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What Makes a Better Smeller?

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Abstract

Olfaction is often viewed as difficult, yet the empirical evidence suggests a different picture. A closer look shows people around the world differ in their ability to detect, discriminate, and name odors. This gives rise to the question of what influences our ability to smell. Instead of focusing on olfactory deficiencies, this review presents a positive perspective by focusing on factors that make someone a better smeller. We consider three driving forces in improving olfactory ability: one's biological makeup, one's experience, and the environment. For each factor, we consider aspects proposed to improve odor perception and critically examine the evidence; as well as introducing lesser discussed areas. In terms of biology, there are cases of neurodiversity, such as olfactory synesthesia, that serve to enhance olfactory ability. Our lifetime experience, be it typical development or unique training experience, can also modify the trajectory of olfaction. Finally, our odor environment, in terms of ambient odor or culinary traditions, can

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influence odor perception too. Rather than highlighting the weaknesses of olfaction, we emphasize routes to harnessing our olfactory potential.

Keywords
chemosensory, olfaction, odor detection, odor discrimination, odor recognition, cross-cultural, individual differences

The sense of smell is regularly underestimated which is illustrated by numerous studies examining the limits of human olfactory perception and cognition (see Classen, Howes, & Synnott, 1994, for a historical account of why this is so). Even experts in the field of olfaction often focus on olfactory *dysfunction* (e.g., ''anosmia''—the inability to perceive odor). This follows a long history in psychology of using dysfunction as a methodological tool to build theories about intact systems (e.g., Amoore, 1967). While this approach is valuable in its own right, in this review we contemplate instead the striking feats humans accomplish with their sense of smell and ask under what conditions olfactory abilities thrive. What can we learn if we focus on what human olfaction *can* do and what it is *good* at, rather than focusing on where it fails?

Many of the reasons why ''our noses are better than we think'' have been eloquently reviewed previously (e.g., Laska, 2011; Shepherd, 2004), and more evidence has accumulated since then. Until a few years ago, popular opinion had it that people can distinguish around 10,000 distinct odors (Gilbert, 2008), a number that seems pitiful in comparison with our other senses. The human visual system can distinguish millions of colors (e.g., Pointer & Attridge, 1998) and the auditory system hundreds of thousands of tones (S. S. Stevens & Davis, 1938). In comparison, then, the olfactory sense seemed paltry. But this conclusion has recently been overturned by the work of Bushdid, Magnasco, Vosshall, and Keller (2014) who estimate people can distinguish trillions of odors. Although estimating the capacity of any perceptual system is fraught with pitfalls and by no means uncontentious (cf., Gerkin & Castro, 2015; Kuehni, 2016; Masaoka, Berns, Fairchild, & Abed, 2013), Bushdid et al.'s study has served to galvanize the discussion about the limits of sensory systems, as well as showing the feats the human sense of smell can accomplish. As Yeshurun and Sobel (2010, p. 223) stated a few years earlier ''Humans are astonishingly good at odor detection and discrimination.''

It appears, however, that not all humans have equally good noses, and this is the focus of the current review. A series of studies by Sorokowska et al. raised the specter of possible cross-cultural variation in the human ability to smell. It appears people from other parts of the world have a better sense of smell than people from the West. In one study, Sorokowska, Sorokowski, Hummel, and Huanca (2013) compared olfactory sensitivity among the Tsimane' (an indigenous forager-farming community from Bolivia) with Germans using the ''Sniffin' Sticks'' olfactory threshold test with *n*-butanol (Hummel, Sekinger, Wolf, Pauli, & Kobal, 1997). Sniffin' Sticks are pens which dispense odors in a constant concentration simply by uncapping. In the threshold task, participants are presented with three pens one after another. Only one pen contains *n*-butanol at different concentrations across trials, while the other two are nonsmelling pens (blanks). Participants have to indicate which pen out of the triplet has an odor. By using the Sniffin' Sticks protocol, Sorokowska et al. found the Tsimane' had greater olfactory sensitivity (i.e., lower thresholds for detecting an odor) than their German counterparts. A later study also found people from the Cook Islands in the South Pacific Ocean had greater olfactory sensitivity than a Polish comparison group (Sorokowska, Sorokowski, & Frackowiak, 2015). These studies underscore the possible differences in olfactory abilities worldwide.

In a different line of work, another long-held dogma regarding our olfactory abilities has also been challenged; namely, the idea that: "Smell is the mute sense, the one without words" (Ackerman, 1990, p. 6). Ackerman goes on to describe this most provocatively:

> If there are words for all the pastels in a hue—the lavenders, mauves, fuchsias, plums, and lilacs—who will name the tones and tints of a smell? It's as if we were hypnotized en masse and told to selectively forget. It may be, too, that smells move us so profoundly, in part, because we cannot utter their names. In a world sayable and lush, where marvels offer themselves up readily for verbal dissection, smells are often right on the tip of our tongues—but no closer—and it gives them a kind of magical distance, a mystery, a power without a name, a sacredness. (pp. 8–9)

The belief that smells are impossible, or difficult, to describe has been touted widely (e.g., Ackerman, 1990; Lawless & Cain, 1975; Levinson & Majid, 2014; Olofsson & Gottfried, 2015; Sperber, 1975; Wilson & Stevenson, 2006; Yeshurun & Sobel, 2010). But this view has been questioned by data from non-Western cultures (Majid, 2015). Challenging the claim that "there is no semantic field of smells" (Sperber, 1975, p. 116), the Aslian languages of the Malay Peninsula have well-articulated lexicons capturing smell qualities (Burenhult & Majid, 2011; Majid & Burenhult, 2014; Wnuk & Majid, 2014). For example, in Jahai, the word *haʔɛ̃t* is used for the smell qualities shared between shrimp paste, sap of rubber tree, tiger, feces, musk gland of deer, rotten meat, and so forth; while *ltpɨt* is used for the smell of flowers, perfumes, durian, and bearcat (*Arctitis binturong)*. Jahai, and another Aslian language Maniq, are spoken by small groups of indigenous hunter-gatherers who inhabit lush tropical rainforests. In both languages, there is a rich vocabulary of 12 to 15 smell terms, dedicated to capturing the olfactory qualities important to these communities. These terms clearly have communicative efficacy. Under experimental conditions, the Jahai are as good at naming smells as they are at naming colors, and clearly better at odor naming than matched English speakers (Majid & Burenhult, 2014).

These findings—and others we review later—demonstrate people can discriminate odors and articulate their olfactory experiences more eloquently than we have been led to think. What might underlie these cross-cultural differences? To begin to answer this question, we must first consider the various factors that influence olfactory function more generally. In this review, we provide a broad perspective on the empirical findings that shed light on our olfactory abilities in a hope to better lay bare the landscape of variation within which cross-cultural diversity sits.

There are at least three factors to consider as foundations of variation: our biological infrastructure, the experiences we navigate during our lifetime, and our physical and social environment. How does each of these contribute to olfactory abilities? Olfactory function itself can be assessed in various ways, from self-report to psychophysical testing. We do not review factors affecting perceptual judgements, such as intensity, pleasantness, and familiarity; since these require a different framework of consideration (i.e., it is less intuitive to know what it means to be "better" at judging pleasantness or intensity). We focus primarily on behavioral studies of odor *detection*, *discrimination*, and *recognition*, while drawing on other data as pertinent. Briefly, tests of odor detection (also known as "sensitivity") establish how little of an odorant is required for a person to be able to sense it (i.e., what the olfactory threshold is). In a discrimination task, the ability to differentiate odors from each other is assessed. Odor recognition measures include forced-choice tasks where people pick a label to go with an odor (odor identification) and free-naming where people have to generate a label themselves (odor naming). The cognitive demands increase from odor detection to odor naming, with the former being more "low-level" than the latter.

While we have attempted to do justice to the available evidence in each case, there are no doubt additional factors still to be considered. It should also be said that topics we discuss under one section could as well be included under another (e.g., sex differences in olfaction are often considered to be a result of biology, but could also be understood from a sociocultural perspective; see "*Sex differences*" section). Regardless of whether the factors we consider under each section rightfully belong there, the broad remit of biology, experience, and environment, nevertheless serves as a useful roadmap of the issues. So, what factors make us better smellers?

Inherit a Particular Biological Infrastructure

Can the attested differences we see in olfactory perception and cognition be attributed to biological differences between groups of people? There is tremendous variation within and between populations in olfactory receptor (OR) genes and pseudogenes (see, e.g., Hoover, 2010, for review). Humans have more than 1,000 OR genes of which around 400 are functioning. Studies show African populations have more functional ORs than non-Africans (Hoover et al., 2015; Menashe, Man, Lancet, & Gilad, 2002, 2003), suggesting they also differ behaviorally; but there has been no direct test of olfactory abilities. There is evidence linking genotypic variants of odor receptors with olfactory abilities within populations, however. Keller, Zhuang, Chi, Vosshall, and Matsunami (2007), for example, found people with the OR7D4 RT/RT genotype were more sensitive to androstenone and androstadienone (but not any other odor) than those with RT/WM or WM/WM genotypes. RT/RT participants also rated high concentrations of androstadienone as "extremely unpleasant," and were more likely to label androstenone "sickening," whereas RT/WM participants were more likely to label it "vanilla." Other studies have similarly linked specific OR genes to olfactory abilities related to particular odors (e.g., Jaeger et al., 2013; Mainland et al., 2013; Menashe et al., 2007; McRae et al., 2013), but have not yet scaled-up so as to account for differences between groups (e.g., African vs. non-African). Despite the exciting leaps in this area, given the vast cultural and ethnic diversity there is worldwide, we are still far from understanding how genetic variation relates to ecologically relevant olfactory behaviors.

The remainder of this section reviews areas with a large body of empirical data directly addressing olfactory abilities. In particular, we examine (a) sex differences, (b) neurodiversity, and (c) cases of trade-offs between the senses. In each of these cases, a biological basis for a boost to olfactory function has been postulated. We critically examine the evidence.

Sex Differences

General wisdom has it that women are better smellers than men. This idea has a long history in Western thought as Classen (1997, p. 4) points out: "men tended to be linked with the 'rational' senses of sight and hearing, and women with the 'corporeal' senses of smell, taste and touch." This belief has wide-spread acceptance today too: Women rate their own sense of smell higher than men do (Wysocki & Gilbert, 1989); they say smell is more important to them (Croy, Buschhüter, Seo, Negoias, & Hummel, 2010; Seo et al., 2011); and that they are generally more attentive and interested in odors (Ferdenzi, Coureaud, Camos, & Schaal, 2008; Havlicek et al., 2008). On the flip side, women also report being more disturbed by odors (Nordin, Bende, & Millqvist, 2004; Nordin, Palmquist, Bende, & Millqvist, 2013); and when they suffer from an olfactory dysfunction, women feel their quality of life is affected much more than men do (Frasnelli & Hummel, 2005). However, none of this speaks to whether women actually have better olfactory abilities. When we turn to the experimental literature for answers, the picture is murky.

Some studies find women are better than men at odor detection for particular odors (e.g., Andersson, Lundberg, Åström, & Nordin, 2011; Cometto-Muñiz & Abraham, 2008; Hedner, Larsson, Arnold, Zucco, & Hummel, 2010; Hulshoff Pol, Hijman, Baare, van Eekelen, & van Ree, 2000; Pinkaew, Assanasen, & Bunnag, 2015), but other studies do not (e.g., Guarneros, Hummel, Martínez-Gómez, & Hudson, 2009; Larsson, Finkel, & Pedersen, 2000; Oberg, Larsson, & Backman, 2002). There is even evidence to the contrary, demonstrating instead that men are better at detecting specific odors (e.g., Olsson & Laska, 2010). The same mixed picture is found for odor discrimination. Data from infants show female, but not male, neonates have a preference for an odor they were exposed to for 24 hours (Balogh & Porter, 1986). More impressively still, they prefer breast odor of a lactating female compared with a nonlactating female (Makin & Porter, 1989). Evidence of better discrimination from adult females is less convincing, however. For example, Hulshoff Pol et al. (2000) found women were better at discriminating which odor was the odd one out from three different concentrations of phenylethyl alcohol—but only at short durations. When comparing adults' discrimination across a number of different odors, others have found no differences (e.g., Hedner et al., 2010; Oberg et al., 2002; Zatorre & Jones-Gotman, 1990).

As we move on to higher level aspects of olfactory abilities, such as odor identification and naming, there is more support for women doing better than men (e.g., Cain, 1979; Cardesín et al., 2006; Doty, Applebaum, Zusho, & Settle, 1985; Nordin, Nyroos, Maunuksela, Niskanen, & Tuorila, 2002; Wysocki & Gilbert, 1989; although see, e.g., Hedner et al., 2010; Larsson et al., 2000). This effect may not reside in the olfactory system per se, however; but could indicate instead differences in cognition (cf., Ohla & Lundström, 2013). For example, Dempsey and Stevenson (2002) taught men and women novel names for odors and found both groups learned odor-name associations at the same rate and were equally good at odor naming on the day they learned them. But a week later, women were significantly better at recalling the odor names. This study is important because it shows differences in odor naming arise because women are better able to consolidate their memories than men—a general cognitive effect.

Contrary to common wisdom, then, the case for women being better smellers than men is not clear-cut after all. There are dozens of studies either directly or incidentally examining sex differences in olfactory function, and yet firm conclusions are still hard to draw. Studies differ in the number and type of odors tested, the method of testing, and generalizations are difficult to draw because studies are often underpowered (see Brand & Millot, 2001; Doty & Cameron, 2009, for reviews). A systematic meta-analysis is called for, but crucial information is likely missing from the original studies hindering firm conclusions even then. For example, Nováková, Havlíček, and Roberts (2014) conducted a meta-analysis focusing on olfactory function during the menstrual cycle and found women were better at odor detection in fertile than nonfertile phases. This was true for "food" and "musky" odors (which have different evolutionary functions) but not for rose odor (phenyl-ethyl alcohol; whose detection has no clear evolutionary significance). Most studies examining sex differences do not report or control for where in her menstrual cycle a woman might be creating a further obstacle to systematic comparison across studies.

More generally, one can ask what causes sex differences in olfaction—to the extent they exist in the first place. As alluded to earlier, hormones could play a role. In addition, brain anatomy could differ. Oliveira-Pinto et al. (2014) compared the number of cells in the olfactory bulbs of men and women postmortem, and found women had significantly more neurons than men, even when correcting for mass. Given olfactory bulb volume correlates with olfactory function (Seubert, Freiherr, Frasnelli, Hummel, & Lundström, 2013), this might provide a biological basis for the odor recognition effects described earlier. However, in the same study examining the relationship between olfactory function and structural anatomy of the brain, Seubert et al. (2013) failed to find any differences in olfactory abilities between men and women. Since Oliveira-Pinto et al. (2014) only compared a small sample of men and women, the reported sex differences in anatomy found may be spurious. In any case, even if there are differences in brain anatomy between men and women, this in itself would not tell us whether biology directly causes these differences, since men and women could have different life experiences with odors, and experience also shapes the brain.

As we summarized earlier, there is a wide-spread belief that women are better smellers than men. Nation-wide comparisons show countries differ in the stereotypes residents hold about gender and science (i.e., the extent to which people believe science = male), and that these beliefs predict science and math achievement (Nosek et al., 2009). So the belief that women can smell better—rather than any biological difference—could explain differences in olfactory function. Some evidence consistent with this comes from Nováková, Valentová, and Havlíček (2013), who found childhood gender conformity predicted olfactory abilities; specifically gender-conforming men were worse at odor identification than gender-nonconforming men irrespective of their sexual orientations. In sum, although women report a greater interest in odors, and may have an advantage in odor recognition, there is little clear evidence they are generally better at odor detection and discrimination.

Neurodiversity and Possible Positive Impacts on Olfactory Function

Much attention has focused on the negative effects conditions such as Parkinson's, Alzheimer's, depression, schizophrenia, and so forth, have on olfaction; but there are other conditions which may boost olfactory function according to some. People with autism spectrum disorders (ASD), attention-deficit hyperactivity (ADHD), and synesthesia have "hyper-excitable" brains (of one sort or another) and for various reasons people have suspected this may have a positive impact on olfactory functions. Let's review each case in turn.

People with ASD experience hyper- or hypo-reactivity to sensory stimuli, often involving atypical reactions to odors and tastes (e.g., Legiša, Messinger, Kermol, & Marlier, 2013; Martin & Daniel, 2014; Rogers, Hepburn, & Wehner, 2003). This has led people to speculate people with ASD are more sensitive to odors. This appears not to be the case, however. Most studies find no differences (Galle, Courchesne, Mottron, & Frasnelli, 2013; Suzuki, Critchley, Rowe, Howlin, & Murphy, 2003; Tavassoli & Baron-Cohen, 2012), with one study finding decreased sensitivity (Dudova et al., 2011) and another increased sensitivity in individuals with ASD compared with controls (Ashwin et al., 2014). For discrimination, one study found no difference between ASD individuals and controls (Galle et al., 2013) and another diminished discrimination in ASD individuals (Wicker, Monfardini, & Royet, 2016). ASD individuals do not clearly differ from controls in odor recognition either (Brewer, Brereton, & Tonge, 2008; Dudova et al., 2011; Luisier et al., 2015), with some studies finding poorer odor identification (Bennetto, Kuschner, & Hyman, 2007; Galle et al., 2013; Suzuki et al., 2003; Wicker et al., 2016). Taken together, it appears having ASD does not lead to enhanced olfactory functions contrary to expectations.

In contrast, ADHD does appear to improve olfactory abilities. ADHD is a neurodevelopmental disorder involving problems with attention and hyperactivity. Romanos et al. (2008) found better odor detection, but not discrimination, in a group of children and adolescents with ADHD, compared with matched healthy participants. This greater sensitivity disappeared with methylphenidate (MPH) treatment, an indirect dopamine receptor agonist. The authors therefore suggest improved odor sensitivity is related to dopaminergic dysregulation. Increased odor sensitivity, but not trigeminal sensitivity, in ADHD has also been reported by Lorenzen et al. (2016). Other studies, however, have failed to find a difference in odor sensitivity when comparing ADHD adults to matched patients with bulimia nervosa (Weiland et al., 2011), or ADHD children to matched controls (Sarı & Taşkıntuna, 2015), with one study even showing ADHD children and adolescents had lower sensitivity than matched healthy controls (Ghanizadeh, Bahrani, Miri, & Sahraian, 2012). But these contradictory results could arise due to the medications ADHD individuals were taking: If people are being tested while on medication (e.g., MPH), or with insufficient time since they last took MPH, then possible positive effects of ADHD would be obliterated in testing (cf., Lorenzen et al., 2016).

Finally, let's turn to synesthesia. This is a neurological phenomenon where perceptual input in one modality (i.e., inducer) leads to involuntary secondary sensation (i.e., concurrent); for example, when a person sees the letter *R* (inducer), they "see" it as having a nonexistent color (e.g., yellow; the concurrent). This "neurodevelopmental synaesthesia" contrasts with what has been dubbed "olfactory-induced synaesthesia" which all people experience (Stevenson, 2009; Stevenson & Tomiczek, 2007). Rather than consider this multisensory interaction between smell, taste, and the trigeminal system as "synaesthesia," it might better be viewed as the unified perception of "flavor" (Auvray & Spence, 2008). To avoid further confusion, we focus on neurodevelopmental synesthesia here.

Some synesthetes have been reported to experience an illusory odor when they see certain people (Simner et al., 2006), objects (Chan et al., 2014), or when reading or hearing words (Ward, Simner, & Auyeung, 2005). Intriguingly the same word can be experienced as having different retronasal and orthonsal concurrents; for example, the word *Alessandro* experienced as having the flavor of "fried potatoes" but the smell of "burnt wool" (reported in Ward et al., 2005). Using fMRI, Chan et al. (2014) found that when a visual object-odor synesthete viewed pictures of objects with an odor concurrent, the piriform cortex was activated to a greater extent than when viewing pictures that did not trigger the synesthetic experience.

A different type of synesthesia has odor as the inducer, so that when it is perceived the odor gives rise to illusory color sensations. Speed and Majid (submitted) found odor-color synesthetes outperformed a group of matched control participants on odor discrimination, but not threshold using Sniffin' Sticks (Hummel, Sekinger, et al., 1997). The same study, as well as an earlier study by Russell, Stevenson, and Rich (2015), also found that odor-color synesthetes were better at odor naming than controls. So, it appears odor-color synesthetes do have enhanced olfactory cognition. The fact that differences do not appear in threshold judgments suggests differences may lie in conceptual rather than perceptual systems. Speed and Majid suggest synesthetic associations to odors strengthen odor concepts, making them more differentiated, thus facilitating odor discrimination and naming. Whether the same holds for synesthetes with odor as a concurrent remains to be established.

Plasticity and Sensory Loss

Is there a trade-off between the senses, such that loss of one sensory modality heightens the activities of the others? Are blind and deaf people, for example, better able to smell than their sighted or hearing counterparts? Children with visual impairments pay more attention to odors than sighted children according to self-report questionnaire data; especially odors related to social and food spheres (Ferdenzi, Coureaud, Camos, & Schaal, 2010).

This seems to confirm anecdotal reports of enhanced olfactory abilities in the blind. So what does the evidence say?

As before, the data are mixed; but overwhelmingly suggests blind people are not better smellers. Most studies report no significant group differences in odor detection between blind and sighted people (congenital or early blind: Cornell Kärnekull, Arshamian, Nilsson, & Larsson, 2016; Diekmann, Walger, & von Wedel, 1994; Guducu, Oniz, Ikiz, & Ozgoren, 2016; Luers et al., 2014; Rosenbluth, Grossman, & Kaitz, 2000; Smith, Doty, Burlingame, & McKeown, 1993; Sorokowska, 2016; Wakefield, Homewood, & Taylor, 2004; late blind: Cornell Kärnekull et al., 2016; Smith et al., 1993; Sorokowska, 2016; onset of blindness unknown: Schwenn, Hundorf, Moll, Pitz, & Mann, 2002). One study even reports diminished olfactory detection (Murphy & Cain, 1986), while only three studies comparing congenital or early blind people to sighted controls find the blind have higher sensitivity to odors (Beaulieu-Lefebvre, Schneider, Kupers, & Ptito, 2011; Çomoğlu et al., 2015; Cuevas et al., 2010).

The evidence for enhanced olfactory discrimination in the blind is also rather mixed, with the weight of evidence suggesting no difference. Some studies find blind people are better at discriminating between odors (Çomoğlu et al., 2015; Cuevas et al., 2010; Cuevas, Plaza, Rombaux, De Volder, & Renier, 2009; Renier et al., 2013; Rombaux et al., 2010), others find no difference (congenital or early blind: Beaulieu-Lefebvre et al., 2011; Cornell Kärnekull et al., 2016; Diekmann et al., 1994; Guducu et al., 2016; Smith et al., 1993; Sorokowska, 2016; late blind: Cornell Kärnekull et al., 2016; Smith et al., 1993; Sorokowska, 2016; onset of blindness unknown: Schwenn et al., 2002), while one reports poorer discrimination in the blind than sighted (Luers et al., 2014).

As with sex differences, it appears there is stronger evidence of better odor naming by the blind (e.g., Cuevas et al., 2009; Murphy & Cain, 1986; Renier et al., 2013; Rombaux et al., 2010; Rosenbluth et al., 2000; Wakefield et al., 2004; although see Cornell Kärnekull et al., 2016; Sorokowska, 2016). Studies of odor identification using a forced-choice paradigm, on the other hand, show no differences between blind people and controls (e.g., Beaulieu-Lefebvre et al., 2011; Çomoğlu et al., 2015; Cuevas et al., 2010; Cuevas et al., 2009; Guducu et al., 2016; Iversen, Ptito, Møller, & Kupers, 2015; Luers et al., 2014; Rosenbluth et al., 2000; Smith et al., 1993; Sorokowska, 2016); although it appears blind people might be better at identifying emotions such as fear and disgust from sweat smells (Iversen et al., 2015).

The majority of studies on possible olfactory boosts as the result of plasticity have focused on loss of vision, whereas studies of the possible impact of hearing loss are few—even though they raise the same questions. Diekmann et al. (1994) and Guducu et al. (2016) both compared olfactory functions between congenitally deaf, blind, and sighted or hearing people, and reported diminished—not enhanced—odor threshold and discrimination for the deaf.

In sum, the speculation of some sort of trade-off between the senses appears weak on closer examination. The strongest evidence of enhanced olfactory function comes from odor naming in the blind. The fact that blind participants appear to do better in free odor naming, and not necessarily in forced-choice odor identification, suggests any advantage here may lie in the language system, rather than the olfactory system per se.

Have the Right Kinds of Experiences

Over our lifetime, we accumulate different histories of experience, some of them in the normal course of development and others because of differential exposure and interest in odors. What sorts of experiences lead to better olfactory function? We review (a) changes over development, (b) the role of mere exposure to odors, and (c) expertise.

Olfactory Changes Over Development

How olfactory perception differs across the lifespan can tell us which factors are important for detection and discrimination abilities. Do such changes co-occur with cognitive changes or do they reflect changes in peripheral function?

Olfactory detection has been shown to improve within the first 4 days of life (Lipsitt, Engen, & Kaye, 1963). There are studies suggesting odor sensitivity changes later during childhood too. Hummel et al. (2011) found odor detection increased continuously from 6 to 17 years. Similarly, testing 4- to 12-year-olds, Monnery-Patris, Rouby, Nicklaus, and Issanchou (2009) found children between 5 and 6 years improved in a suprathreshold detection task, and a threshold task with tetrahydrothiophene (THT), with further improvements on the THT threshold task between 6 and 10. Yet many studies suggest odor detection remains fairly stable in childhood. For example, Hummel et al. (2007) found no difference in threshold for children between 3 and 6, and other studies fail to find differences in threshold between children and adults (age 8–14 vs. 18–28, Cain et al., 1995; participants aged 4–90, Lehrner, Glück, & Laska, 1999). Other studies even suggest odor sensitivity is higher in children than adults (Dorries, Schmidt, Beauchamp, & Wysocki, 1989; Solbu, Jellestad, & Strætkvern, 1990). Two possible explanations have been put forward for these discrepancies. First, differences in findings may be related to cognitive ability. Studies showing improved sensitivity throughout childhood have used tasks that more strongly tax working memory (e.g., Hummel et al., 2011; Monnery-Patris et al., 2009), so the poorer performance in younger children may reflect shorter memory span (Hummel et al., 2011). Second, there may be different developmental trends for different odors. For example, greater sensitivity with age was observed for THT, but not R-(+)-carvone, by Monnery-Patris et al. (2009). THT is an odor used in domestic gas, and therefore its increased sensitivity over time could mirror children's growing knowledge and reactivity to its significance.

In contrast, olfactory discrimination improves throughout childhood; 11-year-olds (and adults) are better at odor discrimination than 6-year-olds (Stevenson, Mahmut, & Sundqvist, 2007; Stevenson, Sundqvist, & Mahmut, 2007), and young adults are better than adolescents (Hummel et al., 2011; Zucco, Hummel, Tomaiuolo, & Stevenson, 2014). These differences could be due to experience: Because younger children have experienced fewer odors, odor percepts for any specific odor should be redolent, increasing confusability between different odors (Stevenson, Sundqvist, et al., 2007). Alternatively, the effects could reflect developmental changes in working memory. Indeed, adolescents benefit more than young and middle-aged adults when short-term memory load is reduced during a discrimination task (Zucco et al., 2014). However, whether this explanation also holds for differences attested at younger ages is not yet clear.

The improvement in discrimination also appears to be independent of any odor naming abilities. There is patent improvement in odor identification and naming throughout childhood (e.g., Bastos, Guerreiro, Lees, Warner, & Silveira-Moriyama, 2015; Cameron & Doty, 2013; Cavazzana et al., 2016; De Wijk & Cain, 1994; Doty et al., 1984; Hugh et al., 2015; Lehrner et al., 1999; Monnery-Patris et al., 2009; Oleszkiewicz et al., 2016; Rothschild, Myer, & Duncan, 1995), related to the growing vocabulary and linguistic prowess of children. So, in principle, children's improved discrimination could rely on a verbal code. But this does not appear to be the case. The improved discrimination between 6- and 11-year-olds remains even when children had to do a secondary task with verbal suppression (i.e., repeating *the, the, the*... between odors). Of course, improvements could also be due to physiological maturation in the olfactory mucosal layer or epithelium (e.g., see Doty & Kamath, 2014, for a review); although it is unclear whether such changes would affect discrimination (Stevenson, Mahmut, et al., 2007).

Into adulthood, the literature almost unanimously shows olfactory function is at its peak, but then declines later in life. This is true for odor detection (e.g., Cain & Gent, 1991; Guarneros, Hudson, López-Palacios, & Drucker-Colín, 2015; Hummel, Barz, Pauli, & Kobal, 1998; Kern et al., 2014; Kobal et al., 2000; Lehrner et al., 1999; Murphy, Nordin, De Wijk, Cain, & Polich, 1994; J. C. Stevens & Dadarwala, 1993), discrimination (e.g., Guarneros et al., 2015; Hummel, Barz, et al., 1998; Hummel, Sekinger, et al., 1997; Kobal et al., 2000; Zucco et al., 2014), and odor identification and naming (e.g., Doty et al., 1984; Fornazieri et al., 2015; Hummel, Sekinger, et al., 1997; Larsson et al., 2000; J. Wang, Sun, & Yang, 2016), although it has been suggested such deterioration may be odorant-specific (Seow, Ong, & Huang, 2016). Hummel, Sekinger, et al. (1997) found such decreases were more pronounced in those aged over 65. One study however found the decline in olfactory ability over 65 was small in a sample of healthy, nonmedicated, nonsmokers, but larger in age-matched medicated smokers, or people with a history of nasal problems (Mackay-Sim, Johnston, Owen, & Burne, 2006). Similarly, there was no difference in detection threshold between young adults and elderly participants when the elderly participants were "successfully aged" in terms of medical health and cognitive ability (Nordin, Almkvist, & Berglund, 2012). In addition, Sulmont-Rosse et al. (2015) found a link between level of dependence (e.g., whether or not an individual lives alone, has assisted living, or lives in a nursing home) and chemosensory abilities, independent of age. So it seems factors secondary to aging, such as poor medical health and cognitive decline, could explain some of these effects. In line with this, a discrimination task with reduced load on short-term memory benefits the elderly more than younger adults (Zucco et al., 2014).

In sum, olfactory functions improve in early childhood but then appear to remain remarkably stable throughout life. This, however, belies further differences which arise as a result of differential experience as adults. We next consider improvements to olfaction in adulthood that accompany training.

Improvements in Olfactory Function Due to Training: Mere Exposure

Can perception of odors be improved from mere exposure to odors? Can it be improved with explicit training, involving more conceptual processing of odors? The olfactory system is thought to possess greater neural plasticity than elsewhere in the central nervous system. The neuroepithelium and parts of the olfactory tract experience neurogenesis throughout the lifespan (e.g., Brann & Firestein, 2010; Lötsch et al., 2014). Because of this neuroplasticity, olfactory training has the potential to improve olfactory perception. Does it?

Some people have problems smelling after having suffered olfactory dysfunction, and one technique to overcome this is "mere exposure" training. A standard protocol involves merely sniffing a small number of odors (usually four), twice a day for a period of 12 to 18 weeks (e.g., Haehner et al., 2013; Hummel et al., 2009; Kollndorfer et al., 2014; Mori, Petters, Valder, & Hummel, 2015; Schriever, Lehmann, Prange, & Hummel, 2014). Mere exposure improves threshold, discrimination, and identification in Parkinson's patients with olfactory loss (Haehner et al., 2013) and patients with olfactory dysfunction (Damm et al., 2014; Hummel et al., 2009; Konstantinidis, Tsakiropoulou, Bekiaridou, Kazantzidou, & Constantinidis, 2013). Two independent meta-analyses found training has a large effect on odor discrimination and identification and a small-to-moderate effect on odor detection (Pekala, Chandra, & Turner, 2016; Sorokowska, Drechsler, Karwowski, & Hummel, 2016). The benefits of training further depend on the severity or characteristics of the olfactory dysfunction and duration of training (Pekala et al., 2016; Sorokowska et al., 2016).

This standard form of training has also been shown to be effective for improving odor threshold and identification in healthy children aged 9 to 15 (odor discrimination was not tested; Mori et al., 2015). Only one study to date used mere exposure training with healthy adults (aged 55–96) and found no significant improvement in detection. However, at the end of the study, the trained group did differ from controls, suggesting olfactory function remained stable in the trained group, but declined in the control group (Schriever et al., 2014).

Other studies have found improved odor perception in healthy participants with mere exposure to odors, but with procedures diverging from those described earlier. Engen (1960) found merely practicing a threshold test with an odor (24 times) improved detection for that odor (in four out of six odors). Olfactory detection improves uniformly over days of practice (Rabin & Cain, 1984), and over 4 days of threshold testing detection can be improved by at least 25% (Cain & Gent, 1991). Sniffing androstenone for 3 min, three times a day, for 3 weeks also significantly improves detection threshold (L. Wang, Chen, & Jacob, 2004); in fact 2 weeks sniffing is enough to improve detection (Boulkroune, Wang, March, Walker, & Jacob, 2007). A striking result comes from training studies with anosmic patients. After sniffing androstenone three times a day for 6 weeks, half the tested participants who were previously anosmic to androstenone could now smell it. No improvement was seen after the same training with amyl acetate (Wysocki, Dorries, & Beauchamp, 1989). Aside from changes in detection, discrimination of androstenone also improves following repeated testing; moreover, this improvement is more pronounced when participants separately sniff androstenone daily on top of the repeated testing (Mörlein, Meier-Dinkel, Moritz, Sharifi, & Knorr, 2013).

While it is evident repeatedly smelling an odor makes a person more sensitive to that specific odor, we do not know whether it also makes people sensitive to other odors (not part of the training). Earlier studies used such disparate odors that it is difficult to make firm conclusions. However, Dalton, Doolittle, and Breslin (2002) found repeated testing improved odor detection for several odors beyond the one specifically trained (although this improvement was only found in women of reproductive age). In an elegant study, Li, Luxenberg, Parrish (2006) exposed people to an odor for 3.5 min and found enhanced differentiation for odorants related in odor quality (e.g., ‘‘floral’’) and functional group (in terms of odorant structure). So simply smelling an odor can make you more sensitive to it and make it more distinct from the other odors you experience.

More Than Mere Exposure—The Making of An Odor Expert

If mere exposure can achieve boosts to olfactory functions, what feats can be accomplished with active training? Here, we turn to olfactory experts and examine whether their olfactory functions are boosted, before returning to the issue of how to train expert noses.

Experts are people with extensive knowledge about a particular domain (e.g., perfume) or who have procedural skills most people would only be able to perform poorly (e.g., for a wine expert, the swirl-sniff-slurp-swish-spit routine; see Weinstein, 1993). Level of expertise can, of course, vary (i.e., one can be on the way to becoming an expert); but substantive knowledge of a domain is usually acquired through extensive training and professional practice (e.g., Caley et al., 2014).

If we construe olfactory expertise broadly—encompassing both orthonasal and retronasal components—then there are many interest groups to explore, aside from perfumers: sommeliers, master chefs, certified baristas, tea sommeliers, cheese mongers, and so forth. In actual fact, most research on olfactory expertise has focused on wine experts, mainly sommeliers and vinologists (see Royet, Plailly, Saive, Veyrac, & Delon-Martin, 2013, for review). There are several reasons for this: There are many wine experts; they are easier to recruit than perfumers, for example, whose knowledge can often be proprietary; their expertise is easier to quantify through certified qualifications and established questionnaires; and the domain of wine is more accessible with open documentation widely available. Given the vast literature on wine experts, we focus our attention primarily on them in this section, with brief forays into other expert domains as relevant.

A wine can have as many as 800 different aromatic volatiles (Ortega-Heras, González-SanJosé, & Beltrán, 2002), and a wine expert has to be able to detect and distinguish the aromas within a wine, as well as between wines. There is evidence experts develop more sensitive noses for some of these aromas (as we discuss later). Wine experts also receive additional benefits in olfactory abilities from "mere exposure" paradigms. When asked to just sniff either diacetyl or linalool every day for 1 month, experts were better able to detect the trained odor (Tempere, Cuzange, Bougeant, Revel, & Sicard, 2012). In fact, just imagining odors appears sufficient to improve detection for the imagined smell (Tempere, Hamtat, Bougeant, de Revel, & Sicard, 2014).

Not all experts are alike. In a large study of over 200 wine professionals, experts who had received specialized training in wine were significantly more sensitive to the smell of both diacetyl and ethylphenols than experts without specialized training (Tempere et al., 2011); moreover, wine-makers—rather than wine-growers or others in the wine industry—also had lower thresholds for ethylphenols (Tempere, Cuzange, et al., 2014). When present in small amounts in wine, ethylphenols produce a desirable "leathery" aroma, but in larger amounts are considered a wine fault (known as "brett" or "horsey"). So this odor is particularly pertinent for wine-makers who need to pinpoint the exact concentration of this aroma in the wine they are making.

That being said, wine experts are not better at detecting all wine-related odors. In one study, 2-isopropyl-3-methoxypyrazine—an undesirable odor also known as "ladybug taint" in wine—was added in different concentrations to three different wines. Wine experts and novices did not differ in their detection thresholds for this odor (possibly because of the large individual differences; Pickering, Karthik, Inglis, Sears, & Ker, 2007). Studies using an odor detection task with *n*-butanol also failed to find differences between wine expert and novice thresholds (Bende & Nordin, 1997; Brand & Brisson, 2012; Parr, Heatherbell, & White, 2002; Parr, White, & Heatherbell, 2004). As well as studying detection for *n*-butanol, Brand and Brisson (2012) also examined detection of three different wines which were each diluted in 20 steps. For all three wines, novices had a lower detection threshold (but only for the left nostril). To explain these somewhat surprising results, the authors suggest experts might have become relatively desensitized to the smell of alcohol since they experience it so often. Taken together, studies examining how sensitive the expert nose is have somewhat contradictory results. While experts might not be more sensitive to smells in general, they may have lower detection thresholds for smells specific to their expertise.

When it comes to odor discrimination, there is a much larger and varied body of evidence to suggest experts are better than novices. In studies where wine experts were asked to select the odd one out from a set of three different wines, they made more correct judgments than novices; although if the wines were very similar to one another, the differences between experts and novices were attenuated (Lawless, 1984; Solomon, 1990). Solomon (1997) asked experts and novices to discriminate between triads of cheap, white Bordeaux wines and found no statistical difference between experts and novices (although the numerical difference was consistent with an expert advantage). Similarly, beer experts were better able to discriminate between beers than novices (Chollet, Valentin, & Abdi, 2005; Valentin, Chollet, Beal, & Patris, 2007). In another study, Fujii et al. (2007) asked Japanese masters of koh-do—an ancient Japanese tradition of incense appreciation—to discriminate between four types of incense while their brain activity was measured using near infrared spectroscopy. The experts appeared to be better than novices at discriminating the incenses, although both groups were equally good at distinguishing between tea odors (a control odor stimulus). Moreover, the experts showed activation of the right prefrontal cortex (PFC) during discrimination of incense, followed by later left PFC activation. The authors conclude this PFC activation reflects reasoning processes that the experts—but not novices—engage in while they process incense odors.

It is not clear whether experts' odor discrimination abilities are general across odors. The Fujii et al. study suggests a limited advantage, since incense experts were no better than novices at distinguishing tea odors, but in a different study wine experts were better at discriminating between solutions of clove and citrus in weaker concentrations than novices (Bende & Nordin, 1997). Although this is an intriguing finding, the fact that experts also show little generalization for odor detection suggests odor discrimination improvements might also be restricted to those that have been specifically trained. Consistent with this, Croijmans and Majid (2016) found wine experts were only better at naming the odors of wines, but not of coffee or everyday objects—again suggesting limited generalization of experts' odor abilities.

In addition, there are limitations imposed on all smellers regardless of their experience. For example, when more than four odors are mixed together both experts (perfumers and flavorists) and novices failed to identify individual components of the odor mixture; but when there were only two to three odors in a mixture, experts were better at discriminating and identifying the components than novices (Livermore & Laing, 1996). This shows that while experts might have enhanced odor perception and cognition, there is nevertheless a ceiling to these improvements.

So, taken together, these studies indicate experts have improved odor detection and discrimination for smells related to their domain of expertise, but they are not more sensitive for smells in general. A number of factors, including type of training, type of odor, and the function the odor plays in their expertise influences expert odor perception and cognition. A question with obvious application is what type and how much training is the most advantageous for developing expert olfactory skills.

It seems that a few hours of training can already lead to substantial improvements in odor discrimination, for example. In one experiment, beer-expert-trainees were trained for just 11 hours to evaluate components of beer and to detect added flavors. In testing, beer-expert-trainees sorted beers more consistently than beer-consumers. When tested on a beer communication task, however, the effect of expertise was more limited. Participants were assigned to pairs and given a series of six beers which they had to match based on verbal descriptions alone. In this task, beer-expert-trainees performed better than beer-consumers when they had to match supplemented beer (which they had previously trained on), but when matching commercial beers, training did not help the beer-expert-trainees; the beer-consumers performed better (Chollet & Valentin, 2001). At the end of 2 years of training, those trained were better able to discriminate between beers, but only for the beers they were specifically trained on (Chollet et al., 2005).

As for what type of training is helpful, Rabin (1988) tested odor discrimination after three different training procedures versus no training. Participants were trained (a) to use consistent labels for the target odors in the experiment (target-label training), (b) to give labels for odors that were *not* the target odors (nontarget-label training), (c) used odor-adjective attribute lists to capture the quality of the odor (odor-profile training), or (d) had no form of training (no training). Training took around 1 hr and was completed the day before the discrimination test, where participants smelled two odors and had to decide if the second odor was the ''same'' or ''different'' to the first. Rabin found discrimination performance was highest in after target-label training, followed by the odor-profile training, but there was no difference between the other conditions. So, training of the target odors either with labels or by profiling likely helped participants focus on discriminative features of the odors, such that ''more familiar stimuli possess sharper categorical boundaries'' (Rabin, 1988, p. 539).

From the small number of studies so far, we can conclude that active training with odors improves odor discrimination. At present, however, it is unclear how such training compares with the mere exposure paradigm, and to what extent the improvements in discrimination generalize to new odors. To our knowledge, no study has utilized a more active training strategy to improve odor sensitivity, except Tempere, Hamtat, et al. (2014) who found mental imagery training for specific odors improved odor detection. It is possible that such active training could benefit odor discrimination performance more (as compared with mere exposure training) because discrimination is a higher level process than odor detection. In support of this, cognitive variables (measures of executive function and semantic memory) have been shown to predict individual odor discrimination scores, but not odor threshold scores (Hedner et al., 2010).

Live in the Right Environment

Given that mere exposure can influence how people perceive odors, it is important to consider the role the environment may play in olfactory detection and discrimination. Temperature, humidity, barometric pressure, air currents will all influence how molecules move and how they are processed by the perceiver (Muller-Schwarze, 2006). This means some environments might, in fact, be more odorous than others (compare a cool damp Glasgow to a humid subtropical summer in Naples).

The positive effects of environment on olfactory perception are little explored; instead the emphasis is often on the role that, for example, pollution might have on olfactory perception. For example, Sorokowska et al. (2015) compared Europeans (i.e., Polish participants) living in a modern industrialized society (with its concomitant environmental pollution) to the Tsimane' who live in a relatively unpolluted natural environment and people from the Cook Islands, apparently one of the least polluted places on the planet. They found people from the Cook Islands had the lowest detection thresholds, followed by the Tsimane' and then Polish people, as predicted. Although this study does not provide causal evidence for a link between environmental pollution and olfactory sensitivity, it dovetails with other data showing everyday pollution negatively affects olfactory perception (e.g., Guarneros et al., 2009; Guarneros, Ortiz-Romo, Alcaraz-Zubeldia, Drucker-Colín, & Hudson, 2013; Hudson, Arriola, Martinez-Gomez, & Distel, 2006), and intensive exposure to airborne smoke and dust can deteriorate odor detection, discrimination, and identification (e.g., Altman et al., 2011; Dalton et al., 2010). Conversely, then, we can conclude that unpolluted environments have a positive effect on olfactory perception and cognition. Interestingly, in this light, an analysis of 65 travel accounts by various authors—such as Balzac, Coleridge, Süskind, Lodge, and Kerouac—showed that odors in rural environments are described much more positively than those in urban environments (Dann & Jacobsen, 2003).

Not all studies show a negative impact of odorous environments on olfaction, however. Perfume retail outlets can be intensely aromatic, as anyone who has shopped in one can attest. So, one could predict that people working in such an environment might also suffer from exposure to these odors. But when Hummel, Guel, and Delank (2004) compared olfactory function of people who have worked in perfume sales for years to control participants matched in age and gender, they found perfume workers were actually better at a standardized odor discrimination task. No differences were found for odor detection or identification. Whether this enhanced discrimination is really due to environmental exposure, however, is unclear. The perfume retailers could also have differed in olfactory knowledge or procedural skills; that is, they could be odor "experts."

Aside from ambient odors, humans play a critical role in creating their own environment. Studies have illustrated the crucial role culture can play in affective responses to odors (e.g., Ayabe-Kanamura et al., 1998; Distel et al., 1999; Ferdenzi, Roberts, et al., 2013; Ferdenzi, Schirmer, et al., 2011; Seo et al., 2011), and how communities categorize odors (e.g., Chrea et al., 2004; Chrea, Valentin, Sulmont-Rossé, Nguyen, & Abdi, 2005), in addition to the olfactory functions we considered in detail in this article. But which specific aspects of cultural experience influence which aspects of olfactory function is not well understood.

One area that has been subject to investigation is diet. In the Alsace region of France anise is an often used ingredient in foods and drinks. A few day old infants whose mothers consumed anise-flavored foods prefer anise odor; while infants whose mothers did not consume anise show clear signs of rejection of the odor (Schaal, Marlier, & Soussignan, 2000). At the same time, rotting odors can become appetizing if part of early culinary exposure. The Chukchi and Yupik of the Beiring Straits eat fermented fish, reindeer blood, and walrus fat and have even been said to have a preference for partially decomposed food (Yamin-Pasternak, Kliskey, Alessa, Pasternak, & Schweitzer, 2014). This is reflected in vocabulary too: for example, Chukchi *veglyt'ul* 'old edible' versus *pegyt'ul* 'old, should not to be eaten'; in Naukan *ushaq* is used for walrus roulade in its earliest consumable fermentation stage; *soniq* when the fat layers of the roulade turn green at which point it has aged into its next edible stage, but beyond this it is *sighleqaq* 'spoiled' and no longer edible (Yamin-Pasternak et al., 2014, p. 629). In the Soviet era, some indigenous people were no longer exposed to these foods and odors; thereafter when the Soviet Union collapsed, younger people who had to go back to the fermented foods (or starve) had difficulties ingesting these potent odors. This goes to illustrate the importance of early experienced environmental odors (Beauchamp, 2014).

In a direct study of the role of food consumption on olfactory abilities, Stevenson et al. (2016) tested whether people with a Western-style diet—rich in processed food with high-saturated fat and sugar content—differed from people with relatively healthier diets. It appears only odor identification was related to diet, whereas odor detection and discrimination were unaffected. But the participants in this study were all Western, and the differences between them were limited. Future studies could explore a more varied dietary intake and its relation to olfactory functions. More generally, different aspects of culture—such as customs and traditions, beliefs and values, artifacts and technology—need to be incorporated into inquiry more seriously (cf., Burenhult & Majid, 2011; O'Meara & Majid, in press; Wnuk & Majid, 2014).

Conclusion

Despite olfaction being traditionally viewed as a limited sense, there are numerous ways in which olfactory skill can be harnessed. Certain biological propensities, experiences and training, and environments make improvements in olfactory abilities possible. To be a better smeller, one must inherit the right biology, live in the right environment, or have the right experiences. Although not all of them are available to each and every one of us, some are, and this is positive news.

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