olfactory bulbs in otherwise healthy participants are typically found, accompanied by a shallow olfactory sulcus [20]. Based on our data, we estimate the prevalence of ICA in the general population to be 1: 5000–10000.

Kallmann's syndrome is an important differential diagnosis characterized by the lack of the olfactory bulb and hypogonadotropic hyopogonadism. The incidence of this disorder is estimated at about 1:86.000 in the general population [21]. Because the hormonal dysfunction in Kallmann's syndrome causes a lot of additional problems, those patients are explicitly not included in the study.

Although there are very few studies and single case reports about patients with ICA, based on the literature and on our experience, we can report that they typically do not complain about a reduced quality of life [9]. The patients are mostly unaware of the olfactory deficit as children [22] and rather the parents become suspicious that something might be "wrong". Typically this occurs when it is obvious that the child is not disturbed by bad smells, like rotten milk, dog's feces, or smells during chemistry lessons at school. However, to our knowledge, there is no systematically collected evidence on the lifestyle of people born without a sense of smell. If the sense of smell is important for ingestive behaviour, environmental hazards and social communication, like described above, how are these domains affected in patients with ICA? Do ICA patients have trouble maintaining their weight or do they obtain no joy in eating, for example? Do they accidentally eat spoiled food? Do they also worry about their body odor? And do they feel different in social situations? Or are people without a sense of smell not affected at all by this deficit and is olfaction just overestimated?

In this study, we wanted to provide a very first step in answering those questions. In a hypothesis-generating design we sent a broad questionnaire covering these topics to patients with ICA.

Methods

Ethics Statement

The study followed the Declaration of Helsinki on Biomedical Research Involving Human Subjects and was approved by the Ethics Committee from the University of Dresden Medical School. All participants provided written informed consent.

Participants

Originally 50 ***patients***, diagnosed with ICA, participated in the study. Because daily life functioning depends on age, we decided to exclude participants older than 60 and younger than 18 years to get a more focused age group. Therefore the questionnaires of 32 participants (aged 18–46years, mean age 31+/−8 years) were analyzed for the study. Congenital anosmia was diagnosed using detailed medical history, psychophysical examination, electrophysiological measurements and magnetic resonance imaging.

Psychophysical examination was performed using the Sniffin' Sticks, including tests for olfactory threshold, discrimiation and identification ability ("Sniffin' Sticks", Burghart GmbH, Wedel, Germany; compare Hummel, 2007). Additionally patients underwent electrophysical measurement. Trigeminal (CO_2) and olfactory (PEA, H_2S) stimuli were presented to patients in order to record event related potentials. Chemosensory nasal stimulation was performed using a stimulator (Olfactometer OM2S, Burghart Instruments, Wedel, Germany), which allows administration of chemical stimuli without causing concomitant mechanical or thermal sensations. Anosmic patients do not show event related potentials in response to olfactory stimuli, but they typically do exhibit response to trigeminal ones. Additionally patients underwent structural magnetic resonance imaging (compare Yousem et al 1996). If no olfactory bulb could be found by a trained physician, if no hint of olfactory function could be found in any of the tests performed, if patients had no memory of ever having been able to smell something and other possible causes of congenital anosmia were excluded (e.g. Kallman's syndrome), isolated congenital anosmia was diagnosed. For illustration, we show a structural magnetic resonance image of an ICA patient in Figure 1 in comparison to an image obtained in a healthy control subject.

Thirty-six age-matched healthy participants (aged 18–50 years, mean age 29+/−7 years; Table 1) served as control group. They were recruited from our database of healthy participants, that took part in other studies. The actual status of health was checked by detailed medical history, olfactory function was checked by an olfactory screening test [23]. Normosmic function was ascertained in all controls. Patients and controls did not differ significantly with regard to age and sex distribution.

Most of the ICA-patients received the questionnaires by mail; four patients filled in the questionnaire in our clinic during their diagnostic routine. Return rate of the questionnaires, sent by mail, was 74%. Most participants of the control group also received the questionnaires by mail without payment; however 14 participants of this group answered the questionnaire in our clinic and received a small amount of money for participating in the study. As some of the questions asked in the questionnaire were very personal, special care was taken in telling the participants (oral or by letter) that data was handled anonymously and that there were no "good" or "bad" answers. Additionally, interviews focusing on the

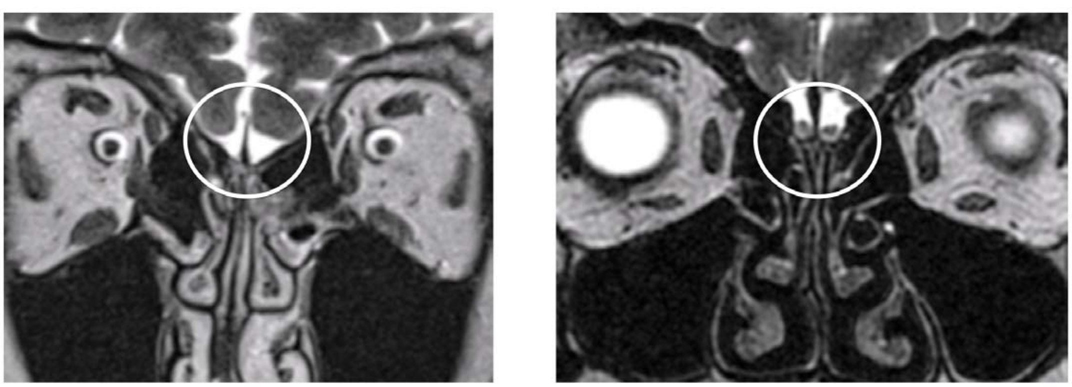

Figure 1. Structural magnetic resonance image of an isolated congenital anosmic patient (left). Within the marked region an olfactory bulb is missing. This becomes obvious compared to the healthy person visualized in the right picture.
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Table 1. Descriptive statistics and comparison between ICA-patients and controls.

			ICA-patients (N = 32)			Healthy controls (N = 36)			Group comparison
			mean	SD	N	mean	SD	N	p-value
	Age		30.50	7.65		29.33	6.57		n.s.*
	Sex	Female			22			21	n.s.+
		Male			10			15	
Ingestion	Size in cm		170.75	9.52		173.60	9.24		n.s.*
	Weight in kg		69.73	12.60		69.94	14.22		n.s.*
	Body mass index		23.81	3.25		23.10	3.71		n.s.*
	Breast-fed	No			7			6	n.s.+
		Yes			25			29	
	Components of preferred food		1.43	.69		1.23	.43		n.s.*
	Eating behavior		2.21	.54		2.26	.47		n.s.#
Environ-mental hazards	household accidents		2.02	.52		1.51	.42		<0.001#
	Washing behavior		2.25	.65		2.16	.66		n.s.#
	Frequency of showering	More than daily			0			1	n.s.#
		Daily			16			24	
		Every two days			10			8	
		More than weekly			4			3	
		Weekly			1			0	
		Rarely			1			0	
Social behavior and communication	Partnership status	Married			8			1	n.s.+
		Divorced			2			2	
		Single			10			17	
		Engaged			12			16	
		widowed			0			0	
	Satisfaction with partnership								n.s.#
	Number of children		.53	.80		.33	.79		n.s.*
	Age of first sexual intercourse		18.10	2.65		19.00	4.76		n.s.*
	Sexual satisfaction		1.76	0.76		1.73	0.81		n.s.#
	Number of sexual relationships		3.34	3.89		6.2	7.00		0.048*
	BBE-Questionnaire	Security mother	4.06	.90		4.38	.62		n.s.*
		Security partner	4.31	.63		4.64	.36		n.s.*
		Dependency mother	2.01	.63		1.96	.60		n.s.*
		Dependency partner	2.85	.61		2.82	.45		n.s.*
	social worries		2.18	.51		1.49	.36		<0.001#
Depression	BDI-Questionnaire		10.47	9.38		4.63	6.61		0.014*

Significant differences have been raised for the components of preferred food, household accidents, the age of the first sexual intercourse, social worries and depression.

Note:

*… t-test;

+… Chi-Square-Test;

#… Mann-Whitney-test. Bonferroni-Correction was applied for p-values within the BBE-Questionnaire.

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ability to cope with daily life were performed with those ICA-patients we saw in our daily routine.

Materials

The questionnaire intended to obtain information about daily life functions related to olfaction. The whole questionnaire is provided as supporting online information (Questionnaire S1). For **ingestion,** participants were asked about their size, weight, preferred food and about their eating behavior. Their answers to "preferred food" were coded into food with 1 component (e.g. "pasta", "soup"), 2 components (e.g. "rice with vegetables") or three components (e.g. "steak with french fries and vegetables"). For "eating behavior", participants had to agree or disagree to three statements on a four-point-scale (arms were "I totally agree" and "I do not agree at all") and a mean was derived from these. The questions are reported in Table 1. Furthermore we originally intended to ask about ingestion as a baby, but about half of the participants stated they were uncertain about their answers to these questions, so we decided not to analyze them. However, we were able to obtain reliable data whether participants were breast fed or not. For **environmental hazards** participants were asked about household accidents. They were asked to respond to five statements and a mean score was built (see Table 2). Additionally we asked about personal hygiene by asking the participants about the frequency of showering, and about their washing behavior (see Table 2). For **Social Behavior and Communication** participants were asked to respond to three statements of social insecurity and a mean score was built (see Table 2). Additionally participants were asked about intimate relationships by asking about the present status of partnership (married, divorced, single, engaged, widowed), self-rated well-being in the partnership (on a five-point scale), the number of children they have, the age of first sexual intercourse, self-reported sexual satisfaction (on a four-point scale) and the number of different sexual partners they had during their life. Furthermore we presented them a questionnaire for personal relationships (BBE) to obtain information about attachment towards the mother and towards the partner [24,25]. This questionnaire consists of 14 items for attachment to the mother and 14 for attachment to the partner, formulated as statements. Participants rated their agreement on a five-point-Likert-scale. Two sub-scores were formed, one for attachment security and one for dependency.

Finally, the Beck Depression Inventory (BDI) was presented to all participants, a widely-used, standardized and validated instrument for measuring depressive symptoms [26].

Statistical Analysis

Data were analyzed using SPSS vs. 17 (SPSS Inc., Ill, USA). T-test was used for the comparison of both groups regarding the variables *size, weight, body-mass index, age of first sexual intercourse, number of sexual relations, components of preferred food*, as well as *BDI-questionnaire* and *BBE-questionnaire*. Bonferroni Correction was applied for p-values within the BBE-Questionnaire. For the comparison of *partnership status* and *breast feeding* Chi-Square testing was applied. All of the other variables, namely *eating behavior, household accidents, washing behavior, frequency of showering, satisfaction with partnership* and *sexual satisfaction* were analyzed using Mann-Whitney test. The level of significance was set at 0.05.

Table 2. Items forming the subscales of eating behavior, household accidents, social insecurity and washing behavior.

Eating behavior	I eat at fixed times (reverse coding).
	I eat when I'm hungry.
	I eat, when I have appetite.
Household accidents	I have accidently eaten spoiled food.
	Accidents in my household often happen to me.
	Occasionally it happens to me, that I scorch food.
	Sometimes I burn clothes when ironing.
	I rarely perceive smoke.
Social insecurity	I have problems in contacting other people.
	I worry about my body odor.
	I avoid eating with other people.
Washing behavior	I wash myself at fixed times (reverse coding).
	I wash myself when I feel dirty.

Al of the items are to be rated on a four-point scale ("I totally agree" to "I don't agree at al"). For subscales the average of the related items is calculated.
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Results

The results are reported focusing on the main olfactory functions mentioned above.

Ingestion

For ingestion, we found no significant difference in breast feeding. For the controls 85% indicated they had been breast fed, but for the IAC-patients 78.1% had been. There was also no significant difference in the weight, size or in the Body-Mass Index of both groups. Both groups did not differ in their eating behavior (see Figure 1 and Table 1).

Environmental Hazards

ICA- patients reported more household accidents than healthy controls ($p = 0.001$, see Table 1 and Figure 2). For personal hygiene, however, no significant difference in the frequency of showering could be revealed. There was also no significant difference in the ratings of washing behavior (see Figure 2 and Table 1).

Social Behavior and Communication

ICA-patients and controls did not differ significantly in their rated attachment towards mother or partner in the BBE-questionnaire. Ratings of both groups were within a normal range [24,25] (see Table 1).

ICA-patients reported more worries about social situations than controls ($p<0.001$), i.e. they reported worrying about their own body odor, having problems in interactions with other people and avoided eating with others (see Table 1 and Figure 2).

For partnership and sexual behavior, there was no significant difference between both groups in the partnership status or the self-reported satisfaction with their partnership. There were also no significant differences in the age of the first sexual intercourse, the self reported sexual satisfaction or in the number of children. However, ICA-patients reported to have had significantly less sexual partners than controls ($p = 0.031$, see Table 1 and Figure 3).

Depression

ICA-patients exhibited higher scores in the Depression Inventory compared to controls ($p = 0.018$, see Table 1).

Discussion

Based on our data, ICA-patients do not seem to differ a lot in their daily life functions from healthy controls. Does this mean that the sense of olfaction is dispensable for humans, at least in the Western world? We do not believe this to be true. Although people who were never able to smell, seem to cope well with this deficit, there are some restrictions, very worthy of further study. Likewise, the domains where we found no differences between people with and without a sense of smell are very interesting and raise further questions about the role of the sense of smell in daily life.

For ***ingestive behavior***, ICA-patients reported they were breast fed as frequently as the controls. This is very interesting because studies suggest that breast-feeding in mammals very much depends on the ability of the newborns to find the nipples by olfactory cues. In rabbits for example, the offspring has almost no chance of survival if they are not able to smell [27]. Interestingly, human mothers seem to be able to compensate for the olfactory

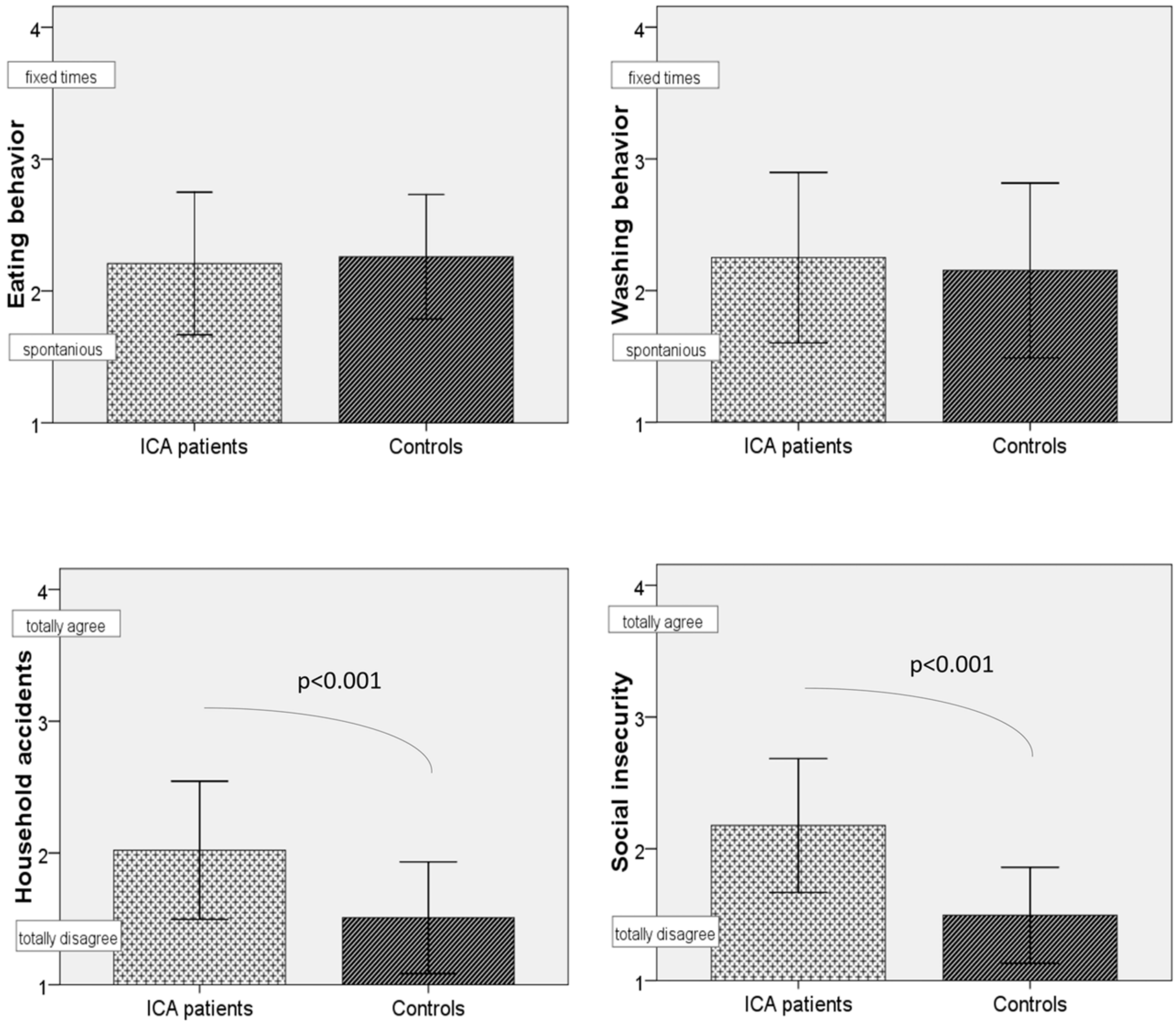

Figure 2. Comparison of ICA-patients (N = 32) and age-matched controls (N = 36) with regard to eating behavior, washing behavior, household accidents and social insecurity. The bars visualize the mean ratings for the scales; error bars indicate the single standard deviation. ICA-patients significantly more often agreed to have household accidents and to be unsure in certain social situations.
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deficit of their babies very well, perhaps because humans normally have to focus on only one baby.

As adults, ICA-patients do not differ in size or weight, have preferred foods and do not exhibit major differences in their eating behavior. As taste is a combined sensation of olfactory, tactile and gustatory senses, the lack of olfaction since birth does not seem to lead to a lack of taste.

Another function of the olfactory system is the avoidance of ***environmental hazards*** [1]. Here, ICA-patients report more household accidents. This fits information about patients who lost their sense of smell in adulthood [11]. The patients told us about different strategies to cope with this, like not leaving the iron alone or asking others whether the milk was still palatable. For hygiene behavior, on the other hand, no significant differences between both groups could be found. Nevertheless, patients reported coping strategies for hygiene, like washing clothes after a certain routine.

Not very surprisingly, for ***social behavior and communication*** there were no hints for major disturbances in relationships with others, like mother or partner. ICA-patients seem to be able to find an intimate partner and to develop a satisfying relationship as frequently as people with normal senses of smell. On average, they start their sexual behavior at the same time as age-matched controls, are as satisfied with their sexual life and have the same number of children. However, we found an ***enhanced social insecurity in ICA-patients***. This social insecurity seems to refer to persons, who are not well-known, like colleagues or distant acquaintances. As olfactory cues are able to confer social information about others [1,2], it is possible that ICA-patients have more problems in assessing other people, because this channel of communication is closed. This may result in an increased social insecurity, which may explain the finding that ICA-patients had only about half of the number of sexual relationships of controls. Alternatively it is conceivable, that the absence of the sense of smell in sexual intercourse leads to a generally lower interest in sexual relationships. In this regard the present study does not provide satisfying answers. However, a closer look into sexual behavior in the absence of a sense of smell would be very interesting (compare [28]).

The ***enhanced ratings of depressive symptoms in ICA patients*** may also relate to the absence of the sense of smell. In

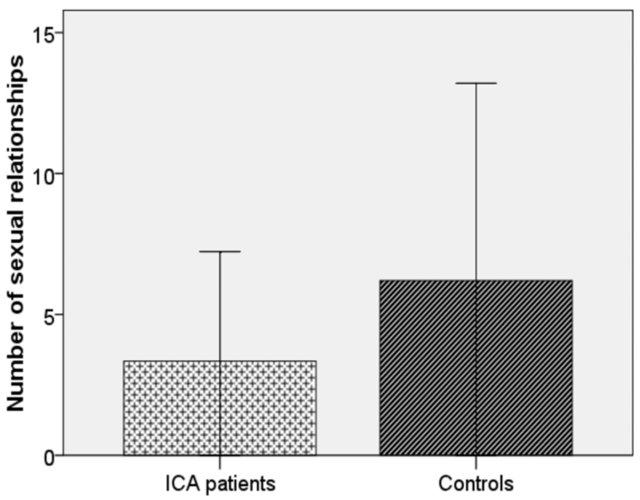

Figure 3. Comparison of the number of sexual relationships in ICA-patients (N = 32) and age-matched controls (N = 40). Controls report to have had significantly more different sexual partners than ICA-patients.
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fact, patients with acquired olfactory loss typically show signs of depression [9,14] However, one could counter that those patients were affected by the loss of the sense of smell (rather than its absence), which is not the case in congenital anosmia. Another possible explanation refers to the application of the questionnaire. Some of the healthy controls received money for participating while the ICA-patients were asked to fill the questionnaires because of their deficit. However, we additionally compared both groups of healthy controls. We could find no significant difference in depression scores between those control participants who answered the questionnaire at home and those who answered it in our laboratory and received a small amount of money. This supports the hypothesis of increased risk for depression in the absence of smell.

There are several studies in humans that support a link between depression and the absence of olfaction. Reduced olfactory sensitivity has been found in patients suffering from Major Depression [29,30,31] and in a line with this, we recently found reduced olfactory bulb volume in depressed patients [32]. One of the hypotheses discussed about this depression-olfaction-coherence refers to shared functionality in limbic and para-limbic brain networks.

Conclusion

ICA-patients differ only slightly in daily life functions related to olfaction. These differences are increased social insecurity, enhanced risk for depressive symptoms and enhanced risk for household accidents. In these domains the sense of olfaction seems to play a key role. Further research with focused assessment would be desirable.

Supporting Information

Questionnare S1 Questionnaire used to obtain information about daily life functions related to olfaction.
(DOCX)

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Author Contributions

Conceived and designed the experiments: IC TH SN LN BL. Performed the experiments: IC LN. Analyzed the data: IC. Contributed reagents/materials/analysis tools: IC TH. Wrote the paper: IC.

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CHAPTER 3

DIFFERENTIAL PATTERNS OF FOOD APPRECIATION DURING CONSUMPTION OF A SIMPLE FOOD IN CONGENITALLY ANOSMIC INDIVIDUALS: AN EXPLORATIVE STUDY

pp. 95-98

Differential Patterns of Food Appreciation during Consumption of a Simple Food in Congenitally Anosmic Individuals: An Explorative Study

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Abstract

Food is evaluated for various attributes. One of the key food evaluation domains is hedonicity. As food is consumed, its hedonic valence decreases (due to prolonged sensory stimulation) and hedonic habituation results. The aim of the present study was to investigate changes in food pleasantness ratings during consumption of a simple food by individuals without olfactory experience with food as compared to normosmics. 15 congenital anosmics and 15 normosmic controls were each presented with ten 10 g banana slices. Each was visually inspected, then smelled and chewed for ten seconds and subsequently rated for hedonicity on a 21-point scale. There was a significant difference in pleasantness ratings between congenital anosmics and controls ($F(1, 26) = 6.71$, $p = .02$) with the anosmics exhibiting higher ratings than the controls, a significant main repeated-measures effect on the ratings ($F(1.85, 48) = 12.15$, $p < .001$), which showed a decreasing trend over the course of consumption, as well as a significant portion*group interaction ($F(1.85, 48) = 3.54$, $p = .04$), with the anosmic participants experiencing a less pronounced decline. The results of the present explorative study suggest that over the course of consumption of a simple food, congenitally anosmic individuals experience differential patterns of appreciation of food as compared to normosmics. In this particular case, the decrease of hedonic valence was less pronounced in congenital anosmics.

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Introduction

Food is evaluated for various attributes through several sensory modalities. The sensory perception of food involves vision, smell, taste, touch, audition and the trigeminal somatosensory system [1] as well as the sensory receptors in the digestive tract and circulatory system [2]. The food's location is identified at a distance using orthonasal olfaction, substantially facilitated by visual cues [3], which may, even at close proximity, override olfactory perception [4]. When the food is delivered to the mouth, but prior to ingestion, it is assessed on the basis of a multimodal sensory integration of retronasal olfaction, taste, and somatosensory input such as mechano-sensation, temperature or irritation [5].

One of the key domains of food evaluation is hedonicity. Over the longer term, it is thought that foods acquire hedonic valence mainly through various learning processes; a unique set of food likes and dislikes is formed over the life course based on the individual's experiences and socially held beliefs. Undoubtedly, one of the key guides in this process is food flavour, and the most widely cited learning models are those based on flavour-based learning, namely those proposing associations between a novel flavour and an existing liked or disliked flavour, or post-ingestive consequences, ingestion of nutrients in particular (for review, see [6]).

Over the short-term, positive hedonic evaluation (liking, pleasantness, appreciation) reflects the immediate experience or anticipation of pleasure from the orosensory stimulation of eating a food. This is referred to as *palatability* [7], and has a positive effect on food intake [8], known as the *appetizer effect* [9]. The driving force behind this effect is the food's flavour, so evidently the retronasal olfactory component comes into play here.

However, the pleasantness of a particular food varies over time. During a meal, the hedonic assessment of the food's visual, olfactory and gustatory properties typically decreases [10]. Accordingly, along with the decline of sensory-mediated pleasantness, the reward value of a particular food decreases during its consumption because of repeated exposure to a particular sensory signal, a phenomenon referred to as *sensory-specific satiation* [11]. In other words, repeated exposure to a food over the course of consumption results in what has been defined as "boredom with taste" [11].

Sensory-specific satiation is facilitated by exposure time [12–13], sensory complexity of the food [14], and intensity [15]. This is not to be confused with *sensory-specific satiety*, a phenomenon that refers to the decline in pleasantness of a particular food when compared to the pleasantness of uneaten foods [16]. Special cases would be the (partial) olfactory and taste sensory-specific satieties, which do not depend on the ingestion of nutrients [17].

Although there is uncertainty as to whether it is the sensory-specific satiation or the satiety phenomenon that bears the major responsibility for the drive for variety and food choice, this makes sense from an evolutionary viewpoint, since it increases the chance of having an adequate intake of various nutrients, and reduces the risk of a toxic overload from one food [18].

Being attracted to a food odor is not the sole driving force for food intake because people with olfactory and gustatory disorders still have a drive to eat and they do not necessarily consume less food than individuals with intact senses of smell and taste [19–20], (although a self-reported decrease of appetite in patients with olfactory dysfunction has been reported [21]). More frequently, people with olfactory loss have reported reduced food appreciation [21–24]. This is of little surprise as, despite normal gustatory function, anosmic individuals have an impaired appreciation of food flavor.

Patients have reported several ways of coping with various olfactory disorders. The most intriguing group of patients are those who have been diagnosed with congenital anosmia. They are of particular interest because of their lifelong lack of olfactory experience with food. Congenitally anosmic individuals tend to focus on the primary tastes, and seek foods with pleasant textures [25] and those which stimulate the trigeminal nerve [26].

Nevertheless, these (often isolated) self-reports, however valuable, do not provide us with an understanding of whether the appreciation of a simple food over the course of consumption is affected by congenital anosmia. This is of interest because the decline of hedonic valence seems to play a crucial role in sensory-specific satiation. We hypothesized that over the course of consumption of a simple, single-food snack-size meal, congenitally anosmic individuals would exhibit a different pattern of change in pleasantness ratings, compared to normosmic controls; namely, that the expected decrease would be delayed and less pronounced in congenital anosmics.

Thus, the aim of the present study was to track the changes in the pleasantness of a simple food over the course of a serving in congenital anosmics and compare them with the results from healthy control subjects.

Materials and Methods

Participants

Fifteen individuals with congenital anosmia (13 women, 2 men; mean [SD] age, 31.0 [9.9] years, range 20–42 years) and fifteen normosmic controls (12 women, 3 men; mean [SD] age, 27.8 [5.2] years, range 21–39 years) participated in the study. The recruitment of congenitally anosmic participants was carried out while another study was being conducted at the research centre. We invited the participation of congenitally anosmic individuals who were listed in the centre's long-term database and who were participating in a study concerning the effects of olfactory loss on taste perception and quality of life. Congenital anosmia was diagnosed using (1) detailed medical history, with participants mentioning no previous taste of flavor experience in their lives, (2) psychophysical examination using the Sniffin' Sticks, with TDI scores less than 15.5, indicative of functional anosmia, (3) electrophysiological measurements based on olfactory event-related potentials, whch were absent in all subjects, and (4) magnetic resonance imaging with severe hypoplasia or aplasia of the olfactory bulb and an olfactory depth of less than 8.0 mm in the plane of the posterior tangent through the eyeballs. The control participants' normal olfactory function was ascertained by use of the extended version of the 'Sniffin' Sticks' test. All of the participants were instructed to refrain from food two hours prior to the commencement of the study. The two groups did not differ in age ($t_{28} = 1.01$, $p = .32$) or age distribution ($\chi^2 = 2.40$, $p = .12$), socioeconomic status based on educational background ($t_{28} = 1.83$, $p = .08$), BMI ($t_{28} = .75$, $p = .46$), time lag between the last meal and their participation in the study ($t_{28} = .27$, $p = .79$), estimated calories consumed prior to participation ($t_{28} = .66$, $p = .52$) or self-assessed hunger ($t_{28} = .40$, $p = .69$), which was indicated on a 21-point scale, ranging from −10 and 10 (extremely hungry and not hungry at all, respectively).

Ethics Statement

Investigations were performed in accordance with the Declaration of Helsinki on Biomedical Research Involving Human Subjects; every participant provided written informed consent. The research was approved by the IRB Charles University, Faculty of Sciences.

Procedure

Before taking part in the study, each participant had already spent an average time of 90 minutes at the clinic, ensuring that no food was consumed immediately before the test began. Since most appointments were scheduled for late in the morning, the last meal reported in the vast majority of cases consisted of moderate amounts of wholemeal bakery products. Care was taken that the room in which the session was to take place was well ventilated and free of any possibly disturbing odors.

Immediately prior to the commencement of the session, ten fresh banana slices were prepared out of the participant's sight. Each portion weighed 10 grams. Banana was chosen as a stimulus due to its low trigeminal activation, soft texture, and the fact that its odor pleasantness is widely agreed upon [27]. In the meanwhile, the participant was seated and asked to fill in a brief questionnaire regarding their last meal in which they were to specify items and amounts consumed, the time elapsed since that last meal and their level of hunger. Subsequently, a plate with the banana slices was placed in front of the participant and a PowerPoint presentation (Microsoft Corporation, Redmond, WA, USA) was run to deliver instructions and to pace the session. To prolong the exposure time, each slice was to be consumed in the following manner: first, the participant was asked to take a slice of banana in the hand and inspect it visually for ten seconds. Next, it was to be smelled and then it was to be chewed without swallowing, each for a period of ten seconds. Finally, ten seconds were allowed for swallowing. After each slice, the participant was repeatedly asked to rate the pleasantness of the particular stimulus on a 21-point scale, anchored at both sides (−10 for very unpleasant to 10 for very pleasant). Each ten-second interval was marked with a non-disruptive sound and a relevant message appeared on the screen, prompting the subject to take the next step. Thus, each banana slice was consumed at an interval of 40 seconds, followed by a pause of approximately 15 seconds for rating.

Before proceeding with analysis, the data were closely inspected for outliers. The following stringent criteria were set to differentiate outliers from naturally occurring fluctuations: an observation that fell beyond two standard deviations from the group mean for each measure, and, at the same time, did so systematically, i.e. in at least 5 measures out of 10 was considered an outlier. Furthermore, the decision to remove such observations from the analysis was further supported by unreliable ratings of self-assessed hunger in which, despite the instructions to refrain from food 2 hours prior to participation, a 10 was given. Even taking into account the subjectivity of the assessments, such reports do not seem credible, be they an indication of the fact that the participant had misunderstood the scale, was careless about his or her responses or that he or she had ignored the instructions not to eat. On these grounds, one case from either group has been excluded from the analysis.

A mixed-design ANOVA with repeated measures (denoted by m1–m10) as a within-subjects factor and group (anosmic subjects and controls) as a between-subjects factor was used. Since for post hoc analysis of small samples nonparametric tests are recommended, we applied Wilcoxon matched pairs signed-rank test (exact test procedure) with Bonferroni correction to follow up the findings. In addition, effect sizes (as denoted by *r*) were computed. Statistica 8.0 was used for all data analysis. All results are reported as significant at $p < .05$ unless stated otherwise.

Results

The analysis yielded a significant main effect of group ($F(1, 26) = 6.71$, $p = .02$). Visual inspection of the data (see Fig. 1) suggests that anosmic participants consistently rated the stimuli as more pleasant than the control group.

Furthermore, there was a significant main effect of repeated measure (portion) upon pleasantness ratings ($F(1.85, 48) = 12.15$, $p < .001$). Mauchly's test indicated that the assumption of sphericity had been violated, $\chi^2(44) = 268.07$, $p < .001$, therefore degrees of freedom were corrected using Greenhouse-Geisser estimates of sphericity ($\varepsilon = .21$). Repeated contrasts revealed that there was a significant change (decrease) between m2 and m3, and m5 and m6 (both ps = .005), m7 and m8, and m8 and m9.

More importantly, a significant portion*group interaction was found ($F(1.85, 48)$, $p = .04 = 3.54$). This turned out to be due to the differential change in pleasantness ratings in the congenital anosmics and controls between m6 and m7 ($p < .01$).

To determine whether there was a continuous significant decline in pleasantness ratings as compared to the baseline in the individual groups and to ascertain at which time point it commenced, we employed the Wilcoxon matched pairs signed-rank test with Bonferroni correction. Whilst multiple comparisons to baseline yielded no significant results at the specified level of significance ($\alpha = .006$) in the anosmic group, in the control group there was a statistically significant decrease in pleasantness ratings between m1 and m8 ($T = 6$, $p = .005$, $r = .52$), m1 and m9 ($T = 4.5$, $p < .005$, $r = .57$), and m1 and m10 ($T = 1.5$, $p < .005$, $r = .58$).

Discussion

In the present study, congenitally anosmic individuals exhibited a more sustained positive response to the stimulus over the course of consumption (relative to baseline) compared with the control group. One line of reasoning, somewhat speculative though, is that the mechanisms underlying hedonic habituation (resulting from repeated prolonged exposure to a simple food and, by extension, possibly also sensory-specific satiation), might be impaired as a consequence of the absence of the sense of smell. Thus, congenitally anosmic participants might exhibit a less-pronounced decline in the hedonic valence of a food than healthy controls do. In other words, to use the original definition, they may not 'get bored with taste' as rapidly as individuals with an intact sense of smell. However, we argue that the hypothesized 'boredom with taste' [11] should be conceived of as 'boredom with flavor' instead, due to smell and taste being closely intertwined in healthy individuals [28]. It is people with this kind of olfactory impairment who are truly in the position to appreciate the sense of taste separately from olfaction; our results indicate that their appreciation of taste might not diminish as rapidly as that of flavor in healthy individuals. However, a recent study [29] showed that sensory-specific *satiety* does not appear to be affected by olfactory dysfunction, as it developed in normosmic and hyposmic/anosmic individuals alike.

An alternative explanation is that being forced to focus on foods with specific characteristics in order to derive some enjoyment from eating may result in considerably fewer choices. In other words, in a world of bland flavors, congenitally anosmic individuals may exhibit a more sustained positive response than healthy subjects would when presented with a food that possesses some redeeming qualities. One of these is sweet tastes, as evidenced by the finding that individuals who have lost olfaction, the most 'sophisticated' sense to enjoy foods simply eat more sweet dishes to reward themselves [21]. Add to this the fact that there is evidence for a biologically-driven hedonic bias in preference for

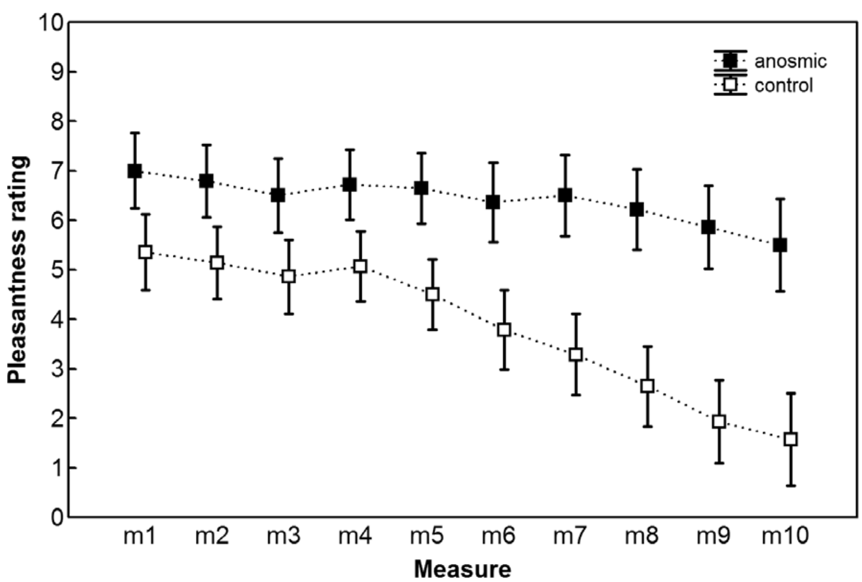

Figure 1. Pleasantness ratings. Pleasantness ratings (mean ± SE) across repeated measures (only the positive side of the scale is displayed).
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sweet taste [30] and it seems understandable why congenitally anosmic individuals would want to derive enjoyment from this particular food characteristic. Food texture might have been another candidate. Clearly, further studies employing a wide selection of diverse foods are needed to test this hypothesis.

Yet another possible explanation is that, being deprived of the sense of smell, which, to a variable extent, constitutes our experience of satiation [17], individuals with this type of olfactory disorder have to 'make do with what they have left'. The knowledge that ten banana bites are usually not enough to ward off hunger, coupled with the limited array of dietary choices congenital anosmics find enjoyable, might have resulted in these participants experiencing a prolonged appreciation of the stimuli. Of course, however, this remains an idea for further research.

Finally, not only did the stimulus elicit a more sustained positive response in the congenitally anosmic participants but it was also rated as more pleasant. This might seem to contradict congenitally anosmic individuals' self-reports of reduced food appreciation in general (i.e. the longer-term overall degree of enjoyment); however, the aim of this study was to investigate the pattern of actual, immediate changes in appreciation of one particular simple, single-food meal over the course of consumption. This particular food may well have happened to be one of their "remedy" or "comfort" foods. Besides, the length of time for which the olfactory loss has been noted (along with the individual's age) appear to be important factors, as older subjects who had been aware of their olfactory loss for more than three years tended to indicate decreased food enjoyment less frequently than younger ones [22].

It is also crucial to understand that the ratings in both the congenitally anosmic and control group were assigned relative to other foods with which they had had experience throughout their lives. When the sense of smell is absent, not only will the pleasantness of food stimuli be judged on the basis of the remaining available sensory attributes, but it will also be judged in the context of non-olfactory experience. However, these interpretations of the general level of food appreciation must be treated with caution, as no non-olfactory stimuli to normalise the scale to have been employed in this study. Furthermore, only one particular stimulus was used in this study. Foods with different characteristics and palatability should be employed in future investigations to ascertain whether the present finding might generalize to other types of stimuli as well.

Although the nature of the present study is explorative, its findings point in the direction of the idea that, at least to some degree, congenital anosmia might affect the hedonic valence of a simple food and/or interfere with the development of sensory-specific satiation (or expression thereof). However, whether this is due to the absence of olfactory stimuli in congenital anosmia or an effect of other properties of this particular olfactory disorder, which have not been addressed in this study, remains to be further explored. The present explorative study contributes towards an issue deserving of more attention than it has been given so far and further investigations should be carried out to explore the possible role of olfaction in inducing or increasing perceived satiation, which, in turn, might lead to a decrease in food intake.

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Author Contributions

Conceived and designed the experiments: LN IC. Performed the experiments: LN VB. Analyzed the data: LN JH. Wrote the paper: LN JH.

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CHAPTER 4

SEX DIFFERENCES IN OLFACTORY BEHAVIOUR IN NAMIBIAN AND CZECH CHILDREN

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Abstract: Sex differences in olfaction are well established, but explanations for those sex differences remain incomplete. One contributing factor could be individual- or cultural-level differences in exposure to odours. We tested whether frequent engagement with common sources of domestic odours (cooking, domestic animals, siblings) was linked to individual differences in olfactory reactivity and awareness among children in southern Namibia, and compared study populations in southern Namibia and the Czech Republic, based on the established COBEL (Children's Olfactory Behaviour in Everyday Life) questionnaire. We did not find any effects of engagement with odour sources, but our results were consistent with usual olfactory sex differences in that girls scored higher than boys in measures of olfactory reactivity and awareness. Among the Czech children, odour identification abilities were positively linked to COBEL scores. Our data contribute to the literature that finds that sex differences in olfactory awareness are apparent across a diverse range of cultures and age groups.

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26 June 2013

Dear Sirs,

Submission of Manuscript: Sex differences in olfactory behaviour

We would like to submit our attached manuscript:

Sex differences in olfactory behaviour in Namibian and Czech children

for consideration in your journal.

The manuscript investigates how differences in sex, age and olfactory exposure might correspond to differences in olfactory ability and orientation in children from Namibia and the Czech Republic. Psychological research on olfactory behaviour is based almost solely on industrialised western countries; our research demonstrates that sex differences in olfactory behaviour are apparent outside of such populations. We also assess the use of a standard questionnaire relating to children's olfactory behaviour in a non-western population, and compare olfactory orientation to children's odour identification abilities. The manuscript comprises 4984 words.

Yours faithfully,

Tamsin Saxton
(corresponding author)

***Title page with author details**

Sex differences in olfactory behaviour in Namibian and Czech children

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***Highlights (for review)**

- We assessed Namibian and Czech children's olfactory orientation
- Girls were more olfaction-oriented than boys
- Olfaction orientation to Environmental and Food odours increased with age
- Olfaction orientation was linked to odour identification among Czech children

Abstract

Sex differences in olfaction are well established, but explanations for those sex differences remain incomplete. One contributing factor could be individual- or cultural-level differences in exposure to odours. We tested whether frequent engagement with common sources of domestic odours (cooking, domestic animals, siblings) was linked to individual differences in olfactory reactivity and awareness among children in southern Namibia, and compared study populations in southern Namibia and the Czech Republic, based on the established COBEL (Children's Olfactory Behaviour in Everyday Life) questionnaire. We did not find any effects of engagement with odour sources, but our results were consistent with usual olfactory sex differences in that girls scored higher than boys in measures of olfactory reactivity and awareness. Among the Czech children, odour identification abilities were positively linked to COBEL scores. Our data contribute to the literature that finds that sex differences in olfactory awareness are apparent across a diverse range of cultures and age groups.

Keywords: cross-cultural; olfaction; olfactory behaviour; sex differences; children

1. Introduction

Sex differences in olfaction are well established, but explanations for those sex differences remain incomplete. On average, women outperform men in odour identification, discrimination, memory, and awareness (e.g. Doty et al. 1985; Havlicek et al. 2008; Herz and Inzlicht 2002; Lehrner 1993; Platek et al. 2001; Velle 1987), and sex differences may be apparent even from very early infancy (Makin and Porter 1989, Balogh and Porter 1986). Brand and Millot (2001) review factors that may contribute to these sex differences, including hormonal (e.g. Doty 1986, Doty and Cameron 2009, Velle 1987), physiological (Hornung et al. 1999), and cognitive (e.g. Öberg et al. 2002).

A factor of a different type that might contribute to sex differences in odour abilities could be greater female than male exposure to, and trained awareness of, different odorants (Brand and Millot 2001). It has been suggested that women may, in general, encounter olfactory cues more often (Brand and Millot 2001), and girls from an early age may be implicitly or explicitly encouraged to pay more attention to environmental and personal odours (Mallet and Schaal 1998; Wysocki et al. 1991). Differences in odorant exposure can lead to measurable differences in olfactory function or awareness. For example, laboratory exposure to odorants or purposeful olfactory training can alter olfactory function (Boulkroune et al. 2007; Dalton et al. 2002; Wysocki et al. 1989). Outside the laboratory, cultural differences in reactions to odours may arise from the prevalence of that odour within that cultural context (Ferdenzi et al. 2008b; Ferdenzi et al. 2011), and include cultural differences in reactions to food odours (Distel et al. 1999; Hudson, 1999; Pangborn et al. 1988; Schleidt et al. 1988), in assessment of odours as pleasant or unpleasant (e.g. Ayabe-Kanamura et al. 1998; Distel et al. 1999; Schaal et al. 1997; Schleidt et al. 1981; Pangborn et al. 1988), and in differential categorisation of odours (Chrea et al. 2004). Seo et al. (2011) report several cross-regional differences in attitudes towards odours; for example, odour is more important in relation to emotions and memories, and is used more in day-to-day life, by Mexican respondents compared with Korean, Czech and German respondents. Similarly, Finnish children report more reactivity and attention to odours than French children (Ferdenzi et al. 2008b). That is, differences in olfactory reactivity may be acquired partly from cultural and social norms and exposure.

Needless to say, endogenous and exogenous factors do not act separately, but interact to give rise to individual differences in olfaction. Nevertheless, we wanted to focus on this question of exogenous factors in individual differences in odour orientation, by examining two questions. Firstly, we examined whether sex differences in olfaction are apparent in a culture and age group that is distinct from more frequently-studied groups; olfaction is very little studied in non-industrialised countries. Secondly, we examined whether individual differences in odour-related activities are associated with individual differences in odour orientation.

To answer these questions, we examined olfactory awareness and sensitivity in children in southern Namibia, using odour identification tests and the COBEL (Children's Olfactory Behaviour in Everyday Life) questionnaire (Ferdenzi et al. 2008a). In order to learn about a child's olfactory environment, we collected data on exposure to pets and other animals, engagement in cooking activities, and number of siblings, because these may represent regular exposure to potential sources of odours in the environment; adult reports of odours that are likely to stimulate nostalgic feelings tend to focus around foods and cooking, family member odours (e.g. perfume, hair spray), and odours linked to nature and animals (e.g. manure, hay) (Hirsch, 2006). A subsidiary aim of our study was to evaluate usage of the COBEL outside of the European cultures where it has been previously used (Ferdenzi et al. 2008a, 2008b). We were also able to make use of COBEL scores and olfactory identification scores collected from children in the Czech Republic, in order to contrast olfactory behaviour in two different cultures.

2. Material and Methods

2.1 Procedure

The study of Namibian children was approved by the [xx] Ethics Committee of the University of [xx]. We recruited participants from urban schools in a southern Namibian town with a population of around 19,000. Questionnaire acceptability was checked with local contacts, research permission was granted by local school principals and teachers, and letters explaining the study were provided to schools for transmission to parents. Teachers arranged for pupils to attend the interviews during school time. Data were collected anonymously during structured interviews with assenting children performed by [xx] and [xx]. Interviews followed the COBEL questionnaire (Ferdenzi et al. 2008a), and also collected basic demographic details such as number of siblings, and language spoken at home. We asked for information on language spoken at home instead of (and as) an indication of ethnicity, which is a sensitive issue. [xx] carried out interviews in English (the official language of Namibia), Afrikaans, and Nama, and [xx] carried out interviews in English, but we were not able to interview every child in the language that he or she spoke at home. Questions about the olfactory environment were included, and an odour identification test given (details below).

The study of Czech children was approved by the IRB of the Faculty of Sciences of [xx]. Informed consent was obtained from the participants' parents. The data were collected in the form of structured interviews performed by [xx] in Czech following the COBEL questionnaire (Ferdenzi et al. 2008a). The English and French versions of the COBEL questionnaire were translated into Czech, and then independently back into the source languages, to reveal any discrepancies. Odour identification data from the Czech participants are also used in ([xx] et al., submitted).

2.2 COBEL questionnaire

The COBEL questionnaire has been published previously in full (Ferdenzi et al. 2008a). It is presented as an interview, and consists of 16 questions designed to understand the importance of odour in children's everyday life. The questions fall into three categories: Food (e.g. whether children try to guess what they will eat for dinner from cooking smells), Social (e.g. whether children realise that people have a natural odour), and Environmental (e.g. whether children seek out smells when feeling sad).

The COBEL questionnaire required adjustment for use in Namibia. Item 9 of the questionnaire asks about the odour of the child's parents' car, and was excluded because most of the Namibian participants' parents would not have had a car; we initially tried asking about the odour of the local supermarket, and a friend's house, as potential replacements, but found that these locations were not visited by all of our participants. Item 11, which asked whether the family members were thought to have a smell, and Item 7, which asked participants to imagine there were no smells outside any more, and report how they would feel, were discarded due to frequent comprehension difficulties in the interviews with Namibian children. Responses to Items 7, 9 and 11 were also deleted from the Czech dataset to allow comparison. Following the deletions, the Social component of the COBEL questionnaire was made from three rather than four items, the Environmental component from seven instead of nine items, and the Food component maintained three items. Due to interviewer error, five Namibian participants for whom we had complete COBEL scores were asked to name things in their bathroom that had a smell, rather than to name things in their bathroom and subsequently to identify which did and did not have a smell (Item 10). These children were given a score of 1 if they named three or more items; 0.5 if they named two items; and 0 if they named one or no items. Item 1 asked why the participant disliked specific foods. Many Namibian children said that they did not like a food because it was not nice. Item 1 was scored according to the proportion of foods that were *spontaneously* described as being disliked because they smelt or tasted unpleasant, and so it was not possible to prompt children by asking whether they meant that they did not like the taste or smell. We scored these answers conservatively, so that a report of not liking a food was not considered to be a report that it tasted unpleasant. In Namibia, Items 6 and 8, which both contribute to the Environmental component, were also problematic. Item 6, which asks whether there are things that are liked just because they smell good, seemed often to be interpreted as though it were asking for items that people liked the smell of. Item 8, which asks whether the participant smells his or her school things, was often answered in relation to things within the school grounds that have an odour. These items were retained to avoid diverting too much from the original questionnaire, but they do suggest that any country-level differences in Environmental scores must be treated with caution.

2.3 Olfactory environment

We noted salient aspects of the olfactory environment by asking the Namibian participants how many siblings and pets they had, and how frequently they helped to cook at home. One child answered only the first of these questions.

2.4 Olfactory identification tests

The Namibian participants were shown four labelled pictures (one target plus three distractors) and asked which one matched the odour. Use of a common test such as the Sniffin' Sticks (see below), which uses odours such as rose, is inappropriate in a culture that does not commonly encounter such odours. Accordingly, we constructed our own test to identify relative strengths and weaknesses in olfactory identification, following discussion with local people, based on locally common odours, and covering a range of different odour types (i.e. fruits, spices, drinks, household products). The tests made use of 12 odorous substances: bottled lemon, orange and peppermint essence, garlic salts, powdered ginger, a crushed cigarette, coffee grounds, beer soaked into a cotton wad, oil/petrol odour sampled onto tissue paper, and a couple of tablespoons of three locally well-known household products (a standard branded washing powder, fabric softener, and cleaning liquid, which are widely and commonly used in the local community). Odour sources were concealed in plastic cups of approximately 0.25 l volume with a perforated aluminium foil cap to allow sniffing. Visual cues to the odorous substances were concealed as necessary (e.g. covering the crushed cigarette with tissue paper). When it transpired after 11 participants that scores were likely to be at ceiling (range: 7 – 12;

mean +/-SD = 11.0 +/- 1.1), we extended the test to precede it by a free-identification test of those same odours. Here, a child was only given the four-alternative forced-choice odour test for an odour if s/he did not identify that odour correctly in the free-identification test.

All but one of the Czech children participated in a Sniffin´ Sticks odour identification test, where odour-dispensing devices shaped like pens were used to test nasal chemosensory performance. This is a well-established test that has been used by researchers in a number of previous studies on children (e.g. Dudova et al. 2011; Ferdenzi et al. 2008b; Renner et al. 2009), as well as by many clinicians across Europe (e.g. Hummel et al. 1997; Kobal et al. 1996). The test consists of 16 odours widely known within European cultural settings (e.g. orange, rose, garlic, fish); participants are asked to select the name of the target odour from a list of four. Scores ranged from 5 – 13 (mean +/- SD = 9 +/- 1.9).

2.5 Participants

Seventy-four Namibian participants answered the COBEL questionnaire, were asked about their olfactory environment, and took part in the odour identification test. Technical problems meant that we did not have the data to calculate complete Food component scores for nine of these children, and problems in question comprehension meant that we could create Food component scores but not overall COBEL scores for six children, including two participants who did not have a bathroom and so were unable to answer Item 10.

To maximise sample size, we also made use of data from a further 32 participants who answered the COBEL questionnaire during a preliminary stage of the study (nine of whom also carried out the odour identification test). Of these 32, we had complete COBEL scores from 23, but Food component scores alone for the remainder (n = 9) due to non-comprehension of, or non-response to, one or more questions making up the Social and Environmental components. Nine of these 32 participants also completed the odour identification test. (An additional eight children were interviewed, but non-comprehension problems meant that we did not have enough data to use their responses in any of the analyses below.)

The sample of 101 Namibian participants whose data are used below comprised 50 boys aged 10-15 (mean +/- SD = 12.3 +/- 1.4 years) and 51 girls aged 9-15 (mean +/- SD = 11.9 +/- 1.5 years) who reported speaking Afrikaans (n = 53), Nama (n = 27), Oshiwambo (n = 13), and other languages (n = 8) at home.

The Czech sample consisted of 92 children (36 boys aged 8-11 years, mean +/-SD = 9 +/-0.8 years; and 56 girls aged 8 – 11 years, mean +/- SD = 9 +/- 0.7 years) from the third and fourth grades of two mixed-sex general education elementary schools in Prague.

2.6 Analysis

Following previous usage of the COBEL (Ferdenzi et al. 2008a; 2008b), we calculated scores for the three components of the questionnaire (Social, Environmental and Food), and summed these together to create a total COBEL score. All of the data arrays that are used in the analysis below are non-normally distributed (Shapiro-Wilk test, $p < .03$). ANOVA is fairly robust to non-normal distribution (Subrahmaniam et al. 1975). Greenhouse-Geisser correction was used in repeated-measures analyses when data appeared to violate assumptions of sphericity (i.e. Mauchley's test of sphericity $p < .05$). Analysis was carried out in SPSS 20. Effect sizes (r) are reported for significant findings.

3. <u>Results and Discussion</u>

3.1 COBEL questionnaire scores

We carried out a repeated-measures ANCOVA using the scores on the Social, Environmental and Food components of the COBEL as within-subjects factors, and including the between-subjects factors of sex and country of residence, and the covariate of age (n = 174).

Girls scored significantly higher than boys ($F(1,169)= 7.95$, $p = .005$, $r = .21$). This replicates findings from Finnish and French children (Ferdenzi et al. 2008a; 2008b), and is consistent with the general finding that the olfactory domain is more significant to females than males (see Introduction). There was no significant interaction between participant sex and COBEL component, but because our main hypothesis concerned sex differences, for completeness, we also examined sex differences for each COBEL component in three separate ANCOVAs (including the between-subjects factor of country of residence, and the covariate of age). Girls scored higher than boys in relation to the Social ($F(1,169)= 7.93$, $p = .005$, $r = .21$) and Environmental ($F(1,169)= 4.58$, $p= .034$, $r = 0.16$) components of the COBEL, but not in relation to the Food component ($F(1,169)= .754$, $p = .387$) (Figure 1).

Figure 1 about here

COBEL scores increased with age ($F(1,169)= 5.51$, $p = .020$), but this was modified by a significant interaction between age and the COBEL component ($F(1.7,294.6)= 5.60$, $p = .006$). Scores increased significantly with age in the Environmental ($F(1,169)= 7.71$, $p = .006$) and Food ($F(1,169)= 4.75$, $p = .031$) components, but not the Social component ($F(1,169)= .304$, $p = .582$). Previous research on the COBEL also found age-linked increases in scores (Ferdenzi et al. 2008a, 2008b).

The COBEL scores of our participants were broadly in line with those reported for French and Finnish children (Ferdenzi et al. 2008a; 2008b and Figure 1 therein; maximum scores in the current study are three points lower than in the previous studies because we removed Items 7, 9 and 11 from the questionnaire). However, the Namibian children, controlling for sex and age, scored significantly higher on the COBEL than the Czech children ($F(1,169)=11.88$, $p=.001$, $r= .26$), and this effect was moderated by a significant interaction between the scores on the three components, and the participant's country of origin ($F(1.7,294.6)=9.41$, $p<.001$). In order to understand this interaction, the scores from the Namibian and Czech children were compared for each of the three COBEL components separately, controlling for sex and age. Namibians scored significantly higher than Czechs in relation to the Environmental ($F(1,169)=14.18$, $p<.001$, $r=.28$) and Social components ($F(1,169)=8.49$, $p=.004$, $r=.22$), but not the Food component ($F(1,169)=.269$, $p=.605$). Figure 2 gives scores on an item-by-item basis in order to illustrate the extent to which the country-level differences are generalisable across the questionnaire Items; interested researchers will find the complete text for each Item in (Ferdenzi et al. 2008a, 2008b). Other research has shown that children from different cultural backgrounds do respond differently to the COBEL (Ferdenzi et al. 2008b). However, misinterpretation in the Namibian context of Items 6 and 8 (see Section 2.2) likely artificially elevated scores on the Environmental component, and further research is needed to separate out cultural differences in olfactory behaviour from alternative explanations (ranging from e.g. the prevalence and salience of scented bathroom items, Item 10, to country-level differences in interviewers, familiarity with interview situations, etc).

Figure 2 about here

3.2 Odour identification scores

We examined possible sex and age differences in odour identification by carrying out ANCOVAs on the odour identification test scores with sex as a between-subjects factor, and age as a covariate. Direct comparison of Czech and Namibian children on the olfactory tests was not possible as they were constructed to fit each culture. Girls' and boys' scores did not differ significantly in relation to the Namibian four-alternative forced choice odour test ($F(1,75)=2.21$, $p = .142$, $n=78$), the Namibian free-choice odour identification test ($F(1,64)=.248$, $p = .621$, $n=67$), or the Czech four-alternative forced choice odour test (F(1,88)=.294, p=.589, n=91). There were no effects of age (all $p > .12$). These results contrast with findings from French and Finnish children in very similar age groups (Ferdenzi et al. 2008b), where girls performed better than boys, and older children performed better than younger children, using the 'Sniffin' Sticks' odour presentation devices used here for the Czech children, although with a larger sample (n = 130).

Next, we looked for possible correlations between odour identification scores and COBEL scores. Among the Namibian participants, there were no significant relationships between overall COBEL scores and either free-choice odour identification scores ($r = .044$, $p = .757$, n = 52) or four-alternative forced-choice odour identification scores ($r = .030$, $p = .818$, n = 64; but note low variability in the data, where the children in this analysis scored between 9 and 12 points). Among the Czech participants, higher overall COBEL scores were associated with higher four-alternative forced-choice scores ($r = .233$, $p = .026$, n = 91; Figure 3). Results were qualitatively identical when non-parametric correlations were used. A similar link was predicted (but not found) in a comparison of odour identification abilities of the highest and lowest quartile of COBEL scores in a smaller sample of French and Finnish children by Ferdenzi et al. (2008b), but other researchers have also found positive relationships between olfactory sensitivity and self-reported attitudes towards olfaction (Seo et al. 2011). Longitudinal studies would help us understand the direction of any causal relationship between olfactory identification and olfactory orientation.

Figure 3 about here

3.3 Participant activities and olfactory measures

The Food component scores did not differ significantly between the Namibian children who sometimes or often cooked ($n = 48$) and those who never cooked ($n = 20$) (F(1,65)= .284, p = .596). We controlled for age but not sex in this analysis, following results above that indicated that age but not sex significantly influenced Food component scores, but results are qualitatively identical with or without these variables. The Namibian participants' overall COBEL score did not differ according to how many siblings they had ($F(1,47) = .031$, $p = .860$), or how many animals were in their family household ($F(1,47) = .831$, $p = .367$), in an ANCOVA that included the covariates of number of siblings, number of animals, and age, and the factor of participant sex ($n = 52$). Similarly, free-choice odour identification scores did not differ significantly according to cooking frequency, or number of siblings or animals (all $p > .6$; ANCOVA as previously, with free-choice odour identification scores instead of overall COBEL scores as dependent variable). It may be that more sensitive measures of individual differences in odour exposure are required, although our null findings imply at least that any effect sizes are unlikely to be large.

A subsidiary aim of the study was to evaluate the use of the COBEL in a population that is geographically and culturally distinct from those in which it has been used previously. The lack of car ownership was the main factor that required adjustments to be made to the questionnaire, although it is also possible that less overt practices, such as potential cultural differences in the salience and proportion of scented bathroom products, might have also had systematic influences on answers. Nevertheless, sex and age were linked to COBEL scores in ways that were consistent across the Namibian and Czech children, and consistent with previously-studied populations, suggesting that the COBEL usefully reveals individual differences in olfactory behaviour in diverse cultures. In particular, we replicated findings of female over male advantage in the olfactory domain from data on olfactory behaviour within cultures that are rarely studied in the context of psychological testing.

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Figure Legends

Figure 1: Boys' and girls' estimated marginal mean scores (controlling for participant sex and country of residence) on the three components making up the COBEL (bars = mean +/- SE). * $p < .05$; ** $p < .01$.

Figure 2: Namibian and Czech estimated marginal mean scores (controlling for participant sex and age) for each questionnaire Item of the COBEL (bars = mean +/- SE). The complete questionnaire Item text is available in (Ferdenzi et al. 2008a, 2008b).

Figure 3: Overall COBEL scores and four-alternative odour identification scores among the Czech participants.

Figure 1

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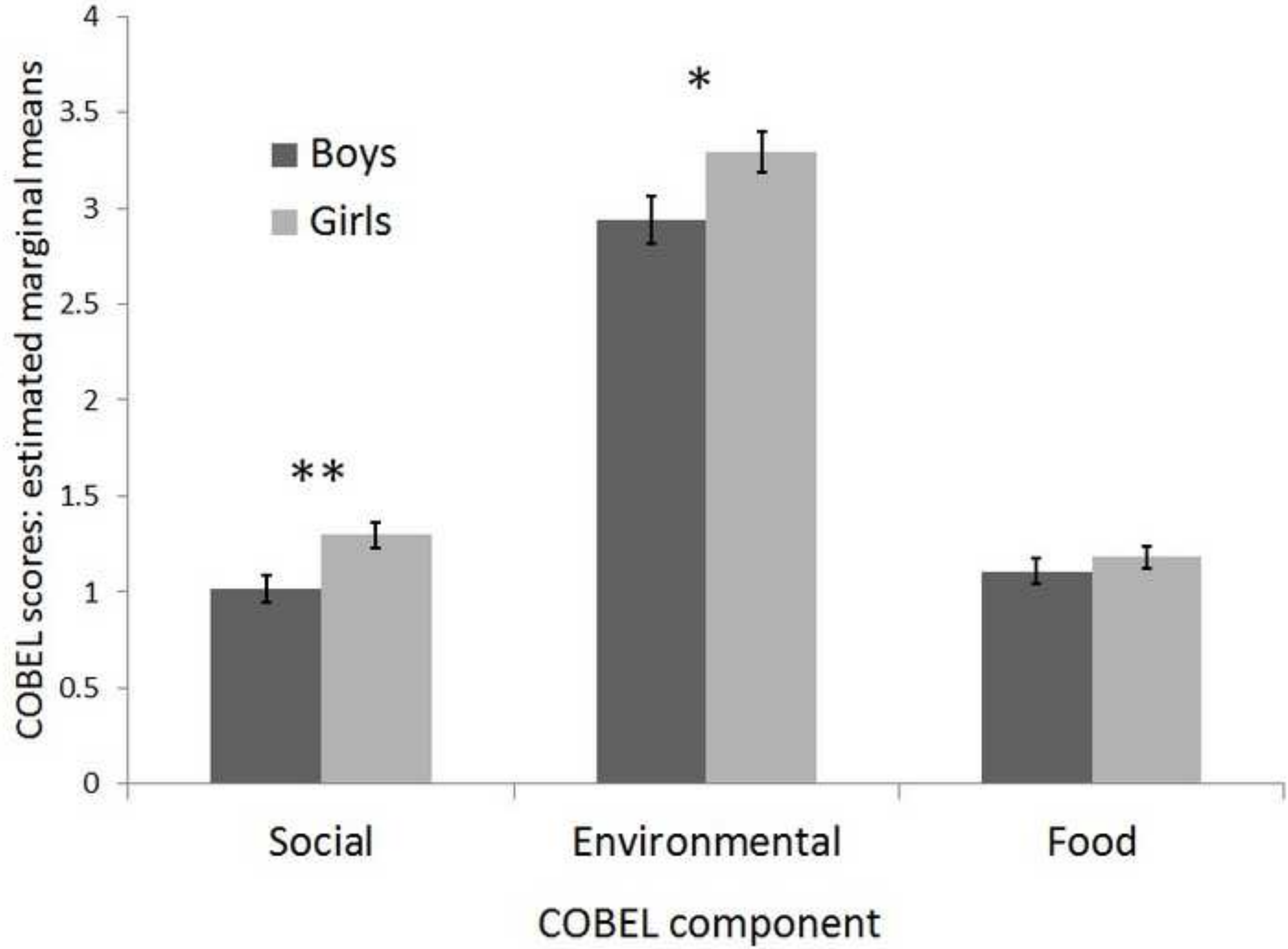

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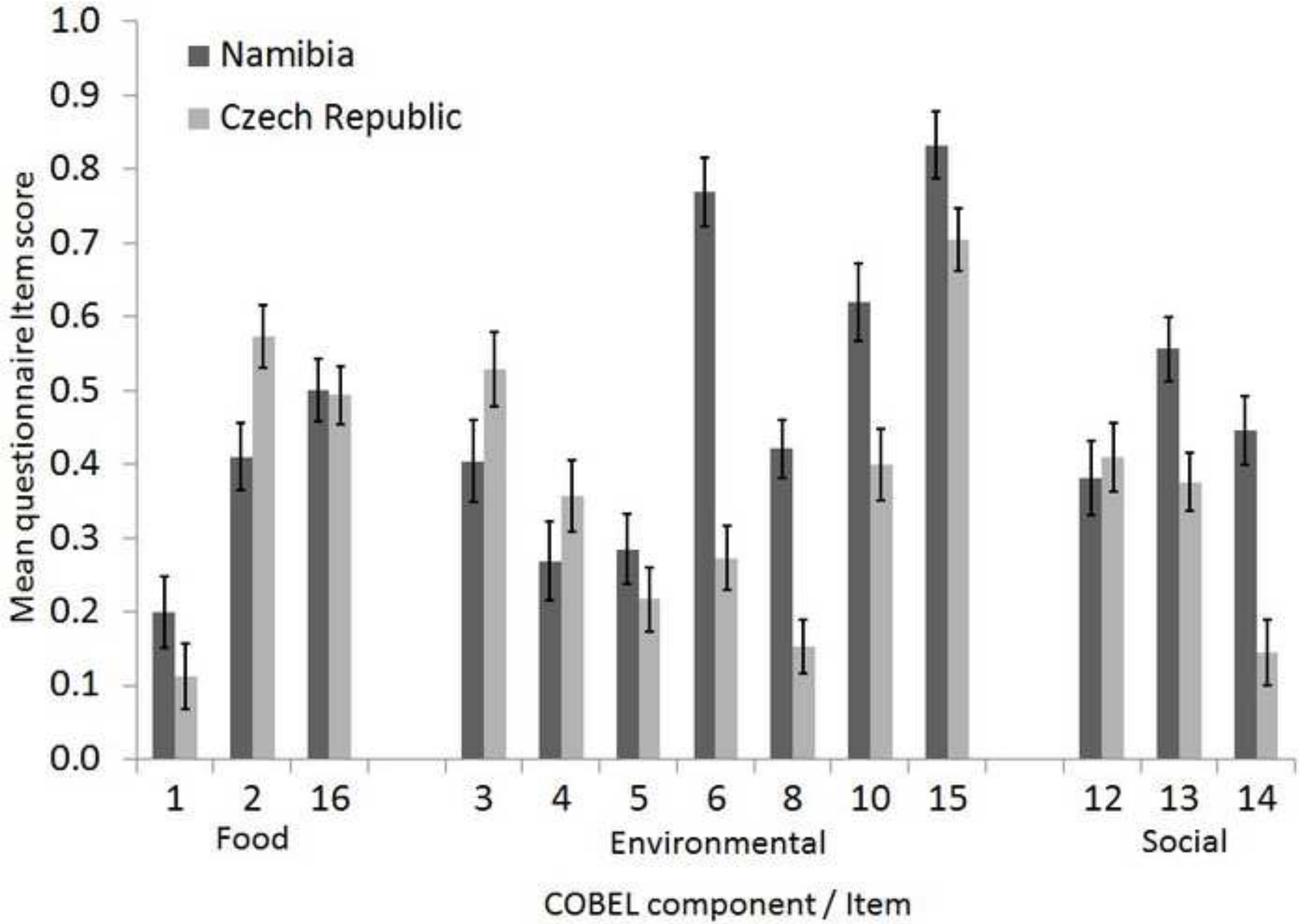

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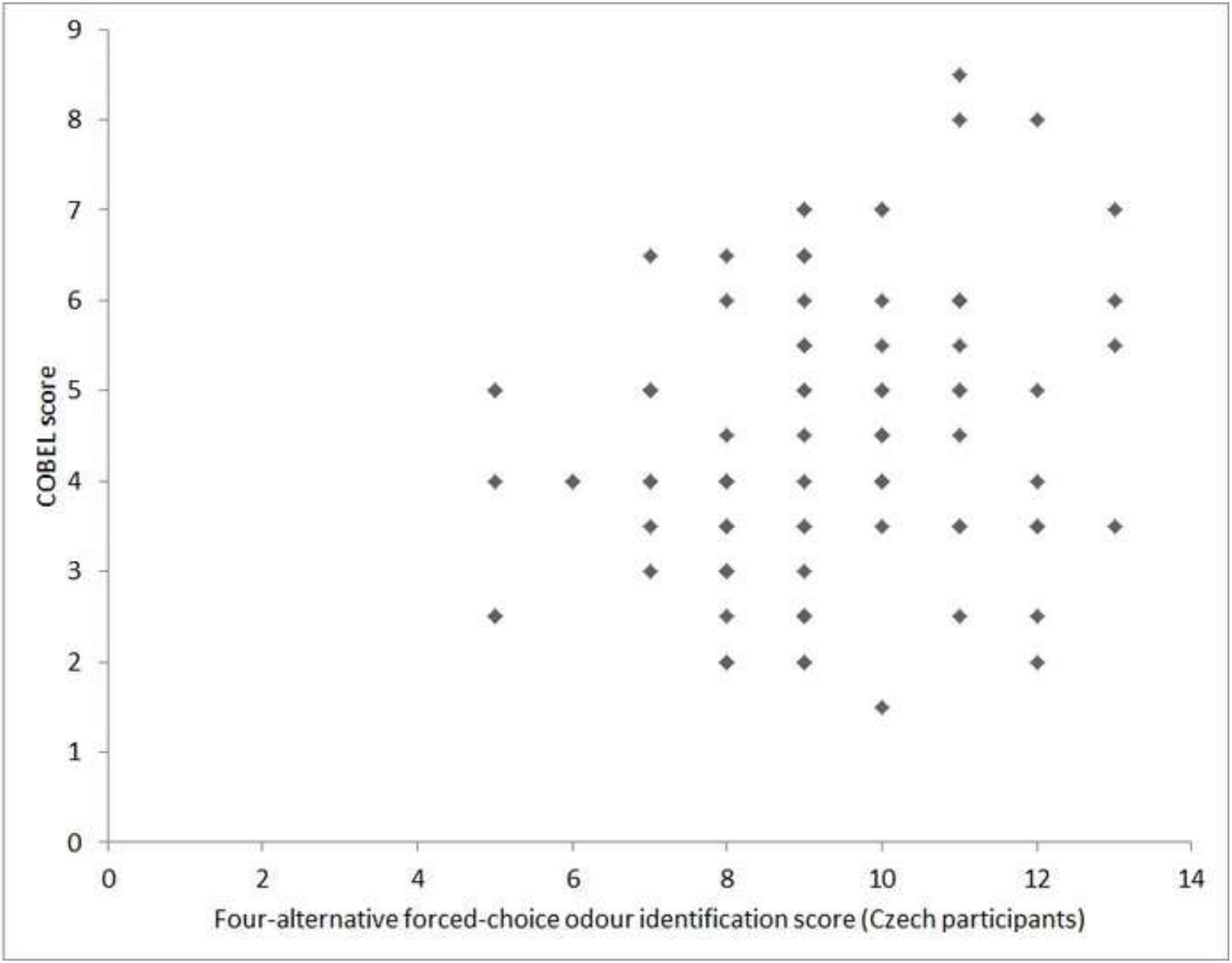

CHAPTER 5

IDENTIFICATION OF UNPLEASANT, BUT NOT PLEASANT ODORS IS RELATED TO HEDONIC RATINGS IN PREPUBERTAL CHILDREN

pp. 126-159

Chemosensory Perception

Identification of unpleasant, but not pleasant odors is related to hedonic ratings in prepubertal children

--Manuscript Draft--

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Abstract:	Hedonic evaluation of odors and olfactory preferences have been shown to have a profound impact on human psychology and behavior in various aspects of our everyday life. These affective responses to odors are influenced by a number of modulating factors, such as prior experience and knowledge about an odor's identity. The present study addresses the effect of knowledge about an odor's identity due to prior experience, assessed by means of a test of cued odor identification, on odor pleasantness ratings. We hypothesised relatively higher pleasantness ratings in cases in which an odor was identified correctly as opposed to instances in which it was not. 91 children aged 8-11 years rated the pleasantness of odors in the Sniffin' Sticks set and, subsequently, took the odor identification test. We found the relation for two of the most unpleasant odors (garlic and fish): relatively higher pleasantness ratings were exhibited by those participants who correctly identified these odors compared to those who failed to correctly identify them. However, we did not find a similar effect for any of the more pleasant odors. The results of this study show that pleasantness ratings of some odors may be modulated by the knowledge of their identity due to prior experience, as evidenced by correct olfactory identification, and we propose that potential involvement of odor pungency and trigeminal stimulation might account for the present pattern of findings.
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Identification of unpleasant, but not pleasant odors is related to hedonic ratings in prepubertal children

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ABSTRACT

Hedonic evaluation of odors and olfactory preferences have been shown to have a profound impact on human psychology and behavior in various aspects of our everyday life. These affective responses to odors are influenced by a number of modulating factors, such as prior experience and knowledge about an odor's identity. The present study addresses the effect of knowledge about an odor's identity due to prior experience, assessed by means of a test of cued odor identification, on odor pleasantness ratings. We hypothesised relatively higher pleasantness ratings in cases in which an odor was identified correctly as opposed to instances in which it was not. 91 children aged 8-11 years rated the pleasantness of odors in the Sniffin' Sticks set and, subsequently, took the odor identification test. We found the relation for two of the most unpleasant odors (garlic and fish): relatively higher pleasantness ratings were exhibited by those participants who correctly identified these odors compared to those who failed to correctly identify them. However, we did not find a similar effect for any of the more pleasant odors. The results of this study show that pleasantness ratings of some odors may be modulated by the knowledge of their identity due to prior experience, as evidenced by correct olfactory identification, and we propose that potential involvement of odor pungency and trigeminal stimulation might account for the present pattern of findings.

INTRODUCTION

Olfactory preferences, a term used throughout this text to refer to “relatively stable evaluative judgements in the sense of liking or disliking a stimulus, or preferring it or not over other objects or stimuli” (Scherer, 2005), have been shown to have a profound impact on human psychology and behavior in varied aspects of life, such as mate choice (Havlicek & Roberts, 2009), mother-infant bonding (Schaal & Marlier, 1998), or dietary habits (Yeomans, 2006). Therefore, it is of essential importance to understand the formation of these affective responses to odors and the effects of factors that may modulate them across the lifespan (for review see Rouby et al., 2009).

Currently, the widely accepted view is that humans are not born with any fixed set of olfactory likes or dislikes but that evaluative reactions towards odors are mainly shaped by means of associative processes (Engen, 1988), namely evaluative conditioning, in the context of everyday individual experience with odors within one’s culture (Herz, 2006). This is a life-long process, although the formation of affective olfactory responses, particularly the negative ones, in isolated, one-off encounters certainly is possible, as evidenced, for instance, by trauma associations to odors (Hinton et al., 2006). Starting as early as in the pre- and perinatal period (Mennella & Beauchamp, 1991; 1999; Mennella et al., 1995; Schaal et al., 1998), these first olfactory experiences have been found to extend their influence well into childhood (Mennella & Garcia, 2000) and adulthood (Haller et al., 1999). On the other hand, some hedonic responses towards odors are subject to change between infancy and middle childhood. This is evidenced by the fact that infants may exhibit responses that are in sharp contrast to those of adults, such as liking the odor of synthetic sweat and feces (Stein et al., 1958). Similarly, four-year-olds’ hedonic reactions to butyric acid (described by adults as “rancid butter” or “vomit-like”) and amyl acetate (“banana-like”) did not differ, even though these odors usually receive very contrasting pleasantness ratings from adults (Engen, 1988).

As noted above, this olfactory learning does not occur within a social vacuum, but always takes place within a certain cultural setting, in which certain odors are encountered more frequently than others, in more or less specific contexts. As a result, they are ascribed a locally specific meaning and hedonic value, which people outside this cultural setting may not share (Cain & Johnson, 1978; Moncrieff, 1967). The influence of similar or dissimilar olfactory experiences (of body and food odors in particular) on our perception of others can be so powerful that gender, class, national, or ethnic identity are often imputed in terms of odors (Manalansan IV, 2006). For example, a cross-cultural study on children’s preferences of essential oil scents has found a trend towards gender and ethnicity differences in Latino and non-Latino U.S. children (Fitzgerald et al., 2007). In another study (Ayabe Kanamura et al., 1998), Japanese and German adult women were asked to rate the familiarity, pleasantness, edibility, and intensity of odors that were familiar to either or both populations and to identify them. Significant differences in odor naming performance (also referred to as ‘free identification’) and ratings of pleasantness, edibility, and intensity between the two populations were noted for many culture-specific odors, suggesting the crucial effect of odor familiarity on olfactory perception and ratings of pleasantness in particular.

What follows is that prior experience with odors constitutes a major factor modulating olfactory perception. It is thus frequently found that ratings of familiarity of a given odor are positively associated with ratings of pleasantness (Royet et al., 1999; Sulmont et al., 2002), although this finding does not invariably reach statistical significance (Bensafi et al., 2002; Savic & Berglund, 2000), or is not consistent (Distel et al., 1999). Delplanque et al. (2008) have, however, demonstrated that the significance and/or strength of the association differs as a function of average odor pleasantness, with odors rated as unpleasant exhibiting nonsignificant, weaker, or negative correlations with ratings of familiarity. However, despite the fact that the use of ratings of odor familiarity as a proxy for prior olfactory experience is well-established, it is important to note that feelings of familiarity are not a direct product of memory; rather, they arise when it is implicitly inferred, on the basis of various clues such as processing fluency, that a stimulus must have been encountered in the past (Jacoby & Dallas, 1981; Lindsay & Kelley, 1996). This inferential process is prone to errors, which may give rise to illusions of familiarity. An alternative approach is to employ the ability of odor identification as a proxy for prior olfactory experience, which was adopted in the present study. The tasks of odor naming (also referred to as 'free identification') and cued identification necessitate the retrieval of odor identity, which, it is presumed, is known to the individual because of previous experience. Moreover, tests of cued odor identification by definition rely on the assumption that an individual's cued choice from an array of possible alternatives actually reflects, at least to a certain degree, his or her knowledge about an odor's source (Jönsson & Olsson, 2012). In the present study, use of a cued odor identification test was motivated mainly by the fact that evaluations of odor familiarity in children raise numerous methodological issues. These relate to substantial developmental differences in childrens' ratings of familiarity, with young children tending to show a smaller range and less variation in their ratings of familiarity (Cycowicz et al., 1997) and, generally, in use of rating scales (e.g., Likert scales; Chambers & Johnston, 2002). Nevertheless, this approach raises its own concerns. These are not only related to perceptual properties of odor stimuli, namely their detectability, discriminability, and recognisability, but also involve the issue of whether the given odor possesses any real-life significance, that is, whether it is at all important for an individual to know what it is or what it signifies. Further, it is also critical to consider the effect of the context provided by the odor label on olfactory perception and any subsequent ratings. Verbal labelling is known to modulate the perceived pleasantness of a given odor in adults and children alike (Bensafi et al., 2007), regardless of whether the identification has been correct or not (AyabeKanamura et al., 1997) and whether or not the odor itself is actually presented (Herz, 2003). Hence, it seems that olfactory evaluations, in the absence of a verbal label, are, to a greater degree, guided by the actual sensory perception, whereas in its presence there is, at least to some extent, reliance on the context provided by the label (de Araujo et al., 2005; Herz & von Clef, 2001; Seo et al., 2008). Thus, in adults, performance on the test of odor identification has been shown to be associated with ratings of perceptual properties of odors, including those of odor pleasantness (Knaapila et al., 2007), with individuals who correctly identified an odor giving it a different pleasantness rating from those who failed to identify it.

In the present study, we aimed to address the generalizability of these findings to children by investigating the relation of knowledge of an odor’s identity due to prior experience (evidenced by its correct identification in a cued identification task) and its pleasantness ratings in a cohort of prepubertal children who may still exhibit some unadult-like olfactory preferences and specificity in odor identification performance (Stevenson et al., 2007a; Stevenson & Repacholi, 2003; Stevenson et al., 2007b). In so doing, we made use of the properties of the particular odor identification test employed (Sniffin' Sticks; Hummel et al., 1997). Firstly, in this test, both the percentages of correct identifications and average pleasantness of the odor stimuli can be expected to vary, as shown in previous studies (Konstantinidis et al., 2006). Secondly, the test consists (except for two items, leather and turpentine) of odors of comestibles, and neither the items nor the labels should have any generally shared, strongly negative (e.g., life-threatening) connotations about them. Thus, we hypothesised a positive effect of knowledge of a given odor’s identity due to prior experience, namely that the odor represents an innocuous and perhaps even perfectly edible item, on its pleasantness ratings, so that higher pleasantness ratings would be found for cases in which it was correctly identified and vice versa. Moreover, we also expected that this knowledge should be more beneficial and its effect more pronounced in the case of odors which, on average, tend to be perceived as relatively more unpleasant.

MATERIALS AND METHODS

Participants

The participants were 91 children of Czech origin (36 boys, mean age 9.31±0.73, range 8-11 years), who were 3rd and 4th graders from two mixed-sex general education elementary schools. There was no significant difference in the proportion of boys and girls across grades in the sample, and they did not differ in terms of mean age or age distribution. Two cases (boys) were not included in the analysis, because the absolute distance of their ratings from median exceeded the cut-off based on the median absolute deviation (Wilcox, 2010) for 8 out of 16 items, and, at the same time, their ratings represented extremes in two out of the total of four plots in which there were outliers and extremes visually detected. The study complies with the Declaration of Helsinki for Medical Research involving Human Subjects and was approved by the IRB of [name of the institution removed for purposes of review](Approval Number 2008/4). The children's parents have provided written informed consent.

Olfactory measures

Olfactory assessment included ratings of odor pleasantness and an odor identification test. The 16-item Sniffin' Sticks odor identification test, a psychophysical test of orthonasal chemosensory performance based on pen-like odor dispensing devices, was employed. The Sniffin' Sticks have been widely used by clinicians as well as researchers across Europe to test olfactory abilities in both adults (Hummel et al., 2007b) and children (Dudova et al., 2011; Ferdenzi et al., 2008; Renner et al., 2009). The identification test consists of odorants familiar to the general European population (Hummel et al., 1997), such as orange, rose, garlic or fish. As spontaneous, free identification of odors is considered difficult, especially for lay subjects (Dewijk & Cain, 1994b), cued identification is employed in which participants select the name of the target odor from a list of four. The resulting score is the sum of correct answers, which can vary between 0 and 16, with 4 as a chance score. The same set of odorants was used to obtain ratings of odor pleasantness assessed on a 5-point Likert scale, which copied the system of grading used in Czech schools (1 being the best grade achievable and 5 being the failing grade) to facilitate scale comprehension by this age group (1=very pleasant odor, 5=very unpleasant odor). The scores have been subsequently recoded to 1=very unpleasant, 5=very pleasant.

Procedure

The children participated in individual testing sessions which were scheduled for the morning during school time, to avoid possible diurnal fluctuation in olfactory abilities. The testing took place in a quiet, ventilated room without strong ambient odors. Since the effect of a verbal label in olfactory perception is well known (e.g., Herz, 2003), the order of the tasks was fixed, with ratings of pleasantness obtained first, followed by odor identification. The order of presentation of the stimuli was fixed and followed that of the recommended standard procedure of the Sniffin' Sticks identification test (Hummel, 2004). Subsequently, for the purposes of another study, they were interviewed about their olfactory awareness using the COBEL questionnaire (Ferdenzi et al., 2008).

Statistical analysis

All analyses were carried out with Statistica 10.0 (Statsoft, Inc.). The data were checked for outliers based on the median absolute deviation (MAD) (Wilcox, 2010) and by visually examining individual boxplots of all relevant variables.

Data normality was checked, firstly, by producing skewness and kurtosis values and their respective standard errors, from which z-scores were computed and compared to the value of 1.96, as suggested by (Field, 2005); secondly, by visually examining individual histograms of all relevant variables, and finally by running the Shapiro-Wilk's W test for either variable. Since results of the Shapiro-Wilk’s test indicated significant departure from normality in all pleasantness ratings and so did visual examination of the respective histograms and many skewness z-scores, nonparametric tests were employed where possible.

Descriptive Statistics

Since the relation between odor identification and pleasantness may vary for odors of different average pleasantness (Knaapila et al., 2007), differences in pleasantness ratings given to the individual odorants were tested with Friedman ANOVA, which was followed up with Wilcoxon signed rank test. Since this relation may also vary with regard to the percentage of correct identifications (Knaapila et al., 2007), differences in correct versus incorrect responses for individual odorants were tested with Cochran’s Q test followed up with McNemar’s tests, to which Bonferroni correction was applied. Given the unplanned nature of the comparisons (N = 120 for the total of 16 items), the level of significance was set to $\alpha = .0004$.

Correlational analyses of children's odor identification performance and median pleasantness ratings

To find out if there was any overall association between individual children's performance on the odor identification test and their median pleasantness ratings given to the items, that is, if the higher-scoring children exhibited a tendency to rate the items as more pleasant and vice versa, Kendall's Tau correlations were performed on the whole set of items, as well as separately for the two subsets of the most pleasant and most unpleasant odorants.

Item-Specific Analyses: Odor Identification as a Predictor of Odor Pleasantness in Individual Items

To find out whether the sought effect could be limited to certain individual items, rather than spanning whole item subsets, we performed item-specific analyses.

First, to determine whether children's pooled responses could be conceived of as a homogeneous sample, we tested for potential differences related to sex and age in odor identification performance and pleasantness ratings of the individual items. Both of these variables are known to affect odor identification in children (Ferdenzi et al., 2008). A generalized linear/nonlinear model (GLZ) was run with ordinal multinomial distribution and a logit link function for pleasantness ratings, and binomial distribution and c-log-log link function for identification, respectively, in which sex was entered as a categorical factor and age as a continuous predictor. The Wald statistic was used as, for fixed effects, it is preferable to likelihood-ratio tests (Bolker et al., 2009).

Second, to test whether odor identification predicted ratings of odor pleasantness, we ran a GLZ analysis for each individual item, assuming an ordinal multinomial distribution for the response variable (pleasantness ratings) and a logit link function, with identification (yes/no) as a categorical predictor. Since we were interested in generalizing the results of the analysis, Likelihood ratio type III test was preferred to the Wald statistic, given its better suitability for testing random effects (Bolker et al., 2009).

RESULTS

Descriptive Statistics

The most pleasant odor was orange (median pleasantness of 5), whose ratings differed from all the other odors at $p < .0001$, except for cinnamon, mint, banana, rose (all *p*s > .05) and apple ($p < .05$). These odors received a median pleasantness rating of 4 and their ratings were not significantly different from one another. On the other hand, the most unpleasant odor was fish (median pleasantness = 1), which differed significantly from all the other odors at $p < .0001$, except for garlic ($p = .008$), clove ($p = .013$) and coffee ($p = .038$). These other three most unpleasant odors, whose ratings did not differ significantly from the fish odor or from one another, all received a median pleasantness score of 2.

Among those most readily identified odors were banana, which was correctly identified by 89.9% of the children, mint (86.5%), cinnamon (78.7%), coffee (77.5%), garlic (75.3%), clove (73.0%) and fish (69.7%). The percentages of correct identifications for these odorants did not significantly differ from one another. Conversely, the least readily identified odors were apple (10.0%), turpentine (31.5%) and lemon (32.6%), whose percentages of correct identifications were not significantly different from one another but differed from those of all the other odors (p*s* < .0001). For complete results on pleasantness ratings and percentages of correct identifications of individual odorants, see Table 1.

Correlational analyses of children's odor identification performance and median pleasantness ratings

Kendall's Tau correlational analyses revealed no significant association between children's total identification scores and their median pleasantness ratings for the total set of items, Kendall's Tau = - .07, p = .36. That is, children who tended to correctly identify more items than others did not exhibit a tendency towards higher ratings of pleasantness in general. Nor was there such an association found for the subsets of the most pleasant (Kendall's Tau = - .06, p = .40) and unpleasant items (Kendall's Tau = .04, p = .58) analysed separately.

Item-Specific Analyses: Odor Identification as a Predictor of Odor Pleasantness in Individual Items

The GLZ revealed a significant effect of age on the identification success rate of orange (Wald $\chi^2(1)$ = 4.33, p = .037), with older children being more likely to correctly identify the odorant. For the percentage of correct identifications of mint, there was a significant effect of sex (Wald $\chi^2(1)$ = 5.47, p = .019) as well as a sex*age interaction (Wald $\chi^2(1)$ = 5.24, p = .022), with girls exhibiting higher percentages of correct identifications and older girls being more successful than anyone else. Thus, for orange and mint, age, and age and sex, respectively, were entered into the subsequent analysis as additional predictors. This revealed odor identification to be a significant predictor of pleasantness for the odor of garlic ($\chi^2(1)$ = 3.95, p = .047) and fish ($\chi^2(1)$ = 4.58, p = .032). Children who had correctly identified these two items also tended to give them more positive ratings of pleasantness than those who had not. None of the values of the ratios of (scaled) deviance and (scaled) Pearson Chi-square over the degrees of freedom were larger than one, indicating overdispersion was not a problem (McCullagh & Nelder, 1989) and goodness of fit could thus be assumed.

DISCUSSION

The key objective of the present study was to investigate the relation between children's knowledge of an odor's identity, assessed with a cued odor identification test, and pleasantness ratings given to these odors. Specifically, we expected that the effect of this knowledge would be such that an odor would be given a higher rating of pleasantness by a child who could correctly identify it. Moreover, we also hypothesised that the effect would be greater for odors rated on average as relatively unpleasant. The results show that identification success or failure only predicted odor pleasantness in the two cases of garlic and fish, both of which also happened to fall among the most unpleasant of odors. Namely, the two odors tended to be given higher ratings of pleasantness by children who could identify them correctly than by those who could not.

Identification as a proxy for prior experience

In the present study odor identification was employed as a proxy for prior experience in order to overcome several issues that may arise when attempting to investigate odor familiarity in the target age cohort. In adult participants, a common method of measuring odor familiarity as well as the olfactory "feeling of knowing" (FOK) and "tip of the nose" (TON) experiences (Jonsson & Olsson, 2003; Jonsson et al., 2005) is the use of Likert scales (Rabin & Cain, 1984), visual analog scales (Sulmont et al., 2002) or whole-number ranges (Ayabe Kanamura et al., 1998; Konstantinidis et al., 2006; Royet et al., 1999). Although young children are capable of evaluating the familiarity of a given odor, they can likely only do so to a limited extent, so that the best approach to response scoring is probably a 'yes or no' one (Dalton et al., 2011), which may not provide sufficient response variability for some research questions. In older children the assessment can be more detailed, but a number of methodological issues arise. For example, developmental differences in children's use of rating scales have been noted, with younger children being more likely to respond at the extremes of the Likert scales (Chambers & Johnston, 2002). Thus, in the light of this evidence, instead of employing ratings of reported familiarity, which may not be properly understood or used by children, we have decided to focus on odor identification.

Irrespective of any age-specific issues, familiarity as a measure of prior experience may be difficult to assess across the lifespan because feelings of familiarity are not a direct product of memory. It is now widely accepted that they are the outcome of an implicit inferential process (e.g. Jacoby & Dallas, 1981; Lindsay & Kelley, 1996). They arise, along with a variety of other possible feelings, such as those of pleasantness (Whittlesea, 1993), when it is inferred, on the basis of various clues, such as the fluency of processing, that a stimulus must have been encountered in the past. The discrepancy-attribution hypothesis (Whittlesea & Williams, 1998; 2000; 2001a; b) however suggests that it is not this fluency per se that the feelings of familiarity are based on but, rather, it is the perceived discrepancy between an individual's actual performance and how they could standardly expect to perform on the given stimulus in that given context. This perceived discrepancy is implicitly attributed to a prior experience and the attribution is consciously experienced as a feeling of familiarity. That is not to say, though, that feelings of familiarity cannot be considered justified or relevant in a number of cases: processing of a given stimulus within a certain context indeed is facilitated by prior experience (which is referred to as the repetition priming phenomenon). However, illusions of familiarity in the absence of actual previous exposure are not infrequent nonetheless.

However, the present approach also poses various methodological challenges. On the most general level, it is assumed that the odor's *identity* is known to the individual, that is, it presumes the availability of some contextual information. This is in contrast to evaluations of familiarity, which, according to the dual process theory (Mandler, 1980), is based on perceptual processing, and no specific information about the encoding episode is needed. Theoretically, an odor can become familiar through mere (repeated) exposure (Zajonc, 2001), which involves no more than a stimulus becoming accessible to the individual's sensory receptors. However, in the case of odor identification, the one concern is whether the items included in the test exhibit substantial real-life significance and are encountered predominantly in similar contexts by the tested individuals, so that some shared knowledge of the odors' identities can be expected. This assumption was met in the population of Czech children, as evidenced by previous successful applications of the test (Dudova et al., 2011; Hrdlicka et al., 2011).

Further, it is also critical to consider the effect of the context provided by the odor label on olfactory perception and any subsequent ratings. Verbal labelling is known to modulate the perceived pleasantness of a given odor in adults and children alike (Bensafi et al., 2007), regardless of whether the identification has been correct or not (AyabeKanamura et al., 1997) and whether or not the odor itself is actually presented (Herz, 2003). Moreover, recently it has been shown that changes in odor liking in children between the ages of 3 to 5 years are related to their language proficiency. More specifically, a higher proportion of odors was categorized as positive after a two-year period only by children who exhibited better language production skills (Rinck et al., 2011). Hence, it seems that olfactory evaluations, in the absence of a verbal label, are, to a greater degree, guided by the actual sensory perception, whereas in its presence there is, at least to some extent, reliance on the context provided by the label (de Araujo et al., 2005; Herz & von Clef, 2001; Seo et al., 2008). Therefore, in terms of the order of the tasks, we followed the procedure employed in previous studies (Degel et al., 2001; Distel et al., 1999; Royet et al., 2001; Sulmont et al., 2002) and first obtained hedonic ratings before investigating what the participants know about an odor's identity.

Focusing now on the specific means of scoring of performance on the cued odor identification test, further challenges arise. Performance on the identification task, which followed the standard procedure (Hummel, 2004), was, on a given trial, only coded as a „success“ (1) or „failure“ (0) to identify an odor correctly. That is, knowledge of the odor's identity has only been assumed for those odors which had been labelled veridically as per the test guidelines. This may seem a crude oversimplification since it could be rightfully argued that some responses classified as „incorrect“ might have been less of a miss than others (the so-called "near- and far- misses"; Cain, 1979). To be able to decide whether choice of a certain label was more or less of a miss within the given item, one would have needed to know how perceptually close or distant the representations of the target and the distractors are within some of the human odor spaces, as well as the level of semantic similarity between the labels, assessed specifically by this age cohort. Thus, we were faced with a trade-off between the unambiguity of response scoring afforded by the present approach and a possible shift in the data caused by our considering all responses other than those involving the veridical label „incorrect“. Therefore, we caution that the reported correct identification percentages for the individual items are not to be considered synonymous with odor knowledge due to prior experience. The relationship between probability of prior experience and identification is a rather asymmetrical one: the ability to choose a veridical label for an odor is, apart from fortuitous instances, more of an evidence that an odor (or a similar one) has been encountered within the real-life context than an inability to do so is of the opposite.

Nevertheless, a covert identification attempt may have occurred at the presentation of the stimuli before the participants were instructed to do so. Thus, the pleasantness ratings, although not affected by the presence of the label, still would have been influenced by the individual's notions of the odor's identity. Although it was the effect of this knowledge about the identity of odors that the present study aimed to investigate, and tests of cued odor identification by definition rely on the assumption that an individual's cued choice from an array of possible alternatives actually reflects, at least to a certain degree, his or her notions of the odor's source (Jönsson & Olsson, 2012), participants might hold multiple hypotheses about this identity (Cain et al., 1998). If this were the case, it would be impossible to know which actually affected the pleasantness ratings.

Finally, as an alternative to the identification task in children, tasks of odor categorization or edibility judgments could have been employed (e.g. Dewijk & Cain, 1994a; Valentin & Chanquoy, 2012), indicating some broader, more general knowledge of an odor's identity. In a study by Dewijk & Cain (1994a), judgments of edibility exceeded the ability to name an odor in 8- to 14-year-olds. However, the benefits of such an approach would seem to outweight its downsides, such as the less specific nature of findings about children's knowledge, in children younger than the present sample.

Correct identification percentages for individual items

Focusing now on the percentages of correct identifications more closely, significant differences can be noted for the individual odors (see Table 1). This finding is in line with previous studies, which show that even with the target population for which the test has been designed, some items in the Sniffin' Sticks identification test typically exhibit markedly lower identification scores than others (Boesveldt et al., 2008; Haehner et al., 2009). There is ample evidence that across the population of European adults, turpentine, along with apple, lemon and sometimes anise quite invariably tend to be misidentified (Catana et al., 2012; Eibenstein et al., 2005; Haehner et al., 2009; Konstantinidis et al., 2008; Orhan et al., 2012), as was the case with children in the present study. The poor performance on the odor identification task for some items may seem odd given the assumption of their general familiarity. It is certainly true that, as some researchers have pointed out (e.g., Engen, 1987), some odors are simply more easily identifiable than others. This may be, for instance, due to their greater real-life significance, that is, it may be particularly important to know their actual identity. Nevertheless, the possibility must also be considered that this might have been due to how realistically some of the items are physically represented within the Sniffin‘ Sticks identification test, as could have been the case with apple, which has been corrently identified by as few as one tenth of the participants.

As regards the issue of age-appropriateness of the items employed, which is specifically relevant to the present study. The Sniffin’ Sticks odor identification test has been successfully used with children before, including children as young as 3 years of age, with a success rate of 81% in children aged 6 years and over (Hummel et al., 2007a). In the olfactory tests deemed suitable for children, turpentine and anise are not typically included but the other items have been successfully used in previous studies employing various other olfactory tests, both orthonasal and retronasal, with children as young as four-year-old (Monnery-Patris et al., 2009; Renner et al., 2009; Richman et al., 1992; Richman et al., 1995). For orange, there was an age effect found in our study. As it was the first item presented, this will likely reflect a lack of concentration in the younger children at the beginning of the session. For mint, there was both the age and gender effect, possibly suggesting that boys and younger children may not have had a particularly good understaing of exactly what mint is, looks or smells like (apart from being some kind of herb) and further specification or context possibly should have been provided, such as „spearmint/peppermint chewing gum“ or „mints“. In the present study, we used the original list of verbal descriptors, though.

The relation of odor identification and pleasantness

The main objective of the present study was to investigate the effect of knowledge of an odor’s actual identity due to previous experience, assessed with a test of cued odor identification, on its pleasantness ratings. A subsidiary aim was to find out whether the effect would be more pronounced for odors rated on average as relatively unpleasant. The Sniffin' Sticks test proved to be suitable for such a purpose as the items have been demonstrated to exhibit sufficient variability not only in terms of correct identification but also in pleasantness ratings, as shown in previous studies (Konstantinidis et al., 2006) and confirmed in the present study (see Table 1). We found the hypothesised effect for the odors of garlic and fish, which tended to be given more positive ratings by children who could correctly identify them. Thus, our data lend support to the hypothesis, although the effect might be limited to specific odors, since for another two odors of comparable pleasantness (coffee and cloves), a similar effect was not found. However, in general, our findings are in line with those reported by Distel & Hudson (2001), who have shown that, in young adults, certain odors of comestibles were rated as more pleasant when correctly named, even though direct comparison of the results is not possible. The study by Knaapila et al. (2007) with adult participants aged 18-78 years, however, does allow some, albeit limited, comparison, as a cued identification test (Brief Smell Identification Test, B-SIT; Doty et al., 1996) was used. To avoid vastly unequal group sizes in group comparisons, the authors only focused on odors correctly identified by less than 80% of the participants, and found that the odors of cinnamon, lemon, rose, and banana were evaluated as more pleasant, and turpentine as less pleasant by individuals who had identified them correctly than those who had not. Thus, their findings suggest that the association between knowledge of an odor's identity and odor pleasantness may possibly take different directions for different odors. Further interpretations are, however, difficult, as, firstly, in the study by Knaapila et al. (2007), the odors did not seem to cluster in any clearly-defined subsets based on rated odor pleasantness and, secondly, like us they have not employed any relevant measure of the semantic properties of the items involved (such as Osgood's semantic scales; Dalton et al., 2008; Osgood et al., 1957). In contrast, Bensafi et al. (2007) found that a shift in pleasantness ratings in correctly identified odors was limited only to those judged as neutral. Future studies should therefore focus on the possible sources of such discrepancies by using a set of odors exhibiting a high degree of variability in hedonic ratings and manipulating the specificity of categorization.

As reported above, our findings did not pertain to the odors of coffee and clove, which also exhibited similar pleasantness ratings and percentages of correct identifications. Consequently, a question that suggests itself then is in which ways, except for the variables assessed within the present study, these two odors differed from those of fish and garlic. Even though we did not collect any data on descriptions of olfactory quality, still it is fairly safe to assume that the odors of fish and garlic are arguably the two most pungent stimuli within the set. Odorants such as trimethylamine (fish odor) and methanethiol or allyl isothiocyanate (garlic odor) are known to produce rather potent trigeminal stimulation at certain concentrations (Amoore & Hautala, 1983; Brand & Jacquot, 2002), whilst the same certainly cannot be said of the odorants for coffee or clove. One could argue that the hypothesised relationship between odor pleasantness and knowledge of the odor’s identity should primarily make sense for those exhibiting such malodor-like properties. This is because from an evolutionary perspective, trigeminal perception was probably largely involved in helping our ancestors avoid digesting rotten, mould-ridden, poisonous, or otherwise inedible foodstuffs. Therefore, it is for such malodors that the knowledge that their source, despite what chemosensation may suggest, is harmless and even perfectly edible, should make any major difference.

Nevertheless, it is this unpleasantness of pungency or odor intensity that could be proposed to have facilitated the correct identification of fish and garlic, as such distinctly perceptible odors may be less prone to confusion than others. Although odorants that comprise the Sniffin' Sticks identification test should be matched for intensity (Hummel et al., 1997), the results of the study by Konstantinidis et al. (2006), in which participants rated the odor of garlic and fish as more intense than that of coffee and cloves, although the statistical significance of this finding is not explicitly stated or inferable, suggest otherwise. Although neither odor intensity nor quality were assessed within the present study, however, the odors of garlic and fish exhibited no greater percentages of correct identifications than the other two unpleasant odors, so intensity or odor quality cannot be considered identification facilitators in this case.

Finally, it is important to note that we need to take into account the potential age-specificity of the observed pleasantness ratings in the present study, such as in the case of cloves of coffee. Konstantinidis et al. (2006) reported that adult pleasantness ratings for the Sniffin' Sticks odors of cloves and coffee were nowhere near those of garlic and fish. If this should be so, then of course the present data do not give us much reason to speculate why the effect was only found for some unpleasant odors, but not for others.

CONCLUSIONS

The present study investigated the effect of knowledge of an odor's actual identity, assessed by means of cued odor identification test, on its pleasantness ratings. In so doing, we recruited an age group that presumably still exhibits some adult-unlike olfactory preferences as well as specificity in odor identification performance. We expected specifically a positive effect, which was found for two unpleasant odors, but not for any pleasant ones. In order to be able to make any generalisations about this effect, and also to investigate that of not knowing the odor's actual identity, future studies should employ a wider range of items for which contrasting pleasantness ratings can be expected, whose veridical as well as distractor labels have both positive and negative connotations about them, and the degree of similarity, perceptual and semantic, can be inferred for both the odors and the labels.

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Table 1. Percentages of correct identifications and median pleasantness for individual items of the Sniffin‘ Sticks identification test (N = 89). Note that pleasantness ratings have been recoded (1 = least pleasant, 5 = most pleasant).

Item	Percent Identified	Median Pleasantness			Mean ± SD Pleasantness		
		Overall	Correctly identified	Not identified	Overall	Correctly identified	Not identified
Orange	40.4%	5	5	5	4.26±1.05	4.22±1.05	4.28±1.062
Leather	47.2%	3	3	3	2.90±1.31	2.76±1.34	3.02±1.29
Cinnamon	78.7%	4	4	5	3.94±1.14	3.86±1.17	4.263±0.99
Mint	86.5%	4	4	5	4.08±1.07	4.03±1.09	4.42±0.90
Banana	89.9%	4	4.5	4	4.16±1.09	4.18±1.08	4.00±1.22
Lemon	32.6%	4	4	4	3.53±1.27	3.76±1.09	3.42±1.34
Liquorice	60.7%	4	3.5	4	3.49±1.28	3.48±1.28	3.51±1.29
Turpentine	31.5%	3	2	3	2.51±1.11	2.50±1.26	2.51±1.04
Garlic	75.3%	2	2	1	2.08±1.28	2.21±1.31	1.68±1.13
Coffee	77.5%	2	2	1	1.99±1.17	2.07±1.20	1.70±1.03
Apple	10.1%	4	4	4	3.90±1.18	4.22±0.83	3.86±1.21
Clove	73.0%	2	2	2	2.07±1.15	2.05±1.18	2.13±1.08
Pineapple	57.3%	4	4	4	3.61±1.35	3.61±1.40	3.61±1.31
Rose	55.1%	4	5	4	4.08±1.15	4.06±1.21	4.10±1.08
Anise	38.2%	3	3	4	3.16±1.22	2.85±1.13	3.35±1.25
Fish	69.7%	1	1	1	1.66±1.00	1.74±0.94	1.48±1.12

CHAPTER 6

OLFACTORY PERCEPTION IS POSITIVELY LINKED TO ANXIETY IN YOUNG ADULTS

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Olfactory perception is positively linked to anxiety in young adults

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Abstract. Olfactory abilities show a high degree of inter-individual variability and this could be partly related to personality differences. Here, in two studies, we tested a potential link between personality dimensions and olfactory perception. Sixty-eight (study 1) and a hundred and fifty-six (study 2) young adults completed the Big Five questionnaire and performed the Sniffin' Sticks test for assessing odour threshold, identification, and (in study 2) discrimination. In neither study did we find a significant link between personality dimensions and olfactory identification scores. However, in study 1, we found a significant positive correlation between the neuroticism dimension and olfactory sensitivity. This was mainly due to the anxiety and self-consciousness subscales, which load onto the neuroticism dimension. In a follow-up study, we again found a significant association between anxiety and odour perception, specifically in odour discrimination. Our results indicate that variability in anxiety could partly explain the high inter-individual variation in olfactory perception.

Keywords: Big Five, odour, olfactory identification, personality, Sniffin' Sticks, threshold, odour discrimination

1 Introduction

Humans use their sense of smell in various domains, particularly in food assessment (Sorensen et al 2003; Novakova et al 2012), avoiding dangerous chemicals (Stevenson 2010), and social interactions including mate choice (Havlicek et al 2008). Although olfactory abilities can be assessed in various ways, the most widely used measures involve the olfactory threshold (also referred to as olfactory sensitivity), odour discrimination, and odour identification. The olfactory threshold refers to the minimum concentration of a tested odorant that an individual is able to reliably differentiate from a blank sample. Odour discrimination is the ability to detect differences between odours and to identify which of a set of stimuli in comparable suprathreshold concentrations is different from the others. Finally, odour identification refers to correct verbal labeling of a given odour (for discussion about the veridicality of verbal labeling see Dubois and Rouby 2002). The major demographic predictor of all three abilities is age. As with many other sensory capacities, olfactory abilities, in general, decrease relatively constantly with age (Doty 1992). Further, results of twin studies suggest that, at least for some compounds, there is a relatively strong heritable component to threshold levels (Gross-Isseroff et al 1992). There is also a robust body of evidence indicating that, on average, women outperform their male counterparts in various odour tests (Brand and Millot 2001; Doty and Cameron 2009). However, even within each sex, there is also high inter-individual variability. Some of this variability could conceivably be related to the personality of the given individual.

The possibility that personality affects olfactory perception was first investigated more than 40 years ago by Koelega (1970). The work was theoretically grounded on Eysenck's three-dimensional personality model (extraversion, neuroticism, and psychoticism). According to this theory, extraverted individuals are marked by prevailing inhibitory processes and individuals scoring high on neuroticism by greater activity of the limbic system (Eysenck 1967). As olfaction is closely related to the limbic system, Koelega expected to find lower olfactory thresholds in neurotics and introverts. In a series of carefully controlled studies, he unexpectedly found lower thresholds in extraverts than in introverts, but no correlation with neuroticism. In a subsequent study by the same author, no general pattern between Eysenck's personality domains and sensitivity was observed (Koelega 1994). However, more recently, Pause et al (1998) reported a positive correlation between olfactory sensitivity and neuroticism in a group of men using the twelve-dimensional Freiburger Personality Inventory. Interestingly, it was recently shown that neuroticism score (assessed by the Big Five inventory) is positively associated with environmental chemosensory responsivity, but not with odour threshold (Cornell Kärnekull et al 2011).

Several other studies have tested the potential link between personality and odour identification. Odour identification was found to be positively related to a high level of neuroticism and openness to experience (Larsson et al 2000). In contrast, the same study found a negative correlation with impulsiveness and assertiveness. Furthermore, a positive relationship between an odour identification score and empathy (Mehrabian and Epstein Empathy Questionnaire) was reported (Spinella 2002).

The above-reviewed studies clearly indicate that a link between olfactory abilities and personality dimensions has not yet been conclusively established. One reason could be the highly variable number of personality measures used in previous studies. Recently, the most extensively used personality assessment tool has been the NEO-PI-R questionnaire, which is based on the Big Five personality model (eg McCrae and Costa 1997). It employs the following broad personality dimensions: neuroticism, extraversion, openness to experience, agreeableness, and conscientiousness. Each of the dimensions is further characterized by 6 subscales (Costa and McCrae 1997). Numerous studies carried out in various cultures and samples demonstrate the NEO-PI-R to be a suitable research tool for the assessment of inter-individual variability, including various aspects of perception (McCrae et al 1998; McCrae and Terracciano 2005; Schmitt et al 2007).

Based on previous findings and characteristics of personality domains, we predict more acute olfactory perception in individuals scoring high on neuroticism and conscientiousness, but no significant link with other Big Five domains. Neurotic individuals are characterised by greater irritability and high vigilance, which might be associated with lower sensory thresholds. On the other hand, conscientiousness is characterised by high self-control, orderliness, and perfectionism. Further, conscientiousness and some of its facets (C4: Achievement Striving and C5: Self-Discipline) tends to predict verbal fluency (Jensen-Campbell et al 2002; Sutin et al 2011). Consequently, one might predict a positive link with ability in odour identification, which also involves verbal fluency (Larsson et al 2005). In addition, we might expect that variation in relative dominance, although it is not included in the Big Five model as a separate dimension, might be of particular relevance. Recently, there has been a growing body of evidence that people are responsive (eg in the form of a startle response), to affective body odours (eg Pause et al 2009). This might be particularly true for individuals low in dominance, as they are more sensitive to potentially socially threatening situations.

Here we tested these predictions regarding possible links between inter-individual variation in olfactory acuity (using measures of odour sensitivity and identification) and personality domains. We controlled for a potential age-related decline in olfactory performance by using a sample of young adults.

2 Study 1

2.1 *Method*

2.1.1 *Participants.* The research sample consisted of 71 students (41 female and 30 male; mean age (SD) = 18.0 (±0.81) years; range 17–22 years) attending two mixed-sex Prague (Czech Republic) high schools. Two men did not complete a personality test and one woman did not finish an odour threshold test, thus leaving 68 participants for the main analysis. All participants were assured about confidential data treatment and none was paid for their participation. All work and data treatment were carried out in accordance with the Declaration of Helsinki.

2.1.2 *Questionnaires.* First, the participants were asked to complete a basic demographic questionnaire which consisted of item concerning age, sex, health problems related to olfaction (cold, allergy, and a history of head injuries) and, for women, their menstrual cycle phase.

Personality profile was assessed using the Czech version of the NEO Personality Inventory (NEO-PI-R) (Hřebíčková 2004). This personality test consists of 240 items loading onto the 5 broad personality dimensions (neuroticism, extraversion, openness to experience, agreeableness, and conscientiousness). Each dimension is loaded by 48 items and can be further separated into 6 subscales (facets); each loaded by 8 items. Participants are asked to assess how well each statement describes themselves using a 5-point Likert scale. The raw scores are computed as a sum of values (0–4) loading onto the individual dimensions (theoretical range 0–192) or facets (theoretical range 0–32), with relevant items reverse-scored (Hřebíčková 2004). The NEO-PI-R does not include dominance as a separate dimension, thus this characteristic was assessed by the 11-item questionnaire from the international personality item pool (Goldberg et al 1999). For descriptive statistics see table 1.

2.1.3 *Olfactory threshold test.* Olfactory threshold/sensitivity was tested using the extended Sniffin' Sticks test. This is a widely used clinical and research tool, which consists of 16 dilution steps of 2-phenylethanol (Hummel et al 1997). Pen-like odour dispensing devices are presented in triplets comprised of one target containing the specific concentration of the chemical and two blanks. The testing starts at the lowest concentration (dilution step 16) and proceeds with every other higher one, prompting a random-order repetition after a correct guess, until the tested individual succeeds in identifying the odorised pen twice in a row, which marks the starting point. The odorised pen in the next presented triplet is one of the nearest lower concentration, which continues to further decrease until the tested individual fails to identify the odorised pen, marking a turning point. The process is then reversed and the nearest higher concentration is presented, further increasing until two correct identifications in a row are attained. The testing is finished after 7 reversals are reached and the threshold is computed as the mean dilution steps value of the last 4 reversals; higher scores signify lower thresholds (ie higher sensitivity). The mean value in our sample was 9.3 (range 2.5–15.75).

2.1.4 *Identification test.* We used a modified version of the extended identification Sniffin' Sticks test which consists of 16 odours commonly known within the European context. The Sniffin' Sticks test presents odours in the form of pen-like dispensing devices; in our study, we used the same set of odorants kept in brown glass jars. One drop (10 μl) of each tested chemical was applied onto a cotton pad which was subsequently deposited in a glass jar. Fresh samples were prepared for each testing session. The chemicals were commercially available essential oils or manufactured odour composites. 4 verbal labels, identical to those used in the Sniffin' Sticks test, were presented for each tested compound. The overall score is simply the number of correct answers. The mean value in our sample was 12.4 (range 9–15).

2.1.5 *Procedure.* All tests were performed during school time in groups of up to 15 students and were carried out by MV and her assistant. The researcher first introduced the procedure, assured the participants that all the data would be treated anonymously and confidentially, and asked them to only provide honest answers. Then they completed the questionnaires and were individually invited to take the odour tests which were performed in another classroom. The order of the threshold and identification tests within the session was randomised. The complete session took, for most individuals, between 60 and 75 min.

2.1.6 *Statistical analysis.* First, we checked whether the continuous variables were approximately normally distributed, by use of Shapiro–Wilk's W tests. Results of the odour identification test (SW-W = 0.95; $N = 69$; $p = 0.005$) and personality dimension agreeableness (SW-W = 0.95; $N = 69$; $p = 0.005$) showed significant deviation from normality (negative skew) and therefore we used more conservative non-parametric tests for further analysis. Sex differences in the olfactory tests were thus analysed by Mann–Whitney U tests. As we had specific predictions about the association between the olfactory tests and personality dimensions, we performed separate Kendall correlation analyses instead of employing a multivariate regression analysis. Descriptive statistics and a correlational matrix of the personality dimensions are shown in table 1.

2.2 *Results*

First, we performed a correlation analysis between personality dimensions and individual measures of olfactory threshold (assessed as dilution steps, ie greater dilution step number signifies higher sensitivity/lower threshold) and identification. Contrary to prediction, we found no relationship between olfactory threshold and either conscientiousness or dominance. However, we did find the predicted relationship (Kendall's tau = 0.17; $N = 68$; $p = 0.04$) between neuroticism and threshold scores (ie more neurotic individuals tended to be more sensitive) (table 1). To find out whether this link was sex-specific, we analysed the male and female samples separately. In men, the correlation between neuroticism and olfactory sensitivity approached the formal level of significance (Kendall's tau = 0.26; $N = 28$; $p = 0.055$); however, it was not significant in the case of women (Kendall's tau = 0.16; $N = 40$; $p = 0.14$) (figure 1). Further, we performed analyses of the threshold values and all 6 subscales loading onto neuroticism to test whether the correlation between the olfactory threshold and neuroticism in men was due to one or more subscales. We found a significant correlation between olfactory sensitivity and both the N1 subscale (anxiety) (Kendall's tau = 0.31; $N = 28$; $p = 0.02$) and the N4 subscale (self-consciousness) (Kendall's tau = 0.27; $N = 28$; $p = 0.05$). To check that the sex-specific correlation between odour sensitivity and neuroticism was not due to sex differences in variance in neuroticism, we performed the Levene test for equality of variance. The results showed no significant difference ($p = 0.30$), indicating comparable variances in women and men.

As predicted, we also found no significant correlation between olfactory threshold and extraversion, openness, and agreeableness. Furthermore, analysis of the odour identification test and personality dimensions showed no significant correlations.

Finally, we analysed sex differences in the olfactory tests. We found no significant difference between men and women in either the threshold (Mann–Whitney U = 527; $N = 68$; $p = 0.68$) or identification test (Mann–Whitney U = 543; $N = 69$; $p = 0.70$). Interestingly, there was also no significant correlation between the threshold and identification tests.

Table 1. Descriptive statistics (mean, SD) and correlation matrix (Kendall's tau) of Big Five dimensions, dominance, odour identification and threshold tests in study 1.

Measure		Measure							
		neuroticism	extraversion	openness	agreeableness	conscientiousness	dominance	odour thresholds	odour identification
	Mean	104.8	111.2	120.2	110.3	100.6	37.1	9.3	12.4
	SD	24.8	23.3	19.3	24.4	27.1	9.3	2.3	1.6
Neuroticism	tau		–0.121	0.273**	0.008	–0.262**	0.133	0.172*	0.037
	p		0.147	0.001	0.926	0.002	0.114	0.043	0.680
	N		69	69	69	69	69	68	69
Extraversion	tau			–0.025	0.015	–0.062	–0.153	–0.081	0.005
	p			0.764	0.860	0.459	0.068	0.342	0.958
	N			69	69	69	69	68	69
Openness	tau				0.239**	–0.245**	0.176	–0.083	0.073
	p				0.004	0.003	0.037	0.326	0.410
	N				69	69	69	68	69
Agreeableness	tau					0.039	0.460**	–0.042	0.014
	p					0.641	<0.001	0.622	0.878
	N					69	69	68	69
Conscientiousness	tau						0.041	0.030	0.047
	p						0.626	0.722	0.594
	N						69	68	69
Dominance	tau							0.096	0.025
	p							0.276	0.764
	N							71	70
Odour thresholds	tau								–0.084
	p								0.349
	N								70

Note. * and ** signify that correlation is significant at the 0.05 and 0.01 level, respectively (two-tailed).

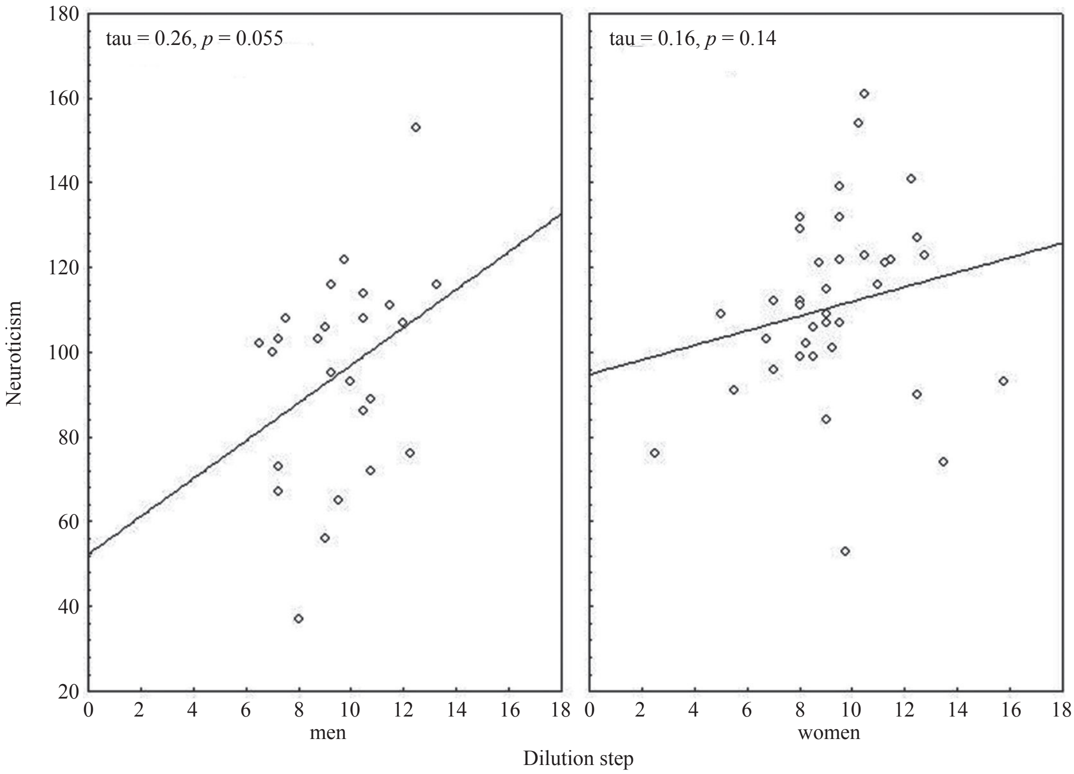

Figure 1. Correlation (Kendall's tau) of 2-phenylethanol dilution steps and neuroticism scores in men (left) and women (right) in study 1. Note that higher values in the dilution step signify lower threshold values.

3 Study 2

The aim of study 2 was to further investigate the trend toward a sex-specific association between neuroticism and olfactory threshold found in study 1. The data presented here were primarily collected for the purpose of a study of the relationship between sexual orientation and olfactory abilities (Nováková et al, submitted). However, the variables that are of interest here (personality traits) were only controlled for and not included in any of the hypotheses. Thus, not only is the present sample categorised according to sex but also with regard to sexual orientation.

3.1 *Method*

3.1.1 *Participants.* A total of 156 university students or alumni (67 female and 89 male; mean age (SD) = 24.2 (± 4.1) years; range 19–35 years) participated in the study. Participants were recruited by means of snowball sampling from students attending both undergraduate and graduate courses lectured by LN and JV, by announcing in the lectures that a study on olfactory perception was to be carried out for which participants were needed, and members of the university's student homosexual association, who received an invitation e-mail by JV. Thus, the majority of participants were current students or alumni of 11 faculties of Charles University (the ratio of graduate students/alumni to undergraduates being 3 : 4). The sample was further subdivided according to participants' self-described sexual orientation, which was indicated on a 7-point Kinsey scale, anchored on either end, with 0 labelled "heterosexual" and 6 labelled "homosexual". We subdivided the sample into the *heterosexual* (ratings of "0" or "1"; $N = 73$; 41 males) and the *non-heterosexual group* (ratings "2" to "6"; $N = 83$; 48 males). To avoid vastly unequal group sizes, data analysis was carried out primarily on these two groups and further verified with participants regrouped to the *heterosexual* and the *homosexual group* (ratings "5" or "6"; $N = 60$; 42 males). This is, however, not reported as the respective results did not differ in any significant way.

Although all participants reported good respiratory health, one case had to be excluded owing to a low olfactory score indicative of moderate hyposmia (for details see olfactory measures below). All women were regularly cycling and reported a usual menstrual cycle length of 24–32 days, were not using hormonal contraceptives, and menstrual cycle phase at the time of testing was random across participants. All participants signed written consent and received financial reimbursement of CZK 300 (approximately USD 15).

3.1.2 *Questionnaires.* For each participant, additional data on sex, education, socioeconomic status, religious beliefs, smoking history, environmental pollution, and olfaction-related health issues and, in women, menstrual cycle phase, were obtained by means of a basic demographic questionnaire. To reduce the time demand on participants, personality profile was assessed with the Czech version of the NEO-Five Factor Inventory (NEO-FFI, Hřebíčková and Urbánek 2001), which is a short version of the Revised NEO Personality Inventory (NEO-PI-R) consisting of 60 items, thereby providing a brief, comprehensive measure of the 5 personality dimensions mentioned earlier. Here, each dimension is loaded by 12 items and can be further divided into 2 to 3 facets, each loaded by 3 to 8 items. Administration and scoring of the NEO-FFI are identical to that of the NEO-PI-R. Correlations between the NEO-FFI and the NEO-PI-R domains were ranging from 0.92 and 0.77 (Costa and McCrae 1992).

3.1.3 *Olfactory measures.* All olfactory measures (olfactory threshold/sensitivity, identification, and discrimination) were obtained using the Sniffin' Sticks test (Burghart Messtechnik GmbH). Olfactory sensitivity was assessed as specified above, only in this particular Sniffin' Sticks set, n-butanol served as a stimulus. Nevertheless, a significant correlation between thresholds for n-butanol and 2-phenylethanol has been found (Croy et al 2009). Identification testing was performed following the exact standard procedure this time (Hummel 2004), identical to that described in study 1, only actually employing the pen-like odour dispensing devices. The Sniffin' Sticks test of odour discrimination is comprised of 16 triplets of "pens" containing odorants in suprathreshold concentrations, of which two are identical. The discrimination task consists in (correct) identification of the odd one. The score is the total number of correct identifications. The sum of the three subtest scores is expressed as the threshold-discrimination-identification (TDI) score (Wolfensberger et al 2000). There were 11 instances of hyposmia in the sample: 10 mild (TDI score of 25–30) and 1 moderate (TDI score of 20–25), predominantly affecting heterosexual men ($N = 7$). The case of moderate hyposmia is excluded from the analysis as more consequential factors than a mere momentary lapse in current olfactory performance are likely to be involved (Hummel et al 2007; Kobal et al 2000).

3.1.4 *Procedure.* Individual, one-per-person testing sessions were conducted by LN in the morning or early afternoon (by 3 pm) in a well-ventilated room. Individuals were instructed to only attend if in good respiratory health, and asked to refrain from smoking or consumption of odorous foods at least 2 h prior to participation, as well as to forego applying perfume. The researcher first introduced the procedure, assured the participant the data would be subject to confidential treatment, and provided financial recompense for participation. Within the olfactory testing part of the session, olfactory sensitivity/odour threshold was tested first, followed by discrimination and identification with a 3 min break after each test to prevent olfactory adaptation, as suggested by Hummel (2004). In addition to the questionnaires mentioned above, for the purposes of the study the data were primarily collected for, there were others that were completed by the participants, namely the Czech versions of the Childhood Gender Nonconformity scale (CGN, Bailey et al 1995), Continuous Gender Identity scale (CGI, Bailey et al 1995), Empathy Quotient (EQ, Baron-Cohen and Wheelwright 2004), the Odor Awareness scale (Smeets et al 2008), and a survey on olfactory-related behaviours from early childhood to present. For this reason the entire session took, in most individuals, 75 to 90 min.

3.1.5 *Statistical analysis.* The assumption of univariate normality for each dependent variable was checked, as suggested by Field (2005, page 593) with multiple Shapiro–Wilk's W tests which showed departure from normality in nearly all variables (for descriptive statistics, see table 2). The assumptions of homogeneity of variances (Levene's test) and homogeneity of covariances (Box's M test) were met for all of the dependent variables. Nevertheless, a MANCOVA is considered to be robust to violations of multivariate normality (as well as to violations of homogeneity of variance/covariance matrices) if N of the largest group is no more than about 1.5 times the N of the smallest group (Field 2005), which was met in the heterosexual–nonheterosexual approach to group categorisation. Prior to performing a MANCOVA, homogeneity of slopes was first checked via the homogeneity-of-slopes model which yielded no significant results, suggesting that a traditional MANCOVA could be performed.

In the multivariate multi-way (multi-factor) between-group design the three olfactory scores (threshold, discrimination, identification) were entered as dependent variables, sex and sexual orientation as categorical factors, and age as a continuous predictor (covariate).

To follow up, separate ANCOVAs on the individual olfactory measures were performed. We ran nonparametric Kendall correlations between age and olfactory measures or personality dimensions to explore the possible associations. Finally, Kendall correlation analyses, or, where appropriate, partial correlation analyses controlling for age, between olfactory measures, and personality dimensions were performed for the total sample, sex, sexual orientation, and each of the 4 groups (non/heterosexual fe/males). All analyses were carried out with Statistica 8.0 (Statsoft, Inc.).

3.2 *Results*

The MANCOVA on olfactory measures revealed no sex differences but a significant effect of the covariate age ($F_{3,148} = 3.73$; $p = 0.013$). Follow-up ANCOVAs revealed this effect was relevant for identification ($F_{1,150} = 8.92$; $p = 0.003$). A Kendall correlation analysis between the covariate age and identification revealed a positive association (Kendall's tau = 0.15; $N = 155$; $p < 0.01$), that is, the older the participant the better the identification score he or she tended to exhibit. Again, we also found no significant correlation between the threshold and identification or discrimination score.

To look for the possible association between individual olfactory measures and personality dimensions, a partial correlation analysis was run for identification (in which age was controlled for), and Kendall correlation analyses were performed for discrimination and sensitivity. For the complete overview of the correlation matrix, see table 2. No association was found between neuroticism and olfactory measures for sex, sexual orientation, or any of the 4 groups (non/heterosexual fe/male) analysed separately.

Although the neuroticism dimension was not significantly associated with any of the olfactory measures, results of the previous study indicate that the association could be limited to some of the components of the neuroticism, namely anxiety. Thus, the analyses were run in the same fashion for the 3 individual components of neuroticism.

Table 2. Descriptive statistics (mean, SD) and correlation matrix of Big Five dimensions and olfactory measures in study 2 ($N = 155$). Please note that Kendall's nonparametric correlations are reported for all associations but those involving identification, in which age was controlled for and thus partial correlations were employed instead.

Measure		neuroticism	extraversion	openness	agreeableness	conscientiousness	odour thresholds	odour discrimination	odour identification
	Mean	20.0	32.2	27.4	30.6	30.0	8.3	13.3	13.7
	SD	8.5	8.8	7.0	7.1	8.8	2.3	1.7	1.4
Extraversion	tau	–0.325***							
	p	0.000							
Openness	tau	0.051	0.012						
	p	0.345	0.829						
Agreeableness	tau	–0.033	0.092	0.088					
	p	0.547	0.090	0.105					
Conscientiousness	tau	–0.294***	0.298***	–0.114*	0.026				
	p	0.000	0.000	0.036	0.636				
Odour threshold	tau	–0.018	–0.081	–0.101	–0.061	–0.017			
	p	0.733	0.133	0.063	0.261	0.750			
Odour discrimination	tau	0.068	0.005	0.019	0.041	–0.061	0.083		
	p	0.209	0.927	0.723	0.449	0.263	0.124		
Odour identification	*r*	0.010	0.165*	0.050	0.060	–0.001	0.047	0.068	
	p	0.903	0.041	0.540	0.459	0.986	0.566	0.405	

Note. *, **, and *** signify that correlation is significant at the 0.05, 0.01, and 0.001 level, respectively (two-tailed).

A positive association was found between the olfactory measure of discrimination and the anxiety component of neuroticism (Kendall's tau = 0.12; $N = 155$; $p = 0.03$; figure 2; see also table 3). For explorative purposes, we further tested whether the association was similarly valid for heterosexual and non-heterosexual individuals separately. The association between discrimination and anxiety was true for heterosexual individuals (Kendall's tau = 0.17; $N = 72$; $p = 0.03$) but not for non-heterosexual ones. This association was not specific to either sex or any of the 4 groups (non/heterosexual fe/male).

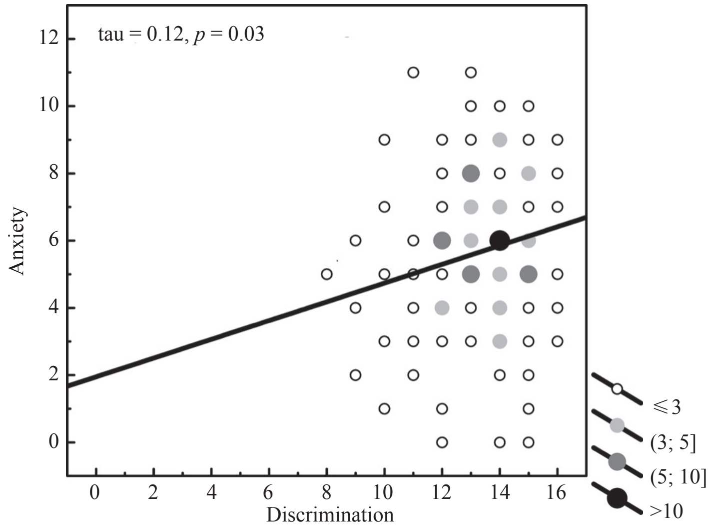

Figure 2. Correlation (Kendall's tau) of the Sniffin' Sticks discrimination score and anxiety scores in the total sample in study 2.

Table 3. Correlation matrix of the three neuroticism facets and olfactory measures in study 2 ($N = 155$). Please note that Kendall's nonparametric correlations are reported for all associations but those involving identification, in which age was controlled for and thus partial correlations were employed instead.

Measure		Measure		
		anxiety	depression	self-reproach
Odour threshold	tau	0.047	–0.001	–0.036
	p	0.384	0.992	0.502
Odour discrimination	tau	0.121*	0.050	0.043
	p	0.025	0.351	0.428
Odour identification	*r*	–0.016	0.035	–0.012
	p	0.847	0.665	0.879

Note. * signifies that correlation is significant at the 0.05 level (2-tailed).

4 Discussion

Initially, we predicted a positive link between olfactory sensitivity and neuroticism, a negative link between sensitivity and dominance, and a positive link between odour identification and conscientiousness. The results of study 1 supported only the association between sensitivity and neuroticism. Further analysis found that this was driven by the anxiety and self-consciousness subscales. The specific association between anxiety and olfactory abilities, namely odour discrimination, was confirmed in study 2.

These findings are consistent with several previous studies. In a sample of men, Pause et al (1998) found neuroticism to be the only personality dimension associated with olfactory sensitivity. More recently, it has been shown that individuals scoring high in neuroticism report elevated environmental chemical sensitivity, suggesting a higher level of odour irritability (Cornell Kärnekull et al 2011), and exhibit high trigeminal sensitivity (but not olfactory sensitivity) (Croy et al 2011). In contrast, three other studies failed to find a link between olfactory sensitivity and neuroticism (Koelega 1970, 1994; Croy et al 2011) and one earlier study found the opposite pattern: women scoring high on the anxiety scale had higher thresholds (were less sensitive) than less anxious ones (Rovee et al 1973; although these authors selected individuals with the highest scores of anxiety, which could explain their opposite results).

What might contribute to such discrepancies? First, each of the studies used a different measure to assess personality traits. However, the discrepancy cannot be accounted for entirely by the use of different measures alone, since neuroticism scores, as measured by Eysenck's, Freiburger's, BFI, NEO-FFI, or NEO-PI-R inventories, are highly correlated (Borkenau and Ostendorf 1989; Larstone et al 2002; McCrae and Costa 1985). Another reason could be that different chemical compounds were used to assess threshold levels. There is some evidence that olfactory thresholds of various compounds can show a relatively high intra-individual variability (Stevens and O'Connell 1991). In turn, sensitivity only to some chemicals might be associated with the given personality dimension. Indeed, personality studies which employed several odorants for threshold assessment (Koelega 1970, 1994; Pause et al 1998) usually found a correlation with some compounds and not with others. In contrast, other threshold studies showed a relatively high intercorrelation between odorants (Cain and Gent 1991). In our research we used 2-phenylethanol (study 1) and n-butanol (study 2), which are generally considered to be good markers of general olfactory sensitivity (Hummel et al 1997). This is further supported by the finding that thresholds for both compounds are highly correlated (Croy et al 2009). Here, the neuroticism dimension, which was found to be positively correlated with olfactory threshold in study 1, was not associated with any of the olfactory measures as an entire dimension in study 2. Only one of its components, namely the anxiety facet, was positively correlated with odour discrimination. A plausible explanation for the present pattern of findings may be the fact that different measures were used to assess both neuroticism and olfactory threshold in the two studies. Furthermore, the fact that no correlation was found between the olfactory threshold and odour discrimination in study 2 prevents direct comparison of the discrepant findings in the respective studies. Nevertheless, because odour threshold in a given individual may exhibit substantial fluctuation over time (Pause et al 1998; Stevens et al 1988), one would expect that, of the two olfactory measures, we would be more likely to find an association between anxiety and odour discrimination, as was the case in study 2.

Interestingly, when men and women were analysed separately, the association between neuroticism and the olfactory threshold in study 1 approached significance in men only. A similar sex-specific pattern was observed by Chen and Dalton (2005). They found that neurotic men, but not women, perceived emotionally valenced odours faster than neutral ones. It is difficult to compare our findings with the above-mentioned studies as Pause et al (1998) examined men only and Cornell Kärnekull et al (2011) and Croy et al (2011) did not test for sex differences. We tested whether this finding could be due to sex differences in variance on the neuroticism dimension, but our results suggest this is not the case. However, as the results of study 2 did not confirm the sex-specific effect, we urge caution in interpreting these findings.

Our results showed no link between personality dimensions and the odour identification score obtained using a forced-choice (cued) paradigm. In contrast, Larsson et al (2000) found in a large sample of ageing participants (mean age = 65 years) that high neuroticism, low impulsivity, and high assertiveness were significant predictors of high odour identification rates even when controlling for age, demographic characteristics, and cognitive abilities. The authors used a mix of free and forced-choice identification. Such a difference in the form of the identification task might result in differences in the link between personality and odour identification. Free identification is known to be much more difficult, and thus there is more variation in the scores (De Wijk and Cain 1994). Further, our participants were young adults (mean age = 18 years in study 1 and 24.2 years in study 2), and they tended to correctly identify the majority of the odours (mean = 12.4, maximum 16 in study 1; and mean = 13.7, maximum 16 in study 2). Thus, it is conceivable that the negative findings in our study could be due to a ceiling effect; if so, a more comprehensive odour identification test (eg free choice, one employing more stimuli and/or distractors) should be used for this age group. Alternatively, the link between personality and odour identification may be expressed only later in life when variability in odour identification increases.

Previously, researchers have tended to interpret associations between olfactory abilities and personality in terms of common underlying biological machinery (Larsson et al 2000; Pause et al 1998). In connection with Eysenck's personality model it was proposed that the activity of the limbic system (eg amygdala) is the underlying brain substrate. The limbic system is known to play a crucial role in odour processing (Zatorre et al 1992; Dade et al 1998) and is also expected to be more activated in neurotic individuals (Eysenck 1998). Furthermore, behavioural genetics studies show a relatively large heritable component in both neuroticism (McCrae et al 2000) and olfactory perception (Gross-Isseroff et al 1992; Knaapila et al 2007). This is also supported by a recent study which found an association between genetic polymorphism in olfactory receptor genes and hypersensitivity to isovaleric acid (Menashe et al 2007). However, the correlational nature of our study (and the same applies to all previous studies on this subject) does not permit conclusions about causality. It is, for instance, plausible that highly neurotic individuals, because of their higher irritability, engage in a greater number of olfactory-related activities, which can in turn result in their higher sensitivity. Future studies should therefore also control for olfactory-related activities. Alternatively, this issue should be addressed in young children where the effect of such activities might be relatively limited.

Interestingly, in both studies there was no significant difference between men and women in threshold values, discrimination, and identification scores. There is a relatively robust body of evidence that women tend to outperform men in various olfactory-related tests (for reviews see Brand and Millot 2001; Doty and Cameron 2009) and report a greater significance ascribed to olfaction (Havlicek et al 2008). On the other hand, sex differences tend to be smallest in young adults (Doty 1992) and have been reported to be restricted to the fertile phase of the menstrual cycle (Navarrete-Palacios et al 2003). Regarding study 1, one might argue that our sample size was not large enough to detect the relatively subtle effect typical for this age category; however, this argument could hardly explain a similar pattern observed in study 2.

As a subsidiary finding, both the comparison of identification scores in study 1 and study 2 (Mann–Whitney U = 2914.5; $N = 224$; $p < 0.0001$), and the effect of age on identification found in study 2, indicate that in the studied age group, older participants tend to exhibit higher identification scores. This is in line with the results of Yousem et al (1999) who report an increase in odour identification score as a function of age, measured by the University of Pennsylvania smell identification test (UPSIT, Doty et al 1984b), in a subgroup of participants in their mid-twenties. However, reports do not tend to be unanimous on this, as, for instance, the authors of the UPSIT themselves found a plateau in odour identification scores for this age cohort (Doty et al 1984a).

We further found no correlation between identification and threshold levels in either of the studies. One may find this surprising, as it is thought that both functions overlap to some extent. Clearly, if one's threshold is very high, it can affect identification ability which is tested with suprathreshold concentrations. Moreover, neuroimaging studies show that odour processing is organised in a hierarchical fashion, and thus different olfactory tasks partly involve specific neural substrates (Royet et al 2001). For instance, both odour detection and discrimination tasks activate areas including the orbitofrontal cortex, thalamus, insula, and piriform cortex; however, areas such as the prefrontal cortex and hippocampus are activated only during odour discrimination (Savic et al 2000). Further, odour identification is heavily dependent on verbal abilities, while sensitivity measures are not (Finkel et al 2001). Consistent with this, most previous studies found only a moderate correlation between threshold values and odour identification scores ($r = 0.18$ in Lehrner et al 1999; $r = 0.24$ in Segal et al 1995). Furthermore, correlational measures vary greatly across study samples, and performance-heterogeneous samples (such as those using a population of the elderly) tend to result in higher correlations. The lack of a significant correlation in our study could perhaps be attributed to the performance-homogeneity of our samples and/or the above-mentioned ceiling effect in the odour identification test.

In summary, the results of our two studies indicate that olfactory perception is associated with a specific personality factor, anxiety. Highly anxious individuals show elevated olfactory perception. We also found some evidence that this effect might be limited to or stronger in men, but further data are needed to confirm this finding. Thus, considering similar findings in previous studies, there is an emerging pattern suggesting that neuroticism, or at least its subscale anxiety, is related to various aspects of olfactory perception. However, we cannot currently distinguish between whether the observed patterns are due to shared underlying biological processes or due to olfactory-linked activities and experience. Future studies should therefore also employ a measure of olfactory awareness and experience to explore these possible connections with neuroticism/anxiety. This, in turn, might improve our understanding of marked individual differences in olfactory perception.

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CHAPTER 7

OLFACTORY PERFORMANCE IS PREDICTED BY INDIVIDUAL SEX-ATYPICALITY, BUT NOT SEXUAL ORIENTATION

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Olfactory performance is predicted by individual sex-atypicality, but not sexual orientation

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Abstract:	Previous studies have reported robust sex differences in olfactory perception. However, both men and women can be expected to vary in the degree to which they exhibit olfactory performance considered typical of their own or the opposite sex. Sex-atypicality is often described in terms of greater gender nonconformity, which, however, is not a perfect correlate of non-heterosexual orientation. Here we explored the intrasexual variability in psychophysical olfactory performance in a sample of 156 individuals (83 non-heterosexual) and found the lowest odor identification scores in heterosexual men. However, when sex-atypicality was entered in the model along with sexual orientation, better odor identification scores were exhibited by gender-nonconforming men, and greater olfactory sensitivity by gender-conforming women, irrespective of their sexual orientation. Thus, sex-atypicality, but not sexual orientation predicts olfactory performance, and we propose that this might not be limited to olfaction, but represent a more general phenomenon.
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7th May 2013

Dear Sirs,

We would like to submit the attached manuscript, 'Olfactory performance is predicted by individual sex-atypicality, but not sexual orientation', for consideration in *PLoS ONE*.

Previous studies have reported robust sex differences in olfactory perception. However, both men and women can be expected to vary in the degree to which they exhibit olfactory performance considered typical of their own or the opposite sex. Sex-atypicality is often described in terms of greater gender nonconformity, which, however, is not a perfect correlate of non-heterosexual orientation. Here we explored the intrasexual variability in psychophysical olfactory performance in a sample of 156 individuals (83 non-heterosexual) and found the lowest odor identification scores in heterosexual men. However, when sex-atypicality was entered in the model along with sexual orientation, better odor identification scores were exhibited by gender-nonconforming men, and greater olfactory sensitivity by gender-conforming women, irrespective of their sexual orientation. Thus, sex-atypicality, but not sexual orientation predicts olfactory performance, and we propose that this might not be limited to olfaction, but represent a more general phenomenon. Moreover, this study is, to the best of our knowledge, the first to demonstrate the effect of sex-atypicality and sexual orientation on olfactory abilities.

This research manuscript is original, not previously published, and not under concurrent consideration elsewhere. All authors have approved the submission of the paper. There are no financial or other conflicts of interest, actual or potential, to declare. The study complies with the Declaration of Helsinki for Medical Research involving Human Subjects and was approved by the IRB of the Faculty of Sciences of Charles University. The participants have provided written informed consent.

Yours faithfully

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Olfactory performance is predicted by individual sex-atypicality, but not sexual orientation

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Abstract

Previous studies have reported robust sex differences in olfactory perception. However, both men and women can be expected to vary in the degree to which they exhibit olfactory performance considered typical of their own or the opposite sex. Sex-atypicality is often described in terms of greater gender nonconformity, which, however, is not a perfect correlate of non-heterosexual orientation. Here we explored the intrasexual variability in psychophysical olfactory performance in a sample of 156 individuals (83 non-heterosexual) and found the lowest odor identification scores in heterosexual men. However, when sex-atypicality was entered in the model along with sexual orientation, better odor identification scores were exhibited by gender-nonconforming men, and greater olfactory sensitivity by gender-conforming women, irrespective of their sexual orientation. Thus, sex-atypicality, but not sexual orientation predicts olfactory performance, and we propose that this might not be limited to olfaction, but represent a more general phenomenon.

Keywords: olfaction; sex differences; sexual orientation; sex-atypicality; childhood gender nonconformity; olfactory abilities

1. **Introduction**

Numerous recent studies have reported sex differences in personality characteristics, cognition, and behavior [1,2]. For instance, robust sex differences have been repeatedly found in physical aggression, which is on average higher in males [3], and in empathy, in which females typically score higher than males [4]. Furthermore, some of these sex differences seem to appear at least as early as during infancy and preschool age, as suggested, for instance, by studies on sex specificity in childhood play behavior [5]. Some of the sex-related differences have also been documented in heterosexual and non-heterosexual individuals. Specifically, it has been shown that, on average, homosexual men tend to show several sex-atypical, i.e. feminine, psychological characteristics. For example, it has been reported that homosexual men exhibit higher empathy and lower physical aggressiveness than heterosexual men [6]. Also, homosexual men outperform their heterosexual counterparts in verbal associations, while the opposite pattern has been found in spatial abilities, particularly in mental rotations [7].

It has been suggested that many sex differences in psychology develop under the influence of context-dependent epigenetic factors. One such factor largely determining sex differences is prenatal or early perinatal exposure to androgen steroids, which affect sex differences in brain anatomy, and consequently sex differences in behavior, cognition, personality factors and others [8,9]. Numerous neuroanatomical differences between men and women have been described, such as those in the percentage and asymmetry of the principal cranial tissue volume, which were found to correlate with cognitive performance [10], or synaptic organization of the medial amygdala, which is hypothesized to provide a sexually dimorphic neural substrate for the effects of hormones on adult social behavior [11]. A well-established example of the linkage between a brain region and sexual behavior is the Third Interstitial Nucleus of the Anterior Hypothalamus (INAH-3), which is generally larger in males than in females [12]. Interestingly, this structure is also larger in heterosexual men than in homosexual ones [13].

Besides differences in neuroanatomy, prenatal hormonal influences on personality and behavioral sex differences have been studied indirectly via physical traits, which also develop in utero under the influence of steroid hormones and remain stable across the lifespan. In particular, the ratio between the second and fourth digit (2D:4D) is considered a marker of prenatal androgen influence [14]. It develops prenatally [15], seems unaffected by postnatal variations in androgen levels [14], and several studies have reported a higher 2D:4D in females [e.g. 16], but see [14]. In homosexual men, sex-atypical 2D:4D has also been demonstrated [17], but see [18].

Furthermore, it has been suggested that similar mechanisms that are supposed to influence the average differences between men and women also give rise to intrasexual variation in such traits [19]. Thus, both men and women vary in the level of development of traits which are typical of their own or the opposite sex and, consequently, both men and women can show rather sex-typical or sex-atypical psychological characteristics [19]. It is worth pointing out that despite an association between sexual orientation and psychological sex-atypicality, which is often described in terms of greater gender nonconformity, empirical evidence suggests that greater gender nonconformity is not a perfect correlate of non-heterosexual orientation since only a proportion of homosexual individuals show sex-atypical traits. For example, about a third of gay men recalled childhood gender-conforming behavior similar to that of heterosexual men [20]. Also, some studies have failed to replicate the previous results on the relationship between sexual orientation and sex-related traits such as 2D:4D [18] or cognition [21]. Consequently, some of the reported differences between heterosexual and non-heterosexual individuals thus might rather represent an epiphenomenon of the variability in gender nonconformity.

To test the spurious association between gender nonconformity and sexual orientation, we chose olfactory abilities, which tend to exhibit significant sex differences in favour of women [for review see 22], especially as regards the ability of odor identification. It is established that performance on this particular test is affected by cognitive factors such as verbal abilities and verbal fluency in particular, in which the female superiority has been widely reported [e.g. 23]. Nevertheless, differences in verbal fluency related to sexual orientation have also been demonstrated, with gay men tending to score the highest or similarly to heterosexual women and lesbian women scoring the lowest or similarly to heterosexual men [24]. Thus, there are reasons to expect similar differences related to sexual orientation in odor identification. However, at the same time, the authors could not demonstrate a clear superiority of heterosexual women over heterosexual men on all the three tests of verbal fluency employed. This might indicate the involvement of sex-atypicality rather than sexual orientation in similar tasks.

The aim of the present study was to explore interindividual differences in olfactory performance related to sex-atypicality, which is often described in terms of childhood gender nonconformity (CGN), and sexual orientation. We expected that, on the test of odor identification, men exhibiting lower CGN scores, and hence being more gender-conforming, would, irrespective of their sexual orientation, be outperformed by the less gender-conforming ones, whose scores would resemble those of the more gender-conforming women. Odor discrimination and the olfactory threshold, in which sex differences are less pronounced, should be less likely to produce such results.

2. **Method**

2.1 ***Ethics Statement***

The study complies with the Declaration of Helsinki for Medical Research involving Human Subjects and was approved by the IRB of the Faculty of Sciences of Charles University. The participants have provided written informed consent.

2.2 ***Participants***

The sample comprised 156 university students or alumni (67 female and 89 male; mean age = 24.2 ± 4.1; range 19-35 years). They were recruited by means of snowball sampling from students attending both undergraduate and graduate courses lectured by LN and JV. In lectures announcements were made that a study on olfactory perception was to be carried out, for which participants were sought. Furthermore, members of the university's student queer association “Charlie” were invited to participate during a lecture. To avoid systematic differences in hormonal contraceptive use between heterosexual and non-heterosexual women that might affect olfactory perception, only non-users were recruited. All participants signed written consent and received reimbursement of CZK 300 (approximately USD 15). The study complies with the Declaration of Helsinki for Medical Research involving Human Subjects.

2.3 ***Questionnaires***

2.3.1 ***General Demographics***

For each participant, data on age, socioeconomic status, religious beliefs, smoking history, living environment pollution, olfaction-related health issues and, in women, menstrual cycle phase were obtained. There were no sex differences in age, Mann-Whitney U = 2769.5, p = .52.

2.3.2 *Sexual orientation assessment (The Kinsey Scale)*

All participants indicated their sexual orientation on the Kinsey Scale [25], prompted by the statement "I regard myself as…". The seven-point ordinal Kinsey Scale, ranging from zero to six, was anchored on either end, with zero labeled "heterosexual" and six labeled "homosexual". It is important to note differences in sexual orientation between men and women. There is a robust body of evidence suggesting greater fluidity in women's sexual orientation compared to that of men, particularly as regards non-heterosexual women [26]. Female non-heterosexuality is significantly less stable than heterosexuality, whilst in men, both heterosexuality and homosexuality are relatively stable [27]. Also, women are more likely than men to use the middle categories of the Kinsey scale to indicate their sexual orientation [28]. Given the unequal numbers of observations in the individual categories both within and between the sexes, for the purposes of the subsequent analysis of variance, the categories were merged to produce the following groups: the heterosexual group (ratings of "0" or "1"; N = 73; 41 males) and the non-heterosexual group (ratings „2" to „6"; N = 83; 48 males). The groups did not differ in terms of age, $F(3,151) = .806$, $p = .49$. Please refer to Figure 1 for the frequency distribution of sexual orientation categories in men and women.

2.3.3 *Childhood Gender Nonconformity*

To retrospectively assess the participants' childhood sex-typed behavior and gender identity, the participants were administered a sex-appropriate form of the Czech version of the Childhood Gender Nonconformity Scale (CGN, [29]). The scale consists of seven items rated on a 7-point Likert scale, anchored on either end with "strongly disagree" (1) and "strongly agree" (7). Items cover internal feelings of maleness or femaleness ("As a child I often felt that I had more in common with girls/boys than boys/girls.") and participation in sex-stereotypic games and activities ("As a child I (dis)liked competitive sports such as football, baseball, and basketball.”). Scores on individual items are added up to produce the overall score, which can range between 7 and 49, with higher scores indicating greater gender nonconformity.

2.3.4 ***Continuous Gender Identity***

To assess the participants’ current self-concepts as masculine or feminine, a sex-appropriate form of the Czech version of the Continuous Gender Identity Scale (CGI; [29]) was administered. The measure includes 10 items rated on a 7-point Likert Scale ranging from “strongly disagree” (1) to “strongly agree” (7) about how masculine or feminine the participant feels (“In many ways I feel more similar to men/women than to men/women.“) and behaves (“People think I should act more feminine/masculine than I do.“). Scores on the individual items are added up to produce the overall score, which can range between 10 and 70. The more masculine a woman’s self-concept is, the higher the score, whereas men scoring high on the CGI tend towards more feminine self-concepts. Both the CGN and CGI were translated to the Czech language by JV and back translation was produced by LN.

Since this study was part of a broader project, including a study by [30] on the relation of Big Five personality traits and olfactory abilities, the participants further completed several other questionnaires.

2.4 ***Olfactory measures***

The Sniffin’ Sticks test ([31]), manufactured by Burghart Messtechnik GmbH, was used to obtain all olfactory measures. This is one of the most widely used tests of (ortho)nasal chemosensory performance, based on pen-like odor dispensing devices. The extended version of the test is comprised of three tests of olfactory function, namely odor threshold (sensitivity), discrimination, and identification.

The olfactory threshold refers to the minimum concentration of a tested odorant (n-butanol) that an individual is able to reliably differentiate from a blank sample. The set consists of 16 dilution steps of the odorant (targets), each of which forms a triplet with two blanks. A single-staircase, three-alternative forced-choice (3-AFC) method is used, in which, starting with the lowest concentration (dilution number 16), an ascending (low to high concentration) series of even-numbered triplets is presented, with successful trials prompting another presentation of the same triplet in a random order. Two successful trials in a row mark a turning point; starting with the nearest lower concentration, a descending series of triplets is presented until the individual fails to detect the target. This marks a reversal towards the higher concentrations and, starting with the next higher concentration, an ascending series of triplets is presented until two correct trials occur, marking another reversal. The testing is finished after the total of 7 reversals is reached. The threshold score is computed as the arithmetic mean of the dilution number at the last four reversals. Ranging from 1 to 16, higher scores indicate greater olfactory sensitivity (i.e. lower threshold).

The test of odor discrimination assesses the degree to which an individual can differentiate between odors in suprathreshold concentrations. The set comprises 16 triplets of odorized pens, of which two are identical, and the individual is asked to indicate the odd one. The score is the total of correct trials (0-16), with higher scores indicating a better ability of odor discrimination.

The 16-item test of cued odor identification involves a 4-AFC task in which the individual is required to choose a label from a list of four, which he or she thinks best describes the odor's source. The score is the total of correct trials. Based on the composite score of the three tests (TDI), individuals can be classified as normosmic (intact sense of smell; TDI > 30), hyposmic (TDI 30-15), or functionally anosmic (TDI < 15) [31].

Although all participants reported good respiratory health, there were 11 instances of hyposmia in the sample: 10 mild (TDI 25-30) and 1 moderate (TDI 20-25). The latter was excluded from the analysis because more consequential factors than a mere momentary lapse in current olfactory performance were likely involved [31].

2.5 ***Procedure***

Individual, one-per-person testing sessions were conducted by LN in the morning hours or by early afternoon (3 p.m.) at the latest in a well-ventilated room. Individuals were instructed to only attend if in good respiratory health and asked to refrain from smoking or consumption of odorous foods at least 2 hours prior to participation, as well as to forego applying perfume or other scented cosmetic products. The researcher first introduced the procedure, assured the participant the data would be subject to confidential treatment, and provided financial recompense for participation. In winter time, participants were first administered the questionnaires upon arrival because the abrupt change in temperature might potentially interfere with olfactory testing. At other times, there was no set order in which questionnaire administration and olfactory testing took place. However, within the olfactory testing part of the session, olfactory sensitivity/odor threshold was always tested first, followed by discrimination and identification, and the participants were allowed a 3-minute break after each test to prevent olfactory adaptation. The entire session took, in most individuals, 75 to 90 minutes.

2.6 ***Analyses***

All analyses were carried out with SPSS 18.0 (IBM Corp.). Data normality was checked firstly by visually examining individual histograms of all relevant variables, secondly by producing skewness and kurtosis values and their respective standard errors, from which z-scores were computed and compared to the value of 1.96, as suggested by [32:72], and thirdly with multiple Shapiro-Wilk's W tests. Since departure from normality in nearly all variables was detected, nonparametric tests were used where possible.

Differences in CGN and CGI scores related to sex and sexual orientation were analysed using the Kruskal-Wallis ANOVA. To analyse differences in olfactory measures, we ran a MANCOVA, which is considered to be robust to violations of multivariate normality, as well as to violations of homogeneity of variance/covariance matrices, if N of the largest group is no more than about 1.5 times the N of the smallest group [32], which was met. To look for possible covariate candidates (e.g. age) to include, a Kendall correlation matrix was produced. Further, for the categorical predictors of sex and sexual orientation, a point-biserial correlation and a biserial correlation were carried out, respectively. Since the identification score turned out to be positively associated with age (Kendall Tau = .15, $p < .01$), it was subsequently entered in the MANCOVA as a covariate. Also, the identification score was correlated with the CGN and CGI scores (Kendall Tau = .15, $p < .01$, Kendall Tau = .14, $p < .05$, respectively). However, the CGN and CGI scores could not be entered as covariates given their significant association with both dichotomous predictors, sex, $r_{pb} = -.34$, $p < .0001$ (both CGN and CGI), and sexual orientation, $r_b = -.45$, $p < .0001$ (CGN) and $r_b = -.25$, $p < .01$ (CGI). This was because in instances in which there is nonrandom group assignment and a variable is intimately associated with any of the independent variables, so that the groups inherently differ on this variable, use of such a variable as a covariate is incorrect [e.g. 33]. Nevertheless, the effect of the CGN, which is the strongest correlate of adult sexual orientation [20], on the prediction of olfactory scores has been tested by means of a regression analysis, as detailed below. Finally, there was an association between the CGN and CGI scores, Kendall Tau = .46, $p < .0001$.

The three olfactory scores (threshold, discrimination, identification) were entered in the MANCOVA as dependent variables, sex and sexual orientation as dichotomous categorical factors, and age as a covariate.

The follow-up to the MANCOVA was twofold, as recommended by [32:594]: firstly, a stepwise discriminant function analysis and a subsequent canonical analysis were run, and, secondly, a separate ANCOVA on identification scores and ANOVAs on discrimination and threshold scores were performed, further followed up by multiple Mann-Whitney U tests for post-hoc comparisons.

To test whether the olfactory scores would be predicted by sexual orientation or, rather, by its strongest correlate, the CGN, we ran a categorical regression analysis, using the SPSS Optimal Scaling (CATREG) feature. The CGI, which was associated with CGN scores, was not included to prevent multicollinearity problems. The assumptions were met since the number of valid cases exceeded the number of predictor variables plus one. Because of the differences in sexual orientation between men and women and their differential use of the Kinsey scale, detailed above, the analysis was run separately for each sex. Moreover, since in men, the categories of 2, 3, and 4 only contained 1, 2, and 3 observations, respectively, these had to be merged so that the analysis could be performed. In women, the same had to be done with categories 3 ($N = 4$) and 4 ($N = 2$). The dependent variables of identification, discrimination and threshold score were treated as numeric measures, and the CGN and sexual orientation as ordinal measures, which were discretized by ranking. A numerical initial configuration was selected, as recommended when no variables are treated as nominal. Multicollinearity did not appear a serious problem, as the two predictors (sexual orientation and CGN) were only found to be moderately associated, Kendall's Tau = .49, $p < .0001$ and Kendall's Tau = .35, $p < .0001$ in men and women, respectively. This was further supported by reviewing the variance inflation factors (VIF), which were nowhere near the value of 10, and the average VIF was not greater than 1 [32:175]. Moreover, a parallel analysis with multiple linear regression showed comparable results.

3. **Results**

3.1 Interindividual differences in CGN and CGI scores

The Kruskal-Wallis ANOVA on CGN scores revealed significant differences H(3, 148) = 55.72, p < .0001, namely between heterosexual men, who exhibited the lowest CGN, and everyone else (all p*s* < .001), and between heterosexual and non-heterosexual women (p = .02), with the former being more gender-conforming. There was also a difference in CGI scores, H(3, 148) = 25.49, p < .0001, namely between non-heterosexual women, who scored second highest, and highest-scoring non-heterosexual men (p = .01) as well as lowest-scoring heterosexual men (p < .0001). Descriptive statistics of CGN and CGI scores are given in Table 1.

3.2 Differences in olfactory measures

The MANCOVA on olfactory measures revealed no sex differences, but a significant effect of the covariate age, F(3, 148) = 3.73, p = .013, which was due to its effect on the identification score. However, there was a significant sex*sexual orientation interaction, F(3,148) = 3.00, p = .033. Results of the first part of the twofold follow-up, the stepwise discriminant function analysis followed by a canonical analysis, suggested that discrimination between groups was significant with Sniffin' Sticks identification and discrimination (but not threshold) scores entered in the model (Wilks' Lambda = .90; F(6,300) = 2.63, p < .02), in which, however, only the identification score was a significant contributor, F(3,150) = 3.63, p = .01. The canonical analysis indicated that there was only one significant discriminant function, accounting for 92% of the explained variance, by means of which the most significant and clear discrimination (although rather small in absolute magnitude) could be made between heterosexual males and the other individuals. To be specific, the lower the identification and, to a lesser extent, the discrimination score on the Sniffin' Sticks test, the more likely it was that such olfactory performance would be exhibited by a heterosexual male.

The results of the second part of the follow-up were in accordance with this. An ANCOVA with identification as a dependent variable revealed a sex difference $F(1,150) = 5.52$, $p = .02$ and a sex*sexual orientation interaction, $F(1,150) = 4.96$, $p = .027$. Post-hoc comparisons showed that heterosexual men scored significantly lower than everyone else, namely than heterosexual women, Mann-Whitney $U = 389$, $N = 72$, $p < .005$, non-heterosexual men, Mann-Whitney $U = 662$, $N = 88$, $p < .01$, and non-heterosexual women, Mann-Whitney $U = 509$, $N = 75$, $p = .04$. An ANOVA with discrimination as a dependent variable revealed a sex*sexual orientation interaction, $F(1,150) = 4.27$, $p = .04$. This was due to a difference between heterosexual men and their non-heterosexual counterparts, who they were outperformed by, Mann-Whitney $U = 713.5$, $N = 88$, $p = .04$. Descriptive statistics of olfactory measures are given in Table 1.

3.3 ***Categorical regression of sexual orientation and CGN scores on olfactory measures***

A categorical regression analysis with sexual orientation and its strongest correlate, the CGN, revealed that in men, CGN but not sexual orientation significantly predicted odor identification scores, $\beta = .403$, $F = 7.259$, $p < .0001$. Men who tended towards greater gender nonconformity exhibited a better ability of odor identification than their more gender-conforming counterparts. CGN thus explained a significant proportion of variance in the odor identification scores of men, $R^2 = .231$, $F(8,87) = 2.960$, $p < .01$. No such association was found for the other two olfactory measures.

Similarly, in women, CGN but not sexual orientation predicted the olfactory threshold, $\beta = -.569$, $F = 10.127$, $p < .0001$, suggesting that women who were more gender-conforming tended to exhibit greater olfactory sensitivity than their more gender-nonconforming counterparts. However, the overal model was not significant on the conventional level of significance, $R^2 = .247$, $F(10,59) = 1.607$, $p = .133$. No associations were found for the other two olfactory measures in women. Odor identification scores and olfactory thresholds in men and women relative to CGN and sexual orientation are plotted in Figures 2 and 3, respectively.

4. Discussion

In the present study, we found a modulating effect of sexual orientation on differences between men and women in olfactory performance. Namely, in odor identification, heterosexual men were outperformed by all other participants, and, in odor discrimination, by non-heterosexual men. However, when separate regression analyses were run for each sex in which, along with sexual orientation, the CGN was entered as a predictor, only the latter turned out to significantly predict performance on some of the olfactory tests. To be specific, in men, those who had been less gender-conforming in childhood exhibited a better ability of odor identification than the more gender-conforming ones, irrespective of their sexual orientation. In women, those who had been more gender-conforming in childhood, exhibited greater olfactory sensitivity. Thus, it would seem that it is CGN rather than sexual orientation that actually modulates differences in olfactory abilities between men and women.

In olfactory research, the number of previous studies which did take into account the possible effect of sexual orientation on interindividual differences in olfaction is very limited. A positron emission tomography (PET) study by [34] revealed a sex-dissociated activation of regions covering the sexually dimorphic nuclei of the anterior hypothalamus in response to the putative human pheromones, namely 4,16-androstadien-3-one in women and estra-1,3,5(10),16-tetraen-3-ol in men. This is one of the key brain regions mediating human sexual behavior (e.g. neuroendocrine and autonomic aspects of sexual drive and sexual orientation [35]). In follow-up PET studies, it was found that what actually mattered was not the biological sex but sexual orientation: homosexual men differed from their heterosexual counterparts and resembled heterosexual women in that their preoptic hypothalamus was activated by androstadienone [36]. Similarly, lesbian women, in whom the pattern was less clear, failed to exhibit activation of the region in response to androstadienone, unlike their heterosexual counterparts, but showed some congruence with heterosexual men in their hypothalamic processing of estratetraenol [37]. Nevertheless, a PET study with male-to-female transsexuals [38], whose hypothalamic activation in response to androstadienone and estratetraenol bore some resemblance to that of both heterosexual men and women, indicates that the pattern will likely be more complex.

By way of explanation, androstadienone is the prominent 16-androstene steroid found in semen, sweat, axillary hair, and blood [39] in much higher concentrations in men than in women, whereas estratetraenol is an estrogen-like steroid reported to be found in the urine of pregnant women [40]. Importantly, some sex-specific effects on the autonomic nervous system as well as mood, memory and sexual arousal, that act in a context- and dose-dependent manner, have been reported for both substances [see 41 for review], although the evidence is less consistent for estratetraenol. The above-mentioned sex-specificity of cerebral activation has been interpreted in terms of the supposed bimodality of the stimuli [34,36,37]. However, implicit is the assumption of the heterosexual orientation of the participants, i.e. their presumed sexual attraction to the opposite sex, which is the context that lends relevance to interpretations that suggest the pheromone-like nature of these steroid compounds. Nevertheless, several researchers [e.g. 41] have questioned the ecological validity, and hence the physiological relevance, of the androstadienone stimuli employed in previous studies in the pure crystalline form, and highlighted the critical effect of concentration.

Thus, as it turns out, the potential effect of sexual orientation on olfactory perception first came to be addressed to help to explain findings on sex-dissociated brain activation in response to components of human body odor, i.e. the so-called social odors. The present study, however, aimed to investigate the effect of sexual orientation on the olfactory abilities of odor identification, discrimination, and the olfactory threshold in men and women, tested with odors that are presumed not to bear any social relevance. Although women's olfactory abilities are often simplistically described as being in general superior to those of men, this, in fact, particularly seems to hold for odor identification, in which their olfactory superiority appears to be established relatively early in ontogeny, holds across the lifespan, and exhibits a later decline with aging [42]. It has been argued that the better ability of odor identification in women may be partly accounted for by cognitive factors. It has been found that performance on odor identification is affected by verbal abilities and verbal fluency in particular [42], in which the female superiority has been widely reported [e.g. 23]. Moreover, differences in verbal fluency related to sexual orientation have also been demonstrated [24,43], with gay men tending to score higher than heterosexual men or similarly to heterosexual women, and lesbian women scoring lower than their heterosexual counterparts or similarly to heterosexual men. Thus, whether the female advantage in odor identification is driven predominantly by women's better verbal fluency or not, this is the primary test in which to look for sexual orientation-related intrasexual differences, with the other two being less likely to produce such results given the less consistent sex differences.

However, in their study, [24] also failed to demonstrate a clear superiority of heterosexual women over heterosexual men on all the three tests of verbal fluency employed. This might indicate the involvement of sex typicality or atypicality of individual performance rather than sexual orientation per se. Sex-atypicality is often described in terms of greater childhood gender nonconformity (CGN), which, mainly in men, is the strongest predictor of sexual orientation in adulthood [20]. Expecting the involvement of CGN, we hypothesized that gender-conforming men, irrespective of their sexual orientation, would perform in a sex-typical manner and exhibit relatively lower identification scores than gender-nonconforming men, who would be likely to exhibit scores similar to those of gender-conforming women.

Our data support the tendency towards the greater CGN in non-heterosexual men and women alike. Also, sex-atypical levels of olfactory performance on odor identification (but not on the other two tests) were found in non-heterosexual men only. Heterosexual and non-heterosexual women exhibited no reliable differences in olfactory abilities in the present study. Further, it has also turned out that in men, the odor identification scores were actually predicted not by sexual orientation, but by the CGN scores. In women, the CGN scores rather than sexual orientation appeared to underlie the intra-sexual variability in the olfactory threshold, although the overall model was not significant on the conventional level of significance.

Given the fact that the female olfactory superiority seems predominantly pertaining to odor identification, sex differences in olfaction have often been suggested to be a mere expression of complex differences in higher levels of brain organization and function [e.g. 44]. If this would be the case, the higher scores of women in odor identification could reflect a cognitive advantage that may manifest itself in many other respects. That odor identification and language processing share some cortical resources has been pointed out for instance by [45]. In non-heterosexually oriented men, the cognitive pattern (particularly as regards verbal fluency and spatial abilities) was different from that of heterosexual men and not significantly dissimilar from that of heterosexual women [43]. Nonetheless, a similar difference has not been found between heterosexual and non-heterosexual women, who tend to perform primarily in a sex-typical manner [46]. This might explain the absence of significant intrasexual differences in odor identification in women in this study.

In their review, [22] put forward the hypothesis that women may in general encounter olfactory stimuli more often than men and thus they can have greater experience with a wider variety of odors. At least in western industrialized societies, this might be due to women's long-term greater odor exposure within specific contexts, such as use of cosmetic products or housework [47], which starts as early as in infancy. Gender non-conforming boys, however, appear to be interested in activities which would be considered typical of the opposite sex, such as doing hair, makeup, dressing-up, cooking or cleaning, as can be gleaned from reports of men who were gender-nonconforming boys [48]. Therefore, gender-nonconforming and gender-conforming men (but not women) may differ in the extent to which they engage in such activities and hence in the level of long-term olfactory experience. In women, the findings are less clear, and thus it could be argued that gender-conforming women may not seek more frequent exposure to a significantly wider variety of odors compared to gender-nonconforming ones, which is why they do not exhibit different olfactory scores.

The significance of the present study lies in the finding that CGN rather than sexual orientation underlies the intrasexual variability in olfactory abilities. We suggest that this may not be limited to olfaction but in fact represent a more general phenomenon. Several studies have failed to find any sexual orientation-related differences in sex-related traits such as 2D:4D [18], salivary testosterone [7], or certain spatial abilities [21], suggesting that at least some of the reported differences between non-heterosexual and heterosexual individuals might be an epiphenomenon of the intrasexual variability in gender nonconformity.

Although still few in number, several studies have recently highlighted the usefulness of quantitative measures of sex-atypicality. The measure of CGN may relate to variability in cognition within and/or between sexual orientation groups, specifically to reading abilities and derived full-scale IQ scores [49] or certain aspects of spatial memory [50]. However, future studies should also test whether the presumed better suitability of the CGN for capturing the full range of variability in some traits is not a mere by-product of the fact that it is measured in a more precise manner than sexual orientation, which is dichotomous, categorical, or assessed on a seven-point scale at best.

5. Conclusions

In conclusion, the present study accentuates the need to employ more comprehensive quantitative measures of sex-atypicality that are known to covary with sexual orientation, such as CGN, to acknowledge the full range of intrasexual variability in traits in which sex differences have been reported. In the present case of olfactory abilities, in which marked differences between men and women are typically noted, the variability observed in various measures was not limited to differences between male and female or heterosexual and non-heterosexual individuals. The measure of CGN has afforded a finer distinction between individual performance on some tasks on the basis of recalled childhood sex-atypicality. At the same time, this study is, to the best of our knowledge, the first to demonstrate the effect of CGN and sexual orientation on olfactory abilities.

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Figure Legends

Fig. 1. Frequency distribution of sexual orientation categories in men and women.

Fig. 2. Odor identification scores in men and women relative to CGN and sexual orientation.

Fig. 3. Olfactory threshold scores in men and women relative to CGN and sexual orientation.

Table 1. Descriptive statistics of childhood gender nonconformity (CGN), continuous gender identity (CGI), and olfactory scores in heterosexual and non-heterosexual men and women.

	N	**mean ± SD gender nonconformity scores**		**mean ± SD olfactory scores**		
		CGN	CGI	identification	discrimination	threshold
men	88	18.35 ± 8.82	25.28 ± 8.22	13.55 ± 1.52	13.28 ± 1.64	8.12 ± 2.52
heterosexual	40	12.55 ± 4.68	22.78 ± 8.40	13.13 ± 1.32	12.88 ± 1.79	7.86 ± 2.82
non-heterosexual	48	23.19 ± 8.56	27.38 ± 7.52	13.90 ± 1.60	13.63 ± 1.44	8.34 ± 2.25
women	67	25.32 ± 10.68	31.58 ± 9.44	13.99 ± 1.24	13.28 ± 1.82	8.52 ± 2.02
heterosexual	32	21.32 ± 10.20	28.87 ± 9.56	14.13 ± 1.21	13.47 ± 1.59	8.55 ± 2.02
non-heterosexual	35	29.59 ± 9.60	34.48 ± 8.53	13.86 ± 1.26	13.11 ± 2.03	8.50 ± 2.05

Figure 1
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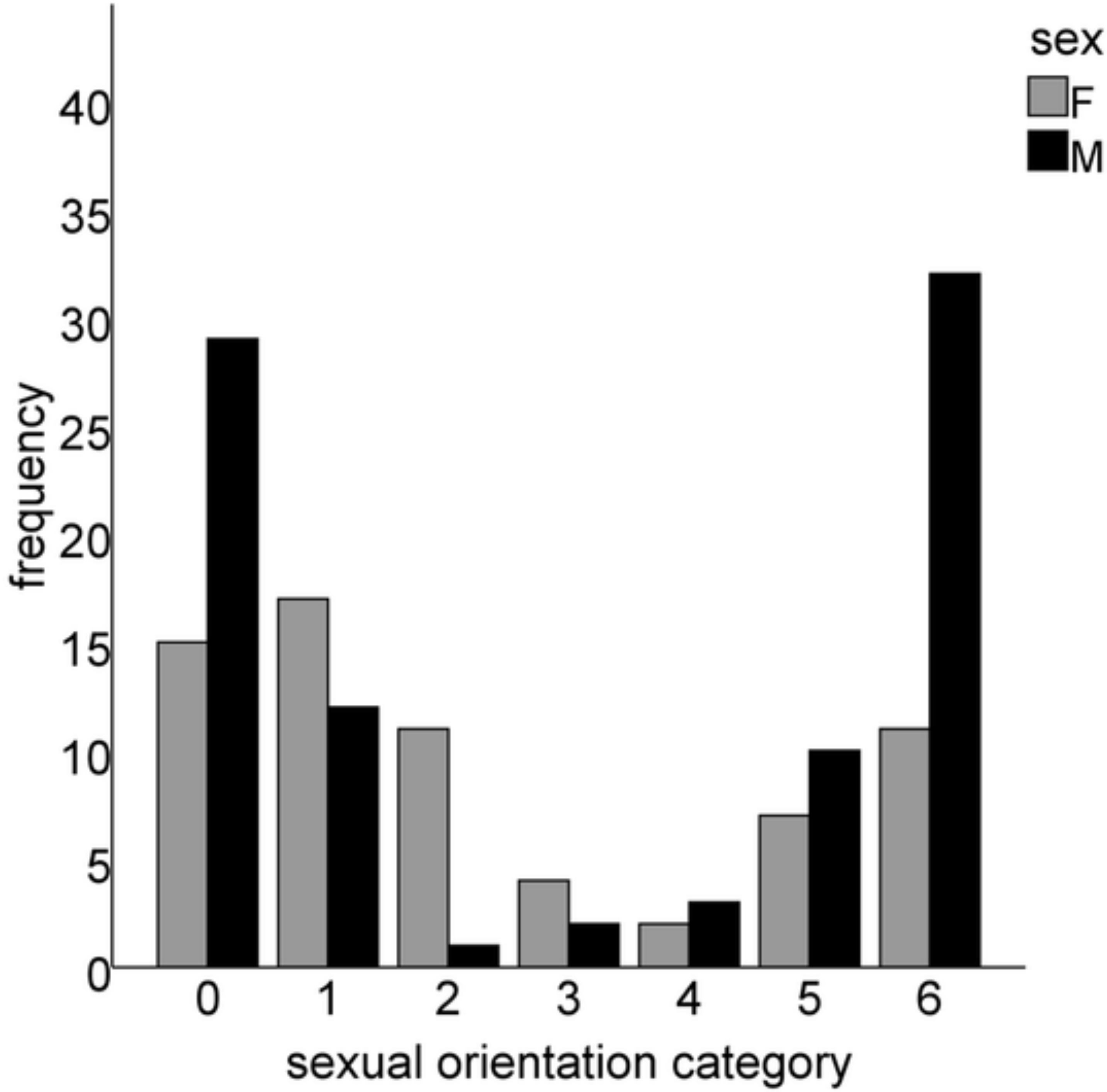

Figure 2
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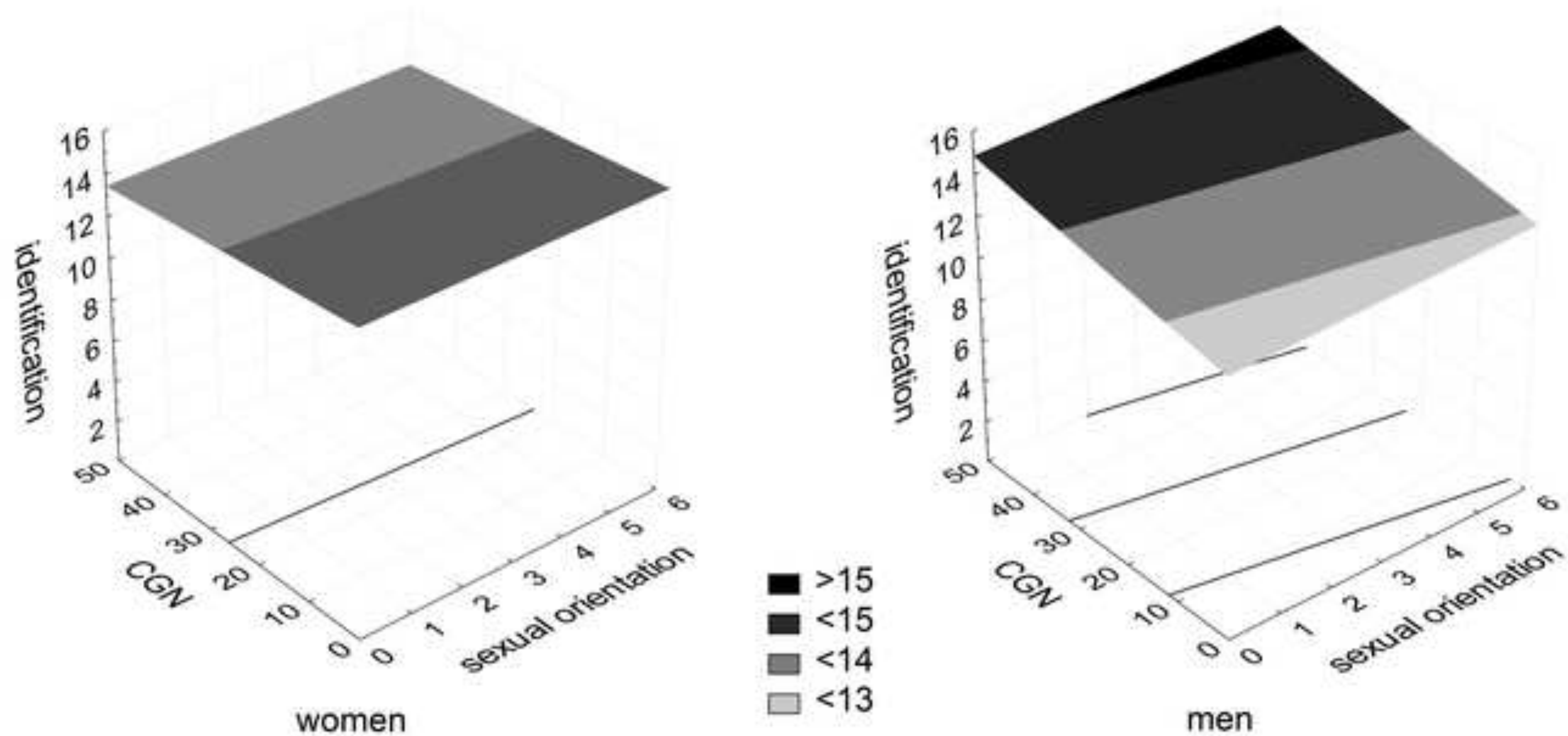

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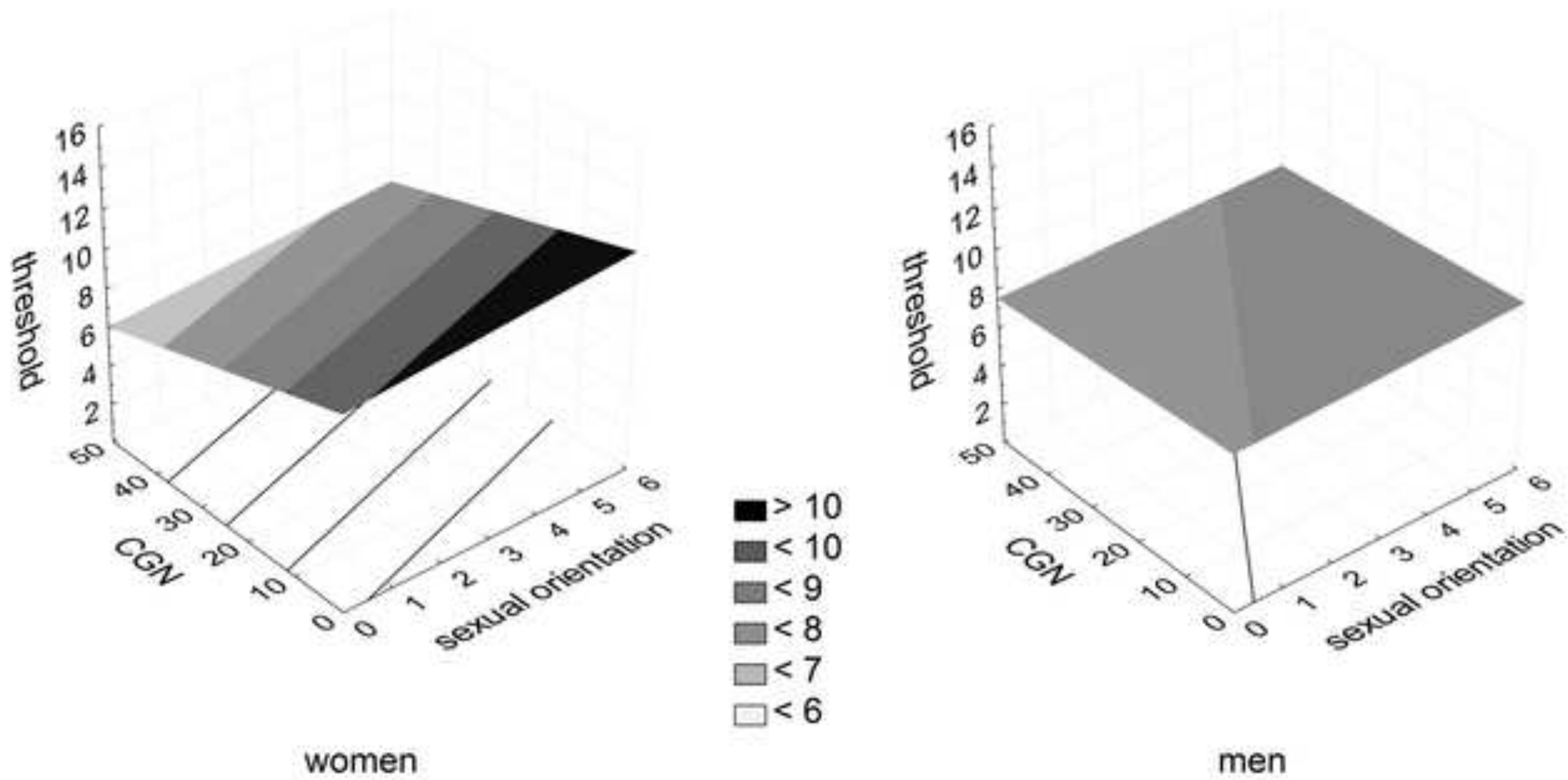

CHAPTER 8

ENGAGEMENT IN OLFACTION-RELATED ACTIVITIES IS ASSOCIATED WITH THE ABILITY OF ODOR IDENTIFICATION AND ODOR AWARENESS

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Engagement in olfaction-related activities is associated with the ability of odor identification and odor awareness

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Engagement in olfaction-related activities is associated with the ability of odor identification and odor awareness

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Abstract

Sex differences in olfactory abilities and odor awareness in favour of women have been proposed to be partly related to women's broader olfactory experience due to their more frequent long-term engagement in activities which could afford greater odor exposure within specific contexts. However, intrasexual variability in odor exposure could also be expected with respect to childhood gender nonconformity. The aim was to explore the potential links between self-reported long-term engagement in selected activities, potentially rich in olfactory stimulation, individual olfactory abilities, and self-reported odor awareness in men and women, and to find out whether the associations were affected by participants' childhood gender nonconformity. In both men and women, it was found that individuals reporting greater engagement in female-stereotyped activities in childhood, including frequency of use of cosmetic products and help with cooking at home, also exhibited higher odor awareness scores. There were also positive associations between more frequent exposure to a greater variety of potentially intense or novel food odors and flavors in childhood and adulthood, odor awareness, and odor identification in both men and women. None of these associations were affected by the participants' childhood gender nonconformity. Our results indicate that self-reported previous olfactory experience acquired through various olfaction-related activities is positively related to odor identification scores and odor awareness.

Keywords: behavior; childhood gender nonconformity; experience; odor awareness; olfactory abilities; sexual orientation

Introduction

Humans are known to exhibit a relatively high degree of interindividual variability in olfactory perception (e.g. Wysocki *et al.* 1991), and, specifically, in the three most widely used measures of psychophysical olfactory performance, namely odor identification, discrimination, and the olfactory threshold. Also, considerable variability between individuals exists in the amount of attention paid to chemosensory stimuli, which is known to significantly affect human chemosensation (Prescott *et al.* 2004; Prescott *et al.* 2008). The perceived olfactory ecology of individuals can be assessed by means of various metacognitive measures, which afford unique insights into how people interact with their daily olfactory environments, which may not be directly observable or reproducible within laboratory settings. These for instance include "odor awareness" (e.g. Smeets *et al.* 2008), "subjective significance of olfaction" (Croy *et al.* 2010), "attitudes towards the sense of smell" (Martin *et al.* 2001), "odors in everyday life" (Cupchik *et al.* 2005), "affective impact of odors" (Wrzesniewski *et al.* 1999) and "children's olfactory behaviors in everyday life" (COBEL; Ferdenzi *et al.* 2008a; Ferdenzi *et al.* 2008b).

Of the demographic factors that have been shown to give rise to interindividual variability in olfactory performance (for review see Hawkes and Doty 2009:37-47), the most consequential seem to be the effects of aging (Doty *et al.* 1984; Wysocki and Gilbert 1989), followed by another major demographic factor, sex. Sex differences in human olfaction, or, more precisely, the female olfactory superiority across virtually all age groups and cultures studied, is a well-established yet poorly understood phenomenon (for review see Brand and Millot 2001), whose robustness has led some to refer to it as an inborn sexually dimorphic trait (Doty *et al.* 1992). This female superiority applies chiefly to the ability of odor identification, which seems to be established relatively early in ontogeny, being present by preschool age (Ferdenzi *et al.* 2008a; Ferdenzi *et al.* 2008b; Richman *et al.* 1992), holds across the lifespan and exhibits a later decline with aging (Doty *et al.* 1984; Larsson *et al.* 2004; Ship *et al.* 1996). In a similar fashion, women report greater awareness of odors (Dematte *et al.* 2011), are more likely than men to be guided in their everyday decisions by their olfactory impressions (Croy *et al.* 2010; Havlicek *et al.* 2008), regard olfactory stimuli as being capable of generating more powerful affective responses (Martin *et al.* 2001), are more careful about masking bad odor (Wrzesniewski *et al.* 1999) and, as early as in preschool age, girls tend to be significantly more olfaction-oriented than boys, especially towards the odors of people, self and the environment (Ferdenzi *et al.* 2008a), which has been noted cross-culturally (Ferdenzi *et al.* 2008b; Saxton *et al.* submitted).

Explanations for these sex differences remain rather incomplete. One of the many contributing factors might be individual differences in long-term olfactory experience. In their review, Brand and Millot (2001) put forward the hypothesis that women may in general encounter olfactory stimuli more often than men and thus they can have greater experience with a wider variety of odors. At least in western industrialized societies, this might be due to women's long-term greater odor exposure within specific contexts, such as cooking, use of cosmetic products or housework (Bianchi *et al.* 2000; Coltrane 2000; Fuwa and Cohen 2007), which starts as early as in infancy. In children, the fact that gender stereotyping of activities is encouraged from very early in ontogeny is reflected in the knowledge of gender stereotyping of household activities demonstrated by girls (but not boys) as young as 24 months of age (Poulin-Dubois *et al.* 2002). Although most evidence for the effect of prior odor exposure on olfactory performance comes from laboratory studies (e.g. Dalton *et al.* 2002; Schab and Crowder 1995), within the real-life context, the long-term effect of olfactory expertise has been demonstrated in perfumers, who show functional reorganisation of olfactory and memory brain regions (Plailly *et al.* 2012), and in other professionals, including chefs (Martin *et al.* 2001).

Nevertheless, besides intersexual variability, intrasexual variability in exposure to odors over the lifespan could be expected as well, particularly with regard to childhood gender nonconformity (CGN, Bailey *et al.* 1996). Gender-nonconforming boys appear to be interested in activities which would be considered typical of the opposite sex, such as doing hair, makeup, dressing-up, cooking or cleaning, as can be gleaned from reports of men who were gender-nonconforming boys (Hockenberry and Billingham 1987), whereas in women the findings are less clear. Besides, especially in men, childhood gender nonconformity tends to be a strong predictor of adult sexual orientation (Bailey and Zucker 1995). It has been shown that both non-heterosexual men and women prefer gender-nonconforming hobbies and occupations (Lippa 2008) and they also exhibit different hobbies and occupational choices compared to their heterosexual counterparts (Lippa 2000). Therefore, individuals with varying degrees of gender nonconformity, particularly men, might also be expected to differ in the extent to which they engage in various everyday activities and hence in the level of long-term olfactory experience.

The aim of the present study was to explore the potential association between self-reported engagement in selected activities, which could afford greater exposure to chemosensory stimulation within common everyday contexts over the long term, and individual olfactory abilities, and self-reported odor awareness in men and women. Moreover, we also sought to find out whether the relationship was affected by the participants' childhood gender nonconformity. In a previous study on the present sample, (Nováková *et al.* submitted) found that in men, those who had been less gender-conforming in childhood exhibited a better ability of odor identification and, moreover, a better ability of odor discrimination than the more gender-conforming ones, irrespective of their sexual orientation. Furthermore, in women, childhood gender nonconformity scores were negatively associated with the olfactory threshold: those who had been more gender-conforming in childhood exhibited greater olfactory sensitivity. Thus, both men and women exhibited significant intrasexual variability in olfactory performance related to childhood gender nonconformity. Here, we sought to find out whether there would be an association between self-reports of engagement in olfaction-related activities, olfactory abilities, and odor awareness, and whether the relationship would hold regardless of the participants' reported childhood gender nonconformity.

Materials and methods

Participants

The sample comprised 156 university students or alumni (67 female and 89 male; mean age = 24.2 ± 4.2; range 19-35 years). They were recruited by means of snowball sampling from students attending both undergraduate and graduate courses lectured by LN and JV. In lectures announcements were made that a study on olfactory perception was to be carried out, for which participants were sought. Furthermore, members of the university's student queer association "Charlie" were invited to participate during a lecture. To avoid systematic differences in hormonal contraceptive use between heterosexual and non-heterosexual women that might affect olfactory perception, only non-users were recruited.

The study complies with the Declaration of Helsinki for Medical Research involving Human Subjects and was approved by the IRB of the Faculty of Sciences of Charles University. The participants have provided written informed consent and received reimbursement of CZK 300 (approximately USD 15).

Questionnaires

General Demographics

For each participant, data on age, socioeconomic status, religious beliefs, smoking history, living environment pollution, olfaction-related health issues and, in women, menstrual cycle phase were obtained. There were no sex differences in age, Mann-Whitney U = 2769.5, p = .52.

Sexual orientation assessment (The Kinsey Scale)

All participants indicated their sexual orientation on the Kinsey Scale (Kinsey *et al.* 1948), prompted by the statement "I regard myself as…". The seven-point ordinal Kinsey Scale, ranging from zero to six, was anchored on either end, with 0 labelled "heterosexual" and 6 labelled "homosexual". Participants were sampled with respect to their sexual orientation, yielding the heterosexual group (ratings of "0" or "1"; N = 73; 41 males) and the non-heterosexual group (ratings „2" to „6"; N = 83; 48 males). The groups did not differ in terms of age, F(3,151) = .806, p = .49. Please refer to Figure 1 for the frequency distribution of sexual orientation categories in men and women.

Insert Figure 1 about here

Childhood Gender Nonconformity

To retrospectively assess the participants' childhood sex-typed behavior and gender identity, the participants were administered a sex-appropriate form of the Czech version of the Childhood Gender Nonconformity Scale (CGN; Bailey *et al.* 1996). The scale consists of seven items rated on a 7-point Likert scale, anchored on either end with "strongly disagree" (1) and "strongly agree" (7). Items cover internal feelings of maleness or femaleness ("As a child I often felt that I had more in common with girls/boys than boys/girls.") and participation in sex-stereotypic games and activities ("As a child I (dis)liked competitive sports such as football, baseball, and basketball."). Scores on individual items are added up to produce the overall score, which can range between 7 and 49, with higher scores indicating greater gender nonconformity.

Participants were also asked to complete the Czech version of the Continuous Gender Identity Scale in the sex-appropriate form (CGI; Bailey *et al.* 1996) to find out whether they assessed their current self-concepts as rather sex-typical or atypical. However, since, firstly, CGI scores showed a positive association with CGN scores, Kendall Tau = .36, $p < .0001$ and Kendall Tau = .56, $p < .0001$ in men and women, respectively, and, secondly, also showed associations with other variables identical to those of CGN scores, but fewer in number, only CGN associations are reported.

Both CGN and CGI scores showed an association with sexual orientation in men (CGN: Kendall's Tau = .49, $p < .0001$; CGI: Kendall Tau = .26, $p = .002$) and women CGN: Kendall's Tau = .35, $p < .0001$; CGI: Kendall Tau = .29, $p = .003$), respectively.

Odor Awareness Scale

To assess individual differences in odor awareness, the Czech version of the 32-item Odor Awareness Scale (OAS; Smeets *et al.* 2008) was administered. This is a metacognitive measure to learn about people's self-assessments of their tendency to notice, pay attention, or attach importance to odors in certain everyday situations, and their knowledge of how olfactory experiences shape their everyday behaviors. Most items are five-category response format ("always", "often", "sometimes", "seldom", and "never"), with greater frequency, degree, or probability scoring more points. The total score is obtained by adding the scores of the individual items and can range between 72 and 151, with higher scores indicating greater odor awareness.

All the three scales (CGN, CGI, and OAS) were translated into Czech and a back-translation was produced by the authors (LN, JV).

Olfaction-Related Activities Inventory

The participants were further asked to complete an inventory, produced by the authors for the purposes of the present study, regarding their current and past involvement in activities which are likely to provide contexts for heightened odor exposure. The selection of these contexts and items was based on the Olfactory Diversity Questionnaire (Ferdenzi 2007), which provides parental reports of their children's odor exposure and lists items involving activities potentially rich in olfactory stimulation. The total score exhibited a moderate to strong association with children's both free and forced-choice Sniffin' Sticks odor identification scores. Contexts relevant to adults and presumably amenable to retrospective assessment were used to produce the inventory items, which include use of various scented (gender non-specific) cosmetic products, help with home cooking, family's and own culinary habits, such as experience with foreign cuisines or exotic foods or use of various spices and herbs, and home processing of herbs and fragrant or aromatic produce. Retrospective assessments were recorded separately for infancy to pre-school age (0-6 years), middle childhood (6-12 years), and puberty to adolescence (12-18) on a 5-point scale. Response categories were „never", „rarely", „sometimes", „often", and „regularly" for frequency and „not at all", „slightly", „moderately", „quite a lot" and „extremely" for intensity. A complete list of the survey items is given in Table 1.

Histograms of the individual survey items showed that retrospective assessments for the 0-6 years age range exhibited very small variability, with the most frequent response being "never" and a significant proportion of participants choosing not to respond at all. Therefore, responses for this age range on all items were excluded from the analysis.

Since this study was part of a broader project, for the purposes of another study (for details see Havlicek *et al.* 2012), the participants further completed the Czech versions of the

NEO-Five Factor Inventory (Hrebickova and Cermak 1996) and Empathy Quotient (Baron-Cohen and Wheelwright 2004).

Olfactory measures

The Sniffin' Sticks test (Hummel *et al.* 1997), manufactured by Burghart Messtechnik GmbH, was used to obtain all olfactory measures. This is one of the most widely used tests of (ortho)nasal chemosensory performance, based on pen-like odor dispensing devices. The extended version of the test is comprised of three tests of olfactory function, namely odor threshold (n-butanol version), discrimination, and identification. Testing was carried out in accordance with the instructions (Hummel 2004).

Although all participants reported good respiratory health, there were 11 instances of hyposmia in the sample: 10 mild, exhibiting a total score (TDI) of 25-30, and 1 moderate (TDI 20-25). The latter was excluded from the analysis because more consequential factors than a mere momentary lapse in current olfactory performance were likely involved (Hummel *et al.* 2007).

Procedure

Individual, one-per-person testing sessions were conducted by LN in the morning hours or by early afternoon (3 p.m.) at the latest in a well-ventilated room. Individuals were instructed to only attend if in good respiratory health and asked to refrain from smoking or consumption of odorous foods at least 2 hours prior to participation, as well as to forego applying perfume or other scented cosmetic products. The researcher first introduced the procedure, assured the participant the data would be subject to confidential treatment, and provided financial recompense for participation. In winter time, participants were first administered the questionnaires upon arrival because the abrupt change in temperature might potentially interfere with olfactory testing. At other times, there was no set order in which questionnaire administration and olfactory testing took place. However, within the olfactory testing part of the session, olfactory sensitivity/odor threshold was always tested first, followed by discrimination and identification, and the participants were allowed a 3-minute break after each test to prevent olfactory adaptation. The entire session took, in most individuals, 75 to 90 minutes.

Analyses

All analyses were carried out with SPSS 18.0 (IBM Corp.). Data normality was checked firstly by visually examining individual histograms of all relevant variables, secondly by producing skewness and kurtosis values and their respective standard errors, from which z-scores were computed and compared to the value of 1.96, as suggested by (Field 2005:72), and thirdly with multiple Shapiro-Wilk's W tests. Since departure from normality in nearly all variables was detected, nonparametric tests were used where possible.

To explore the structure underlying the reports of various olfaction-related activities, we performed categorical PCA using the IBM SPSS CATPCA (Optimal Scaling) option. As reports of past and current engagement in activities may cluster differently, the analysis was performed separately on the retrospective (age ranges of 6-12 and 12-18 years) and current part of the survey, which involved 14 and 8 items, respectively. Frequencies of use of the various categories of (gender non-specific) cosmetic products (bath, body, facial etc. products) were expressed as median values of use of cosmetics in general for the age ranges of 6-12 years, 12-18 years, and present, respectively. The assumptions of the analysis were met since a survey of correlations between the variables entering the analyses showed that extreme multicollinearity (>.9) or singularity (=.0) was not a problem and all data were positive integer. The CATPCA settings involved discretizing the ordinal variables by means of ranking and selecting variable principal as the normalization method. Dimensions in solution were ascertained upon several trials in order to obtain the most interpretable structure of loadings. The recommendation of Stevens (1992:382-384) on factor loadings with respect to sample size was followed and loadings greater than .512 were considered significant.

Of the total of 156 cases, 9 cases in which the survey had not been completed were excluded from the analysis. The resulting factors, the original survey items and their wording, and analysis items and their loadings are given in Table 1.

Insert Table 1 about here.

Given the non-random sampling, sex and intrasexual differences could not be analysed with single ANCOVA models. This was because in instances in which there is nonrandom group assignment and a variable (such as CGN) is intimately associated with any of the independent variables (sex, $r_{pb} = -.34$, $p < .0001$), so that the groups inherently differ on this variable, use of such a variable as a covariate is incorrect (e.g. Miller and Chapman 2001).

Sex differences in object scores for the factors which showed no departure from normality were analysed using independent t-tests, otherwise a Mann-Whitney test was used. Since OAS scores showed significant association with age in the total sample, Kendall Tau = .15, $p = .008$, to analyse sex differences in odor awareness, an ANCOVA on odor awareness scores was run with sex as a categorical predictor and age as a covariate.

Kendall Tau correlations and, where appropriate, semi-partial (part) correlations between olfactory abilities, OAS scores, object scores, sexual orientation categories, and CGN scores were produced separately for men and women, respectively. This was due to the expected opposite direction of associations between CGN scores (or sexual orientation categories) and object scores in men and women, respectively. Besides, it is important to note differences in sexual orientation between men and women. There is a robust body of evidence suggesting greater fluidity in women's sexual orientation compared to that of men, particularly as regards non-heterosexual women (Diamond 2008). Female non-heterosexuality is significantly less stable than heterosexuality, whilst in men, both heterosexuality and homosexuality are relatively stable (Mock and Eibach 2012). Also, women are more likely than men to use the middle categories of the Kinsey scale to indicate their sexual orientation (Lippa 2006).

Results

Sex differences in OAS and object scores

A one-way ANCOVA on OAS scores revealed that the effect of sex marginally missed significance, $F(1,151) = 3.85$, $p = .052$, with women tending towards higher OAS scores than men. Furthermore, it also revealed an effect of age $F(1,151) = 11.48$, $p < .001$, with older participants exhibiting higher OAS scores, Kendall Tau = .15, $p < .01$, and sex*age interaction $F(1,151) = 5.16$, $p < .05$, with older women, but not men, exhibiting higher OAS scores, Kendall Tau = .29, $p < .001$.

In CATPCA object scores, a significant sex difference was found in the factor of Female-stereotyped activities in favour of women, $t(145) = 5.40$, $p < .0001$, and Frequency of use and intensity of scented products, Mann-Whitney U = 2031.5, $p = .026$, also in favour of women.

Intrasexual differences in OAS and object scores

There were no associations of OAS scores with CGN scores or sexual orientation in men or women. In men, there was a positive association of the retrospective factor Flavor diversity and aroma with sexual orientation and also a trend thereof with CGN scores. In women, CGN scores exhibited a negative correlation with the factor Flavor diversity and aroma at present. Besides, sexual orientation showed a trend of a positive and negative association with Female-stereotyped activities in men and women, respectively.

Correlational analyses of TDI, OAS and object scores

In men, the ability of odor identification was positively associated with the factor Flavor diversity and aroma at present. Controlling for the effect of age, CGN, or both age and CGN on odor identification in a semi-partial correlation had no effect on the strength of this association. There was also a marginally significant negative correlation of odor identification and the factor Frequency of use and intensity of scented products. However, this association was no longer significant after the effect of age on odor identification was controlled for in a semipartial correlation. Finally, there was also a positive association of the olfactory threshold and Frequency of use and intensity of scented products, that marginally missed the level of significance.

Odor awareness in men was positively associated with Female stereotyped activities in childhood. Although there was a trend of a positive association of this factor with sexual orientation (with non-heterosexually oriented men reporting greater engagement), the relation retained its significance and strength when sexual orientation was controlled for. Further, there were trends of an association between higher OAS scores and reports of more frequent exposure to a greater variety of potentially novel food odors and flavors, both in childhood and at present.

There were no associations between either of the three olfactory measures and odor awareness in men.

In women, there was only a trend between the ability of odor identification and the factor Flavor diversity and aroma in childhood. As in men, odor awareness also exhibited a positive association with Female stereotyped activities, whereas the positive correlations between OAS scores and the two factors Flavor diversity and aroma, both in childhood and at present, were more pronounced in women. A semipartial correlation in which the effect of age on odor awareness in women was controlled for yielded similar results, as well as one in which the effect of CGN on the factor Flavor diversity and aroma at present was controlled for.

Finally, odor awareness was positively associated with the ability of odor identification in women. A semipartial correlation in which the effect of age on odor awareness in women was controlled for, however, yielded only a trend. There were no associations between odor awareness and the other two olfactory measures. The complete results are given in Table 2.

Insert Table 2 about here.

Discussion

The aim of the present study was to explore the potential association between self-reported engagement in selected activities, which could afford greater exposure to chemosensory stimuli within common everyday contexts over the long term, individual olfactory abilities, and self-reported odor awareness in men and women. Moreover, we also sought to find out whether the relationship was affected by the participants' childhood gender nonconformity. Since childhood gender nonconformity has been shown to be a strong predictor of sexual orientation in adulthood (Bailey and Zucker 1995), we recruited equal samples of men and women of both heterosexual and non-heterosexual orientation.

Higher odor awareness scores were exhibited by older participants, particularly by women, but the sex difference marginally missed significance. In previous studies, a clear sex difference in odor awareness was found (e.g. Buron *et al.* 2011; Dematte *et al.* 2011). One may ascribe the relatively modest sex difference in odor awareness to the higher ratio of sex-atypical to sex-typical individuals in the sample. However, no association of odor awareness with CGN scores or sexual orientation was found. This suggests that whatever potentially differential engagement in olfaction-related activities individuals exhibiting varying degrees of gender nonconformity may report, it does not translate into gender-nonconforming men's and gender-conforming women's greater proficiency in knowledge and use of their sense of smell.

In both men and women, it was found that those who reported greater engagement in olfaction-related Female-stereotyped activities in childhood, including frequency of use of gender non-specific cosmetic products and help with cooking at home, also exhibited higher odor awareness scores. Despite the trend of an association of this factor with sexual orientation in both men and women (with non-heterosexually oriented men reporting greater engagement, whereas non-heterosexually oriented women reporting a lesser degree, respectively), in both cases the relation retained its significance and strength when sexual orientation was controlled for. Although it is not possible to decide solely on the basis of the present findings whether children exposed over the long term to a greater variety of odors grow up to become more olfaction-oriented individuals or, rather, whether adults who have come to exhibit greater awareness of odors tend to describe themselves as having had more opportunity to gain olfactory experience as children, it is perhaps safe to assume the role of a developmental aspect as well as continuity over the lifespan. Besides, men and women who reported more frequent exposure to a greater variety of potentially intense or novel food odors and flavors at present and in childhood, respectively, exhibited higher scores on the test of odor identification, which does not rely on self-reports.

To the best of our knowledge, there are no longitudinal developmental studies addressing this issue, but this assumption would seem in line with indirect evidence, which comes from cross-sectional studies with children and young adults. Using the COBEL questionnaire to obtain children's self-reports of their everyday olfactory behaviors, Ferdenzi *et al.* (2008a) found a marked increase in children's self-reported attention and reactivity to odors in the context of their daily settings between the ages of 6 – 10, although this was partly due to the greater verbal fluency exhibited by older children. More specifically, older children were more likely to explain their food dislikes in terms of an item's unpleasant odor, seemed to appreciate the fact that people had natural body odor, exhibited better memory of odors encountered on the previous day, and could name more odorous bathroom objects. The age effect on the same items of the COBEL questionnaire, as well as on the total score, was also found in another, cross-cultural study by Ferdenzi *et al.* (2008b). In a sample of adults aged 20 – 59, Dematte *et al.* (2011) also demonstrated the effect of age on OAS scores, with older participants exhibiting higher scores, which is in line with the results of the present study. Thus, at least as far as the assumption of development of odor awareness across the lifespan is concerned, it does seem to be in accord with the evidence available thus far.

Besides, there were positive associations (or trends thereof) between self-reports of more frequent exposure to a greater variety of potentially intense or novel food odors and flavors in childhood and odor awareness in both men and women, and, moreover, odor identification in women. The factor Flavor diversity and aroma at present showed a similar, yet more pronounced pattern of associations, with the exception that the relation with the ability of odor identification was found in men but not in women. The finding that of the three olfactory measures, it was the ability of odor identification that turned out to be associated with any of the factors, is in line with results obtained by Ferdenzi (2007) with the Olfactory Diversity Questionnaire, on which the selection of contexts and some of the items was based in the present study. Namely, parental reports of the frequency of occurrence of children's activities assumed to provide heightened olfactory stimulation showed a moderate to strong association with children's both free and forced-choice Sniffin' Sticks odor identification scores. Also, the association of the measure of odor identification with reported experience with this factor seems understandable given the fact that the 16-item Sniffin' Sticks odor identification test set consists (but for two odors) of odors of comestibles.

Nevertheless, a note of caution must be sounded on the finding that the factors of olfaction-related activities seem to exhibit more associations with odor awareness in men and women than with olfactory measures. A possible cause of this finding may lie in the self-report, ordinal nature of these two measures, as some participants may consistently favor or avoid extreme response categories regardless of the specific item content, which is known as the extreme response style (Greenleaf 1992; Hamilton 1968; Merrens 1970). This is not an infrequent phenomenon, since extreme responders constitute up to 30% of all respondents (Austin *et al.* 2006; Eid and Rauber 2000).

Finally, odor awareness scores and performance on the test of odor identification did not seem to be reliably related in our study. This also appears in accord with previous studies, as Smeets *et al.* (2008) reported that individuals scoring high on OAS did not outperform the low-scoring ones on the test of odor identification, and in the study by Dematte *et al.* (2011), no association between participants' self-reported odor awareness and odor identification performance emerged. Similarly, in children, no differences in odor identification were found between the most and least olfaction-oriented individuals (Ferdenzi *et al.* 2008b).

To conclude, the results of the present study show that self-reports of both childhood and current behavior that might afford olfactory experience in certain specific functional contexts are associated with individual odor awareness and, albeit to a more limited degree, with odor identification in men and women. These associations are not affected by sexual orientation or gender nonconformity. Semi-longitudinal and longitudinal research in verbally proficient children, employing both own and parental reports of children's actual everyday olfactory behaviors as well as repeated psychophysical measurements, might provide us with answers as to whether children exposed more frequently to a greater variety of odors over the long term grow up to become individuals who exhibit greater awareness of odors or superiority in certain olfactory abilities, and whether these children more often than not tend to be gender-conforming girls and gender-nonconforming boys.

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Figure Legends

Fig. 1. Frequency distribution of sexual orientation categories in men and women.

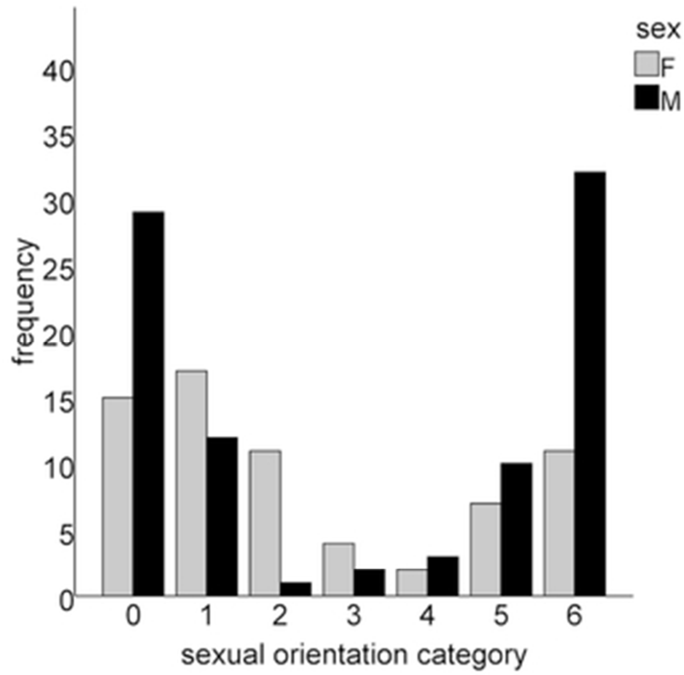
Table 1. An overview of the factors, original survey items, their wording, analysis items, and their loadings. Items with weak loadings (< .512) are given in gray at the factor on which their loadings have been the highest.

Factor	% Total variance	Survey Item	Item Wording	Analysis Item	Loading
Childhood and Adolescence (responses indicated separately for age ranges of 6-12 and 12-18 years)					
Flavor diversity and aroma in childhood	34.29%	Experience with foreign cuisines or exotic foods	*How often did you try out foreign cuisines or exotic foods?*	Frequency 6-12	**.641**
				Frequency 12-18	**.641**
		Use of spices and herbs in cooking	*How often did you or your family use various spices and herbs to season your home-cooked meals?*	Frequency 6-12	**.788**
				Frequency 12-18	**.775**
		Intensity of food aroma	*How aromatic were the foods prepared at your home?*	Intensity 6-12	**.730**
				Intensity 12-18	**.678**
		Consumption of fragrant herbal teas	*How often did you or your family prepare fragrant herbal teas?*	Frequency 6-12	**.690**
				Frequency 12-18	**.640**
Home processing of herbs and fragrant produce	14.88%	Home processing of herbs and fragrant produce	*How often did you or your family grow or gather herbs, edible flowers or fruit and process them at home?*	Frequency 6-12	**.734**
				Frequency 12-18	**.753**
Female-stereotyped activities	12.10%	Frequency of use of gender non-specific scented cosmetic products	*How often did you use cosmetic products belonging to each of the following categories? (bath, body products, facial (non-decorative) products, deodorants and fragrances, hair styling products)*	Median frequency 6-12	.385
				Median frequency 12-18	**.687**
		Frequency of help with home cooking	*How often did you help prepare food at home?*	Frequency 6-12	**.566**
				Frequency 12-18	**.519**
Present					
Flavor diversity and aroma at present	34.37%	Experience with foreign cuisines or exotic foods	*How often do you try out foreign cuisines or exotic foods?*	Frequency	**.707**
		Use of spices and herbs in cooking	*How often do you use various spices and herbs to season your meals?*	Frequency	**.764**
		Intensity of food aroma	*How aromatic are the foods you prepare?*	Intensity	**.731**
		Consumption of fragrant herbal teas	*How often do you prepare fragrant herbal teas?*	Frequency	**.678**
		Home processing of herbs and fragrant produce	*How often do you grow or gather herbs, edible flowers or fruit and process them?*	Frequency	.504

Frequency of use and intensity of scented products	21.26%	Frequency of use of gender non-specific scented cosmetic products	*How often do you use cosmetic products belonging to each of the following categories? (bath, body, facial (non-decorative) products, deodorants and antiperspirants, fragrances, hair styling products)*	Median frequency	**.665**
		Preferred intensity of scented cosmetic products	*How fragrant are the cosmetics products you prefer to buy?*	Intensity	**.802**
		Preferred intensity of scented household products	*How fragrant are the household products you prefer to buy?*	Intensity	**.539**

Table 2. Kendall Tau correlational analyses of the TDI, OAS scores, and factors of olfactory-related activities. * denotes p < .05, ** < .01, and *** < .001, † denotes a trend p < .1; ns denotes nonsignificant semipartial association.

	retrospective			present		OAS
	Flavor diversity and aroma in childhood	Home processing of herbs and fragrant produce	Female-stereotyped activities	Flavor diversity and aroma at present	Frequency of use and intensity of scented products	
__men__						
OAS	.139†	-.120	__.196**__	.138†	.011	
identification	.111	-.091	.045	__.210**__	__-.154*__^{ns}	.125
discrimination	-.099	-.075	-.073	-.054	-.002	.047
threshold	-.004	.014	-.093	.023	.143†	.022
CGN	.127†	-.133†	.049	.091	-.002	.069
sex. orient	__.213**__	-.130	.135†	.131	-.059	.133
__women__						
OAS	__.186*__	.100	__.218*__	__.296***__	-.019	
identification	.182†	.129	.132	.117	.024	__.185*__^{ns}
discrimination	-.029	-.092	.002	.095	.065	.021
threshold	.050	-.056	-.062	.057	-.008	.073
CGN	-.078	-.068	-.043	__-.178*__	.073	-.044
sex. orient	.101	-.037	-.161†	-.010	.147	.001



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