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REVIEW

The navigational nose: a new hypothesis for the function of the human external pyramid

Lucia F. Jacobs*,‡

ABSTRACT

One of the outstanding questions in evolution is why *Homo erectus* became the first primate species to evolve the external pyramid, i.e. an external nose. The accepted hypothesis for this trait has been its role in respiration, to warm and humidify air as it is inspired. However, new studies testing the key assumptions of the conditioning hypothesis, such as the importance of turbulence to enhance heat and moisture exchange, have called this hypothesis into question. The human nose has two functions, however, respiration and olfaction. It is thus also possible that the external nose evolved in response to selection for olfaction. The genus *Homo* had many adaptations for long-distance locomotion, which allowed *Homo erectus* to greatly expand its species range, from Africa to Asia. Long-distance navigation in birds and other species is often accomplished by orientation to environmental odors. Such olfactory navigation, in turn, is enhanced by stereo olfaction, made possible by the separation of the olfactory sensors. By these principles, the human external nose could have evolved to separate olfactory inputs to enhance stereo olfaction. This could also explain why nose shape later became so variable: as humans became more sedentary in the Neolithic, a decreasing need for long-distance movements could have been replaced by selection for other olfactory functions, such as detecting disease, that would have been critical to survival in newly dense human settlements.

KEY WORDS: Climate, *Homo*, Olfaction, Primate, Respiration, Neolithic

Introduction

The function of one of the most striking features of the human face is still somewhat unclear. This is the unique external pyramid of the nose (Lieberman, 2011) (Fig. 1). This external protrusion, along with its inferiorly oriented nostrils, is unique among anthropoids and even among great apes (Ankel-Simons, 2007). Because the external nose can be reconstructed from cranial remains (Rynn et al., 2010), the appearance of the external pyramid can be dated to the appearance of *Homo erectus*, approximately 1.6 million years ago (Franciscus and Trinkaus, 1988).

There is currently only one accepted hypothesis for the evolution of the human nose, based on its respiratory function. What I will refer to as the conditioning hypothesis proposes that the external nose evolved to warm and humidify air before it reaches the lungs. This hypothesis was introduced by Arthur Thomson in 1913, who had observed that taller, thinner (i.e. leptorrhine) noses were found

Department of Psychology and Helen Wills Neuroscience Institute, University of California, 2121 Berkeley Way, Berkeley, CA 94720-1650, USA.
*Present address: Radcliffe Institute for Advanced Study, Harvard University, 8 Garden Street, Cambridge, MA 02138, USA.

‡Author for correspondence (jacobs@berkeley.edu)

L.F.J., 0000-0003-0330-9700

in cold, dry climates and shorter, flatter (i.e. platyrrhine) noses were found in warm, humid climates. He hypothesized that the narrower the channel through which air passes, the greater would be the exchange of heat and moisture, and thus the leptorrhine nose could be an adaptation for respiration in cold, dry climates (Thomson and Buxton, 1923).

Thomson and Buxton (1923) tested their hypothesis using the metric of nasal index, the ratio of nose height to breadth, which can be measured in living tissue, as seen in Fig. 2, or from cranial measurements, where the nasal index is the height and breadth of the nasal aperture, the area defined by the nasal and maxillary bones (Fig. 1). A global map of nasal indices, based on cranial measurements from Davies (1932) and redrawn by Leong and Eccles (2009), is shown in Fig. 3A, with a recent map of global climate zones for comparison (Fig. 3B) (Peel et al., 2007). It should be noted that the nose is particularly amenable to reconstruction from cranial remains, as there is a high correlation between measurements of the cranium and the living tissue. Forensic reconstructions can thus reconstruct the nose accurately, validating the methods using ante-mortem photos (Rynn et al., 2010) (Fig. 4). In contrast, other facial structures, such as ears, must be invented by the reconstructionist (Wilkinson, 2010).

Since the pioneering work of Thomson and Buxton (1923), the conditioning hypothesis has served as an important framework for studies of human cranial variation in relation to climate, with over a century of data on population differences in the nasal index (see von Cramon-Taubadel, 2014, for a review of the history of this field, including its relationship to phrenology and eugenics). The conditioning hypothesis has also complemented new theories of human evolution, specifically the evolutionary impact of the human ability to sustain long-distance running and walking, a physical exertion that would also require greater conditioning of air before respiration (Lieberman, 2008; Bramble and Lieberman, 2004).

However, after a century of study, some of the predictions and assumptions of the conditioning hypothesis are being questioned. For example, an important assumption is that the geometry of the narrower nasal chamber will add turbulence to the flow of air. This is important because it is assumed that the maximum heat and moisture exchange must occur in a turbulent, non-laminar, regime (Lieberman, 2008). Thus, the narrower, leptorrhine nose (Fig. 2C,D) is assumed to create more turbulence and condition more effectively than the broader, platyrrhine nose (Fig. 2A,B). Although, as will be discussed later, computational studies have recently shown that a specific feature of the narrowed human nose creates an airflow vortex, the effect of this vortex is found in a different function of the nose, olfaction (Li et al., 2018). In terms of nasal index and climate, early studies indeed showed a strong positive correlation between measures of absolute humidity and nasal index (Weiner, 1954) and an inverse relationship with the degree of nasal protrusion of the cranium (Carey and Steegmann, 1981). Yet, recent studies have found a mismatch between the prediction of the conditioning hypothesis that the
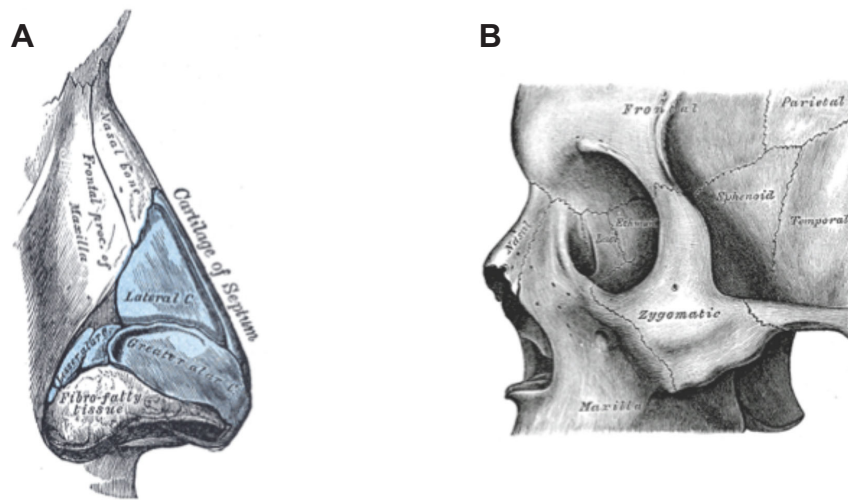
Fig. 1. Anatomy of the human nose. (A) Cartilages (fig. 852 of Gray, 1918). (B) Nasal bone articulation with maxilla (fig. 164 of Gray, 1918).

enlarged nasal chamber in a leptorrhine nose causes increased turbulence and hence increased conditioning. For example, contrary to expectations, nasal index was not highly correlated with the internal dimensions of the nasal chamber (Yokley, 2009), nor did nasal index predict nasal resistance, a measure of air flow (Patki and Frank-Ito, 2016). Using acrylic models of living tissue, the size of the internal nasal chamber did not predict the degree of turbulence (Churchill et al., 2004). In this and other studies, the greatest area of contact of air flow was also in the anterior nasal chamber (Churchill et al., 2004; Inthavong et al., 2014). Finally, Maddux et al. (2017) correlated measures of climate with four morpho-functional units of the nose: the external pyramid, the nasal aperture, the internal nasal fossa (i.e. chamber) and the nasopharynx. Of these, the only correlation with climate that emerged was the size of the internal nasal chamber. The authors also remark on similarities between short, wide

nasal apertures in populations from hot, dry climates (e.g. Khoisan) that are similar to those from hot, humid equatorial regions (Maddux et al., 2017), a pattern that goes against the predictions of the conditioning hypothesis. A more recent study, calculating nasal index from photographs of living tissue, however, did find a relationship between nasal breadth (but not height) and absolute humidity (but not temperature) (Zaidi et al., 2017). The state of the field is thus currently in flux.

Comparative studies have not further clarified the relationship between conditioning and nasal structure. A comparative study of primate internal noses concluded that, in comparison to the internal nose of the chimpanzee and macaque, the human nose would impede rather than enhance heat and moisture exchange (Nishimura et al., 2016). A new computational study of air flow in the mammalian nasal skeleton called even the assumption of turbulence into question. This model of the role of passage geometry in fluid mechanics concluded that the nasal passage is optimized to produce a laminar, not turbulent, airflow (Zwicker et al., 2018). This does not mean that the human nose does not condition air. What it does mean is that we lack a working hypothesis to explain why nasal index varies with climate.

Given that the nose mediates both respiration and olfaction, there are at least two possible alternative hypotheses. The first is that variation in nasal index is the result of neutral evolutionary forces such as genetic drift. This hypothesis has been evaluated by studying cranial variation, using geographic separation among populations as a proxy for genetic distance (Relethford, 2004). What has been found is that most cranial variation can be explained by neutral evolutionary forces (von Cramon-Taubadel, 2014). In contrast, nasal structures show strong positive selection, similar to the levels of heritability found for human skin color (Relethford, 2004; Guo et al., 2014). This positive selection has been found for measures of nasal aperture (Hubbe et al., 2009; Crognier, 2009; Roseman and Weaver, 2004; Roseman, 2004), nasal skeleton protrusion (Carey and Steegmann, 1981) and living tissue measures (Zaidi et al., 2017), even in children (Cole et al., 2017).

If nose shape is under positive selection, then, barring the hypothesis of Dr Pangloss that the human nose evolved to hold up spectacles (Gould and Lewontin, 1979), we must consider the hypothesis that it could function in olfaction. Subtle changes in nasal anatomy can be associated with significant differences in olfactory function (Zhao, 2004). For example, the shape of the tissue immediately past the nostrils (i.e. nasal vestibule) can have a
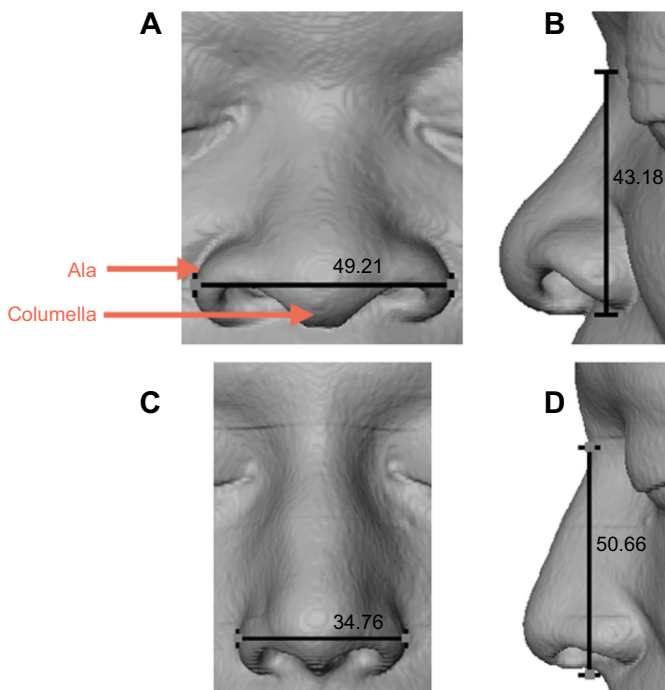

Fig. 2. Human nasal index measurements. Platyrrhine nose (A, breadth; B, height) and leptorrhine nose (C, breadth; D, height). Reproduced with permission from Patki and Frank-Ito (2016).
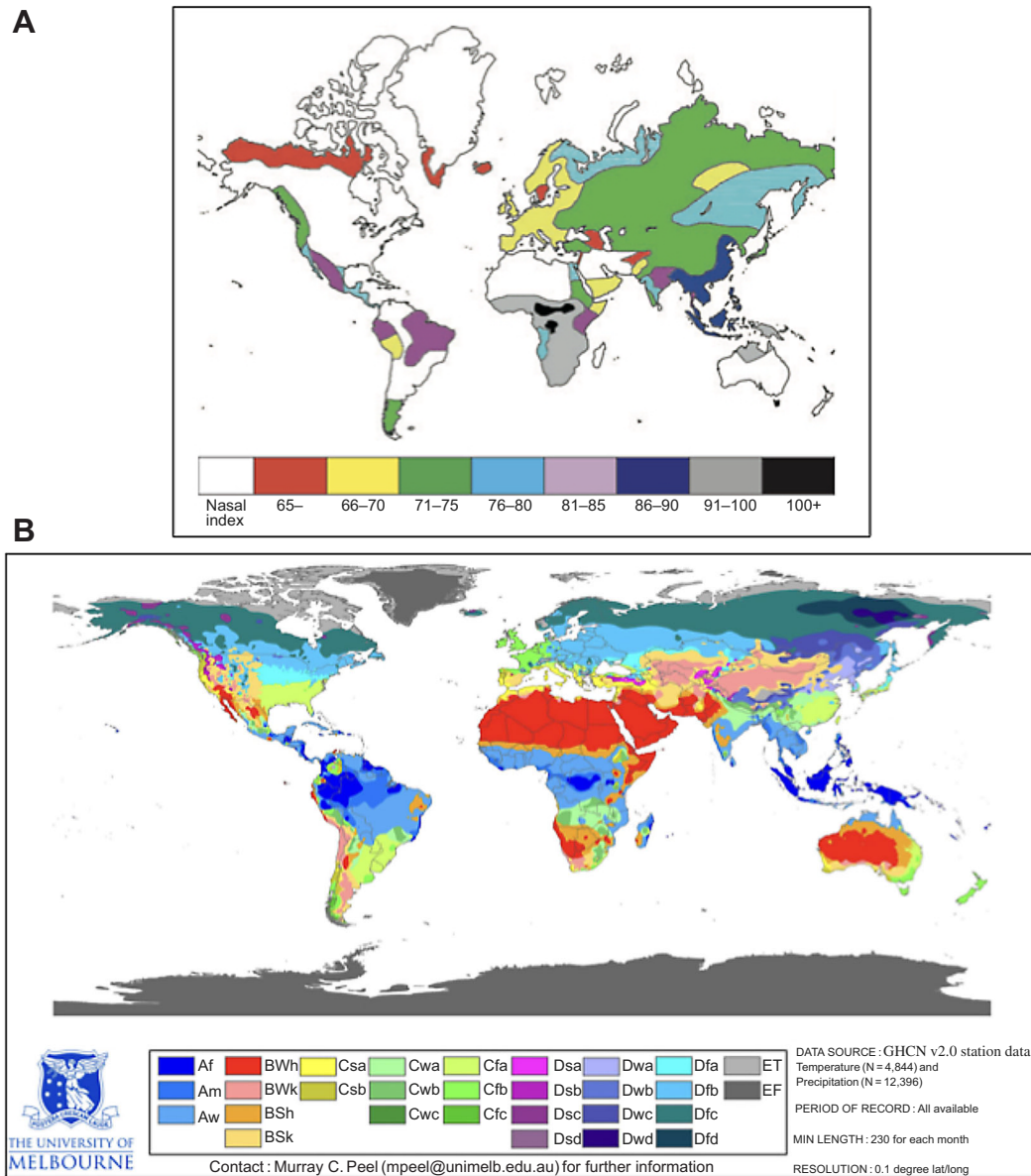
Fig. 3. Global patterns of climate and nasal index. (A) Nasal index map. Reproduced with permission from Leong and Eccles (2009). (B) Climate map (Peel et al., 2007; this work is licensed under the Creative Commons Attribution-Non Commercial-Share Alike 2.5 License).

significant effect on the flow of air to the olfactory epithelium (Zhao and Jiang, 2014). There are large individual differences in this area, with some individuals showing a distinctive notch (Ramprasad and Frank-Ito, 2016). Because the perception of intensity for soluble odorants increases when airflow is lower (Sobel et al., 1999), Li et al. (2018) hypothesized that the notch would produce a vortex that would increase sensitivity to more soluble odors, which their results confirmed. Moreover, narrower noses had larger notches, more intense vortices and higher sensitivity to soluble odorants (Li et al., 2018). Thus, there may be local turbulence in specific regions in the nasal chamber that can influence olfactory as well as respiratory function (Zhao and Jiang, 2014).

An olfactory hypothesis
If structure influences sensory function, then this structure may be adapted to a specific use. In humans, the shape of the external ear can be predicted from the statistics of the auditory landscape (Parise et al., 2014). The relative size of the eye in birds and mammals

scales with the speed of movement (Heard-Booth and Kirk, 2012). If human nose shape has an olfactory function, it may have been similarly shaped by its olfactory landscape.

One reason why there should be a relationship between olfaction, nose morphology and climate is that the conditions supporting olfaction are also climactic. Odorants may become easier to detect with increased absolute humidity because water molecules compete with odorant molecules for substrate positions (Igue et al., 1972; Vander Wall, 2003), although the exact relationship between humidity and the behavior of molecules can vary in complex ways (Emanuelsson et al., 2013). Laboratory studies of olfactory threshold in humans confirm that odors are easier to detect in conditions of higher humidity and temperature and lower barometric pressure (Kuehn et al., 2008). Thus, one might predict that using olfaction would be favored in hot, humid climates but not in climates that are cold, dry or found at high altitude. In fact, there is a positive association between nasal breadth and absolute humidity (Zaidi et al., 2017; Maddux et al., 2016).
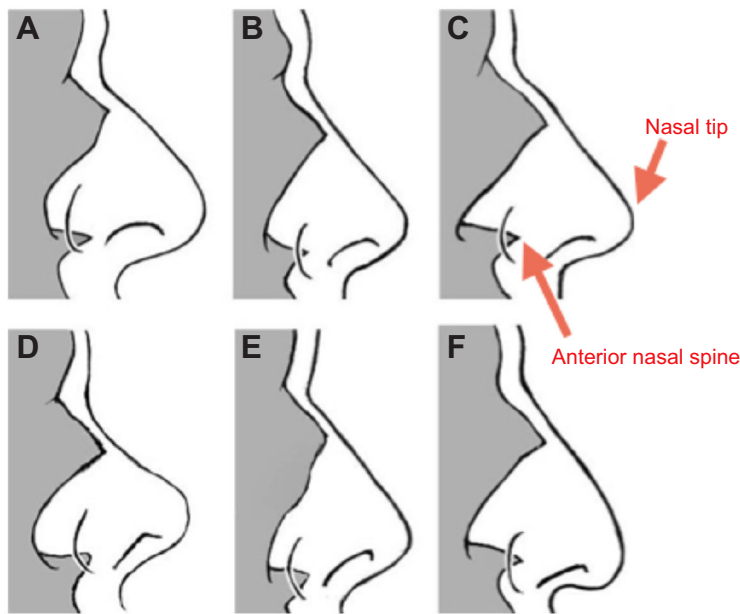
Fig. 4. Reconstruction of the nose from cranial landmarks.
Examples of corresponding bony (gray) and soft nasal profiles.
(A) Rounded aperture and nasal tip. (B) Average aperture and nasal tip. (C) Sharply angled aperture and nasal tip. (D) Rounded aperture and nasal tip, upturned nose. (E) Angled aperture and nasal tip, upturned nose. (F) Angled aperture and nasal tip, down-turned nose. Reproduced with permission from Rynn et al. (2010).

The observation that nasal breadth associates with a climate conducive to olfaction may be a clue to an olfactory function for the human external nose: the use of odors in spatial orientation. The reason is that the use of olfaction in orientation makes specific demands on the external morphology of the olfactory sensors. This is because olfactory navigation is enhanced by using stereo olfaction, where paired olfactory sensors (antennae, nares) that can compare independent samples increase the accuracy of orientation to an odor source, as I will review below. Perhaps the evolution of the external pyramid in *Homo* is an adaptation for spatial olfaction and hence is another contribution to the integrated suite of adaptations for efficient long-distance travel that has been characteristic of the genus since *Homo erectus*.

Human olfactory navigation

Olfaction is often underestimated as a sensory basis for navigation (Jacobs, 2012). This neglect is particularly acute in the study of human navigation (Jacobs et al., 2015). This is partly because primates, and particularly humans, have erroneously been assumed to have exceptionally poor olfactory abilities (Laska et al., 2000; McGann, 2017; Shepherd, 2004). Yet, in many species, including humans, the largest gene superfamilies are those for olfactory receptors (Hasin-Brumshtein et al., 2009). And while primates are indeed highly visual (Smith et al., 2007, 2014), visual acuity does not preclude the use of olfaction for long-distance movements in other highly visual animals such as birds (Wallraff, 2005).

Descriptive reports of humans using odors to navigate have a long history (Porteous, 1985; Gatty, 1983), especially in the visually impaired (Koutsoklenis and Papadopoulos, 2011), although there are to date only two experimental studies of olfactory navigation in humans. In the first study, humans were shown to accurately follow an odor trail of chocolate across a grassy field, and their accuracy was enhanced by stereo olfaction (Porter et al., 2007). In another study, humans were able to learn and map an arbitrary location in a room using only odor gradients (Jacobs et al., 2015).

Clearly, the human ability to orient to odors is not as highly developed as that of olfactory specialists, such as the domestic dog. First, the human internal nasal chamber is smaller than expected for a mammal of its body size (Zwicker et al., 2018). Its chamber lacks an olfactory recess, a feature found in the domestic dog that separates the olfactory air stream from the respiratory air stream. The recess is thought to retard and enhance the processing of air to extract odors (Craven et al., 2010, 2007).

But to make the analogy with birds once again: just because human olfaction is inferior does not mean it is not functional. Modern birds also have a reduced olfactory system in comparison to their archosaur ancestors (Zelenitsky et al., 2011). Yet, bird olfactory bulb size may be adapted to different ecological niches (Corfield et al., 2015), including long-distance travel: diverse bird species rely primarily on olfaction for orientation during migration and experimental displacement (Wallraff, 2005; Gagliardo, 2013; Holland et al., 2009; Wikelski et al., 2015). Air-borne odors can be stable across time and hence may offer unique value to navigators, as a long-distance sensory highway (Safi et al., 2016). This property of air-borne odors could lead to selection for olfactory navigation skills, even in highly visual and auditory species, such as birds and bipedal apes.

Stereo olfaction

Comparative studies can offer clues as to what properties of the human nose would support such olfactory navigation. A primary function would be stereo olfaction, or the spatial separation of paired sensors to increase the accuracy of directional orientation, similar to stereo audition (von Békésy, 1964). von Békésy's (1964) hypothesis has been supported by studies from a wide range of invertebrate and vertebrate species: honey bee (*Apis mellifera*) (Martin, 1965), desert ant (*Cataglyphis fortis*) (Steck et al., 2010), fruit fly (*Drosophila melanogaster*) (Borst and Heisenberg, 1982), terrestrial snail (*Achatina fulica*) (Chase and Croll, 1981), giant garden slug (*Limax maximus*) (Gelperin, 1974), blacktip shark (*Carcharhinus limbatus*) (Gardiner et al., 2015) and sharks in general (Gardiner and Atema, 2010), brown bullhead catfish (*Ictalurus nebulosus*) (Bardach et al., 1967; Johnsen and Teeter, 1980), the bifurcated tongue of snakes (Schwenk, 1994), laboratory rat (*Rattus norvegicus*) (Rajan et al., 2006; Khan et al., 2012), eastern American mole (*Scalopus aquaticus*) (Catania, 2013), domestic dog (*Canis lupus familiaris*) (Craven et al., 2010) and

human (Porter et al., 2007). The manipulation of crossing the inputs also eliminates the ability to orient in space to odors, both in animals with antennae (Martin, 1965) and in those with nares (Catania, 2013).

The critical variable in stereo olfaction is the physical separation of the catchment areas in the fluid, whether air or water, in which odorants are suspended. Sensor mobility will be critical in determining the volume of fluid sampled and the separation of the catchment areas, with greater separation allowing for greater accuracy in orientation. For example, a honey bee with two fixed antennae oriented less accurately to an odor source than a bee with two mobile antennae (Martin, 1965). For vertebrates with nares, Stoddart (1979) proposed that the key variable may instead be the length and flexibility of the neck, suggesting this could explain why vertebrates with less flexible necks, such as salamanders, have more widely spaced nares. This increased nasal breadth would theoretically increase the separation of the samples and hence compensate for the lack of head mobility seen in vertebrates with less flexible necks (Stoddart, 1979). The same reasoning has been used to study the separation of nostrils in sharks such as the hammerhead shark, where computational models predict that this separation increases the shark's accuracy in directional orientation (Rygg et al., 2013; Gardiner and Atema, 2010).

A third principle that has been proposed to enhance stereo olfaction, in addition to using the movement of antenniform structures or increasing the spatial separation of the nares, is the addition of a tube-like vestibule to the nares. The use of tube noses to increase the accuracy of stereo olfaction was first proposed by Stoddart (1979) to explain the distribution of tube noses in several bat families (Vespertilionidae subfamilies Nyctimeninae and Murininae; also in Pteropodidae). A recent study of the physics of siphons offers direct support for Stoddart's (1979) hypothesis. When fluids are siphoned into a simple vertical tube, the size and separation of the catchment area are determined by the velocity of movement of the fluid and the height of the tube entrance from the bed on which it stands. The greater the distance between the bed and the siphon opening, the greater the spatial separation between the siphon and the catchment area from which the siphon draws in fluids. There is a further additive effect of fluid velocity, such that a tall tube, pulling in fluid at a higher velocity, will be sampling from areas that are farther apart than a siphon that is flush with the bed's surface or is pulling in fluids at a lower velocity (True and Crimaldi, 2017).

This result has important implications for understanding the adaptive significance of tube noses. A longer tube would therefore increase the spatial separation of odor samples, effectively increasing the distance between the sensors. Additionally, the further separation of these samples could be controlled by varying the intensity of the inhalation, which would increase the velocity of the fluid, further separate the catchment areas and thus further enhance stereo olfaction.

The hypothesis that a tube nose enhances stereo olfaction may explain the presence of this trait not only in bats but in birds. Tube-nosed seabirds (Procellariiformes), which include shearwaters and albatrosses, are well known for their ability to orient to odors, such as the krill metabolites that are odor proxies for the presence of prey (Nevitt, 2008). Tube-nosed seabirds are also thought to use olfaction to orient during long-distance movements over water, in the absence of proximal visual landmarks (Reynolds et al., 2015; Safi et al., 2016; Dell'Ariccia et al., 2014). In addition, the relative size of the olfactory bulbs is also larger in aquatic bird species (Corfield et al., 2015). It is therefore possible that the demands faced by these seabirds have led to the evolution of tube-like appendages

to further separate catchment areas and thus enhance olfactory navigation accuracy.

It is interesting that tube noses have evolved in vertebrate taxa that have evolved powered flight; relatively larger olfactory bulbs are associated with increased space use in homing pigeons (Mehlhorn and Rehkämper, 2009), which navigate using odors (Wallraff, 2005). Mapping an odor gradient may be done more accurately with the greater number of samples possible over larger distances and hence may be more valuable in species using long-distance movements, such as flying insects and vertebrates (Jacobs and Menzel, 2014). But this logic might also apply to terrestrial vertebrates that cover large distances, e.g. cursorial vertebrates, such as carnivores and humans; relatively larger olfactory bulbs are also found in terrestrial carnivores that range over longer distances (Gittleman, 1991). If increases in space use are associated with an increased use of olfactory navigation, then this constraint may be relevant to the genus *Homo*, the first hominid to significantly increase space use and leave Africa (Antón et al., 2014). To answer this, we must first consider the question of the hominid nose in the context of other primates.

Spatial olfaction in primates

Primates are characterized by their external noses and were even originally classified using the Greek suffix -rhin, for 'nose' (Ankel-Simons, 2007) (Fig. 5). The primate groups are: suborder Strepsirrhini ('strepsisor' or 'turning inward' nose), i.e. prosimians, a group which includes lemurs, galagos and bushbabies. Strepsirrhines are characterized by curved nostrils and a rhinarium, the glabrous tissue on the nose tip. The second major group is the suborder Haplorrhini ('haplous' or 'simple' nose), including the group Catarrhini ('kata' or 'down' nose for downward facing nostrils), i.e. the Old World monkeys and apes, and the group Platyrrhini ('platt' or 'flat' nose), which comprise the New World monkeys (Ankel-Simons, 2007) (Fig. 5). Although these terms no longer accurately capture primate diversity (e.g. there are flat-nosed catarrhine species; Hofer, 1980), it is nonetheless characteristic enough of the order Primates that the terms have been retained. Why primates have evolved this radiation of external nose types, however, remains unclear.

A possible hypothesis for primate external nose morphology is that it serves as an adaptation for spatial orientation. Strepsirrhines are a highly olfactory group (Drea, 2015). The strepsirrhine external nose is superficially similar to that of the dog (Hofer, 1980). In the dog, the slit-like lateral openings of the nares are adapted for stereo olfaction (Craven et al., 2010), and it is possible that a similar structure has the same function in strepsirrhines. The strepsirrhine nose is also characterized by a rhinarium that is similar in appearance to that of the dog. The behavioral function of the rhinarium, a common mammalian nasal structure, has not been identified (Gläser and Kröger, 2017), although the strepsirrhine rhinarium is highly sensitive to touch (Elofsson et al., 2015). Because the mammalian rhinarium lacks olfactory receptors, it is possible that it functions in orientation to wind movement (anemotaxis), information critical for stereo olfaction. An anemotactic function for the rhinarium might work similarly to that demonstrated for the vibrissae of the rat, where inputs from the vibrissae are used to encode wind direction (Yu et al., 2016).

In contrast, haplorrhine primates lack a rhinarium (Ankel-Simons, 2007). The two haplorrhine groups, platyrrhines and catarrhines, also vary significantly in their external nose morphology. The platyrrhine nose is characterized by a wider internasal cartilage than that of catarrhine monkeys, with nares that are oriented laterally, as opposed to a frontal orientation in catarrhines (Ankel-Simons, 2007) (Fig. 5). Hofer has suggested
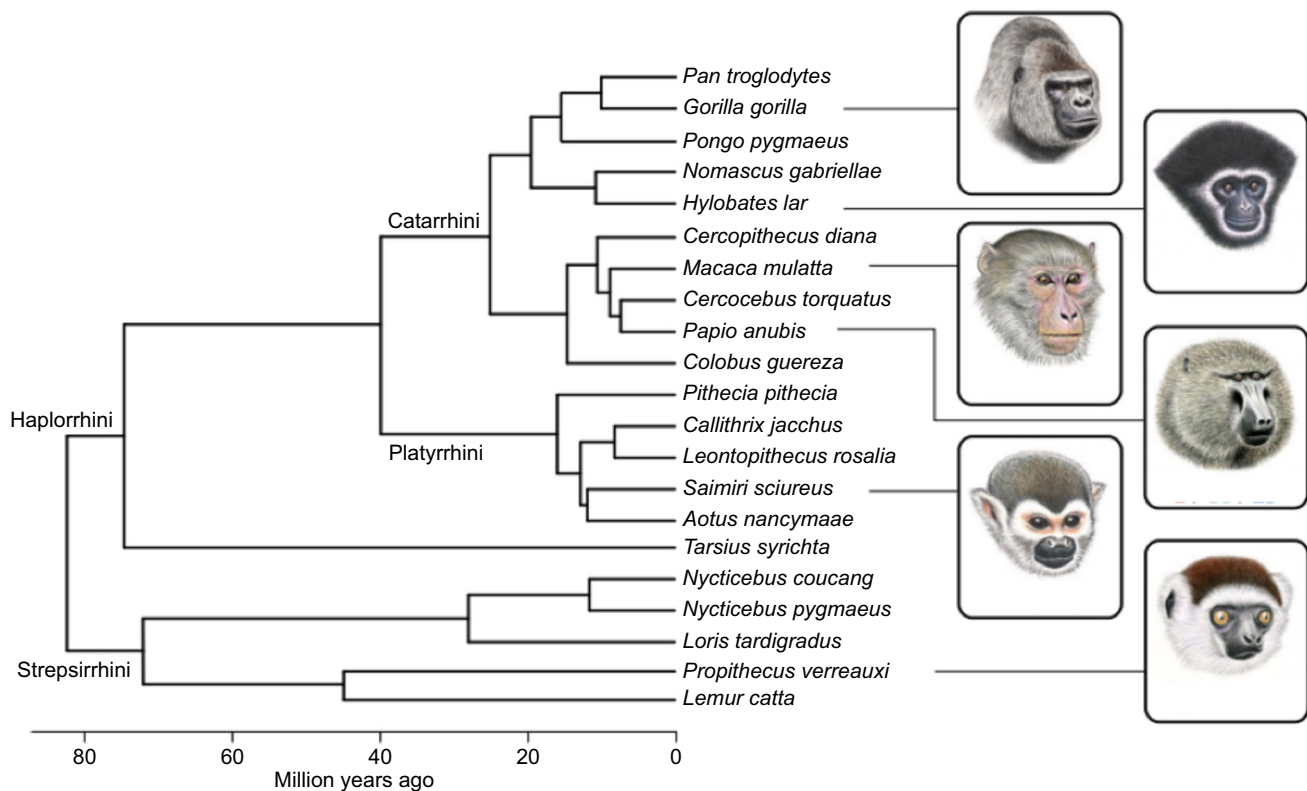
Fig. 5. Phylogeny of primates illustrating facial diversity. Note the lateral orientation of the nostril in Platyrrhini. Reproduced with permission from Santana et al. (2014).

that this lateral orientation of the platyrrhine nostril might contribute to spatial orientation to odors (Hofer, 1980, 1979). Of the two groups, catarrhines are less olfactory, having lost a secondary olfactory system, the vomeronasal system, and having gained routine trichromacy (Liman, 2012), although the loss of vomeronasal function preceded the change in color vision (Matsui et al., 2010). Catarrhines rely heavily on color vision to detect physiological state changes (e.g. sexual skin) in social interactions (Dixson, 2012) and to discriminate the faces of closely related species (Allen et al., 2014; Santana et al., 2014, 2013).

Olfaction in *Homo*
Perhaps external nose morphologies in primates, including *Homo*, can also be explained by the olfactory spatial hypothesis (Jacobs, 2012). As a catarrhine, the genus *Homo* is one of the least olfactory primates, yet it is the only primate to have evolved a large external nose. The only exception to this is the catarrhine proboscis monkey (*Nasalis larvatus*), but in this case the external nose is used by males in audiovisual communication and does not appear to be specialized for olfaction (Koda et al., 2018).

The human external nose shows several unique features (Figs 1 and 2). The external pyramid encloses generally inferior-orienting nares, a trait not found in other great apes. The pyramid encloses the nares within the alae nasi, the cartilaginous structures surrounding each naris, separated by a third structure, the columella, a protrusion between the two alae. No current hypothesis posits a respiratory function for the alae nasi or columella.

Yet, such structures could theoretically enhance olfaction, specifically stereo olfaction. It is a testable hypothesis that the alae nasi could act as tube noses, where a greater length of nasal vestibule would correspond with greater separation of the catchment

areas of inspired air. The unique inferior orientation of the human nares, separated by the columella, might also further separate the geometry of the catchment areas during inspiration. Finally, the external pyramid itself could increase the distance between the nares and, to a greater extent than that seen in platyrrhine monkeys, could also enhance stereo olfaction. These predictions could be tested by measuring the effect of nasal metrics on a human's accuracy in orienting to an odor gradient. Using standard methods, it should be possible to measure the effect of nasal breadth on orientation accuracy to odors distributed in plumes. If supported, then the navigational nose hypothesis could then be used to address the remaining questions about the human external nose: why did it appear when it did and why did nasal breadth and height subsequently become so variable in modern humans?

Why did it evolve?
The external pyramid first appeared in *Homo erectus* (Franciscus and Trinkaus, 1988) (Fig. 6). Early *Homo* evolved in an increasingly unpredictable climate, with periods of great aridity, and forest habitats changing to grasslands (Antón et al., 2014). This change in climate and habitat structure led to selection in *Homo* for a suite of traits to increase bipedal locomotory efficiency, such as increased lower limb length, which allowed archaic humans to forage more economically for widely dispersed resources (Steudel-Numbers, 2006; Bramble and Lieberman, 2004; Kuhn et al., 2016; Antón et al., 2014; Antón, 2012; Lieberman, 2011).

Another major behavioral shift in *Homo* at this time was an increase in carnivory, a shift that brought the genus into direct competition with other mammalian carnivores (Churchill et al., 2016). Given this interspecific competition between humans and other African carnivores, it may be most fruitful to ask not what species humans

Fig. 6. A reconstruction of *Homo erectus*. An early African *Homo erectus*, based on the skull KNM-ER 3733. Reproduced with permission from Gurche (2013).

are most closely related to but to which species they are most ecologically similar (Schaller and Lowther, 1969). Humans were competing not only with cursorial carnivores but also with olfactory specialists, species that used olfaction both to detect prey and to orient in space. Carnivory, space use and olfactory bulb size may be generally associated, as they are in terrestrial carnivores (Gittleman, 1986) and theropod dinosaurs (Zelenitsky et al., 2011, 2009); a similar association between carnivory, space use and olfaction may be seen in piscivorous birds (Wikelski et al., 2015) and sharks (Nosal et al., 2016).

Many African carnivores, such African lions (*Panthera leo*), wild dogs (*Lycaon pictus*) and spotted hyenas (*Crocuta crocuta*), are also highly social and hunt cooperatively (Smith et al., 2012). To compete in this environment, *Homo sapiens* also became, like their competitors, increasingly social, both hunting and breeding cooperatively (Hrdy, 2007). The ability to hunt cooperatively, even before the development of weaponry, changed many aspects of human socio-ecology. One behavior that may have evolved at this time is the use of endurance pursuit to capture large game (Carrier et al., 1984; Bramble and Lieberman, 2004). Endurance pursuit requires accurate spatial orientation, while tracking and returning to camp (Liebenberg, 2008). Such long-distance travel could also have selected for new navigational skills, such as olfactory navigation.

There are additional navigational costs of carnivory beyond prey search and handling. Carnivory carries with it a higher risk of foraging with zero return than does foraging for non-meat foods. Hence, a primary mechanism that has been shown to insure against such risk is to maintain large social networks for food sharing (Grove, 2009). In models of hunter–gatherer food sharing, greater cooperation and the elimination of free riders is supported primarily by increased mobility (Lewis et al., 2014). One of the true costs of carnivory may therefore be the need for cooperative hunting and a widely dispersed social network for food sharing, a behavior that would be made efficient with more accurate spatial navigation.

Thus, olfactory navigation in *Homo* could have represented an important new technical skill to increase the efficiency of space use. This, in turn, would have selected for mechanisms of stereo olfaction. It has also been proposed that it was these adaptations for increased mobility that allowed archaic humans to subsequently expand their species distribution (Kuhn et al., 2016); by 1.8 million years ago, *Homo erectus* had expanded out of Africa and become established in Georgia, Indonesia and possibly China (Antón et al., 2014).

Implications for sex differences

Both the conditioning hypothesis and the navigational hypothesis posit that the human external nose evolved as an adaptation for long-distance movement. Thus, both hypotheses are predicated on the same ecological demand: increased space use in an arid environment, necessitating efficient conditioning and efficient navigation. Individual differences in long-distance travel should therefore be reflected in nasal structure.

Although men generally have larger range sizes than women (Gaulin, 1992), women may also forage over long distances (Jones et al., 1994). Both may orient using odor and hence both could benefit from stereo olfaction. The advantage of stereo olfaction may operate at different spatial scales. In a landscape defined both by arrays of local landmarks and distant cues that supply compass directions, females weight proximal landmark cues more heavily than do males (Jacobs and Schenk, 2003; Chai and Jacobs, 2010; Bettis and Jacobs, 2013). But it is not clear at what scale stereo olfaction is most effective when tracking an odor plume; stereo olfaction is clearly important in close-range orientation to odors (Catania, 2013; Porter et al., 2007). Unlike a distant visual object that provides direction, plumes are not contiguous in space but are a collection of discrete filaments (Murlis et al., 1992). Thus, the local structure must be analyzed to deduce the global structure. In this light, stereo olfaction might be valuable for the analysis of both close and distant resources. The key factor is the added value of a second sensor, as has been recently demonstrated in an information theoretical model of optimal sampling for spatial orientation in an empirically measured odor plume (Boie et al., 2018). In short, the evolution of the external pyramid could have been equally adaptive for women building high-resolution maps of resources near the home base or men building low-resolution maps of distant resources.

The use of long-distance foraging by men, in particular endurance pursuit, may also explain sex differences in the relative size of the external and internal nose. In a sample of European-descent Americans, men had larger external noses, both absolutely and relative to body size, than did women (Holton et al., 2014). In a study using crania from diverse worldwide populations, males also had a relatively larger nasal chamber volume than women, including relative larger choanae, i.e. the posterior opening leading to the lungs (Bastir et al., 2011). The authors conclude that the larger internal chamber and choanae in males would allow a greater

volume of air to be conditioned during exercise (Bastir et al., 2011). A similar sex difference in internal nose dimensions has been documented in imaging studies of German and Chinese adults, with men showing a relatively larger nasal aperture than women (Schlager and Rüdell, 2015).

Such sex differences in nose morphology could have arisen via sexual selection in males for enhanced respiration during long-distance travel. The choanae, for example, which are relatively larger in males, have a purely respiratory function (Bastir et al., 2011). Thus, while the original appearance of the external nose in *Homo erectus* may have been due to natural selection for increased space use in both sexes of the species, other nasal structures could have been shaped by sexual selection to enhance a male's ability to compete with other men, such as in endurance pursuit. Male hunting skill in hunter-gatherer societies can often be interpreted as a trait driven by female choice and may be the product of both natural selection for foraging and sexual selection for male–male competition (Hawkes and Bird, 2002).

Sexual selection for navigation might also explain patterns in olfactory bulb size. In a German sample, both absolute olfactory bulb size and olfactory function developed gradually between the ages of 6 and 17 (Hummel et al., 2011). It increased throughout adulthood to peak around age 40 and then declined in both women and men, although the absolute size of the olfactory bulb was consistently larger in men (Buschhüter et al., 2008). Forty is also the age at which mortality begins to increase in hunter–gatherers, peaking at a model adult death of 70 years (Gurven and Kaplan, 2007). Finally, olfactory bulb size is positively correlated with olfactory function (discrimination and threshold) in humans (Buschhüter et al., 2008; Hummel et al., 2011, 2013; Mazal et al., 2016; Seubert et al., 2013). This suite of characters in human males could be an adaptation for efficient foraging, a difference that might emerge at puberty and extend over the peak hunting years, where accurate spatial orientation to odors might be enhanced by a larger external nose, while the capacity for oxygen exchange would be increased by a larger internal nasal chamber and choanae.

In contrast, women might have evolved a different suite of olfactory specializations, in addition to the stereo olfaction afforded by an external nose. Women consistently outperform men on measures of odor identification, for both social and non-social odors (Doty and Cameron, 2009). In a cross-cultural study of Japanese, Italian and German participants, women more accurately identified the sex and individual identity of an axillary odor (Schleidt et al., 1981); in a study of American college students, women could more accurately identify their own axillary odor than could men (Platek et al., 2001). Thus, in social encounters, women may have access to more accurate olfactory information than men.

These sex differences could arise from sex differences in olfactory system plasticity. The olfactory system changes rapidly (e.g. within months) if given repeated exposures to an odor, even in humans that are initially anosmic to the odorant (e.g. androsterone) (Wysocki et al., 1989). Repeated exposures both decreased the threshold of detection and increased absolute olfactory bulb size in the subject (Haehner et al., 2008). Even when only one nostril is exposed to the odor, both olfactory bulbs increased 11–13% in volume after 4 months (Negoias et al., 2017). This effect of repeated exposure decreasing the threshold of detection for an odor is significantly stronger in women than in men (Dalton et al., 2002).

Therefore, experience-dependent sex differences in social experiences and hence olfactory exposure could lead to the observed female advantage in olfactory identification. These female advantages might also arise via sexual selection, in this case selection for enhanced social intelligence. This form of neural plasticity could also support related skills, such as tracking and mapping the distribution of other resources, e.g. food and medicinal plants, that could be identified most accurately by odor. Relevant to this, a new study has demonstrated that a human's ability to identify odors co-varies with their ability to learn landmark locations in a virtual environment. These cognitive skills also co-varied with the size and integrity of brain structures involved in both spatial navigation (right hippocampus) and olfaction (left orbitofrontal cortex) (Dahmani et al., 2018), in accordance with the olfactory spatial hypothesis (Jacobs, 2012). This tight relationship between olfaction and spatial memory could have evolved via selection for mapping resources via chemical cues.

The predictions of these proposed sex-specific specializations, whether long-distance travel in men or resource tracking in women, are amenable to empirical testing. Re-framing the human external nose as an olfactory structure could lead to new insights into human perception and brain plasticity and their modulation by natural and sexual selection.

Why did it narrow?

If *Homo* evolved a broad nose to facilitate long-distance navigation, why then did the *Homo sapiens* nose undergo a subsequent global radiation in breadth and height? Given the evidence for positive selection in nasal structures (von Cramon-Taubadel, 2014), why, once humans migrated out of Africa, did their nose, change its shape so many times (Fig. 3)? If it served a navigational function, then one simple interpretation is that decreased nasal breadth resulted from a reduced need for stereo-olfactory navigation. Such a shift could have occurred for at least two reasons: first, humans could have moved into climates less amenable to the use of olfaction for navigation or second, and not excluding the first, humans could have become less mobile and hence had less need for long-distance olfactory navigation.

In fact, both of these events occurred after the genus left Africa. As discussed earlier, the ideal conditions for olfaction combine low altitude, high temperature and high absolute humidity. The demonstrated association between nasal breadth and absolute humidity in living tissue (Zaidi et al., 2017) suggests that such habitats may select for stereo olfaction, i.e. a greater nasal breadth. In contrast, the greatest shifts in nasal index have been seen in habitats that are most hostile to olfaction, such as extreme cold, which is characterized by a reduction in vapor pressure and hence low absolute humidity (Hubbe et al., 2009; Maddux et al., 2016). The higher nasal index seen in tropical South America, compared with Arctic populations, suggests that after crossing Beringia, the human nose once again broadened to re-adapt to an olfactory environment that supported olfactory navigation (Fig. 3).

The other factor that could have contributed to this change, however, is not just a decline in olfactory navigation but a decline in space use altogether. The human species underwent rapid changes in social ecology in the Holocene. Human mobility decreased dramatically in the Neolithic, a change which has been calculated from decreases in lower limb proportions. This change in morphology was specifically associated with a change in food production, with the shift from nomadic hunting to sedentary agriculture (Ruff et al., 2015). Such a sudden decrease in space use would have reduced selection for navigational skills, including stereo olfaction.

The Neolithic nose: from navigation to diagnostics

If so, this does not answer the question of why the nose was under positive selection to decrease breadth and increase height in the early Neolithic, before the migration to northern latitudes with cold,

dry climates. One hypothesis is that this narrower and taller nose was an adaptation in response to three olfactory challenges related to selective pressures that were becoming increasingly important: disease, social status and cooking.

Non-human vertebrate species rely heavily on olfactory discrimination to detect disease states in conspecifics, information that influences their behavior, including mate choice (Kavaliers and Colwell, 1995; Penn and Potts, 1998). Even humans can detect an induced immune response in another human based on odor alone (Olsson et al., 2014). Until recently, human medical training included knowledge of the characteristic odor of a disease; this knowledge is now being revived with the training of dogs to sniff out human disease (Bijland et al., 2013). Neolithic societies were characterized by significant increases in disease, both infectious disease and disease as a result of the agricultural diet. Societies were also larger and living in more densely settled areas, with close proximity to livestock; all of these created an ideal environment for an increase in disease (Larsen, 2006). Being able to detect disease more accurately, either in potential mates or to avoid infectious individuals, would have been a valuable survival and reproductive trait.

The second olfactory challenge that might have increased during the Neolithic is related to social intelligence. Humans rely on olfactory information in diverse social contexts that are often competitive (Lübke and Pause, 2015): detecting emotions (de Groot et al., 2012), and identifying individuals (Meadow et al., 2015) and their degree of relatedness (Havlíček and Roberts, 2009; Milinski et al., 2013). The large, sedentary societies that emerged in the Neolithic were characterized by increased social stratification, as the accumulation of wealth became possible (Larsen, 2006; Mummert et al., 2011). This brought with it a host of new social ills (van Schaik and Michel, 2016). All of these factors would have led to greater levels of social selection, i.e. competition for social status and reproductive success (West-Eberhard, 1983). The need for greater social intelligence, arguably one of the driving features of human evolution (Dunbar and Shultz, 2007), might also have increased at this time, including the ability to diagnose the emotional states of potential competitors or allies. Modern humans, like other species (Caro et al., 2015; Tibbetts and Dale, 2007; Wyatt, 2010), still use odors to make decisions in these realms, including detecting emotions in social encounters (de Groot et al., 2012), mate choice (Wedekind et al., 1995; Milinski et al., 2013; Havlíček and Roberts, 2009), offspring identification by fathers (Alvergne et al., 2010) and the identification of individual-specific odors (Meadow et al., 2015). Thus, an increase in sedentism, with the accompanying increase in social competition, might have favored enhanced abilities to discriminate physiological states and social status using socio-chemicals.

Finally, a potential third category of function for a different nose is the human development of cooking, a behavior which by then had already led to changes in cranial evolution (Zink and Lieberman, 2016), foraging efficiency and diet breadth (Wrangham and Conklin-Brittain, 2003; Wrangham et al., 1999). The use of olfaction for selecting and preparing ingredients, as well as detecting spoilage in stored food, with the addition of retronasal olfaction via the specialized human nasopharynx (Shepherd, 2013; Ni et al., 2015), would have added yet another selective force for olfactory function at this time. The former advantages of stereo olfaction and the spatial separation of nostrils would be replaced by selection for a narrowed nose, creating internal vortices that enhance olfactory discrimination.

Such seismic changes in the social ecology of Neolithic humans could have shifted the adaptive function of human olfaction away from navigation and towards diagnostics. Behavioral changes may have been accompanied by changes in nasal structure. Cheronet et al. (2016) documented cranial changes in three Neolithic populations (Levant, Iberia and Ukraine), where the transition to sedentism began at different times. In the Levant, where the transition to the Neolithic first began around 15,000 years ago, there was a significant increase in nasal height (Cheronet et al., 2016). This could be consistent with olfactory function and nasal structure adapting to the new sedentism, with nasal height increasing first in the earliest adopters of sedentism.

If the Neolithic nose was becoming specialized for olfactory discrimination, then this could explain why there is a relationship between nasal index and olfactory function. The results of Li et al. (2018), showing that low nasal index is associated with notch-related vortices in the anterior nose and specific olfactory sensitivities, could be evidence for this. A narrower human nose, at the cost of decreased stereo olfaction, could have allowed increased sensitivity to odorants with greater survival and/or reproductive value. Selection for specific sensitivities could have been fueled by the high inter-individual variation in functional olfactory genomes in humans, comparable only to the level of genetic variation in the major histocompatibility complex (Menashe et al., 2003), which humans identify via olfaction (Havlíček and Roberts, 2009). These lines of evidence suggest that nasal structure and the olfactory genome could be locally co-adapted for specific olfactory functions, creating a spectrum of adaptive nose solutions, from the broad navigational nose to the narrow diagnostic nose.

Conclusion

This Review has only sketched a hypothesis for future research. The question of the function of the human external nose demands large scale, cross-disciplinary and quantitative studies of geometry and olfactory function, as is the tradition in this field (von Cramon-Taubadel, 2014; Lieberman, 2011). Yet, to quote John Tukey, 'Far better an approximate answer to the *right* question, which is often vague, than an *exact* answer to the wrong question, which can always be made precise' (emphasis as in original) (Tukey, 1962). For a century, research has focused on the respiratory function of the human external pyramid and it is time to reconsider its role in olfaction, both spatial and non-spatial.

This is not to say that this will be easy. The mammalian nose is a complicated and dynamic structure (Van Valkenburgh et al., 2014). The field of olfactory neuroscience, despite many breakthroughs, has yet to identify the code by which an odorant is perceived as an odor by the brain (Murthy, 2011). Understanding the evolution and diversity of human noses will require an integrated synthesis of the costs and benefits of respiration and olfaction under different climatic and social ecological conditions. But if this effort is successful, we might re-evaluate statements such as, 'The only area in which the size and shape of the nose is of relevance is in aesthetic and reconstruction surgery' (Leong and Eccles, 2009) and instead celebrate the diversity of human noses for their functional individuality.

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