REVIEW

An Initial Evaluation of the Functions of Human Olfaction

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Abstract

Although referred to in passing in several places, there have been few attempts to specify the functions of the human olfactory system. This article presents an initial effort at identifying and categorizing these functions, using 3 sources of information as a guide: 1) losses experienced by anosmic participants; 2) olfactory function in other mammals; and 3) capacity, namely, whether the human olfactory system can support the suggested function and whether there is evidence that it does. Three major classes of function were identified, relating to Ingestion (Detection/identification prior to ingestion; Detection of expectancy violations; Appetite regulation; Breast orientation and feeding), Avoiding environmental hazards (Fear related; Disgust related), and Social communication (Reproductive [inbreeding avoidance, fitness detection in prospective mates]; Emotional contagion [fear contagion, stress buffering]). These suggested functions were then examined with respect to 1) issues of ecological validity in human olfactory research; 2) their impact on olfactory loss; and 3) their general and specific implications for the study of human olfaction.

Key words: function, human, olfaction

Introduction

The aim of this manuscript is to identify and categorize the functions of the human olfactory system. Perhaps surprisingly, there appears to be few attempts at addressing this before, although it is referred to briefly in several places (e.g., Cullen and Leopold 1999; Mann 2002; Hummel and Nordin 2005; Wilson and Stevenson 2006). It is important to think about function for several reasons. Understanding the mechanisms, which underpin olfaction requires an awareness of what it is used for by the organism in its natural environment. Although this may seem an obvious statement, the literature suggests that such considerations are often ignored. For example, as Hudson (1999) points out, the olfactory system typically encounters complex chemical mixtures in the environment, yet many studies, rightly striving for precise stimulus control, present single pure chemicals against an odorless background. Findings based on such an approach may fail to uncover important mechanisms that support the detection of complex odor objects against a background of chemical "noise," an arguably crucial and routine aspect of olfactory perception in humans and animals (Stevenson and Wilson 2007).

A further reason for studying function is in trying to assess olfaction's value in day-to-day life. Value is used here in rather strict utilitarian terms, not to reflect the pleasure of the smell of rain or a musky perfume—although these aspects of olfactory perception are clearly important (e.g., Miwa et al. 2001)—but rather its value when assessing financial compensation for olfactory loss. The American Medical Association's (AMA 1993) "Guides to the evaluation of permanent impairment" rates anosmia as being equivalent to a rather trifling 3% impairment of the whole person, in contrast to a 35% impairment for complete loss of hearing and an 85% impairment for complete loss of vision. Although it has been reported that compensation payouts for anosmia often exceed the amount expected based on the AMA's evaluation (Doty et al. 2006), questioning the validity of this "3%" value is difficult without an understanding of the functional loss that actually accompanies anosmia. Several recent papers have started to address this issue by surveying anosmic participants to quantify the impacts of olfactory loss (e.g., Van Toller 1999; Santos et al. 2004; Aschenbrenner et al. 2007). This approach could be augmented by asking questions that are based on a more

complete understanding of function, because some aspects of anosmia may exert significant indirect effects on health and behavior that are not currently appreciated or understood (e.g., on mood, propensity for depression, reproductive, and immune functions). Finally, and perhaps most importantly of all in the context of the scientific understanding of human olfaction, is that identifying function can suggest new areas for study, which might not otherwise be apparent. In the context of this manuscript, one such example is the emergence of an interesting nexus between olfaction and the immune system. Another, albeit far better appreciated, is the olfactory system's reliance on learning and memory.

How then does one go about identifying the functions of a particular biological system? The approach adopted here involves 3 components. The first is to use, where possible, data from the limited number of "deficit studies," namely, what functional loss do participants with anosmia actually report? The second is to use the extensive animal olfaction literature, especially for other mammals, as a guide to inform the putative functions of human olfaction. Some caution is obviously required here, as humans seem to lack an accessory olfactory system, and because different ecological niches place different demands upon an organism's sensory systems. The third approach is to examine capacity. That is, does the human olfactory system have the capacity to fulfill a particular function, and is there evidence in the human literature that it did or does? It is important here to note the distinction between a function and a capacity. A washing machine, for example, has the capacity to heat water and to spin and agitate the contents of its tub. Its function can be to clean clothes or any other purpose that the user can employ these capacities for.

In reviewing the extensive literature on human olfaction, it was apparent that there were probably 3 major classes of function, relating to ingestive behavior, avoidance of environmental hazards, and social communication. Accordingly, the manuscript is organized into 3 major sections reflecting this division. Within each section, more specific functions are described, along with the supporting evidence drawn from the animal, human capacity, and human-deficit literatures. The final part of the manuscript examines the broader implications of the various functions described below.

Ingestive behavior

Brillat-Savarin's "Physiologie du goût" (1825) is significant not only for initiating the art of the gastronomic essay, but also because his work highlighted the importance of olfaction in many aspects of eating and drinking. Although Brillat-Savarin's observations are clearly well founded—after all odor is a key component of flavor—specifying the particular functional roles that olfaction serves in ingestive behavior has not been attempted before. Based on the literature reviewed below, a case can be made for 4 specific functions. First, orthonasally detected odors can assist in the

distal location of food. More proximally, odor can be used to identify a food's suitability for ingestion, reflecting prior learning about the food's immediate and delayed consequences. Second, when a food is placed in the mouth, volatiles are released during chewing or swallowing. These then stimulate the olfactory receptors via the nasopharynx–retronasal olfaction. Under conditions where there is a large discrepancy between the perceived flavor (the combined experience of retronasal olfaction, taste, and somatosensation) and the expectation formed prior to ingestion, this can lead to rejection without further consumption and hence the avoidance of microbial contamination or poison. Third, both the smell of food before or after a meal, and the experience of flavor during a meal, may act to regulate appetite—including both its stimulation and inhibition—by a variety of mechanisms. Fourth, in neonates, olfaction may have an age-delimited function in initiating and promoting breast feeding. Each of these 4 putative functions is considered in turn.

Detection and identification

Animal data

Foraging behavior in many mammals, including fruit-eating bats (Raghurm et al. 2009), root-eating subterranean rodents (Schleich and Zenuto 2007), seed-eating mice and rats (Vander Wall et al. 2003), and fruit-eating tamarins (Garber and Hannon 1993)—along with other examples too numerous to mention—have been shown to depend strongly on the olfactory system for the distant detection of a food source. In addition, the olfactory system has also been shown to be important more proximally in establishing the suitability of a potential food source for consumption. For example, spider monkeys utilize both vision and olfaction to select suitable fruit, but under conditions where the quality of the fruit is questionable (unusual color) or where color is a poor cue, the animals sniff the fruit before either ingesting or rejecting it (Hiramatsu et al. 2009). A further approach seen in several mammals is to sniff the mouth area of a conspecific either while they are eating (Laidre 2009) or after they have eaten (Galef and Stein 1985). Such actions appear to enhance an animal's preference for the food odor smelled on the conspecific's breath or body.

Human-capacity data

A key element in the distal detection of an odorous object is the capacity to follow an odor plume or a scent trail, as observed in many animal species including mammals (Vickers 2000; Lytridis et al. 2001). Although humans in industrialized countries will rarely use olfaction for the distal detection of food, we still have the capacity to follow scent trails, and this ability can improve with practice (Porter et al. 2007). Unfortunately, there does not appear to be any empirical work exploring the capacity of humans to follow an odor plume to its source, but this would appear possible given

the scent-trail findings. It is also worth noting here that the capacity to follow trails/plumes in humans may suggest a further latent ability, namely, using olfactory cues for spatial orientation. This has been observed in a number of animal species but not as yet in humans.

The capacity to identify a food's suitability for consumption is quite well established in humans. In a series of studies, Rozin and colleagues (e.g., Fallon and Rozin 1983; Rozin et al. 1985) examined how humans come to learn what is and is not food. In developing their taxonomy of food and nonfood categories, they found strong evidence that participants make evaluative judgments of a food's likely edibility, well before it is placed in the mouth. These judgments were quite consistent over a number of preconsumption scenarios, including seeing the "food," smelling the food, seeing someone else eat it, and thinking about eating it (Fallon and Rozin 1983). The important point here is that the food's likely acceptability is judged "before" ingestion and orthonasal olfaction is considered by human participants to play a significant role in this process.

An illustrative example of this process is provided by Yeomans et al. (2007). They examined whether odor-taste and odor-caffeine pairings would affect liking for these and control odors, when the odors were tested both orthonasally and retronasally, following conditioning. Evidence of learning (increased liking for caffeine-paired and aspartame-paired odors) was present "to an equal degree" in both test conditions, reflecting the ability of orthonasal olfaction to benefit from prior experience acquired retronasally, thus offering the potential for this information to be used in food selection prior to consumption.

As the example above suggests, identifying an odor as indicative of a potential food source, draws heavily on the capacity to learn about prior ingestive episodes. The ability to learn the flavor of a food has been demonstrated extensively in human research, as has the capacity to learn associations between a food's volatile signature and its delayed consequences (Yeomans 2008). Humans can learn to associate an odor with a liked taste, and that odor is then judged to smell more pleasant on test (e.g., Zellner et al. 1983). Similarly odors paired with unpleasant tastes, notably sour or bitter ones, are judged to smell less pleasant following such pairings (e.g., Baeyens et al. 1990). Humans can also learn about the delayed consequences of ingestion, with calorically dense foods being liked more (e.g., Capaldi and Privitera 2007), and those that induce nausea being liked less (e.g., Cannon et al. 1983).

Learning the flavor of food during ingestion also affects the perceptual properties of food-related odors when they are later smelled alone, including their likely taste (e.g., sweet, bitter, or sour) and fat content (Stevenson et al. 1995; Sundqvist et al. 2006). Not only does this capacity to learn influence the selection and identification of food, but it also provides the information utilized in some forms of appetite regulation and of course in detecting expectancy

violations (more below). In sum, the retronasal and orthonasal olfactory routes provide, respectively, an avenue to learn about flavor, and an avenue to draw on this learning when encountering that particular food-related odor in the environment. Relatedly, they also provide, respectively, the basis for enjoying the rewarding properties of food during ingestion and for generating a desire (or not) to consume them before (or after) eating.

Human-deficit data

Anosmia has an impact on several aspects of ingestive behavior (Mattes et al. 1990; Aschenbrenner et al. 2007), but the key question here is whether it impairs the detection and identification of suitable food. Obviously, certain impairments are likely to be difficult to detect in contemporary society, as food foraging is typically restricted to shopping. However, functional deficits might be observed in relation to consumption of food that appears edible but whose smell would normally indicate that the food was not suitable for ingestion (e.g., microbial decay, unripe, etc.). Several papers have documented this type of impairment in anosmic participants. Temmel et al. (2002) reported that in a sample of 278 patients who were either hyposmic or anosmic, 50% reported problems in identifying spoiled food. In the Miwa et al. (2001) study of 1093 patients with abnormal taste and smell, 75% noted a similar problem. Santos et al. (2004) surveyed 445 patients who had undertaken olfactory testing for suspected anosmia, and one-quarter of this sample reported experiencing an actual incident in which they had consumed spoiled food. Finally, Bonfils et al. (2008) examined 106 hyposmic and anosmic participants, and half reported that they had accidentally eaten rotten food. So although orthonasal olfaction may no longer be involved in the distal location of food (at least in industrialized nations), it clearly serves a demonstrable role in identifying the suitability of a food item for consumption.

Expectancy violation

A second specific function for olfaction in the context of ingestive behavior is in detecting expectancy violations. In this case, retronasal olfaction, taste, and oral somatosensation will all contribute to this judgment.

Animal data

Laboratory rats are clearly able to form a wide range of expectancies based on prior learning, including ones pertaining to olfaction (e.g., Freeman 2000). More specifically, rats are able to reject foods that "appear" palatable but that have been tainted in some way, such as by poison (Rzoska 1953). This suggests that rats have the ability to form an expectation of the likely flavor of a familiar food and to attend to violations of it.

Human-capacity data

In humans, visual variables are probably central to forming an expectation of a food's flavor. Although small deviations

may not be noticed unless attention is drawn to them, large deviations are attention demanding and typically aversive. For example, participants told to expect an ice cream, but who were in fact given a savory salmon flavored mousse (which looked like strawberry ice cream), reported significantly more negative evaluations when they tasted it, than participants who received no information or those who were told to expect salmon flavored mousse (Yeomans et al. 2008). Most notably, a capacity to reject foods where the flavor violates expectations must again depend on a capacity to learn flavor experiences. As described in the section above, this capacity is clearly well developed in humans.

Human-deficit data

Although an adequate sense of smell may typically guard against consuming a spoiled food, presumably its detection by anosmic participants may depend on a functional gustatory–somatosensory system. So although an intact sense of smell may augment this process in the mouth, a capacity for rejection based on other sensory properties clearly exists.

Intake regulation

Olfactory cues may serve to regulate food intake by stimulating appetite under conditions of hunger. Changes in hedonic responsiveness to a particular flavor can occur both during a meal, thus providing the first part of the satiety cascade, and more generally to other food-related odors following a meal. Prior experience with a particular flavor and its postingestive consequences, can also affect the quantity of food consumed.

Animal data

Laboratory rat-feeding studies suggest that preferred foods promote appetite, whereas nonpreferred foods do not. This is reflected, for example, in the eating rate of rats across a meal, which shows the effect of 2 discrete components, the stimulating effects of the orosensory properties of the food, and its satiating effects (Davis and Levine 1977). Although a food's orosensory properties might initially promote ingestion, sensory-specific satiety may slow or ultimately stop intake. The latter effect can be demonstrated by varying the types of food available, because sensory-specific satiety is less effective in reducing a rat's food intake when multiple flavors are presented (Treit et al. 1983). Longer-term state-dependent changes in affective responsiveness to foods have also been documented in rats. For example, ingestive cosummatory responses to sucrose are reduced following glucose infusion into the stomach (Cabanac and Lafrance 1990). Although this is a gustatory alliesthesia, it would appear likely that such findings would also extend to olfactory cues (see Cabanac 1971). Finally, rats can learn to meter their intake of a particular food based on having learned its satiating consequences and this too—along with

the other mechanisms above—may contribute to the animals' short-term ability to regulate food intake (Booth 1972).

Human-capacity data

Hunger and satiety are associated with particular changes in the hedonic response to food-related odors. Cooking bacon may smell delicious when hungry and serve to stimulate appetite (i.e., wanting or desire), but it may smell unpleasant when replete. This type of food-related alliesthesia effect has been observed in humans for both sweet tastes and food-related, but not for non–food related, odors (Cabanac 1971; Duclaux et al. 1973).

Three regulatory effects occur specifically during ingestion. The more palatable a food, the more hungry this appears to make participants, and the more food they subsequently consume (the appetizer effect; Yeomans 2000). This effect is driven by the food's flavor, thus clearly including its retronasal olfactory component. A further effect is sensory-specific satiety, which can be demonstrated in humans, as in animals, by the effect of dietary variety on food intake as well as by changes in self-report hedonic ratings (Rolls et al. 1981; Hetherington 1996). This too has a significant olfactory component, as hedonic ratings of the odor of a food eaten to satiety, relative to a control (uneaten) food odor, show significant negative shifts from the start (like) to the end of a meal (dislike; Rolls and Rolls 1997). A further mechanism is learned satiety, whereby the satiating properties of a flavor come to regulate the amount of that food that is consumed on a subsequent occasion (Birch et al. 1990). Although learning is the principal basis for this regulatory mechanism, it is important to note its role in all of the others as well. Ingestive alliesthesia operates selectively on food-related odors, and this designation has to be learned, and sensory specific satiety and the appetizer effect are both impacted by the "initial" hedonic value of the flavor, which will also reflect prior learning (e.g., if the flavor had been paired with an energy-dense food).

Human-deficit data

Both weight gain and loss have been reported following the onset of anosmia, suggesting that it can influence appetite in various ways (Mattes et al. 1990; Aschenbrenner et al. 2007). This variability in body mass following the onset of anosmia might be accounted for by people's reaction to a loss of flavor. In some cases, this may result in dietary shifts to foods that are palatable based on taste and somatosensory qualities alone (i.e., sweet and fat) and hence weight gain, and by others in a loss of interest in food, and hence weight loss. Loss of interest in food, and weight loss, has also been observed in the elderly, where hyposmia is quite common (Cain and Gent 1991). Although a number of factors are known to contribute to impaired food intake in the elderly

(see Hickson 2005), weight loss solely attributable to hyposmia has been documented (Schiffman 1992).

Breast feeding

Although the functions above are primarily operative following the broadening of the diet that occurs during early childhood, olfactory influences on feeding behavior are present from birth, and these constitute a further functional class.

Animal data

Neonates from many mammalian species including rats, rabbits, cats, dogs, sheep, and pigs, all rely on olfactory cues to assist detection of the mother's nipple and to promote feeding (Porter and Winberg 1999; Schaal et al. 2009). The importance of these olfactory cues has been extensively studied, especially in rabbits, and impairing odorant release from the mother's nipple or rendering the neonatal animal anosmic can result in the pup's death from starvation (e.g., Hudson and Distel 1983). The olfactory cues that are utilized to guide the neonate and to promote feeding behavior appear to include both mother-specific cues, reflecting diet, as well as an apparently innate preference for mother's milk, at least in rabbits (Coureaud et al. 2002). This ability to find the nipple, to suckle and feed, appears to be highly conserved in mammals (Porter and Winberg 1999; Schaal et al. 2009).

Human-capacity data

Human neonates have a functional sense of smell, and as discussed later, a capacity to acquire memories of odors to which they have been exposed. Schmidt and Beauchamp (1992) in considering the function of olfaction in neonates suggest that it may play a role in promoting appropriate feeding behavior (i.e., promoting suckling of the mother's breast) and avoidance of suckling unfamiliar stimuli. Varendi and Porter (2001) provide some support for this as they found that newborn infants tended to move toward a pad scented with their mother's breast odor in contrast to a clean control pad. For human neonates at least, it may be exposure to the chemical signals in the mother's amniotic fluid that results in this preference for things maternal, including breast odor (Porter and Winberg 1999). Exposure to milk or breast odor may be important in promoting feeding, and evidence favoring this has been observed in preterm infants (Raimbault et al. 2007). The functional significance of orienting to the breast and promoting feeding may be of considerable importance where the mother is inexperienced and where support services are absent, such as in the third world and in our evolutionary past, as a failure to start feeding will result in dehydration and ultimately death (see Schaal et al. 2009, p. 347).

Human-deficit data

No deficit data are available on this topic.

Conclusion

Olfaction has a number of demonstrable functions relating to human ingestive behavior, including the detection and identification of food suitable for eating, rejection of foods that have an unexpected flavor, modulation of appetite, and promoting breast feeding in neonates. All of these functions rely heavily on the olfactory system's capacity to learn.

Environmental hazards

In any environment, there will be a range of volatile chemicals present, some as discussed above from food, and others relating to the presence of predators, pathogens, or kin. The ability to identify and react appropriately to olfactory signals that connote danger is clearly well developed in humans, as evidenced by the use of volatile agents to signal the presence of odorless airborne hazards (Cain and Turk 1985; Cain et al. 1987) and by the ability of certain chemicals resulting from biological decay processes to potently engage avoidance (Rozin et al. 2000). There is a case to be made that chemical hazard signals can be split into 2 functional categories broadly reflective of these latter examples—nonmicrobial hazards (e.g., predators, fire, degraded air, and poisons), and microbial threats (e.g., feces, vomit, and organic decay). One important reason for this division is that each class of hazards seems in humans to be associated with a different emotion, namely, fear and disgust, respectively.

Although the majority of the focus here is on these negative dimensions'—fear and disgust—it is important to stress that just as many vertebrates have the capacity to learn that certain odors signal something to be avoided, they can equally learn associations between odors and things to be approached. Indeed, the capacity of odors to reinstate emotive memories (positive or negative) in humans, even after a considerable passage of time, reflects the power of this signaling function. A large number of human studies have demonstrated this by showing that odors, relative to other sensory cues, are especially adept at reinstating emotional memories, even ones acquired decades ago (e.g., Willander and Larsson 2007).

Nonmicrobial hazards

Although there is a clear link between threat detection and the role of olfaction in identifying the suitability of food for ingestion (i.e., "signals danger"), the 2 are distinguished by the motivational state of the organism and the response produced if the odor signals a non–food related threat. The evaluation of food is likely to take place in a state of hunger and will result in further food-seeking behavior if the target food is rejected. In contrast, detection of

predators, fire, or other such threat signals is salient irrespective of motivational state and results in different behavioral outcomes. In respect of predation, this might include avoidance of open areas, altered feeding behavior, and the psychological and physiological arousal. Relatedly, signs of airborne or waterborne contaminants, will lead to evasion and movement away from the source of these items as well as generating arousal.

Animal data

Many animals show defensive reactions to predator odors (Apfelbach et al. 2005). Such reactions have been observed in mammals, including rats (Staples and McGregor 2006) and primates (Sudermann et al. 2008). Although defensive responses have been frequently documented, drawing firm parallels from predator avoidance in animals to avoidance of "all" fear-related responses in humans may be problematic for a number of reasons.

In humans, many defensive reactions to odors are probably learned, yet although there is evidence of plasticity in animals in this regard (e.g., Ferrari et al. 2006), there is also evidence to suggest that responses to certain "indicators" of predators may be innate and common to many species (e.g., fecal markers of a carnivorous diet—making feces an especially interesting cue as it can signal both the presence of a carnivore "and" microbial threat). For example, work by Kobayakawa et al. (2007) in mice suggests that there are glomeruli solely dedicated to supporting innate responses to predator-related odorants, and these are independent of glomeruli that support learned responses to odorants. Although hedonic plasticity is often considered the norm in humans (e.g., Wilson and Stevenson 2006), here too reactions may be driven, at least in part, by physiochemical factors, suggesting that we may also possess some innate hedonic dispositions (Khan et al. 2007). It "could be" then that humans, like many animals (notably rodents), react adversely (or are prepared to do so) to certain odorants because they contain chemicals that have been reliable indicators of predators in our ancestral past.

A further reason for caution concerns the systems that are used to detect and orchestrate reaction to the target odorant in animal predator avoidance. At least in some instances, predator odors in animals serve to activate the accessory or vomeronasal olfactory system, the accessory olfactory bulb, and then the amygdala (Apfelbach et al. 2005), as well as the main olfactory system. The former observation has led some authors to regard certain aspects of predator odor as having pheromonal characteristics, which would square with the discussion above concerning the innate basis of such capabilities. In humans, at least, there is considerable controversy surrounding the functionality of the vomeronasal system (this is discussed more extensively in the Social communication section), and so even if certain aspects of our hedonic response to odors were innate, this may not always be mediated by the same sensory and neural pathways that control predator-related odorant responding in animals. Nonetheless, the functional significance of detecting biologically salient odors would still hold even if the details of how this were operationaliszd differed between humans and other species.

Human-capacity data

Humans clearly have the capacity to learn the meaning of odors that they have not encountered before and thus to learn that they signal danger (Cain and Turk 1985; Cain et al. 1987). Gas attacks in the First World War by chlorine, phosgene, and mustard gas (among 15 others) could not at that time be detected by any machine-based sensor, but rather detection relied on seeing the approaching gas cloud, the hiss of escaping gas from a shell, or the smell associated with particular agents. The US Army's publication "Defensive measures against gas attacks" (Headquarters American Expeditionary Forces 1917) provides details of the typical visual and olfactory cues associated with gas attacks. Similar details were provided on Second World War Japanese posters designed to warn civilians about impending gas attacks, such as the hay-like odor of phosgene and the geranium-like odor of mustard gas. These warnings suggest rather clearly that the meaning associated with an odor can be acquired.

Setting aside historical examples, laboratory work also indicates a clear capacity for both learning an odor's name (e.g., Cain 1979) and for acquiring a dislike for it (orthonasally) if it is associated with adverse physiological effects (Van den Burgh et al. 1999). Moreover, Herz and von Clef (2001) have demonstrated that simply providing verbal information that offers either a positive or negative interpretation of the smell is sufficient to induce an appropriately consistent hedonic response. It also appears that in many cases of adverse reactions to odors that are scientifically evaluated as harmless, these reactions can reflect participants' beliefs about the noxious nature of the stimulus (Dalton 1996). Although these beliefs may be incorrect, they illustrate how easily odors can come to serve as a warning signal.

Human-deficit data

The deficit literature also suggests that a significant consequence of anosmia is the loss of ability to detect certain chemical signals that uniquely warn of danger. Temmel et al. (2002) reported that 30% of his sample of hyposmic and anosmic participants reported problems identifying burning food. In the Miwa et al. (2001) study, 61% of anosmics had problems spotting gas leaks and 50% smoke. In a further study, Santos et al. (2004) asked participants to actually identify hazardous incidents, and 23% reported having failed to detect a gas leak and 7% a fire. Indeed, prior to the use of natural gas in the United Kingdom, many elderly people accidentally died of coal gas poisoning, and it has been suggested that a significant proportion of these deaths

related directly to the hyposmia that commonly accompanies aging (Chalke and Dewhurst 1957). A similar concern relates to the odorization of natural gas, as these additives may not be detected by the elderly if a gas leak of some kind occurs (Cain and Turk 1985). Finally, Bonfils et al. (2008) reported that 47% of their sample had problems with detecting gas leaks and 26% with identifying fire-related hazards. Detection of non–food related hazards is clearly a significant and notable impairment following olfactory loss and points to the functional significance of olfaction in this regard.

Microbial threats

The second alerting function concerns potential microbial threats. As above, it is also necessary here to consider why microbial threat cues should be categorized as being functionally discrete from food-related rejections driven by microbial threats. Unlike for human fear–related avoidance above, functionally dissociating food and non–food related microbial threat avoidance is more problematic. This is because both food and non–food related microbial threats are likely to engender a common emotion in humans, disgust. However, it seems logical to deal with avoiding or accepting potential energy sources for ingestion as one discrete function, and avoiding disease sources outside the context of food as another, as both have different overarching goals (obtaining food vs. avoiding getting sick). It is for this reason that the 2 are treated discretely here.

Animal data

It has been argued that it is beneficial, from an evolutionary standpoint, to avoid contact with feces, decaying organic matter, etc, because of the likelihood of them containing infectious pathogens (Curtis and Biran 2001; Oaten et al. 2009). On this basis one would expect to see avoidance of these objects and their associated cues in many animal species, and this does appear to be the case. In an extensive review on disease-avoidant behaviors in animals, Hart (1990) identifies 3 particular features that are pertinent to the discussion here. First, many mammals, especially grazing ungulates, avoid pasture that is contaminated by feces. Second, many mammals, including certain primates, cats, dogs, ungulates, and pigs, avoid defecating in sleeping or nesting sites. Third, certain carnivorous and omnivorous species, avoid eating their dead conspecifics. In many cases, these avoidant behaviors involve the use of olfactory cues. For example, rats will not eat dead conspecifics unless their skin has been removed, and visual and olfactory cues are the principal means by which sheep avoid fecal-contaminated pasture when grazing (Cooper et al. 2000). The latter example is an interesting one, because it points to a broader issue. Avoiding disease-related cues might arguably overwhelm all activities, especially those that involve a significant infection risk such as nurturance and reproduction. However, this is

clearly not the case, and the way in which this is dealt with is nicely illustrated by the next example. Ewes with lambs will tend to graze clumps of pasture with tall standing grass that is avoided by ewes without lambs. Such clumps are usually indicative of feces and parasite density and provide a short-term gain (i.e., increased milk production) for the lamb—but are potentially costly to the ewe (Hart 1990). A similar "trade-off" argument can be made for coprophagy, as it may supply essential nutrients in some species, and in others it may only occur during periods of malnutrition (Brooks 1999). In addition, any disease-related risk is reduced by the fact that coprophagy usually involves the ingestion of the animals' "own" feces (Hörnicke and Björnhag 1979). Overall, these data suggest that certain olfactory cues that elicit disgust in humans can generate avoidance in animals.

Human-capacity data

Odors associated with feces, vomit, and organic decay evoke disgust in most adults, and reactions to these odors are most likely learned (Rozin et al. 2000). In a recent study (Stevenson et al. 2009), we tested adult and child responses to a range of disgust elicitors, including 2 odors, a fecal and a urinous one. In adults, sniffing these 2 odors generated significantly more facial expressions of disgust (72% of participants for fecal and 65% for urinous) than the next best cue, live maggots (27% of participants; Sign test Z's > 5.00). In addition, most adults reported these odors to be foul smelling (91% for urinous and 96% for fecal). Children, especially the youngest (aged 2–3 years), evidenced far less disgust in response to these odors on all our measures (facial expression, self-report, and behavioral avoidance).

Other smells can also evoke disgust, notably those associated with the human body such as genital, oral, and axillary odors (McBurney et al. 1977). However, the situation is more complex for these cues, as the context in which they are encountered may have an important bearing upon the reaction the odor provokes. For example, genital odors may be highly desirable in a state of sexual arousal but not at other times (note the parallel with the discussion of trade-offs in the animal data above), and axillary odors may be desirable when they are from kin or a lover but not when they are from a stranger (Stevenson and Repacholi 2005). More importantly, although the odors of feces, vomit, and decay all signal the likely presence of pathogens (Curtis and Biran 2001), the same argument cannot be made with the same force for genital, oral, and axillary odors, a point returned to below.

Humans also demonstrate an implicit association between disease and smell. Bulsing et al. (2009), using the Implicit Attitude Test, found that participants were faster at associating odor with sickness-related words than they were with health-related words. The presence of this implicit association between sickness-related concepts and odor is also reflected in human history, with the belief prominent for over

2000 years, that places "where the air is dank and foul" are associated with ill health and disease (see Bulsing et al. 2009).

Although certain odors are effective predictors of pathogen-rich objects, others are not, and yet such smells can still evoke disgust. The observation that axillary odor from an unknown adult, for example, is found to be disgusting (Stevenson and Repacholi 2003) may be accounted for by the tendency to associate odors with disease-related concepts (in this case poor personal hygiene). In the case of axillary odor, there is a good case to be made that prior to the latter part of the 19th Century, most adults were not particularly bothered by this smell (see Soo and Stevenson 2006). With the advent of a societal push to improve personal hygiene and the availability of cheap soap, this attitude progressively changed, so that poor personal hygiene came to acquire strong negative meaning, sufficient to induce disgust.

Several authors have suggested that the relationship between disgust, smell, and disease may be considerably more intimate than the discussion above would suggest (Rubio-Godoy et al. 2007; Moscavitch et al. 2009). In particular, exposure to disgust eliciting stimuli, including odors, may act to prepare the immune system for a potential microbial attack. In animals and humans (Riether et al. 2008), odors can serve as conditioned cues to both stimulate immune responses (Ramirez-Amaya and Bermudez-Rattoni 1999) and suppress them (Mei et al. 2000). Olfactory cues can also act to regulate cutaneous allergic reactions (Hosoi and Tsuchiya 2000). All 3 of these effects are solely mediated via associative learning, and it is important here to differentiate these from direct pharmacological effects of odorants on the immune system, which have also been documented. More generally, and for reasons that are not yet understood, olfactory and taste cues are especially prepared to become associated with immune-system effects, in the same way that they are for conditioned taste aversions (Riether et al. 2008).

Human-deficit data

Although we do not know whether anosmia brings with it a heightened risk of illness either due to a failure to avoid disease-related cues or via some form of odor-related immune-system impairment, it certainly does affect a related concern, namely, personal hygiene. In the Miwa et al. (2001) study, 60% of the olfactory impaired group (relative to 35% of controls) reported concerns about their bodily odors. Anosmic participants also reported here that they washed their clothes more, cleaned their homes more, and used deodorants more extensively, than did controls. Similar hygiene-related issues were also identified in the Temmel et al. (2002) study, with 41% of olfactory impaired participants reporting concern about their own bodily odors.

Conclusion

Odors can serve as warning cues for microbial threats, which are typically accompanied in humans by a specific emotion—disgust—and by an intriguing, but as yet poorly understood, link to the immune system. Odors can also serve as cues for a variety of nonmicrobial hazards. Responses to these cues seem in humans to be accompanied by the emotion of fear. In both cases, humans can learn responses to new olfactory signals, but there is also some evidence albeit rather limited, to suggest an innate component to such reactions.

Social communication

So far, most of the functions that have been considered reflect interactions between an organism and its chemosensory environment. However, there is a further class of function relating to the detection and exchange of chemosensory information between conspecifics that is of major significance to certain species. In many invertebrates, this may be the dominant channel of communication, and although vertebrates also utilize this method, it is not generally as important (D'Ettorre and Hughes 2008). Humans also have the capacity to communicate information via a chemical channel, but the functional significance of this can often be hard to gauge and the potential range of specific functions is large and disputed (e.g., see Wysocki and Preti 2004; Schank 2006). A related and additional issue here is gender-related difference in human olfaction, whereby females typically outperform males on most tasks (Cain 1982; Doty and Cameron 2009). The functional significance of these gender differences for social communication, and indeed for the other functions reviewed above, are either not well understood or contentious (e.g., see recent work on pregnancy and food choice; Cameron 2007).

The functions identified in this section have been selected because they appear well supported in the literature, both in terms of their use by other mammals and in that each one has generally 2 or more strands of evidence in humans. Unfortunately, almost no human-deficit data are available. The selected functions are grouped into 2 broad classes: reproductive, including inbreeding avoidance and mate selection; and emotional contagion, including enhanced vigilance and stress-buffering effects.

Reproductive functions—introduction

Of all areas of human olfactory function, the role of smell in reproductive behavior has consistently attracted the most popular attention (e.g., Hassett 1978; Kohl and Francoeur 1995). Historically, there has long been a suspicion of an intimate relationship between sex and smell, which may in part have been driven by casual observation of domestic animals (see Talbot 1904). Perceptions of this sex–smell relationship have changed over the last 150 years. Fliess and many of his medical contemporaries considered that disturbances in the olfactory mucosa were causal agents in abnormal sexual behavior (Mackenzie 1898; Fabricant 1960). However, during the early and midpart of the 20th century, various workers

from a psychodynamic perspective reorientated this emphasis on to a role for olfaction in normal sexual development (Brill 1932; Kalogerakis 1963), whereas others stressed a far more modest role (Ellis 1911)—a view echoed in more recent reviews (e.g., Rogel 1978; Doty 1981). Much current thinking has been shaped by the pheromone concept (e.g., Wysocki and Preti 2004), which has perhaps brought us back the full circle to the study of reproductive behavior in animals.

Olfaction clearly has a role in human sexual behavior. The most concrete illustration of this comes from perfume sales, which in the late 1990s were estimated at around 5 billion USDs per year (Herz and Cahill 1997). Relatedly, Franzoi and Herzog (1987) found that female participants described the scent of a prospective mate as among the most important determinants in assessing attractiveness. Similarly, Herz and Cahill (1997) reported that females claim smell is "the" most significant factor in mate choice, a finding replicated in a later study (Herz and Inzlicht 2002). Relating this back to perfume sales, it is not surprising then that females account for a far greater share of this market than do men.

In reviewing the large literature on olfaction and reproduction, 2 principal functions emerge, inbreeding avoidance, and prospective mate fitness detection in adults. Notably, there are several function-related claims in the literature that are not well supported. One of these is menstrual synchrony. Apart from a growing uncertainty about its empirical footing (e.g., Schank 2006; Ziomkiewicz 2006), Trevathan et al. (1993) have suggested that menstrual synchrony does not appear to have a function in humans. Indeed, it has been argued that menstrual "asynchrony" may be functionally useful, at least in primates (Matsumoto-Oda et al. 2007). For these reasons, it is not included here. Another unsupported function concerns the ability of certain odors to affect the behavior of a potential mate, typically a female conspecific. This body of research is most notable for its preponderance of "published" negative effects (i.e., no impact on female selection of potential male partners).

In vertebrates, many reproductive-related chemosignals were thought to function primarily via the vomeronasal system, but more recent work has demonstrated that the main olfactory system is also sensitive to reproductive chemosignals (e.g., Keverne 2005; Baum and Kelliher 2009; Touhara and Vosshall 2009). Humans do not appear to have a functional vomeronasal organ (Witt and Hummel 2006; Mast and Samuelson 2009). Although the vomeronasal duct may be present in many human adults (Johnson et al. 1985; Trotier et al. 2000; Besli et al. 2004), immunohistochemical and genetic studies strongly suggest that it is nonfunctional (Kouros-Mehr et al. 2001; Witt et al. 2002; Liman and Innan 2003). In addition, recent work on the main olfactory system in the mouse suggests the existence of receptors that might be sensitive to chemosignals that transmit reproduction-related information (Liberles and Buck 2006). Liberles and Buck (2006) suggest that similar receptors may also be present in humans, based on evolutionary conservation, although it is not currently known whether such receptors are expressed in the human olfactory epithelium. In sum, the lack of a functional vomeronasal organ may be of little significance for any consideration of the functional role of olfaction in human reproductive–related activities (Knecht et al. 2003).

Reproductive functions—inbreeding avoidance

Several authors have suggested that inbreeding avoidance in animals and humans may be driven, at least in part, by olfactory cues (Penn and Potts 1998). Although it is clearly the case that a taboo against inbreeding (incest) is present in many human societies, whether this has a psychobiological, social, or psychodynamic explanation is still disputed (Schneider and Hendrix 2000). However, the psychobiological case appears to provide the most parsimonious explanation of the animal and human data.

Animal data

In many animal species, inbreeding results in perceptual and cognitive deficits, as well as compromising immune function in the offspring (Ross-Gillespie et al. 2007; Van Oosterhout et al. 2007; Ilmonen et al. 2008). Outbreeding on the other hand has been suggested to confer benefits associated with heterozygosity, including resistance to infectious agents (Hamilton 1982; Hamilton and Zuk 1982). These findings lend support to Bateson's theory of optimal outbreeding, namely, selecting a mate that is genetically different from self but not too different (Bateson 1983).

It has been suggested that olfactory cues may be one means by which animals detect genetic relatedness to self (Levy and Keller 2009). In mice and rats, which have been studied extensively, genetic relatedness may be expressed via chemical means—that is in a suitable form for olfactory detection—by variation in the major histocompatability complex (MHC). Not only does MHC reflect relatedness but it is also instrumental in influencing the available selection of antigens (Kuby 1991). Thus, variability in an offspring's MHC, generated by mating with a nonrelated conspecific, should enable the production of a larger range of antigens and so ultimately confer greater protection against infectious disease (Apanius et al. 1997).

Mice and rats are capable of discriminating different MHC genotypes based on volatiles present in urine, and these differences are also apparent to humans (Gilbert et al. 1986). The most likely chemical basis for expressing variations in MHC genotypes is via a range of volatile carboxylic acids that are present in blood serum and that are expressed in all bodily fluids, including urine (Yamazaki, Beauchamp, et al. 1999; Yamazaki, Singer, and Beauchamp 1999). Whether mice and rats actually utilize such olfactory cues

in mate choice is not so well established, with favorable and unfavorable evidence having been obtained (Beauchamp et al. 1988; Eklund 1997). A further point of contention is whether animals learn their own smell or that of their parents or foster parents. Evidence favoring the acquisition of parent/foster-parent odor has been demonstrated (Beauchamp et al. 1988). Notwithstanding these uncertainties, olfactory cues clearly offer a reliable and valid cue to relatedness, and this information is used in mate choice by certain strains of rats and mice to avoid inbreeding.

Human-capacity data

Several lines of evidence indicate that early exposure to an individual of the opposite sex inhibits the formation of sexual relationships in later years. Studies on unrelated children, raised in the communal system of the Kibbutz, find that they are unlikely to marry or have sex with individuals with whom they were raised (Shepher 1983). Similar observations have also been obtained from Taiwanese ''sim-pua'' marriages, where the female child bride-to-be goes to live with her future spouse. Such marriages typically produce fewer offspring, have higher divorce rates, and greater rates of adultery than would otherwise be expected (Wolf 1995). Similar exposure effects may also account for the apparent rarity of sexual relationships between opposite sexed siblings raised within the same family.

One factor that has been hypothesized to inhibit the formation of sexual relationships following exposure during childhood is olfactory cues. Neonates have a demonstrable capacity to learn the odor signature of their mother (Cernoch and Porter 1985; Schleidt and Genzel 1990; Schaal et al. 1998). This ability to learn an odor profile also extends to other individuals to whom one is or has been exposed, and it appears to be an especially robust finding (e.g., Porter et al. 1986; Weisfeld et al. 2003; Olsson et al. 2006).

As with animals, humans too have distinct odor profiles that are in part dictated by the person's inherited complement of immune-system genes, notably those for human leukocyte antigens (HLAs—akin to MHC in animals). Trained rats can distinguish between HLA types in urine, and specific volatiles in these samples reliably distinguish these different HLA types (Eggert et al. 1999). Odor differences in human sweat are also detectable based on HLA type (Zavazava et al. 1990), and it has been suggested that a similar chemical basis—volatile organic acids—reflect HLA odor types as they do for MHC odort ypes in mice and rats (Wysocki and Preti 2004).

There are good functional grounds for avoiding mating with someone whose HLA pattern is similar to one's own. In humans, a high degree of similarity between partners' HLA is associated with higher rates of spontaneous abortion (Beer et al. 1985; Ober et al. 2003), and if a baby is born to such a couple, the baby has a higher chance of being of low birth weight (Reznikoff-Etievant et al. 1991). If the olfactory hypothesis is correct, then it would suggest that the early exposure effects that are presumed to be responsible for the sexual inhibition observed in the Kibbutzim and simpua marriage studies result in part from acquiring memories of the other children's odors.

Evidence for mate choice based on olfactory-driven HLA detection is moderately favorable. Two studies on the closed Hutterite community in the United States have suggested that couples tend to have more dissimilar HLA than one would expect by chance alone and that this dissimilarity effect, so it has been argued, may be driven by olfactory cues (Ober et al. 1997; Ober 1999). However, 2 conceptually similar studies, one on Japanese couples (Ihara et al. 2000) and another on a group of Amerindians (Hendick and Black 1997), have failed to obtain evidence favoring this hypothesis, which may imply that avoidance based on such cues may (perhaps) be obscured by a range of culturally specific factors (see Beauchamp and Yamazaki 1997).

Another approach adopted to explore the role of olfactory-driven HLA selection is to determine whether people express a preference for body odors associated with a dissimilar HLA to their own. Wedekind and Furi (1997) found just such an effect (and see Wedekind et al. 1995). In addition, Milinski and Wedekind (2001) found that perfume selection was also related to HLA expression and so complemented choice rather than masking it. Finally, Matchock and Susman (2006) have argued that delayed menarche in daughters with ''live-in'' fathers may also serve to reduce the chance of inbreeding, and this too they suggest is driven by olfactory cues.

Human-deficit data

There are currently no data available on the impact of anosmia on mate choice and only anecdotal evidence that it might be influential in inbreeding avoidance. In this regard, Schneider and Hendrix (2000) quote from a book on sexual abuse of minors where a biological father who had abused one of his daughters could not bring himself to abuse the other because her smell ''turned me off'' (op cit, p. 81.). As Schneider and Hendrix (2000) suggest, it would be of considerable theoretical and practical interest to determine whether anosmia or hyposmia is a contributing factor in cases of incest.

Reproductive functions—fitness detection in potential mates

A variety of signals are used by animals and humans to gauge the genetic fitness of potential mates, and relatedly, whether the potential mate reveals any sign of illness. Several authors have suggested that olfactory cues may provide one such fitness signal, as well as being indicative of general health (e.g., Penn and Potts 1998; Garver-Apgar et al. 2008).

Animal data

Sexual-selection studies have found that females of some species avoid breeding with diseased males. Able (1996) suggests that females select unparasitized males because they obtain the direct benefit of avoiding parasitic infection, as these "may impair fertility, induce abortion, or cause malformations in the young" (Hart 1990, p. 281). Female mice can detect disease by the urinary odor of males and avoid mating with male mice that are infected with viruses, protozoa, and larval nematodes. Disease-free males have also been shown to refuse copulation with infected females and to avoid parasitized conspecifics thus reducing likelihood of infection (Kavliers et al. 2003). Finally, mice can determine information about social status, as the territorial marking odor of male mice that subsist in a dominant mouse's territory are less preferred by females relative to those of the dominant mouse—a further indicator of fitness (Hurst 2009). No studies have as yet detailed the nature of the chemical cues on which these olfactory-driven effects are presumed to be based.

Human-capacity data

Sick humans frequently emit odors that are notable for being different (and often unpleasantly so) from those emitted by healthy individuals (Penn and Potts 1998). Such abnormal bodily odors can be generated by both infectious agents and by metabolic abnormalities. Although appearing sick is likely to be an equally reliable predictor of unhealthiness, olfactory cues may act as a further and potent (i.e., disgust inducing) means of eliminating sexual desire.

Other olfactory fitness signals have also been identified. In a series of studies, female participants at the peak of fertility (during the menstrual cycle) were found to prefer the body odor of males who were more symmetrical (Gangestad and Thornhill 1998; Rikowski and Grammer 1999; Thornhill and Gangestad 1999; Thornhill et al. 2003), and this cyclic change in preference is driven by variations in progesterone and estrogen (Garver-Apgar et al. 2008). Body and facial symmetries are reliable indicators of fitness (Geary et al. 2004) and seem to be reflected in adult male body odor. Whether this particular type of signal has an animal equivalent is not currently known, nor is the chemical nature of the signal. However, Thornhill et al. (2003) suggest that the chemosignal underlying the scent of symmetry is independent of that used in HLA-type detection.

Human-deficit data

There are currently no data in this regard.

Emotional contagion

Rats and mice, as well as humans, appear able to detect threat-related chemical signals that emanate from a stressed conspecific, and these cues may then act to enhance vigilance.

In addition, certain odorants expressed by a familiar or an unfamiliar conspecific may have a stress-buffering effect on the perceiver. The nature of the chemical signals that underpin these examples is not currently known.

Animal data

Several studies in rats and mice indicate that they can detect and respond to odorants that are released by stressed conspecifics (Valenta and Rigby 1968; Zalaquett and Thiessen 1991). When the odors of stressed mice and rats are collected and presented to other conspecifics, these animals exhibit avoidance of the odor source, and more generally, behaviors that reflect enhanced vigilance (Zalaquett and Thiessen 1991; Abel 1994).

Stress responses can also be buffered in some animal species by various social factors, including mother–infant bonding, and adult social bonds (DeVries 2002). These types of social interactions can result in downregulation of the hypothalamic–pituitary–adrenal (HPA) axis, resulting in a protective effect against acute and chronic stressors (DeVries et al. 2003). The precise role of olfaction (or indeed the vomeronasal system) in this form of stress buffering is only starting to be explored, but it is likely to be important because of the ability of olfactory cues to modulate HPA activity (i.e., immune function and olfaction) and because olfaction is clearly an important means of social communication in many mammals. In a recent study using rats, Kiyokawa et al. (2007) found that social buffering of a conditioned stress response was mediated by olfactory cues, as lesioning the olfactory epithelium eliminated the buffering effect, as did eliminating olfactory cues from the donor animal.

Human-capacity data

As with rats and mice, a number of studies suggest that humans can detect fear-related cues via an olfactory channel, with arguably similar effects, although whether this is mediated preattentively and equally in male and female recipients, remains in question (Prehn-Kristensen et al. 2009). Ackerl et al. (2002) found that female participants were able to correctly identify sweat samples from fearful donors, suggesting that the stimuli can under some circumstances be consciously evaluated and detected. In terms of responses, a range of phenomena have been observed, including enhanced identification of fearful faces in ambiguous stimuli by women (Zhou and Chen 2009), enhanced performance on a word association task in women, along with slowing on a task with ambiguous content (Chen et al. 2006), and enhanced startle blink amplitude in male participants (Prehn et al. 2006)—all when exposed to sweat donated by anxious or fearful participants. These findings suggest that humans are sensitive to chemosensory fear signals from conspecifics and that these may act to enhance vigilance.

As described above, adults, children, and neonates have the capacity to learn the smell of those individuals to whom

they are frequently exposed. Schaal (1986) has suggested that a mother's odor may exert a calmative effect on her infant offspring. This calmative effect, evidenced by a reduction in physical activity, may have interesting developmental consequences, especially as there is evidence that milk and lavender odors can buffer cortisol levels in neonates exposed to stress, relative to a nonodor control group (Kawakami et al. 1997). Higher stress and cortisol levels are associated with a range of later behavioral and neural impairments (e.g., Sanchez 2006; Champagne and Curley 2009), and the role of familiar maternal odor in reducing neonatal stress may have hitherto unrecognized impacts on this.

An arguably similar effect may be suggested by the finding that adults can find the smell of their partner or a close family member comforting in that person's absence. Shoup et al. (2008) found that not only women, but also men, reported sleeping with the clothes of an absent partner or family member. In the same way that a familiar odor related to the mother may reduce stress and arousal in a neonate, a related effect may be occurring in adults. Indeed, one might speculate whether findings that demonstrate the mood-improving effects of sweat components (e.g., Jacob et al. 2002), and axillary odor itself (e.g., Chen and Haviland-Jones 1999), may be exerting this effect via their similarity to a loved one's odor.

Conclusion

Olfactory social communication is important to many species, including certain vertebrates, and so its presence in humans should not be surprising. Two broad classes of communicative function were described, namely, a role for olfaction in human mate selection in respect of inbreeding avoidance and fitness detection, and in emotional contagion of fear and safety, although the evidence for the latter is far less developed. Two further points warrant comment. First, in 3 of the functions described here, there is no clearly identified candidate chemosignal, making it hard to determine the effect of such an agent on behavior. Second, and as with many of the other functions considered in this manuscript, learning again is seen to play a key role, especially in acquiring odor profiles of individuals to whom one has been exposed.

Discussion

This article presents a preliminary attempt at identifying the major functions that olfaction serves in humans. The 3 major classes of function described here relating to ingestive behavior, environmental hazard avoidance, and social communication would not seem particularly contentious, as good evidence exists for grouping into these categories. What is likely to provoke more argument is the nature of the specific functions identified within each category and especially those relating to social communication. In respect of the latter, this probably arises in part from the sheer complexity of social communication in humans and from the fact that in many cases the nature of the chemosignal itself is not fully understood.

It was noted in the Introduction that a focus on function might suggest generic shortcomings in the literature. In the food and flavor literature, there has been considerable interest in multisensory processing (e.g., Small and Prescott 2005). This multisensory perspective acknowledges the contribution that all of the senses make to our experience of flavor and to the regulation of ingestive behavior. This approach is useful for 2 reasons. First, it provides a better perspective on the importance of individual senses (i.e., redundancy), which is highly relevant when thinking about the practical consequences of olfactory loss. Second, it can identify hitherto unknown synergistic and antagonistic effects between sensory systems. It is notable that this multisensory approach is almost completely absent in the hazard-related and social communication literature reviewed above. A cynic might suggest that this is because visual and other nonolfactory cues might completely swamp the olfactory channel, yet the only studies that attempt anything like this in the reproductive (Herz and Cahill 1997; Herz and Inzlicht 2002) or hazard literature (e.g., Willander and Larsson 2007) find that olfaction may be very salient in mate selection and emotive memory retrieval, relative to the other senses. In the same way that Hudson (1999) suggested that more attention should be paid to ecologically valid "stimulus" selection, this review suggests that far more attention should be given to multimodal processing. The benefit of this approach would be 2-fold. First, it would delineate the relative importance of olfaction in contrast to the other senses. Second, it would identify olfaction's interactions with the other senses.

Odors are especially adept at eliciting negative emotions in humans such as disgust and fear. Anosmic participants often report affective disturbances, including depression, following symptom onset (Frasnelli and Hummel 2005; Hummel and Nordin 2005), and this has usually been ascribed to the distress associated with sensory loss (Van Toller 1999). It is intriguing to speculate whether an additional cause of affective disorders in anosmic participants results from flattened affect, a consequence of the reduction in the experience of olfactory driven alterations in emotional state. Not only can odors evoke negative states, but they can also evoke positive emotional responses. These may also have functional significance, such as liking the olfactory components of flavors associated with a pleasant taste or an energy dense food, an odor associated with a mate, or a smell associated with a particularly good time in our personal history. Kant in his treatise "In critique of Judgment" suggests that a distinction be drawn between purely sensory pleasures (i.e., what essentially amounts to the discussion in this paragraph) versus the capacity of a sensory experience to engage reflective contemplation (i.e., as art or music might). The extent to which any olfactory experience engages "reflective

contemplation"—thus becoming an esthetic experience— has not been considered in the literature. Indeed the possibility of esthetic loss may be a further and hitherto unconsidered consequence of anosmia.

As noted in the Introduction, considering function can also lead to unanticipated research questions. The extent and nature of the link between the olfactory system and the immune system is one such question. Immune-olfaction links are suggested by the role of olfaction in detecting disease-related cues, by olfactory-related stressors, by the need to detect the health and HLA status of prospective mates, by the finding in humans and animals that odors and taste can selectively serve as cues to modulate various aspects of immune function, and that certain odorants may directly affect immune function (i.e., a pharmacological effect). This nexus has not been systematically explored in human olfaction (although it may be incidentally exploited by aromatherapy), and uncovering the nature and extent of this relationship might have interesting implications for evolutionary psychology (i.e., disease avoidance strategy and mate selection) as well as unanticipated practical implications for promoting immune function in vulnerable groups such as the elderly (e.g., see Miletic et al. 1996).

A further unanticipated research question concerns infant development. There is wide agreement in the literature that exposure to significant stress during the first 2–3 years following birth has adverse consequences on behavioral development and later with the adult's ability to cope with stress (Sanchez 2006; Champagne and Curley 2009). So far, we know remarkably little about the calmative effects of familiar odors, particularly maternal odors, on human neonates. Are familiar maternal odors able to reduce cortisol levels in babies, and relatedly, can the baby's odor produce a calmative effect (behaviorally and physiologically) on the mother? As neonates are probably far more dependent on the olfactory channel in the first several weeks of life, it would be interesting to explore whether olfaction is instrumental (possibly in association with other cues) in modulating stress reduction, particularly during the postpartum period.

Another observation that emerges from this review is the importance and ubiquity of learning in supporting all aspects of olfactory function. Although this capacity has been noted before (Gottfried 2008), and is widely exploited in animal research (e.g., Slotnick and Katz 1974; Wilson et al. 2004), the role of learning in human olfaction has arguably not received the attention that it warrants, despite some notable studies suggesting its importance (e.g., Lawless and Cain 1975; Rabin and Cain 1984). Apart from the fact that human-olfactory learning may have properties that differentiate it from learning in other modalities (notably its speed, resistance to extinction, and often implicit nature; Brunstrom 2004), it is such a central feature of olfactory processing that it cannot be ignored in any complete account of human olfaction.

In conclusion, it is possible to point with a reasonable degree of certainty to 3 major classes of olfactory function relating to ingestive behavior, environmental hazards, and social communication. Within each of these categories, there is likely to be more disagreement about the specific functions that olfaction might fulfill in humans and their importance in day-to-day life, and this is especially so for the category of social communication. Nonetheless, this manuscript represents an initial attempt to detail what these specific functions might be, what we do and do not know about them, and how this approach might be used to further research in olfactory science.

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