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Olfaction scaffolds the developing human from neonate to adolescent and beyond

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Abstract

The impact of the olfactory sense is regularly apparent across development. The foetus is bathed in amniotic fluid that conveys the mother's chemical ecology. Transnatal olfactory continuity between the odours of amniotic fluid and milk assists in the transition to nursing. At the same time, odours emanating from the mammary areas provoke appetitive responses in newborns. Odours experienced from the mother's diet during breastfeeding, and from practices such as pre-mastication, may assist in the dietary transition at weaning. In parallel, infants are attracted to and recognise their mother's odours; later, children are able to recognise other kin and peers based on their odours. Familiar odours, such as those of the mother, regulate the child's emotions, and scaffold perception and learning through non-olfactory senses. During adolescence, individuals become more sensitive to some bodily odours, while the timing of adolescence itself has been speculated to draw from the chemical ecology of the family unit. Odours learnt early in life and within the family niche continue to influence preferences as mate choice becomes relevant. Olfaction thus appears significant in turning on, sustaining and, in cases when mother odour is altered, disturbing adaptive reciprocity between offspring and caregiver during the multiple transitions of development between birth and adolescence.

Key-words: Olfaction, Maternal effects, Social cognition, Emotion, Attachment, Communication.

1. Introduction

Like other mammalian offspring, human infants thrive through a predictable sequence of developmental transitions: embryonic and foetal growth; birth, breastfeeding and attachment; diversification in sociality and sustenance (weaning); motor autonomy and wariness of novelty; puberty and risk-taking; and dispersal, social enculturation through affiliation networks, and initiation of mate choice. Each transition comes with its particular timing, tensions, and threats to offspring viability [e.g. 1-3], requiring physiological, perceptual-cognitive and behavioural co-adaptations in the dependent infant and the investing parents.

This paper aims to review the adaptive contribution of olfaction in alleviating the challenges raised by these developmental transitions. It will describe how the foetal environment primes the growing offspring to their forthcoming environment, where neonates will need to discern the mother promptly in order to ingest colostrum/milk and reach physiological stability. Next, it will survey the nursing niche, where infant responsiveness to odours can assist in self-regulation and managing the uncertainties of emerging social and dietary novelty. Finally, parent-to-child olfactory communication will be considered in the context of expanding affiliative networks within the family and beyond. In all this, we aim to provide an overview of empirical research on parent-to-infant odour exchanges, identify gaps in current understanding, and suggest new directions for future research.

1 2. From the prenatal to the postnatal niche: the birth transition

2 2.1. Interacting physiologies: materno-foetal odorant transfers and transnatal olfactory continuity

3 An infant's olfactory preferences have their origins in the prenatal period. Nasal chemoreception begins
4 functioning during the last gestational trimester [4], bathed in an amniotic pool that is permeated by
5 odorous compounds that are regulated by the mother's genetic, immune and physiological constitution,
6 modulated by her stress and health, and paced by her dietary, cosmetic, or addictive inclinations. Odorous
7 metabolites pass easily into amniotic fluid (AF) , and such transplacental penetration can be so stark that
8 the newborn's body odour is occasionally pungent [5,6]. Neonates favour the odour signature of AF [7],
9 particularly their own AF [8], and react to odours experienced during gestation (e.g. anise [9]; alcohol
10 [10]). Regular gestational exposure to strongly odourised foodstuffs (garlic, carrots, fish, cheese, green
11 vegetables) influences the progeny's preferences for related odorants over periods that can last several
12 months or even years [11-13].

13
14 The amniotic environment provides the foetus with an olfactory repertoire that prepares it for the outside
15 world by virtue of transnatal olfactory continuity (TOC). Thus, amniotic and milk odours are equivalently
16 attractive to neonates up to postnatal d3, at which point, conspecific milk odour becomes more appealing
17 [14]. Such initially undifferentiated responses between AF and colostrum have been found in the
18 newborns of other species , suggesting a pan-mammalian convergence in TOC from both compositional
19 and perceptual points of view [6]. Many of the maternal dietary odorants that infiltrated AF will permeate
20 colostrum/milk, as will remnants of the mother's chemical ecology (tobacco smoke, cosmetics), and
21 odour-active compounds deriving from her normal metabolism and lactogenic process, such as steroids or
22 fatty acids [reviewed in 15,16]. Nurslings are sensitive to these odour changes in milk [17-21].

23
24 TOC represents a maternal sensory information transfer system that impinges both on the stimuli and on
25 the receptive system of the offspring. Indeed, maternal physiology not only conveys odorant metabolites
26 to foetuses, but also attunes the conceptus's olfaction to detect a range of odorants that will occur on her
27 body surface and in her milk. In animal models, exposure to an odorant *in utero* induces epigenetic
28 changes in olfactory receptor expression and orients neurogenesis and synaptic organisation in the
29 olfactory bulbs, eventually tuning olfactory sensitivity in newborns [e.g. 22,23]. Prenatal olfactory
30 experience is then reinforced through postnatal reconsolidation, thereby facilitating newborn
31 responsiveness to that odorant [24,25]. Thus, under normal mammalian circumstances, the mother, via
32 odorants transferred in AF, designs the offspring sensors (foetal chemoreception), the medium (odour
33 cues), and the message (familiarity between the prenatal and postnatal niches) [reviewed in 15,26].

34
35 The fitness value of the TOC is best demonstrated with reference to the consequences of its disruption.
36 Several non-human examples show that drastic odour mismatches between the prenatal and birth
37 environments result in altered nipple grasping [24,25], increased stress levels [27], and even lethality [4].
38 In humans, one such perinatal odour mismatch is created by feeding neonates non-human milks or
39 artificially-engineered formulas. When infants are breastfed from birth they show a preference for milk
40 over AF in a paired-choice odour test run on d4. In contrast, when exclusively fed cow-based formulas,
41 same-age infants turn more to AF odour than to the reinforcing formula odour [14,28], indicating a
42 differential path of preference development as a function of a progressive change based on TOC vs. a
43 saltational change of it. Another such mismatch is created when the AF odour is washed away right after
44 birth. AF odour elicits a positive orientation response in newborns [7,29,30], and infants' own spreading
45 of AF on the breast facilitates their motivated responses. When the neonate's AF covering is left intact for

1 at least 12 h after birth, infants evince better weight gain, revealing more optimal feeding responses
2 [31,32]. Along the same lines, recreating the prenatal odour environment postnatally facilitates the
3 neonates' adaptive responses. For example, providing AF odour to term or preterm newborns eases self-
4 regulatory responses in reducing fussing and crying [e.g. 29,33-35]. In sum, prenatal odours not only
5 guide the first directional actions, but also promote neonates' energy allocation to anabolism and growth
6 as opposed to catabolic wasting during a period of great metabolic vulnerability (see below).

7 8 2.2. Birth and the rapid learning of the mother's body surface odours

9 The normal birth process represents both the last AF odour encoding and an upsurge of novel perceptual
10 experience for the foetus as it becomes a newborn. The physiological/sensory upheavals of labour affect
11 the brain, with rising catecholamines coinciding with high arousal levels [36]. Not only does labour set a
12 last sensory update of the amniotic "smellscape" [37], but it promotes neonatal learning of odours, as
13 found in the rat [25], and inferred in human neonates. When exposed to an odorant for 30 min after a
14 Caesarean section made before/after labour engagement, and then re-exposed to that odour 1-5 d later,
15 only those neonates who were subjected to contractions preferred the familiar odour compared to a novel
16 odour [38]. Thus, labour-related events mediate high arousal states during the first few postnatal hours
17 when the brain appears especially receptive to incoming stimulation. Human neonates exposed to an
18 odorant for 30 min during the first postnatal hour go on to display a preference for the familiar odorant 2-
19 3 d later, unlike those exposed later (after 12 h postpartum) [39]. Likewise, 4-d-olds mouth more to their
20 mother's milk odour (than to another mother's milk odour) when they have been in contact with the
21 mother's skin right after birth [40]. Thus, the birth process itself creates a neurosensory context that
22 engages fast learning of odours associated with the mother's body.

23
24 Aversive perinatal odorants might also contribute to newborn performance. Odorous steroids (e.g.,
25 androstenone) or conjugates of acidic or thiol compounds occur in AF, milk, and axillary sweat, where
26 they convey salient odour notes, and are aversive to newborns (perhaps inherently so) when administered
27 in pure form [41,42]. In AF/milk, the aversive value of these odorants may be attenuated when combined
28 with positively-valenced compounds, and indeed such a blend of positive and negative constituents leads
29 to an attention-capturing contrast effect [43], perhaps optimising the learning of the odour qualities of AF
30 or milk [41]. Axillary odours containing the above compounds elicit crying in 2-4 d-old newborns [44],
31 although these odours become secondarily acceptable after pairing with maternal care: 2-w-olds orient to
32 maternal axillary odours [45].

33 34 2.3. Odour communication during nursing

35 Human nipples constitute an evolved multisensory trap that concentrates conspicuous tactile, gustatory,
36 olfactory, and visual cues, and function as vital interfaces between lactating females and neonates [46,47].
37 Darwin foresaw that a natural scent might drive the newborn to the nipple [48], but corroborating
38 evidence awaited another century. The test consisted in presenting odorous cotton pads hanging over each
39 side of the face of supine infants. When so exposed to one pad impregnated with the mother's breast
40 odour against a clean control pad, 17 of 20 breast-fed infants (aged 2-7 d) turned their nose longer to the
41 former stimulus, indicating attraction [49]. A later study verified the specificity of mammary odour for
42 neonates: 2 w-old infants bottle-fed from birth turned longer to an unfamiliar lactating mother's breast
43 odour than to the odour of their familiar formula [50]. Similarly, 2 w-old bottle-fed infants facing the
44 breast odour of an unfamiliar lactating woman, against either i) the breast odour of a nonparturient
45 woman or ii) the axillary odour of that same woman, oriented more to the odour of the lactating breast

1 [51]. As these (formula-fed) infants had never engaged with their mother's breast for feeding, this is
2 consistent with the evidence that women emit a more attractive odour from the (lactating) mammary area
3 than from the axilla. Finally, when laid prone on the mother's torso within an hour of birth, newborns
4 crawl to the breast [52,53], with breast odour possibly driving directional actions [54]. Likewise, when
5 left prone on a mattress, infants are swifter to approach a pad scented with their mother's breast odour
6 than a scentless pad [55]; and when presented with mother's breast odour under the nose, infants display
7 more rooting responses (than to control stimuli), and produce more efficient arm- and footsteps [56].
8 Finally, in different contexts, breast/milk odour can provide comfort, actualized in infants' reduced motor
9 output [57], delayed onset of crying [58], and attenuated expressions of stress and pain [59,60].

10
11 The source of the breast's attractive and reinforcing odorants is unclear. The human areolar-nipple
12 structure harbours skin glands of all types (eccrine, apocrine, and sebaceous). Human nipples bear
13 sebaceous glands at their distal end, that open into milk ducts as well as onto the nipple tip surface [61].
14 The areolae are dotted with Montgomery's glands (MG) [62,63], which are coalesced sebaceous and milk
15 glands [64] that give off a whitish fluid during lactation [47,65]. When 3 d-old infants were exposed to
16 their mother's entire breast, or isolated areola, or isolated nipple, or drops of milk [58], they responded
17 alike to the odour of these different conditions, suggesting overlapping or equivalent attractive potencies
18 in underlying mammary substrates. However, the odour of Montgomerian secretions, when presented
19 separately, elicited a typical respiration pattern and more mouthing responses than milk, sebum, and
20 various controls [66]. Montgomerian odour may thus play a special role in the human infant's attraction
21 to, and coordinated action upon, the lactating breast [47].

22
23 The most obvious contributor to breast odour is colostrum/milk. Infants born at term [67,68] or preterm
24 [69] react to colostrum/milk odour by positive head-turning and appetitive facial-oral responses [28,70],
25 even before they have been directly exposed to the breast. The odour of the mother's milk, compared to a
26 familiar formula feed, increases the efficacy of nutritive sucking during a regular formula feed [71], and
27 affects the pattern of non-nutritive sucking in premature infants [69,72]. Colostrum, milk, or lactating
28 breast odours further elicit cortical activation [as assessed by EEG or near infrared spectroscopy, NIRS;
29 73-75], and milk vs formula odours give rise to different patterns of cortical activation in infants'
30 orbitofrontal regions, irrespective of their prior experience with formula [76]. Thus, human lacteal
31 secretions are olfactorily detectable to infants aged from 2 m pre-birth to at least 2 m post-birth, and they
32 affect infants' arousal, attraction, and appetitive responses.

33
34 The chemical nature of behaviourally-active human milk odorant(s) remains unknown. Chemo-analytical
35 attempts report various odorants in human milk [e.g., 77,78], but their methodological diversity leaves us
36 short of a comprehensive view [79]. The extraction, separation, and identification of milk volatiles is
37 challenging because of their low concentration and instability, yet behaviourally-active milk compounds
38 can be characterised, as shown by work in the European rabbit. A single component of fresh rabbit milk,
39 2-methyl-but-2-enal (2MB2), was as effective as whole rabbit milk odour in eliciting pups' oral grasping.
40 Occurring in milk from varying rabbit genotypes and ecologies, being highly selective in releasing oral
41 responses in other mammalian newborns, and requiring no prenatal/postnatal exposure to become
42 functionally specified, 2MB2 was designated a 'mammary pheromone' [80]. However, there is no
43 evidence to date that milk-based predisposed chemosignalling generalises to other mammalian nursing
44 systems [81-83].

45

1 It seems then that the relative constancy of the mammary chemical signature drives infants' continued
2 attraction/appetitive responses to breastfeeding, and this is further evidenced in settings where the breast
3 chemosignature is altered experimentally or physiologically. For example, the mother's diet or physical
4 exercise can modify the odour of milk and transitorily affect the offspring's sucking behaviour [19,84],
5 and nipples with alien odorants are rejected [85,86]. In undiagnosed cases of unilateral malignant tumour
6 of the breast, nurslings have been reported to refuse the affected breast while accepting the healthy one
7 [87]. Thus, infants can disengage their appetitive or consummatory responses following unacceptable
8 fluctuations in their mothers' breast/milk chemosignature.

9
10 In sum, mammalian newborn attraction to the maternal body, mammary areas, and nipples appears
11 overdetermined. Convergent processes of tactile, visual, and in particular odour signalling, all work to
12 optimize the infant's attentional, integrative, and motor responses. First, foetal olfactory memory biases
13 neonates to sense the chemicals that post-parturient mothers present on their body. Second, odours in the
14 lactation niche, some aligned with foetal experience, others novel, favour an infant's rapid learning of the
15 idiosyncratic odour signatures of the mother. Any odour sensed at the breast may then be promptly
16 acquired as a signal that reinforces interaction and, as such, elicits positive attraction [88,89]. Third, in
17 addition to such opportunistic odour cues learned *in amnio* or *in lacto*, unconditional odour signals
18 conveyed in mammary secretions may operate in humans as they do in other mammals, but evidence is
19 lacking so far [90,91]. Human mammary odorants are indeed effective in eliciting appetitive social
20 responses in infants before direct exposure to the breast or conspecific milk. Such specialized, species-
21 specific signals need now to be chemically characterised and behaviourally assayed in humans [92].
22

23 3. Odour-based maternal weaning strategies

24 A growing infant's energetic/nutritional needs must be balanced against the continuation of the mother's
25 investment in other offspring, among many other duties. Accordingly, exclusive offspring sustenance
26 from human milk must be replaced by the local diet. Across human history, this weaning transition has
27 been, and under harsh conditions continues to be, another period of high infant vulnerability due to the
28 new wave of challenges and pathogens brought in with non-milk foods [93,94]. One of several important
29 challenges of weaning relates to confronting infants with multisensory ingestive novelty without
30 provoking rejection, and mammalian females rely on multiple, non-exclusive olfactory strategies prior to
31 and during weaning to boost gradual acceptance of non-milk foods. *First*, as already mentioned, human
32 foetuses are primed to flavours from the pregnant mother's diet, and retain them postnatally for months.
33 *Second*, foetal familiarisation extends as maternal dietary flavours pass into milk. Such early odour
34 experience favours the emergence of human infants' selective responsiveness to foods [12,13,95,96]. That
35 odour cues positively associated with human milk support infant acceptance of novel feeding contexts
36 [bottle: 97] or of novel foods [11] attests to the strength of these initial maternal olfactory effects. *Third*,
37 beyond experience of dominant flavour qualities *in amnio* or *in lacto*, early and prolonged exposure to
38 chemosensory variety induces weanlings to tolerate ingesting more of a food that is *a priori* repulsive
39 because it is unusual. A diversified maternal diet renders her milk variable in flavour, thus exposing the
40 suckling to a tonus of ever changing, low-intensity chemosensory fluctuations. The infant's daily
41 exposure to such flavour variety increases later tolerance for flavour novelty, further widening the
42 repertoire of accepted flavours [98,99]. Upon first contact with non-milk foods (e.g. at 5-6 m of age), such
43 chemosensory variety experience may influence acceptance of novel foods at least during childhood [up
44 to 6 y; 100].
45 *Fourth*, another pan-mammalian solution to olfactorily cue safe foods relies on an offspring's attraction to

1 the mother's mouth or breath during ingestion [e.g. 101-103]. Such flavour-charged mouth or breath
 2 directs offspring multisensory scrutiny toward the eating mother, inducing attention and observational
 3 learning of palatable foodstuffs [e.g., 104,105]. This incidental "maternal demonstrator" effect can be so
 4 powerful that it induces offspring to adopt atypical or maladaptive ingestive habits [e.g., kitten eating
 5 banana: 106]. There is circumstantial evidence that human infants and young children want to taste foods
 6 following caregivers' oral food odours. Such mother-induced odour learning may be secondary to
 7 intentionally giving infants premasticated foods, a commonplace practice [e.g. 107-109] which makes
 8 non-milk foods more digestible, and exposes infants to pre-treated highly odorous foodstuffs [110],
 9 whose novelty may be attenuated by the caregiver's added saliva and other oral odour substrates (labial
 10 sebaceous glands, breath). But, so far, nothing is known about whether human maternal saliva channels
 11 chemosensory information to offspring as it does in other species [e.g. 111,112].

12
 13 In other mammals, additional olfaction-based weaning strategies imply switch-like processes based on
 14 specific, unconditional chemosignals. Pheromones emitted in milk [rabbit: 80] or in breath [murine
 15 rodents: 113,114] tag as attractive any co-occurring odorant. The appetitive mammary pheromone of the
 16 rabbit is interesting in that context because its concentration in milk declines in parallel with its
 17 decreasing reactogenic potency for pups in the week preceding complete weaning [115], literally turning
 18 off milk-feeding. Another such odour-based "weaning gadget" has been described in the lactating female
 19 rat, whose (unknown) caecal 'pheromone' attracts offspring to her faeces [116]. In many mammals,
 20 infants are coprophagic of maternal faeces [e.g. 117], thereby taking in information on mother's dietary
 21 composition, as well as safe-tested microbiota (e.g. [118]; but see [119]). However, such unconditional
 22 odour-based biological switch processes seem absent from human weaning. But, at least in some human
 23 groups, efficient weaning-switch processes have been devised culturally by adulterating the breast with
 24 unfamiliar, irritating or disgust-eliciting odorants/flavours [e.g. 120].

25
 26 In sum, comparative evidence indicates that human mothers might familiarise their offspring with a range
 27 of odorants, and habituate them to cope with low-level environmental novelty, by presenting them with
 28 variable odour cues in milk or foods. Food odour-based familiarisation, which sometimes appears
 29 imprinting-like, is achieved through multiple, redundant processes, some operating pre-functionally
 30 (perinatal learning), and others working alongside postnatal opportunities and constraints. Thus, human
 31 mothers shape draft versions of the food environment that their offspring will later face directly. In
 32 addition to these psychobiological facilitators of the weaning process, human societies have developed
 33 additional abrupt or progressive weaning strategies matching their own sociocultural settings [e.g.
 34 121,122].

35 36 4. Development of odour-based social cognition

37 4.1 From discriminating parts to recognising whole individuals

38 Nursing-related odour experience may kick off discriminative processes that initiate the recognition of
 39 distinct classes of conspecifics. Odour signatures in AF, milk, maternal skin or sweat potentially convey
 40 nested odour traits or states characteristic of multiple socio-cognitive levels: 1) species, 2) classes of
 41 conspecifics, and 3) individuals. Informative level 1 is exemplified in infants' differential treatment of
 42 human breast/milk odour and odours of heterospecific milk (e.g. bovine milk) [66,67,70]. Informative
 43 level 2 allows categorising classes of conspecifics: i.e., lactating women vs non-lactating women or males
 44 [50], or possibly early vs late lactational stage among lactating women [as in mice, 123]. Finally,
 45 newborns discriminate idiosyncratic odour traits of the mother: breast-fed newborns turn their head more

1 to their mother's milk odour than to another woman's milk odour [14], and similar results arise in 6 w-old
2 infants with breast odour [67].

3
4 Selectiveness for the mother's odour increases with age and suckling experience: 2-d-olds respond
5 randomly, whereas >6-d-olds turn longer to their mother's breast odour [49], while motor activity change
6 reveals such differentiation from d2 [57]. Finally, the mother's neck [57] and axillae [45,124,125] may
7 also emit informative odours. Oral sources (lips, breath, saliva), head (scalp, hair, ears, tears, neck),
8 hands, and other odour sources await further testing. Mothers might thus be sensed as olfactory mosaics
9 with the possibility that some cues work as time-givers because of their regular contingency with different
10 affordances or social configurations (e.g. breast+sucking, neck+upright carrying, axilla+arm-carrying,
11 face+kissing-vocally interacting, etc.). Additionally, mothers may convey redundant identity cues
12 stemming from different body areas [e.g., skin and milk, 40].

13
14 It is not clear at what level newborns recognise their mother. Do they orient to her breast scent because it
15 carries inherently attractive chemosignals emitted by any lactating female, because they anticipate the
16 recurrence of a rewarding experience, and/or because they view the mother as a unique individual? Tests
17 on newborn olfactory recognition are so far equivocal because they have used odour stimuli from donors
18 differing in both familiarity and relatedness [126]. The critical test for odour-based individual recognition
19 would oppose the odours of donor individuals who are genetically equivalent and equally familiar to the
20 tested subject (e.g. kin of equivalent exposure). Another paradigm to gauge individual recognition relies
21 on artificial odorants, which can, when associated with maternal care, promptly release liking and
22 wanting responses in babies [88,89,127], with a final attractive potency which equates to that of a natural
23 odour [89]. Using easily controllable synthetic odorants constitutes a suitable way to understand stimulus-
24 , subject- and development-related processes that convert an 'emotionally neutral' odorant into a
25 meaningful cue.

26
27 Beyond early odour-based recognition of individuals, olfaction may boost social learning through other
28 senses. Maternal odours appear to modulate early visual processing. When exposed to their mother's
29 breast, neonates open their eyes more during the inhalation of a corresponding odour [58]. Thus, breast
30 odour can mobilise vision and touch to approach the pigmented/warm areola of the breast. Indeed,
31 synchronous olfactory-visual inputs recruit more oro-motor actions than each of those inputs
32 independently [58], presumably facilitating both latching and attention to the contiguous mother's face.
33 Overall, from the start of postnatal life, maternal odours, so far mostly investigated unimodally, may
34 expedite the growth of multisensory social cognition [128].

35
36 Olfactory recognition and discrimination of parts of an individual, as described above, may pave the way
37 to the representation of individuals as whole agents. Other investigations of the impact of odours in early
38 social recognition have altered a conspecific's typical odour and documented the impact on social
39 representations. In squirrel monkey neonates, olfactory and visual cues interact early to form what we
40 think is a maternal representation; when the odour cue is altered, the visual representation is disturbed,
41 degrading recognition [129,130]. Human mothers often alter their olfactory presence with artificial scents
42 and, although we know infants easily learn synthetic odorants made contingent with the mother as
43 familiarity cues [88,89,127], virtually no data exist on how they affect infants' social (re)cognition.
44 Infants certainly integrate odour with traits detected in other modalities when performing recognition
45 within multisensory scenes [reviewed in 128]. Indeed, when 4-m-olds view a female face vs a car, they

1 look at the face (particularly the eyes) longer than at the car in the presence of the mother's odour [131].
2 At another level, the mother's body odour enhances a face-selective EEG response over the right occipito-
3 temporal cortex in the infant brain [132]. Thus, in her physical absence, the mother's odour triggers face-
4 selective behavioural and neural processes in infants. However, the specificity of the mother's body odour
5 remains to be ascertained against another mother's/father's odour, or against any arbitrary intensity-
6 matched odorant.

7

8 4.2. Social diversification and olfactory recognition of conspecifics

9 Beyond infancy, when toddlers can voice or otherwise indicate their choices, evidence for odour-based
10 individual identification should become clearer. When children aged 3.5-5 y took an olfactory recognition
11 test based on t-shirts from their mother vs an unfamiliar woman, 18 of 26 chose the mother's t-shirt in
12 >60% of the trials, but only 8 in a statistically significant manner [57]. In another study, 3-5-y-olds had to
13 select their mother's t-shirt among 5 others: only 6 of 19 succeeded [133]. A further test [134] assessed
14 whether 6-15 y-old children could identify their mother's or father's t-shirt (relative to a t-shirt worn by a
15 sex-matched unrelated participant). The father's odour was identified by daughters and sons alike. The
16 mother's odour was chosen at random across the sample, but correctly by only the older group when the
17 participants were split into 6-8 vs 9+ y-olds, illustrating how data processing can affect outcomes [135].
18 A last within-family odour recognition study found children's identification of their parents to be
19 unreliable [7-18 y-old English sample; 136]. Finally, older daughters (11-21 y) recognise their mothers'
20 neck odour, but not her axillary odour [137]. This inconsistency in recognition performance of parents'
21 body odour by their offspring is quite surprising. It may be related to contrasts in methods (instructions,
22 context/social setting, nature of odour, collection and conservation, odour-distractor ratio), among other
23 sources of variation pertaining to parental factors (nature/intensity of odour, prevalence of perfumes),
24 child factors (sensitivity, attentional demand of tests: distractibility, boredom, fatigue) or both
25 (attachment-related proxemics). Perhaps the mother's olfactory presence is dominated by artificial scents,
26 on which children might rely more to recognise the mother than on cues originating from her natural skin
27 [but see 138]. Indeed, 5-y-olds express accurate recognition of their mother's perfume and greater desire
28 to wear it as a scent [139]. Olfactory recognition of parents, especially mothers, is perhaps no longer
29 functionally relevant when children begin to escape the family and engage with same-age groups, and
30 there may be no strong pressure in children's everyday life to recognise parents by olfaction alone when
31 more reliable distal (vision, audition) cues are available.

32

33 Other studies have examined children's olfactory recognition of siblings and peers. Three-8-y-olds could
34 tell apart the t-shirts of their own full siblings from those of unrelated age-mates [140]. Among sibships
35 sharing different degrees of consanguinity [full (.5), half- (.25), step-siblings (0)], 4-11 y-old children
36 correctly identified only the odour of full siblings; either genetic makeup affects body odours more than
37 sharing the same environment, or the degree of relatedness is confounded with social experience
38 (proximity, familiarity) that translates into greater odour awareness. Thus, children can recognise sibling
39 odour, but the evidence for true individual recognition remains weak as tests often contrast two donors,
40 related vs unrelated [but c.f. 134], which prevents confirmation of whether an odour characterises an
41 individual or a higher-level category (e.g. familiarity, gender, age). Additional data on odour-based social
42 recognition concern schoolchildren in whom genetic effects are minimized and familiarity effects
43 maximized. For example, 4-5-y-olds can identify classmates from their neck odour, with girls succeeding
44 in 69% of tests (36/52) and boys in only 33% (21/62) [141]. Otherwise, when 9 y-old classmates were
45 asked to recognise the t-shirts worn by 6 different odour donors [i.e., self, most liked peers (same/opposite

1 sex), least liked peer (same-sex), and mere acquaintances (same/opposite sex)], they could identify the
2 donors better than chance [142]. Same-sex peers were more accurately identified than opposite-sex peers,
3 in line with preferential same-sex affiliations at this age [143]. Thus, children's peer recognition appears
4 to vary under the joint constraints of the gender of the smeller, the gender of the donor, and their mutual
5 familiarity/relatedness. The odour cues used in this latter recognition task are unclear as, for the sake of
6 ecological validity, children's natural body odour was not separated from artificial scents. Both natural
7 and artificial olfactory signatures are recognisable to children, as shown by their identification of t-shirts
8 from unrelated donors [144], categorisation of gender based on the perfumedness of body odour [142] or
9 reliance on mother's perfume [139]. Thus, children's odour-based social cognition is a particularly
10 interesting area to analyse the developmental dynamics of biology-culture interactions. Conclusions
11 around whether children are better able to use olfactory cues to recognise peers than parents await a direct
12 test of that question, comparing the different odour donors with one group of children.

13

14 4.3. Children's use of parents' odours in socio-emotional and cognitive contexts

15 Beyond mere recognition, body odours may subconsciously drive differentiated social behaviour.
16 Newborns and young infants turn toward familiar body odour sources, consistent with the general trend of
17 attraction to the familiar. The same trend appears for artificial odorants associated with the lactating
18 mother [88,127], the reinforcing effects of which carry over to later object choices in novel contexts
19 [127,145], and could influence later social selectivity. Such memories of the sensory features acquired in
20 contingency with the caregiver might elicit differential affective treatment of conspecifics at later ages.

21

22 Children can draw from the emotional content of social odours. For example, the axillary odour of
23 stressed adults augments startle responses as potently in prepubertal children as in adults [146], and
24 children may thus be able to detect, monitor, and remember adults' emotional states. Children also
25 monitor extraneous odorants associated with emotion-arousing contexts such as alcohol or tobacco [e.g.
26 147,148]. In sum, children can single out the odours of individuals or categories of individuals, but might
27 also tag such odours as cues to emotions transmitted or induced by them. Such odours may mediate
28 strong discriminative treatment (affiliation/rejection; favouritism) between sibling or extra familial group
29 members [e.g. 149-151]].

30

31 Children's self-regulation of negative emotions may constitute another context to confirm the long-term
32 impact of parental odours, and perhaps even provide evidence of positive imprinting. Adolescents and
33 adults often report that the highly pleasurable odour memories of conspecifics, especially of the mother,
34 trace back into childhood [152,153]. In principle, subject to individual variations, maternal odours may
35 provide cues of physical proximity and corresponding affordances, such as feelings of security,
36 homeliness, reliance or trust. This informative content of maternal odours appears general among other
37 mammals, where separated offspring are systematically soothed by the mere delivery of the mother's
38 odour [e.g. 154]. Children and young adults often seek the body odour of familiar and/or related
39 individuals in adverse situations (stress, anxiety, separation). The fact that they also rely on their own
40 odours retained on an 'attachment object' suggests that familiarity is decisively soothing [e.g., 155].

41

42 Other paradigms have gauged effects of maternal odours on children's socio-emotional functioning. One
43 particularly interesting approach found that children aged 13 years with autistic spectrum disorders (ASD;
44 but not those without) demonstrated enhanced automatic imitation in the presence of their own mother's
45 axillary odour [156,157], indicating that children with ASD have greater attendance to social odours.

1 Finally, through its buffering effects and the provision of an olfactory secure base, maternal odour may be
2 beneficial in reducing fear, optimising attention and learning, and easing response to novelty [158, for
3 similar effects with familiar odorants]. More investigation is needed into the emotional balancing and
4 trust-enhancing effects of parent-related odorants, relying on behavioural markers of interpersonal trust
5 and compliance (e.g. following behaviour, contact seeking, joint attention, eye contact, smiling, lexical
6 content) in mutual infant-parent attention or in joint attention paradigms.

7 8 5. Homeostatic potency of maternal odours

9 Maternal odours are usually concurrent with the mother's presence. But the mother's odours (unlike her
10 appearance, touch, warmth, sounds, etc) can persist in the offspring's immediate environment in her
11 physical absence, as an effluvium or on an object. They can thus prevent or accelerate recovery from the
12 negative effects of separation, novelty, aggression, or pain, and support the postnatal establishment of
13 basic homeostatic processes in infants.

14
15 In line with the buffering effects mentioned above, restituting maternal odour to separated infants reduces
16 the activation of the hypothalamo-pituitary-adrenal (HPA) axis and related behavioural and endocrine
17 manifestations. Thus, cortisol release induced by acute pain inflicted upon separated neonates is tempered
18 by the administration of human milk odour [159], or of dodecalactone, alleged to resemble milk odour
19 [160]. This effect is stronger when the odour arises from own mother's milk than another mother's milk
20 or formula, pointing to the involvement of a familiar, individual-specific chemical signature. Similar
21 effects have been obtained in separated premature neonates who, with or without a pain challenge,
22 evinced lower salivary cortisol when exposed to the odour of own mother's milk [against formula odour:
23 59,161], an early response that can be interpreted in relation to the TOC. Replication in older infants and
24 children awaits, although non-human studies find that maternal (and sometimes paternal) stimuli buffer
25 stress only in pre- and post-weaning individuals [e.g. 162]. Similar processes were noted in 7 m-old
26 infants looking at happy vs. fearful faces during EEG recording. While exposed to own mother's t-shirt
27 odour, the typical brain response to the fear stimulus did not occur, whereas it clearly appeared in the
28 control contexts (another mother's odour or no odour) [163]. The social buffering effect of maternal
29 stimuli on HPA activation decreases in adolescents compared to children [164], but we do not know
30 whether this also occurs for maternal odours. Do odour stimuli from other social partners (agemates)
31 become potent buffering agents? By adulthood, a partner's odour (e.g. on clothes) can provide comfort
32 and attachment in their absence, although some individuals report using their mother's odour [e.g.
33 165,166]. Clearly, further research is needed on the coping-aid function of maternal odours in the face of
34 distress caused by separation and/or pain.

35
36 Maternal odour has also been shown to induce soothing and engage sleep in various mammalian infants
37 (e.g. rats [167], cats [168], chimpanzees [169]), including human infants [57,170]. This fact has been
38 translated into practice in exposing hospitalised infants/children to a cloth carrying maternal odour with
39 the goal of aiding them to cope with separation anxiety in unfamiliar settings [e.g. 171,172]. But parent-
40 infant separation arises regularly with sleep, at least in Euro-American cultures where sleeping apart
41 prevails [173]. To cope with this recurrent transition, infants frequently rely on odorous 'sleep-aids'
42 (pieces of cloth, fluffy objects, or their own hands [e.g. 174,175]. The mother's odour appears to be
43 effective in her absence, and thus may be an efficient regulator of calm and sleep in infants left alone.
44 One experiment [173] explored this hypothesis longitudinally in infants aged 3, 6, 9 and 12 m who slept
45 alone with a t-shirt containing the mother's odour, and did not find that the t-shirt was privileged in

1 inducing soothing, but (suboptimally) only renewed the odour stimulus every month.

2
3 Maternal odour could also influence the structure of sleep and sleep-dependent cognition, as olfaction is
4 clearly functional during infant sleep, especially in the active sleep stage (equivalent to adult REM sleep)
5 [e.g. 68,174]. When co-sleeping, mothers and infants mostly face each other, thereby exchanging body
6 odours as well as non-odorant volatiles from breath (CO₂, NO), an exchange thought to stimulate the
7 sleeping infants' respiration and awakenings [176,177]. So far, there is little paediatric research on
8 whether and how information from social odours is acquired, integrated, or consolidated during sleep [as
9 shown in adults, e.g., 178,179]. Considering that i) the newborn brain is receptive to odour information
10 for at least 50% of its sleeping time (totalling 70% of the 24-h cycle), ii) olfactory memory and its
11 multisensory and hedonic connections are sleep-dependent [180], and iii) learning and consolidation
12 function well in sleeping infants when external interference is reduced [181,182], the fact that information
13 co-occurring with mother's body odour can be acquired and up-dated *in somno* is a promising research
14 topic in infants and children.

15
16 6. Parental olfactory influences in juvenility and adolescence

17 6.1 Olfactory psychobiology of adolescence

18 Juvenility to adolescence is a period of increased developmental plasticity. Having benefited from family
19 resources for somatic and psychological growth, juveniles' interests shift from relative neophobia to
20 novelty seeking in all domains; their social interests shift from parents to peers, increasingly befriending
21 opposite-sex peers; and their psychobiology enters the reproductive phase. This transition imposes novel
22 constraints within the familial group, with increased risks of interpersonal conflict, inbreeding and
23 precocious pregnancy [183]. Evolved strategies should have emerged to curb these risks toward fitness in
24 modulating interpersonal attractions within families, regulating sexual maturation of offspring and
25 somehow canalising the ontogeny of mate choice. What roles could olfaction play in these strategies?

26
27 The advent of visible and non-visible secondary sexual characters advertise pubertal changes, when
28 hypothalamo-pituitary-gonadal (HPG) activation precipitates menarche or spermarche, and boosts all
29 types of skin glands and body excretions into divergent body odours in females and males. In parallel,
30 non-visible changes occur in olfactory sensitivity and reactivity especially toward adult body odours and
31 components therefrom. For instance, odour thresholds toward the odorants 2-methyl-3-sulfanyl butanol,
32 androstenone, and androstadienone, all occurring in axillary sweat, increase during puberty in males but
33 not females [184-186]. But androstenone thresholds tend to decrease through puberty in female
34 participants [184]. When asked to hedonically evaluate androstenone, younger participants rated it as
35 smelling bad more frequently than older ones, and females more so than males. This is in line with the
36 notion that a high sensitivity to androstenone comes along with a more unpleasant perception of its odour
37 [187]. Also late pubescent subjects (15 y-old) become more sensitive than prepubescent subjects to
38 musky-urinous and sulphurous odorants conveyed in axillary sweat, saliva or sexual discharges
39 [186,188], with pubescent females being more sensitive than their male counterparts [186]. To shed some
40 coherent light on this topic, however, psychophysical research is necessary together with ecologically
41 valid investigations in the same subjects, as developmental changes in the sensitivity to individual body
42 odour constituents may result in different perceptions of odours. Thus, late pubescent children express
43 much stronger aversion than prepubescents (8 y-old) to the odour of t-shirts worn by unfamiliar young
44 adults [189]. Within families, pubescent girls and boys tend to avoid the odour of fathers' t-shirts (6-15 y-
45 old Canadian sample; [134] or to clearly reject it [136]). However, Czech postpubescent girls report a

1 liking for adult male odours [153] and indeed androstenone was shown to become attractive to females as
2 a function of their association with sexual experience [190]. Thus, body odours from adults tend to evoke
3 intense dislike before/during puberty and to become attractive in later adolescence. Post-menarcheal
4 variations of olfaction during the fertile phase of the ovarian cycle [191] may also contribute to
5 intermittently attenuate this repulsion.

6 7 6.2 Olfaction and pubertal timing

8 The menarche milestone, easier to objectivate than spermatarche, has attracted competing theories
9 exploring the mechanisms of its onset and calibration during infancy and childhood [192]. Among
10 multiple, complexly interactive drivers (heritability, nutrition, population density, urban lifestyle, socio-
11 economic status, matrimonial regimen, stress, psychosocial development, exposure to endocrine-
12 disrupting chemicals), some speculate that the chemosensory context inherent to the early developmental
13 ecology may influence menarcheal onset. These speculations rely on epidemiological studies relating
14 family variables and reproductive maturation in females [e.g., 192-196]. First, family stability (presence
15 of biological father) and lower stress levels are thought to provide developmental niches that delay
16 reproductive maturity. Second, father absence and the presence of (an) unfamiliar adult male(s), with
17 possibly co-occurring higher stress levels, would engender environments that translate into accelerated
18 reproductive maturity in female offspring. The proximate mechanisms have been hypothesised to depend
19 on the “pheromonal climate” of their family group [193,196]. In the ‘father present’ family environments,
20 the chemosphere would tend to extend childhood, viz. delay the onset of menarche, following
21 mechanisms akin to the inhibition of neuroendocrine processes controlling oestrus or pubertal timing by
22 chemical cues from the dominant female or older familiar siblings in primates [e.g. 197-199]. In contrast,
23 the chemosphere from the ‘father absent’ familial groups would tend to shorten childhood by accelerating
24 pubertal onset. The Vandenberg effect, defined as pubertal acceleration by unfamiliar adult males’
25 odour, is suggested to function here as it does in other mammals [e.g. 200].

26
27 While these hypotheses may be consistent with the nonhuman literature, they are problematic to put to the
28 test in humans because: 1) human studies on priming pheromones mediating socio-ecological conditions
29 into neuroendocrine responses [201-203] have been so far unsuccessful in chemically identifying and
30 functionally validating any candidate compounds responsible for so-called pheromonal effects [e.g.
31 92,204- 206]; 2) the likelihood of olfaction dependence of human menarcheal timing, although enticing,
32 appears dauntingly complex, contingent on multisensory events (particularly touch) and mitigated by
33 multileveled, interactive internal and external causes [192]; 3) the olfactory priming of female puberty in
34 other mammals occurs after exposure in early development, often in synergy with exposure to stress,
35 meaning that human studies would have to engage in longitudinal designs to measure events 10-15 years
36 before they are translated into recordable physiological events. Thus, even overlooking the challenge of
37 determining which human-produced compounds to measure in the household atmosphere, it would be
38 difficult to assess the differential “pheromonal climate” hypothesis of menarcheal timing. As a
39 noteworthy aside, the “pheromone climate” notion should be parsimoniously referred to as “odour
40 climate”, as domestic effluvia are composed of thousands of biological volatiles emitted by humans [e.g.,
41 207,208,209] plus thousands of artificial volatiles [210,211], the latter being probably attended to by
42 children as much as the former as potential cues to the affective climate of the family group [e.g.
43 147,148]. But perhaps a methodological leap will be possible if atmospheric chemists venture to sample
44 familial environments contrasting in, e.g., social composition, affective stability, conflict or stress [cf
45 212,213].

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6.3 Developmental calibration of mate affiliation

Early olfactory experience within the familial group may also influence adolescents' reproductive behaviour by calibrating social preferences along which future mates will be selected. Is there a possibility of positive reproductive imprinting in human offspring as in other mammalian offspring [e.g. 214-217]? Such imprinting-like effects of early odour experience have been shown in the ingestive domain [127,218,219], and the perinatal and weaning phases are suggested to be sensitive periods for chemosensory learning in humans [12,13,220,221].

No parallel evidence is currently available for such positive olfactory imprinting effects in human mate selection, although body odour is reported to influence seduction and sexual interaction, especially in females [at least in Western samples of young adults; 222-224]. One study on adult response to Human Leukocyte Antigen (HLA)-covarying odour cues [225] hints in that direction, however. Jacob et al. (2002) asked women to rate 6 male odour donors after they had been HLA-typed and the number of allelic matches specified between the male donors, the women, and the women's parents [226]. The body odour of men who bore a low, intermediate level of HLA dissimilarity with the donor was preferred. More important for our argument, these women preferred the body odour of the males whose HLA-type matched that of their father, but not that of their mother. Thus, if fathers' HLA-type covaries with their body odour, a logical assumption would be that young adult females are more attracted to males sharing some odour cues with their own father. However, as mentioned above, negative appraisals of fathers' body odour by prepubertal and pubertal daughters does not predict such an outcome [134,136]. One possible explanation is that a shift occurs somewhere during development, when a father's body odour changes from being perceived as non-repulsive or even attractive instead of somewhat repulsive. The developmental process involved may be posterior to pubertal perceptual changes, perhaps involving a reversal in olfactory incentives linked with experience of sexual reward [190]. Alternatively, it might be that daughters like odours that are similar (i.e., matched in HLA) but not identical to those of their father, in the same way as women are attracted to faces that resemble their father rather than being attracted to their father himself [e.g. 227].

In sum, an odour-mediated aversion towards the opposite-sex parent is suggested in prepubertal girls that reverses after puberty to orient preference toward cues of this same parent. This positive imprinting-like process between daughters and fathers is an area open to further investigation. Extant data do not suggest any symmetric pattern for boys and their mothers [134]. This positive imprinting phenomenon goes in parallel with the Westermarck effect [228], a negative imprinting process actualised in later sexual disinterest between individuals who lived in physical proximity during their first 5 years of life [229]. This effect is hypothesised to: i) depend partly on an odour-based process, ii) operate during an early sensitive period, iii) arise when adult-like sexual interests emerge, and iv) be more potent among females [230]. Thus, similar processes may underlie two different types of imprinting-like phenomena that may be consequential for the avoidance of inbreeding in mate selection. It may be added that the father's odour may have a special status in these processes as it appears more recognisable to children than the mother's odour [134,136], probably due to its perceptual saliency in terms of intensity and/or quality.

7. Conclusions and prospects

We would flag up four headline conclusions.

1. *Chemocommunication tracks specific demands of early life-history stages*; note the perinatal and

1 pubertal periods in particular. Newborns' keen olfactory sensitivity appears somehow synchronised with
 2 maternal chemo-emissions. Attractive prenatal odorants coat the maternal body areas near to the
 3 neonate's nose. The postparturient's body odour is also influenced by intensified seborrhoea and chemo-
 4 emissions from the breast, leading to a probable early lactation-specific odour signature that may scaffold
 5 breastfeeding initiation. Adolescence clusters together changes in sensitivity, hedonic valuation, and the
 6 psychological salience of parental body odours, as well as own body odour production and nascent
 7 attraction to others (perhaps canalised by earlier experience of parental odours).

8 *2. Offspring detect multiple informative cues in body odours.* Neonates sense maternal odours and may
 9 create an odour-map that relates different maternal body regions to their reward value, recognising
 10 familiarity/individuality and lactational status. Later, children appear able to use adults' or age-mates'
 11 body odours to detect familiarity, kin, gender, friends or foes, emotional states, perfumedness, and
 12 atypical odour cues caused by illness. The informative and related chemical contents of all this
 13 chemocommunication is wide open to empirical investigation.

14 *3. The offspring's perception of social odours draws from general and specialized perceptual*
 15 *mechanisms.* Domain-general perceptual mechanisms (familiarisation, conditioning) trace the sensory
 16 regularities that pace typical human development. For instance, odour familiarity provides TOC that
 17 supports breastfeeding. Suckling also facilitates neonatal learning of the mother's odour after birth,
 18 potentially during sensitive windows. Alongside this, domain-specific processes may detect invariant
 19 odorant(s) of high survival value. The mammary structure may emit such inherently attractive
 20 chemosignals, the perceptual failure of which may compromise neonatal viability [47]. Well documented
 21 in other mammals [46,90,231], neonatal response to such specialised signals (pheromones) is a mother-to-
 22 infant chemosignalling option that needs to be fully explored in humans.

23 *4. Parental chemomessages have far-reaching outcomes.* Existing data raise the possibility of social
 24 imprinting in human infancy, but this phenomenon needs to be addressed properly as it has begun to be in
 25 the food domain. Further, chemosignals nested in paternal (maternal?) odours have been conjectured to
 26 prime children's endocrine functions, contributing to the regulation of pubertal onset. The functional
 27 viability of such hypothetical pheromonal processes needs now to be assessed in humans.

28
 29 The developmental study of social olfaction can serve to further illuminate important theoretical issues,
 30 such as:

31 a) *Olfactory contributions to social cognition.* Although audio-visual communication usually prevails in
 32 our species, odour may be more impactful early in life, when the audio-visual mode is still maturing.
 33 Further research in this area could unveil unexpected functions of olfaction in human cognition. For
 34 instance, social odours may pave the way to appreciating individuals as single entities, despite incessant
 35 shifts in vocality and visual appearance (posture, orientation, gestures, clothing). There may well be other
 36 unexpected functions of olfaction in human cognition, and focussed studies may be able to demonstrate
 37 how early olfaction permeates the development of multiple non-olfactory cognitive domains.

38 b) *Emotional state-dependent odour signalling.* The maternal olfactory profile constitutes a safe haven for
 39 offspring, although one that can be vulnerable to maternal emotional perturbations (anxiety, depression,
 40 fear). Understanding whether such odour cues of perturbed safety occur is a key issue within mother-to-
 41 infant communication, with far-reaching consequences for the offspring's sensitivity to emotional
 42 contagion, and the development of their "landscape of fear".

43 c) *Sniffing behaviour.* Questionnaires or interviews have been the principal methodology to understand
 44 how offspring engage in olfactory investigation (sniffing) of conspecifics [e.g. 153,232-234]. While these
 45 can uniquely capture elusive behaviours or intimate feelings, they focus participants' attention on a

1 particular feature of conspecifics and are prone to reconstructive bias and social desirability effects. So
 2 far, we are missing ethologically-valid behavioural studies of children's social odour-seeking behaviours.
 3 Thus, innovative research designs and devices are needed to objectively record sniffing behaviour in
 4 social contexts.

5 d) *Biology-culture interactions*. Infants are born in culturally-constructed olfactory niches: mothers'
 6 scents are shaped by local practices (washing, perfuming) and odour-bearing rituals are enacted on
 7 offspring [e.g. 235]. Thus, natural and cultural systems of olfactory signs operate simultaneously and it is
 8 interesting to gauge whether they do so in synergy or in competition. Effects of this extended maternal
 9 odourtype has rarely been considered within early life transitions.

10 e) *Generalisability of research*. Finally, some methodological prospects are warranted to improve species-
 11 wide generalisability of results. First, research on mother-to-infant chemocommunication should involve
 12 bigger samples than those typically studied so far, with a better distribution across ages and with
 13 psychobiologically-defined age slices. For example, among studies on peripubertal olfactory functioning,
 14 rare are those that consider physiological markers of puberty. Second, the studied phenomena should be
 15 extended to non-WEIRD societies [236] to better incorporate the wide range of parental care practices
 16 (distal vs proximal care systems; different reliance on olfaction) and how this affects
 17 chemocommunication. Relatedly, attention to infants and children afflicted with definitive (i.e.,
 18 congenital anosmia) or incidental (e.g. enlarged adenoids) olfactory deprivations, or with atypical hypo-
 19 or hypersensitivity to odours (ASD, blindness), may be helpful to understand what odours do during
 20 development, in the same way as (the very limited number of) studies of adults with olfactory
 21 impairments have helped further our understanding of the functions of olfaction [237]. The
 22 characterisation of odorant-response patterns that are robust across individuals and cultures is required in
 23 order to identify species-specific phenomena.

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