Northumbria Research Link

Olfaction scaffolds the developing human from neonate to adolescent and beyond

Benoist Schaal[1], Tamsin K. Saxton[2], Hélène Loos[3,4], Robert Soussignan[1], and Karine Durand[1]

[1] Developmental Ethology and Cognitive Psychology Laboratory, Centre des Sciences du Goût, UMR 6265 CNRS-Université de Bourgogne Franche-Comté, Inra-AgroSup, Dijon, France.
[2] Department of Psychology, Northumbria University, Newcastle upon Tyne, United Kingdom.
[3] Chair of Aroma and Smell Research, Friedrich-Alexander-Universität Erlangen-Nürnberg, Erlangen, Germany.
[4] Department Sensory Analytics, Fraunhofer Institute for Process Engineering and Packaging IVV, Freising, Germany.

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 odorised 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

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

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

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

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

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].

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].

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].

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 infanthood, 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 (CO_2, 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

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

6.2 Olfaction and pubertal timing

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

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

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

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

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

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

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

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

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

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

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

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

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

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

References

[1] Konner, M. 2010 *The evolution of childhood: Relationships, emotion, mind*, Harvard University Press.

[2] Volk, AA, Atkinson, JA. 2013 Infant and child death in the human environment of evolutionary adaptation. *Evol. Hum. Behav.* **34**, 182-192. (DOI:10.1016/j.evolhumbehav.2012.11.007).

[3] Lawn, JE, Cousens, S, Zupan, J. 2005 4 million neonatal deaths: when? Where? Why? *Lancet* **365**, 891-900. (DOI:10.1016/S0140-6736(05)71048-5).

[4] Smotherman, WP, Robinson, SR. 1987 Psychobiology of fetal experience in the rat. In *Perinatal development: A psychobiological perspective* (eds. NA Krasnegor, EM Blass, MA Hofer, WP Smotherman), pp. 39-60. Orlando, Academic Press.

[5] Mennella, JA, Johnson, A, Beauchamp, GK. 1995 Garlic ingestion by pregnant women alters the odor of amniotic fluid. *Chem. Senses* **20**, 207-209. (DOI:10.1093/chemse/20.2.207).

[6] Schaal, B. 2005 From amnion to colostrum to milk: Odor bridging in early developmental transitions. In *Prenatal development of postnatal functions* (eds. B Hopkins, SP Johnson), pp. 52-102. Westport, CT, Praeger.

[7] Schaal, B, Marlier, L, Soussignan, R. 1995 Neonatal responsiveness to the odour of amniotic fluid. *Biol. Neonate* **67**, 397-406. (DOI:10.5546/aap.2013.105).

[8] Schaal, B, Marlier, L, Soussignan, R. 1998 Olfactory function in the human fetus: Evidence from selective neonatal responsiveness to the odor of amniotic fluid. *Behav. Neurosci.* **112**, 1438-1449. (DOI:10.1037/0735-7044.112.6.1438).

[9] Schaal, B, Marlier, L, Soussignan, R. 2000 Human foetuses learn odours from their pregnant mother's diet. *Chem. Senses* **25**, 729-737. (DOI:10.1093/chemse/25.6.729).

[10] Faas, AE, Spontón, ED, Moya, PR, Molina, JC. 2000 Differential responsiveness to alcohol odor in human neonates: Effects of maternal consumption during gestation. *Alcohol* **22**, 7-17. (DOI:0.1016/S0741-8329(00)00103-8).

[11] Mennella, JA, Jagnow, CP, Beauchamp, GK. 2001 Prenatal and postnatal flavor learning by human infants. *Pediatrics* **107**, e88. (DOI:10.1542/peds.107.6.e88).

[12] Hepper, PG, Wells, DL, Dornan, JC, Lynch, C. 2013 Long-term flavor recognition in humans with prenatal garlic experience. *Dev. Psychobiol.* **55**, 568-574. (DOI:10.1002/dev.21059).

[13] Wagner, S, Issanchou, S, Chabanet, C, Lange, C, Schaal, B, Monnery-Patris, S. 2019 Weanling infants prefer the odors of green vegetables, cheese, and fish when their mothers consumed these foods during pregnancy and/or lactation. *Chem. Senses* **44**, 257-265. (DOI:10.1093/chemse/bjz011).

[14] Marlier, L, Schaal, B, Soussignan, R. 1997 Orientation responses to biological odours in the human newborn. Initial pattern and postnatal plasticity. *C. R. Acad. Sci. Paris* **320**, 999-1005. (DOI:10.1016/S0764-4469(97)82473-0).

[15] Schaal, B. 2016 How amniotic fluid shapes early odor-guided responses to colostrum and milk (and more). In *Flavor* (eds. A Voilley, E Guichard, C Salles), pp. 23-53. Amsterdam, Elsevier.

[16] Spahn, JM, Callahan, EH, Spill, MK, Wong, YP, Benjamin-Neelon, SE, Birch, L, Black, MM, Cook, JT, Faith, MS, Mennella, JA. 2019 Influence of maternal diet on flavor transfer to amniotic fluid and breast milk and children's responses: a systematic review. *Am. J. Clin. Nutr.* **109**, 1003S-1026S. (DOI:10.1093/ajcn/nqy240).

[17] Mennella, JA, Beauchamp, GK. 1991 Maternal diet alters the sensory qualities of human milk and the nursling's behavior. *Pediatrics* **88**, 737-744.

[18] Mennella, JA, Beauchamp, GK. 1991 The transfer of alcohol to human milk: Effects on flavor and the infant's behavior. *N. Engl. J. Med.* **325**, 981-985. (DOI:10.1056/NEJM199110033251401).

[19] Mennella, JA, Beauchamp, GK. 1996 The human infants' response to vanilla flavors in mother's milk and formula. *Infant Behav. Dev.* **19**, 13-19. (DOI:10.1016/S0163-6383(96)90040-5).

[20] Mennella, JA, Beauchamp, GK. 1999 Experience with a flavor in mother's milk modifies the infant's acceptance of flavored cereal. *Dev. Psychobiol.* **35**, 197-203. (DOI:10.1002/(sici)1098-2302(199911)35:3<197::aid-dev4>3.0.co;2-j).

[21] Hausner, H, Bredie, WL, Mølgaard, C, Petersen, MA, Møller, P. 2008 Differential transfer of dietary flavour compounds into human breast milk. *Physiol. Behav.* **95**, 118-124. (DOI:10.1016/j.physbeh.2008.05.007).

[22] Todrank, J, Heth, G, Restrepo, D. 2010 Effects of in utero odorant exposure on neuroanatomical development of the olfactory bulb and odour preferences. *Proc. Biol. Sci.* **278**, 1949-1955. (DOI:10.1098/rspb.2010.2314).

[23] Youngentob, SL, Kent, PF, Sheehe, PR, Molina, JC, Spear, NE, Youngentob, LM. 2007 Experience-induced fetal plasticity: the effect of gestational ethanol exposure on the behavioral and neurophysiologic olfactory response to ethanol odor in early postnatal and adult rats. *Behav. Neurosci.* **121**, 1293. (DOI:10.1037/0735-7044.121.6.1293).

[24] Pedersen, PE, Blass, EM. 1982 Prenatal and postnatal determinants of the 1st suckling episode in albino rats. *Dev. Psychobiol.* **15**, 349-355. (DOI:10.1002/dev.420150407).

[25] Alberts, JR, Ronca, AE. 2012 The experience of being born: a natural context for learning to suckle. *Int. J. Pediatr.* **2012**, 129328. (DOI:10.1155/2012/129328).

[26] Robinson, SR, Méndez-Gallardo, V. 2010 Amniotic fluid as an extended milieu intérieur. In *Handbook of developmental science, behavior, and genetics* (eds. K Hood, C Halpern, G Greenberg, R Lerner), p. 234. New York, Blackwell.

[27] Oostindjier, M, Bolhuis, JE, van den Brand, H, Kemp, B. 2009 Prenatal flavor exposure affects flavor recognition and stress-related behavior of piglets. *Chem. Senses* **34**, 775-787.

[28] Marlier, L, Schaal, B, Soussignan, R. 1998 Neonatal responsiveness to the odor of amniotic and lacteal fluids: A test of perinatal chemosensory continuity. *Child Dev.* **69**, 611-623.

[29] Varendi, H, Porter, R, Winberg, J. 1996 Attractiveness of amniotic fluid odor: evidence of prenatal olfactory learning? *Acta Paediatr.* **85**, 1223-1227.

[30] Contreras, CM, Gutiérrez-García, AG, Mendoza-López, R, Rodríguez-Landa, JF, Bernal-Morales, B, Díaz-Marte, C. 2013 Amniotic fluid elicits appetitive responses in human newborns: fatty acids and appetitive responses. *Dev. Psychobiol.* **55**, 221-231. (DOI:10.1002/dev.21012).

[31] Preer, G, Pisegna, JM, Cook, JT, Henri, A-M, Philipp, BL. 2013 Delaying the bath and in-hospital breastfeeding rates. *Breastfeed. Med.* **8**, 485-490. (DOI:10.1089/bfm.2012.0158).

[32] Khadivzadeh, T, Karimi, FZ, Tara, F, Bagheri, S. 2017 The effect of postpartum mother–infant skin-to-skin contact on exclusive breastfeeding in neonatal period: A randomized controlled trial. *Int. J. Pediatr.* **5**, 5409-5417.

[33] Akcan, E, Polat, S. 2016 Comparative effect of the smells of amniotic fluid, breast milk, and lavender on newborns' pain during heel lance. *Breastfeed. Med.* **11**, 309-314. (DOI:10.1089/bfm.2015.0174).

[34] Alemdar, DK, Özdemir, FK. 2017 Effects of having preterm infants smell amniotic fluid, mother's milk, and mother's odor during heel stick procedure on pain, physiological parameters, and crying duration. *Breastfeed. Med.* **12**, 297-304. (DOI:10.1089/bfm.2017.0006).

[35] Alemdar, DK, Tufekci, FG. 2017 Effect of smelling amniotic fluid on comfort and crying in preterm infants during peripheral cannulation: A randomized controlled trial. *Acta Clin. Croat.* **56**, 650-657. (DOI:10.20471/acc.2017.56.04.11).

[36] Lagercrantz, H, Slotkin, TA. 1986 The" stress" of being born. *Sci. Am.* **254**, 100-107.

[37] Molina, JC, Chotro, MG, Domínguez, HD. 1995 Fetal alcohol learning resulting from alcohol contamination of the prenatal environment. In *Fetal Development. A Psychobiological Perspective* (eds. J-P Lecanuet, WP Fifer, NE Krasnegor, WP Smotherman). Hillsdale, NJ, Lawrence Erlbaum.

[38] Varendi, H, Porter, RH, Winberg, J. 2002 The effect of labor on olfactory exposure learning within the first postnatal hour. *Behav. Neurosci.* **116**, 206-211. (DOI:10.1037/0735-7044.116.2.206).

[39] Romantshik, O, Porter, RH, Tillmann, V, Varendi, H. 2007 Preliminary evidence of a sensitive period for olfactory learning by human newborns. *Acta Paediatr.* **96**, 372-376. (DOI:10.1111/j.1651-2227.2006.00106.x).

[40] Mizuno, K, Mizuno, N, Shinohara, T, Noda, M. 2004 Mother-infant skin-to-skin contact after delivery results in early recognition of own mother's milk odour. *Acta Paediatr.* **93**, 1640 - 1645. (DOI:10.1111/j.1651-2227.2004.tb00856.x).

[41] Loos, HM, Doucet, S, Soussignan, R, Hartmann, C, Durand, K, Dittrich, R, Sagot, P, Buettner, A, Schaal, B. 2014 Responsiveness of human neonates to the odor of 5α-androst-16-en-3-one: A behavioral paradox? *Chem. Senses* **39**, 693-703. (DOI:10.1093/chemse/bju041).

[42] Loos, HM, Doucet, S, Védrines, F, Sharapa, C, Soussignan, R, Durand, K, Sagot, P, Buettner, A, Schaal, B. 2017 Responses of human neonates to highly diluted odorants from sweat. *J. Chem. Ecol.* **43**, 106-117. (DOI:10.1007/s10886-016-0804-x).

[43] Grabenhorst, F, Rolls, ET, Margot, C. 2011 A hedonically complex odor mixture produces an attentional capture effect in the brain. *Neuroimage* **55**, 832-843. (DOI:10.1016/j.neuroimage.2010.12.023).

[44] Varendi, H, Christenson, K, Porter, RH, Winberg, J. 1998 Soothing effect of amniotic fluid smell in newborn infants. *Early Hum. Dev.* **51**, 47-55. (DOI:10.1016/S0378-3782(97)00082-0).

[45] Cernoch, JM, Porter, RH. 1985 Recognition of maternal axillary odors by infants. *Child Dev.* **56**, 1593-1598. (DOI:10.2307/1130478).

[46] Blass, EM. 1990 Suckling: Determinants, changes, mechanisms, and lasting impressions. *Dev. Psychol.* **26**, 520-533. (DOI:10.1037/0012-1649.26.4.520).

[47] Schaal, B, Doucet, S, Soussignan, R, Klaey-Tassone, M, Patris, B, Durand, K. 2019 The human mammary odour factor: Variability and regularities in sources and functions. In *Chemical Signals in Vertebrates, Vol 14* (ed. C Buesching), pp. 118-138. Cham, Springer.

[48] Darwin, C. 1877 A biographical sketch of an infant. *Mind* **2**, 285-294.

[49] Macfarlane, A. 1975 Olfaction in the development of social preferences in the human neonate. *Parent-Infant Interaction* **33**, 103-117.

[50] Porter, RH, Makin, JW, Davis, LB, Christensen, KM. 1991 An assessment of the salient olfactory environment of formula-fed infants. *Physiol. Behav.* **50**, 907-911. (DOI:10.1016/0031-9384(91)90413-I).

[51] Makin, JW, Porter, RH. 1989 Attractiveness of lactating females' breast odors to neonates. *Child Dev.* **60**, 803-810. (DOI:10.1016/0140-6736(90)92579-7).

[52] Righard, L, Alade, MO. 1990 Effect of delivery room routines on success of first breast-feed. *Lancet* **336**, 1105-1107.

[53] Widström, AM, Lilja, G, Aaltomaa-Michalias, P, Dahllöf, A, Lintula, M, Nissen, E. 2011 Newborn behaviour to locate the breast when skin-to-skin: a possible method for enabling early self-regulation. *Acta Paediatr.* **100**, 79-85. (DOI:10.1111/j.1651-2227.2010.01983.x).

[54] Varendi, H, Porter, R, Winberg, J. 1994 Does the newborn baby find the nipple by smell? *Lancet* **344**, 989-990. (DOI:10.1016/S0140-6736(94)91645-4).

[55] Varendi, H, Porter, R. 2001 Breast odour as the only maternal stimulus elicits crawling towards the odour source. *Acta Paediatr.* **90**, 372-375. (DOI:10.1111/j.1651-2227.2001.tb00434.x).

[56] Hym, C, Forma, V, Anderson, DI, Provasi, J, Carpe, E, Teulier, C, Durand, K, Schaal, B, Barbu-Roth, M. submitted Newborn crawling and rooting in response to maternal breast odor.

[57] Schaal, B, Montagner, H, Hertling, E, Bolzoni, D, Moyse, A, Quichon, R. 1980 Les stimulations olfactives dans les relations entre l'enfant et la mère. *Reprod. Nutr. Dev.* **20**, 843-858.

[58] Doucet, S, Soussignan, R, Sagot, P, Schaal, B. 2007 The "smellscape" of mother's breast: effects of odor masking and selective unmasking on neonatal arousal, oral, and visual responses. *Dev. Psychobiol.* **49**, 129-138. (DOI:10.1002/dev.20210).

[59] Maayan-Metzger, A, Kedem-Friedrich, P, Bransburg Zabary, S, Morag, I, Hemi, R, Kanety, H, Strauss, T. 2018 The impact of preterm infants' continuous exposure to breast milk odor on stress parameters: A pilot study. *Breastfeed. Med.* **13**, 211-214.

[60] Baudesson de Chanville, A, Brevaut-Malaty, V, Garbi, A, Tosello, B, Baumstarck, K, Gire, C, Cozannet, RL. 2017 Analgesic effect of maternal human milk odor on premature neonates: a randomized controlled trial. *J. Hum. Lact.* **33**, 300-308. (DOI:10.1177/0890334417693225).

[61] Montagna, W, Macpherson, EE. 1974 Some neglected aspects of the anatomy of human breasts. *J. Invest. Dermatol.* **63**, 10-16.

[62] Montgomery, WFH. 1839 *An exposition of the signs and symptoms of pregnancy: The period of human gestation, and the signs of delivery*, A. Waldie.

[63] Schaal, B, Doucet, S, Sagot, P, Hertling, E, Soussignan, R. 2006 Human breast areolae as scent organs: Morphological data and possible involvement in maternal-neonatal coadaptation. *Dev. Psychobiol.* **48**, 100-110. (DOI:10.1002/dev.20122).

[64] Smith, JD, Peters, T, Donegan, W. 1982 Montgomery's areolar tubercle. A light microscopic study. *Arch. Pathol. Lab. Med.* **106**, 60-63.

[65] Doucet, S, Soussignan, R, Sagot, P, Schaal, B. 2012 An overlooked aspect of the human breast: areolar glands in relation with breastfeeding pattern, neonatal weight gain, and the dynamics of lactation. *Early Hum. Dev.* **88**, 119-128. (DOI:10.1016/j.earlhumdev.2011.07.020).

[66] Doucet, S, Soussignan, R, Sagot, P, Schaal, B. 2009 The secretion of areolar (Montgomery's) glands from lactating women elicits selective, unconditional responses in neonates. *PLoS One* **4**, e7579. (DOI:10.1371/journal.pone.0007579).

[67] Russell, MJ. 1976 Human olfactory communication. *Nature* **260**, 520-522. (DOI:doi: 10.1038/260520a0).

[68] Soussignan, R, Schaal, B, Marlier, L, Jiang, T. 1997 Facial and autonomic responses to biological and artificial olfactory stimuli in human neonates: re-examining early hedonic discrimination of odors. *Physiol. Behav.* **62**, 745-758. (DOI:10.1016/S0031-9384(97)00187-X).

[69] Bingham, PM, Churchill, D, Ashikaga, T. 2007 Breast milk odor via olfactometer for tube-fed, premature infants. *Behav. Res. Meth.* **39**, 630-634. (DOI:10.3758/BF03193035).

[70] Marlier, L, Schaal, B. 2005 Human newborns prefer human milk: conspecific milk odor is attractive without postnatal exposure. *Child Dev.* **76**, 155-168. (DOI:10.1111/j.1467-8624.2005.00836.x).

[71] Mizuno, K, Ueda, A. 2004 Antenatal olfactory learning influences infant feeding. *Early Hum. Dev.* **76**, 83-90. (DOI:10.1016/j.earlhumdev.2003.10.003).

[72] Meza, CV, Powell, NJ, Covington, C. 1998 The influence of olfactory intervention on non-nutritive sucking skills in a premature infant. *Occup. Ther. J. Res.* **18**, 71-83. (DOI:10.1177/153944929801800301).

[73] Yasumatsu, K, Uchida, S, Sugano, H, Suzuki, T. 1994 The effect of the odour of mother's milk and orange on the spectral power of EEG in infants. *J. UOEH* **16**, 71-83. (DOI:10.7888/juoeh.16.71).

[74] Bartocci, M, Winberg, J, Ruggiero, C, Bergqvist, LL, Serra, G, Lagercrantz, H. 2000 Activation of olfactory cortex in newborn infants after odor stimulation: a functional near-infrared spectroscopy study. *Pediatr. Res.* **48**, 18. (DOI:10.1203/00006450-200007000-00006).

[75] Frie, J, Bartocci, M, Kuhn, P. 2019 Neonatal cortical perceptions of maternal breast odours: A fNIRS study. *Acta Paediatr.* (DOI:10.1111/apa.15114).

[76] Aoyama, S, Toshima, T, Saito, Y, Konishi, N, Motoshige, K, Ishikawa, N, Nakamura, K, Kobayashi, M. 2010 Maternal breast milk odour induces frontal lobe activation in neonates: A NIRS study. *Early Hum. Dev.* **86**, 541-545. (DOI:10.1016/j.earlhumdev.2010.07.003).

[77] Shimoda, M, Yoshimura, T, Ishikawa, H, Hayakawa, I, Osajima, Y. 2000 Volatile compounds of human milk. *J, Fac, Agric, Kyushu Univ,* **45**, 199-206.

[78] Buettner, A. 2007 A selective and sensitive approach to characterize odour-active and volatile constituents in small-scale human milk samples. *Flav. Fragr. J.* **22**, 465-473. (DOI:10.1002/ffj.1822).

[79] Loos, HM, Reger, D, Schaal, B. 2019 The odour of human milk: Its chemical variability and detection by newborns. *Physiol. Behav.* **199**, 88-99. (DOI:10.1016/j.physbeh.2018.11.008).

[80] Schaal, B, Coureaud, G, Langlois, D, Ginies, C, Sémon, E, Perrier, G. 2003 Chemical and behavioural characterization of the rabbit mammary pheromone. *Nature* **424**, 68. (DOI:10.1038/nature01739).

[81] Schaal, B. 2014 Pheromones for newborns. In *Neurobiology of Chemical Communication* (ed. C Mucignat-Caretta), pp. 483-515. New York, CRC Press.

[82] Logan, DW, Brunet, LJ, Webb, WR, Cutforth, T, Ngai, J, Stowers, L. 2012 Learned recognition of maternal signature odors mediates the first suckling episode in mice. *Curr. Biol.* **22**, 1998-2007. (DOI:10.1016/j.cub.2012.08.041).

[83] Al Aïn, S, Mingioni, M, Patris, B, Schaal, B. 2014 The response of newly born mice to odors of murine colostrum and milk: unconditionally attractive, conditionally discriminated. *Dev. Psychobiol.* **56**, 1365-1376. (DOI:10.1002/dev.21220).

[84] Wallace, JP, Inbar, G, Ernsthausen, K. 1992 Infant acceptance of postexercise breast milk. *Pediatrics* **89**, 1245-1247.

[85] Garbini, A. 1897 Evoluzione del senso olfattivo nella infanzia. *Arch Antropolg Etnolog Firenze* **26**, 339-286.

[86] Kroner, T. 1882 Uber die Sinnesempfindungen der Neugeborenen. *Dtsch. Med. Wochenschr.* **8**, 282-283.

[87] Goldsmith, HS. 1974 Milk-rejection sign of breast cancer. *Am. J. Surg.* **127**, 280-281.

[88] Schleidt, M, Genzel, C. 1990 The significance of mother's perfume for infants in the first weeks of their life. *Ethol. Sociobiol.* **11**, 145-154.

[89] Delaunay-El Allam, M, Marlier, L, Schaal, B. 2006 Learning at the breast: preference formation for an artificial scent and its attraction against the odor of maternal milk. *Infant Behav. Dev.* **29**, 308-321. (DOI:10.1016/j.infbeh.2005.12.008).

[90] Schaal, B. 2010 Mammary odor cues and pheromones: mammalian infant-directed communication about maternal state, mammae, and milk. In *Vitam. Horm.* (pp. 83-136, Elsevier.

[91] Schaal, B, Al Aïn, S. 2014 Chemical signals 'selected for' newborns in mammals. *Anim. Behav.* **97**, 289-299. (DOI:10.1016/j.anbehav.2014.08.022).

[92] Wyatt, TD. 2015 The search for human pheromones: the lost decades and the necessity of returning to first principles. *Proc. Biol. Sci.*, 20142994. (DOI:10.1098/rspb.2014.2994).

[93] McDade, TW, Worthman, CM. 1998 The weanling's dilemma reconsidered: a biocultural analysis of breastfeeding ecology. *J. Dev. Behav. Pediatr.* **9**, 286-299. (DOI:10.1097/00004703-199808000-00008).

[94] Hrdy, SB. 1999 *Mother nature: A history of mothers, infants, and natural selection*. New York, Pantheon Books; 315 p.

[95] Harris, G, Coulthard, H. 2016 Early eating behaviours and food acceptance revisited: breastfeeding and introduction of complementary foods as predictive of food acceptance. *Curr. Obes. Rep.* **5**, 113-120. (DOI:10.1007/s13679-016-0202-2).

[96] Beckerman, JP, Slade, E, Ventura, AK. 2019 Maternal diet during lactation and breast-feeding practices have synergistic association with child diet at 6 years. *Publ. Health Nutr.* (DOI:10.1017/S1368980019001782).

[97] Coyle, S, Arnold, HM, Goldberg-Arnold, JS, Rubin, DC, Hall, W. 2000 Olfactory conditioning facilitates diet transition in human infants. *Dev. Psychobiol.* **37**, 144-152. (DOI:10.1002/1098-2302(200011)37:3<144::AID-DEV3>3.0.CO;2-Z).

[98] Gerrish, CJ, Mennella, JA. 2001 Flavor variety enhances food acceptance in formula-fed infants. *Am. J. Clin. Nutr.* **73**, 1080-1085. (DOI:10.1093/ajcn/73.6.1080).

[99] Maier, AS, Chabanet, C, Schaal, B, Leathwood, PD, Issanchou, SN. 2008 Breastfeeding and experience with variety early in weaning increase infants' acceptance of new foods for up to two months. *Clin. Nutr.* **27**, 849-857. (DOI:10.1016/j.clnu.2008.08.002).

[100] Maier-Nöth, A, Schaal, B, Leathwood, P, Issanchou, S. 2016 The lasting influences of early food-related variety experience: a longitudinal study of vegetable acceptance from 5 months to 6 years in two populations. *PLoS One* **11**, e0151356. (DOI:10.1371/journal.pone.0151356).

[101] Chauvin, C, Thierry, B. 2005 Tonkean macaques orient their food search from olfactory cues conveyed by conspecifics. *Ethology* **111**, 301-310. (DOI:10.1111/j.1439-0310.2004.01066.x).

[102] Lupfer-Johnson, G, Ross, J. 2007 Dogs acquire food preferences from interacting with recently fed conspecifics. *Behav. Process.* **74**, 104-106. (DOI:10.1016/j.beproc.2006.09.006).

[103] Laidre, ME. 2009 Informative breath: olfactory cues sought during social foraging among Old World monkeys. *J. Comp. Psychol.* **123**, 34. (DOI:10.1037/a0013129).

[104] Ueno, A, Matsuzawa, T. 2005 Response to novel food in infant chimpanzees: Do infants refer to mothers before ingesting food on their own? *Behav. Process.* **68**, 85-90. (DOI:10.1016/j.beproc.2004.09.002).

[105] Voelkl, B, Schrauf, C, Huber, L. 2006 Social contact influences the response of infant marmosets towards novel food. *Anim. Behav.* **72**, 365-372. (DOI:10.1016/j.anbehav.2005.10.013).

[106] Wyrwicka, W. 1981 *The development of food preferences: parental influences and the primacy effect*. Springfield, IL, Charles C. Thomas.

[107] Pelto, GH, Zhang, Y, Habicht, JP. 2010 Premastication: the second arm of infant and young child feeding for health and survival? *Maternal Child Nutr.* **6**, 4-18. (DOI:10.1111/j.1740-8709.2009.00200.x).

[108] Auer-Hackenberg, L, Thol, F, Akerey-Diop, D, Zoleko, RM, Rodolphe Mackanga, J, Adegnika, AA, Mombo-Ngoma, G, Ramharter, M. 2013 Premastication in rural Gabon - a cross-sectional survey. *J. Trop. Pediatr.* **60**, 154-156. (DOI:10.1093/tropej/fmt082).

[109] Zhao, A, Zheng, W, Xue, Y, Li, H, Tan, S, Zhao, W, Wang, P, Zhang, Y. 2018 Prevalence of premastication among children aged 6–36 months and its association with health: A cross-sectional study in eight cities of China. *Maternal Child Nutr.* **14**, e12448. (DOI:10.1111/mcn.12448).

[110] Van Ruth, S, Roozen, J. 2000 Influence of mastication and saliva on aroma release in a model mouth system. *Food Chem.* **71**, 339-345. (DOI:10.1016/S0308-8146(00)00186-2).

[111] Teicher, MH, Blass, EM. 1977 First suckling response of the newborn albino rat: the roles of olfaction and amniotic fluid. *Science* **198**, 635-636. (DOI:10.1126/science.918660).

[112] Block, ML, Volpe, LC, Hayes, MJ. 1981 Saliva as a chemical cue in the development of social behavior. *Science* **211**, 1062-1064. (DOI:10.1126/science.7466378).

[113] Galef Jr, BG, Mason, JR, Preti, G, Bean, NJ. 1988 Carbon disulfide: a semiochemical mediating socially-induced diet choice in rats. *Physiol. Behav.* **42**, 119-124. (DOI:10.1016/0031-9384(88)90285-5).

[114] Munger, SD, Leinders-Zufall, T, McDougall, LM, Cockerham, RE, Schmid, A, Wandernoth, P, Wennemuth, G, Biel, M, Zufall, F, Kelliher, KR. 2010 An olfactory subsystem that detects carbon disulfide and mediates food-related social learning. *Curr. Biol.* **20**, 1438-1444. (DOI:10.1016/j.cub.2010.06.021).

[115] Coureaud, G, Langlois, D, Perrier, G, Schaal, B. 2006 Convergent changes in the maternal emission and pup reception of the rabbit mammary pheromone. *Chemoecol.* **16**, 169-174. (DOI:10.1007/s00049-006-0345-9).

[116] Moltz, H, Lee, TM. 1981 The maternal pheromone of the rat: Identity and functional significance. *Physiol. Behav.* **26**, 301-306. (DOI:10.1016/0031-9384(81)90026-3).

[117] Hirakawa, H. 2001 Coprophagy in leporids and other mammalian herbivores. *Mammal Rev.* **31**, 61-80. (DOI:10.1046/j.1365-2907.2001.00079.x).

[118] Kort, R, Caspers, M, van de Graaf, A, van Egmond, W, Keijser, B, Roeselers, G. 2014 Shaping the oral microbiota through intimate kissing. *Microbiome* **2**, 41. (DOI:10.1186/2049-2618-2-41).

[119] Han, CS, Martin, MA, Dichosa, AE, Daughton, AR, Frietze, S, Kaplan, H, Gurven, MD, Alcock, J. 2016 Salivary microbiomes of indigenous Tsimane mothers and infants are distinct despite frequent premastication. *PeerJ* **4**, e2660. (DOI:10.7717/peerj.2660).

[120] Oflu, A. 2020 Weaning practices of Turkish mothers: A mixed-model research. *Breastfeed. Med.* (DOI:10.1089/bfm.2019.0262).

[121] DeLoache, JS, Gottlieb, A. 2000 *A world of babies: Imagined childcare guides for seven societies*. Cambridge, Cambridge University Press.

[122] Winikoff, B, Castle, MA, Laukaran, VH. 1984 *Feeding infants in four societies: Causes and consequences of mothers' choices*. New York, Greenwood Press.

[123] Al Aïn, S, Belin, L, Patris, B, Schaal, B. 2012 An odor timer in milk? Synchrony in the odor of milk effluvium and neonatal chemosensation in the mouse. *PloS One* **7**, e47228. (DOI:10.1371/journal.pone.0047228).

[124] Zucco, GM, Grassi, L, Orizio, S. 2000 Riconosciemento olfattivo neonate-madre nelle prime ore di vita. *Life Span Disab.* **3**, 25-36.

[125] Marin, M, Rapisardi, G, Tani, F. 2015 Two-day-old newborn infants recognise their mother by her axillary odour. *Acta Paediatr.* **104**, 237-240. (DOI:10.1111/apa.12905).

[126] Schaal, B. 1988 Olfaction in infants and children: developmental and functional perspectives. *Chem. Senses* **13**, 145-190. (DOI:10.1093/chemse/13.2.145).

[127] Delaunay-El Allam, M, Soussignan, R, Patris, B, Marlier, L, Schaal, B. 2010 Long-lasting memory for an odor acquired at the mother's breast. *Dev. Sci.* **13**, 849-863. (DOI:10.1111/j.1467-7687.2009.00941.x).

[128] Schaal, B, Durand, K. 2012 The role of olfaction in human multisensory development. In *Multisensory Development* (eds. AJ Bremner, DJ Lewkowicz, C Spence), pp. 29-62. Oxford, Oxford University Press.

[129] Redican, WK, Kaplan, JN. 1978 Effects of synthetic odors on filial attachment in infant squirrel monkeys. *Physiol. Behav.* **20**, 79-85. (DOI:10.1016/0031-9384(78)90206-8).

[130] Kaplan, JN, Cubicciotti III, DD, Redican, WK. 1979 Olfactory and visual differentiation of synthetically scented surrogates by infant squirrel monkeys. *Dev. Psychobiol.* **12**, 1-10. (DOI:10.1002/dev.420120102).

[131] Durand, K, Baudouin, J-Y, Lewkowicz, DJ, Goubet, N, Schaal, B. 2013 Eye-catching odors: Olfaction elicits sustained gazing to faces and eyes in 4-month-old infants. *PLoS One* **8**, e70677. (DOI:10.1371/journal.pone.0070677).

[132] Leleu, A, Rekow, D, Poncet, F, Schaal, B, Durand, K, Rossion, B, Baudouin, JY. 2019 Maternal odor shapes rapid face categorization in the infant brain. *Dev. Sci.*, e12877. (DOI:10.1111/desc.12877).

[133] Roberts, SC, Eryaman, F. 2017 Mutual olfactory recognition between mother and child. *Hum. Eth. Bull.* **32**, 42-52. (DOI:10.22330/heb/321/042-052).

[134] Weisfeld, GE, Czilli, T, Phillips, KA, Gall, JA, Lichtman, CM. 2003 Possible olfaction-based mechanisms in human kin recognition and inbreeding avoidance. *J. Exp. Child Psychol.* **85**, 279-295. (DOI:10.1016/S0022-0965(03)00061-4).

[135] Wyatt, TD. 2020 Reproducible research into human chemical communication by cues and pheromones: learning from psychology's renaissance. *Phil. Trans. Roy. Soc. B.* (DOI:10.7287/peerj.preprints.27908v1).

[136] Ferdenzi, C, Schaal, B, Roberts, SC. 2010 Family scents: developmental changes in the perception of kin body odor? *J. Chem. Ecol.* **36**, 847-854. (DOI:10.1007/s10886-010-9827-x).

[137] Johnson, LN. 1994 Mother-daughter olfaction identification. *Modern Psychol. Stud.* **2**, 13-174.

[138] Gaby, JM, Dalton, P. 2019 Discrimination between individual body odors is unaffected by perfume. *Perception* **48**, 1104-1123. (DOI:10.1177/0301006619872055).

[139] Durand, K, Schaal, B, Zucco, G. 2014 Body odor and perfume of caregivers are salient to developmentally typical and atypical young children. *Chem. Senses* **40**, 258.

[140] Porter, RH, Moore, JD. 1981 Human kin recognition by olfactory cues. *Physiol. Behav.* **27**, 493-495. (DOI:10.1016/0031-9384(81)90337-1).

[141] Verron, H, Gaultier, C. 1976 Processus olfactifs et structures relationnelles. *Psychol. Franç* **21**, 205-209.

[142] Mallet, P, Schaal, B. 1998 Rating and recognition of peers' personal odors by 9-year-old children: An exploratory study. *J. Gen. Psychol.* **125**, 47-64 (DOI:10.1080/00221309809595576).

[143] Carlson Jones, D. 1984 Dominance and affiliation as factors in the social organization of same-sex groups of elementary school children. *Ethol. Sociobiol.* **5**, 193-202. (DOI:10.1016/0162-3095(84)90023-2).

[144] Olsson, SB, Barnard, J, Turri, L. 2006 Olfaction and identification of unrelated individuals: examination of the mysteries of human odor recognition. *J. Chem. Ecol.* **32**, 1635. (DOI:10.1007/s10886-006-9098-8).

[145] Mennella, JA, Beauchamp, GK. 1998 Smoking and the flavor of breast milk. *N. Engl. J. Med.* **339**, 1559-1560. (DOI:10.1056/NEJM199811193392119).

[146] Lübke, KT, Busch, A, Hoenen, M, Schaal, B, Pause, BM. 2017 Chemosensory anxiety signals prime defensive behavior in prepubertal girls. *Physiol. Behav.* **173**, 30-33. (DOI:10.1016/j.physbeh.2017.01.035).

[147] Forestell, CA, Mennella, JA. 2005 Children's hedonic judgments of cigarette smoke odor: effects of parental smoking and maternal mood. *Psychol. Addict. Behav.* **19**, 423-432. (DOI:10.1037/0893-164X.19.4.423).

[148] Mennella, JA, Forestell, CA. 2008 Children's hedonic responses to the odors of alcoholic beverages: A window to emotions. *Alcohol* **42**, 249-260. (DOI:10.1016/j.alcohol.2008.03.129).

[149] Todd, WA. 1979 Psychosocial problems as the major complication of an adolescent with trimethylaminuria. *J. Pediatr.* **94**, 936-937. (DOI:10.1016/s0022-3476(79)80224-3).

[150] Ferrari III, ND, Nield, LS. 2006 Smelling like dead fish: a case of trimethylaminuria in an adolescent. *Clin. Pediatr.* **45**, 864-866. (DOI:10.1177/1073858406295287).

[151] Lee, CW, Yu, JS, Turner, BB, Murray, KE. 1976 Trimethylaminuria: fishy odors in children. *N. Engl. J. Med.* **295**, 937-938. (DOI:10.1056/NEJM197610212951706).

[152] Lenti-Boero, D. 1994 Sedici odori per molti ricordi: una ricerca preliminare sull'olfatto e la vita quotidiana. *Studi Urbinati (Urbino)* **5**, 167-181.

[153] Martinec Nováková, L, Plotěná, D, Havlíček, J. 2017 Age and pubertal status-related changes in reports of perception of personal odors. *Perception* **46**, 484-497. (DOI:10.1177/0301006616686096).

[154] Kikusui, T, Winslow, JT, Mori, Y. 2006 Social buffering: Relief from stress and anxiety. *Phil. Trans. Roy. Soc. B.* **361**, 2215-2228. (DOI:10.1098/rstb.2006.1941).

[155] Passman, RH. 1976 Arousal reducing properties of attachment objects: Testing the functional limits of the security blanket relative to the mother. *Dev. Psychol.* **12**, 468. (DOI:10.1037/0012-1649.12.5.468).

[156] Parma, V, Bulgheroni, M, Tirindelli, R, Castiello, U. 2013 Body odors promote automatic imitation in autism. *Biol. Psychiatry* **74**, 220-226. (DOI:10.1016/j.biopsych.2013.01.010).

[157] Parma, V, Bulgheroni, M, Tirindelli, R, Castiello, U. 2014 Facilitation of action planning in children with autism: The contribution of the maternal body odor. *Brain Cogn.* **88**, 73-82. (DOI:10.1016/j.bandc.2014.05.002).

[158] Coffield, CN, Mayhew, EM, Haviland-Jones, JM, Walker-Andrews, AS. 2014 Adding odor: Less distress and enhanced attention for 6-month-olds. *Infant Behav. Dev.* **37**, 155-161. (DOI:10.1016/j.infbeh.2013.12.010).

[159] Nishitani, S, Miyamura, T, Tagawa, M, Sumi, M, Takase, R, Doi, H, Moriuchi, H, Shinohara, K. 2009 The calming effect of a maternal breast milk odor on the human newborn infant. *Neurosci. Res.* **63**, 66-71. (DOI:10.1016/j.neures.2008.10.007).

[160] Kawakami, K, Takai-Kawakami, K, Okazaki, Y, Kurihara, H, Shimizu, Y, Yanaihara, T. 1997 The effect of odors on human newborn infants under stress. *Infant Behav. Dev.* **20**, 531-535. (DOI:10.1016/S0163-6383(97)90041-2).

[161] Badiee, Z, Asghari, M, Mohammadizadeh, M. 2013 The calming effect of maternal breast milk odor on premature infants. *Pediatr. Neonatol.* **54**, 322-325. (DOI:10.1016/j.pedneo.2013.04.004).

[162] Hennessy, MB, Kaiser, S, Sachser, N. 2009 Social buffering of the stress response: diversity, mechanisms, and functions. *Front. Neuroendocrinol.* **30**, 470-482. (DOI:10.1016/j.yfrne.2009.06.001).

[163] Jessen, S. 2019 Maternal Odor Reduces the Neural Threat Response in Human Infants. *bioRxiv*, 827626. (DOI:10.1101/827626).

[164] Hostinar, CE, Johnson, AE, Gunnar, MR. 2015 Parent support is less effective in buffering cortisol stress reactivity for adolescents compared to children. *Dev. Sci.* **18**, 281-297. (DOI:10.1111/desc.12195).

[165] Shoup, ML, Streeter, SA, McBurney, DH. 2008 Olfactory comfort and attachment within relationships. *J. Appl. Soc. Psychol.* **38**, 2954-2963. (DOI:10.1111/j.1559-1816.2008.00420.x).

[166] McBurney, DH, Streeter, S, Euler, H. 2012 Olfactory comfort in close relationships: You aren't the only one who does it. In *Olfactory Cognition* (eds. GM Zucco, RS Herz, B Schaal), pp. 59-72. Amsterdam, NL, John Benjamins.

[167] Shair, HN, Masmela, JR, Hofer, MA. 1998 The influence of olfaction on potentiation and inhibition of ultrasonic vocalization of rat pups. *Physiol. Behav.* **65**, 769-772. (DOI:10.1016/S0031-9384(98)00218-2).

[168] Rosenblatt, JS. 1972 Learning in newborn kittens. *Sci. Am.* **227**, 18-25.

[169] Blackman, TM. 1947 Observations on sense of smell in chimpanzees. *Am. J. Phys. Anthropol.* **5**, 283-294. (DOI:10.1002/ajpa.1330050303).

[170] Sullivan, RM, Toubas, P. 1998 Clinical usefulness of maternal odor in newborns: soothing and feeding preparatory responses. *Neonatol.* **74**, 402-408. (DOI:10.1159/000014061).

[171] Robertson, J. 1970 Young Children in Hospital. (2nd ed. London, Tavistock Publications.

[172] Ybarra, GJ, Passman, RH, Eisenberg, CS. 2000 The presence of security blankets or mothers (or both) affects distress during pediatric examinations. *J. Consult. Clin. Psychol.* **68**, 322. (DOI:10.1037/0022-006X.68.2.322).

[173] McKenna, JJ, Ball, HL, Gettler, LT. 2007 Mother–infant cosleeping, breastfeeding and sudden infant death syndrome: What biological anthropology has discovered about normal infant sleep and pediatric sleep medicine. *Am. J. Phys. Anthropol.* **134**, 133-161. (DOI:10.1002/ajpa.20736).

[174] Mahalski, PA. 1983 The incidence of attachment objects and oral habits at bedtime in two longitudinal samples of children aged 1.5–7 years. *J. Child Psychol. Psychiatr.* **24**, 283-295. (DOI:10.1111/j.1469-7610.1983.tb00576.x).

[175] Wolf, AW, Lozoff, B. 1989 Object attachment, thumbsucking, and the passage to sleep. *J. Am. Acad. Child Adolesc. Psychiatr.* **28**, 287-292. (DOI:10.1097/00004583-198903000-00024).

[176] McKenna, JJ, Mosko, SS. 1994 Sleep and arousal, synchrony and independence, among mothers and infants sleeping apart and together (same bed): an experiment in evolutionary medicine. *Acta Paediatr.* **83**, 94-102. (DOI:10.1111/j.1651-2227.1994.tb13271.x).

[177] Richard, C, Mosko, S, McKenna, J, Drummond, S. 1996 Sleeping position, orientation, and proximity in bedsharing infants and mothers. *Sleep* **19**, 685-690. (DOI:10.1093/sleep/19.9.685).

[178] Arzi, A, Shedlesky, L, Ben-Shaul, M, Nasser, K, Oksenberg, A, Hairston, IS, Sobel, N. 2012 Humans can learn new information during sleep. *Nat. Neurosci.* **15**, 1460-1465. (DOI:10.1038/nn.3193).

[179] Schredl, M, Atanasova, D, Hörmann, K, Maurer, JT, Hummel, T, Stuck, BA. 2009 Information processing during sleep: The effect of olfactory stimuli on dream content and dream emotions. *J. Sleep Res.* **18**, 285-290. (DOI:10.1111/j.1365-2869.2009.00737.x).

[180] Barnes, DC, Wilson, DA. 2014 Sleep and olfactory cortical plasticity. *Front. Behav. Neurosci.* **8**, 134. (DOI:10.3389/fnbeh.2014.00134).

[181] Reeb-Sutherland, BC, Fifer, WP, Byrd, DL, Hammock, EA, Levitt, P, Fox, NA. 2011 One-month-old human infants learn about the social world while they sleep. *Dev. Sci.* **14**, 1134-1141. (DOI:10.1111/j.1467-7687.2011.01062.x).

[182] Callaghan, B, Fifer, WP. 2017 Perinatal attention, memory and learning during sleep. *Enfance*, 349-361.

[183] Hochberg, Ze, Belsky, J. 2013 Evo-devo of human adolescence: beyond disease models of early puberty. *BMC Med.* **11**, 113. (DOI:10.1186/1741-7015-11-113).

[184] Dorries, KM, Schmidt, HJ, Beauchamp, GK, Wysocki, CJ. 1989 Changes in sensitivity to the odor of androstenone during adolescence. *Dev. Psychobiol.* **22**, 423-435.

[185] Hummel, T, Krone, F, Bartsch, O, Lundström, JN. 2005 Androstadienone odor thresholds in adolescents. *Horm. Behav.* **47**, 306. (DOI:Androstadienone odor thresholds in adolescents).

[186] Chopra, A, Baur, A, Hummel, T. 2008 Thresholds and chemosensory event-related potentials to malodors before, during, and after puberty: Differences related to sex and age. *Neuroimage* **40**, 1257-1263. (DOI:10.1016/j.neuroimage.2008.01.015).

[187] Keller, A, Zhuang, H, Chi, Q, Vosshall, LB, Matsunami, H. 2007 Genetic variation in a human odorant receptor alters odour perception. *Nature* **449**, 468. (DOI:10.1038/nature06162).

[188] Koelega, HS. 1994 Prepubescent children may have specific deficits in olfactory sensitivity. *Percept. Mot. Skills* **78**, 191-199. (DOI:10.2466/pms.1994.78.1.191).

[189] Stevenson, RJ, Repacholi, BM. 2003 Age-related changes in children's hedonic response to male body odor. *Dev. Psychol.* **39**, 670-679. (DOI:10.1037/0012-1649.39.4.670).

[190] Knaapila, A, Tuorila, H, Vuoksimaa, E, Keskitalo-Vuokko, K, Rose, RJ, Kaprio, J, Silventoinen, K. 2012 Pleasantness of the odor of androstenone as a function of sexual intercourse experience in women and men. *Arch. Sex. Behav.* **41**, 1403-1408. (DOI:10.1007/s10508-011-9804-7).

[191] Moshkin, M, Litvinova, N, Bedareva, A, Bedarev, M, Litvinova, E, Gerlinskaya, L. 2011 Odor as an element of subjective assessment of attractiveness of young males and females. *J. Evol. Biochem. Physiol.* **47**, 69-82. (DOI:10.1134/S0022093011010099).

[192] Ellis, BJ. 2004 Timing of pubertal maturation in girls: An integrated life history approach. *Psychol. Bull.* **130**, 920-958. (DOI:10.1037/0033-2909.130.6.920).

[193] Burger, J, Gochfeld, M. 1985 A hypothesis on the role of pheromones on age of menarche. *Med. Hypotheses* **17**, 39-46. (DOI:10.1016/0306-9877(85)90018-0).

[194] Moffitt, TE, Caspi, A, Belsky, J, Silva, PA. 1992 Childhood experience and the onset of menarche: A test of a sociobiological model. *Child Dev.* **63**, 47-58. (DOI:10.1111/j.1467-8624.1992.tb03594.x).

[195] Ellis, BJ, Garber, J. 2000 Psychosocial antecedents of variation in girls' pubertal timing: Maternal depression, stepfather presence, and marital and family stress. *Child Dev.* **71**, 485-501.

[196] Matchock, RL, Susman, EJ. 2006 Family composition and menarcheal age: Anti-inbreeding strategies. *Am. J. Hum. Biol.* **18**, 481-491. (DOI:10.1002/ajhb.20508).

[197] Keverne, EB. 1983 Pheromonal influences on the endocrine regulation of reproduction. *Trends Neurosci.* **6**, 381-384. (DOI:10.1016/0166-2236(83)90170-4).

[198] Vandenbergh, JG, Coppola, DM. 1986 The physiology and ecology of puberty modulation by primer pheromones. *Adv. Study Behav.* **16**, 71-107. (DOI:10.1016/S0065-3454(08)60188-6).

[199] Vandenbergh, JG. 1989 Coordination of social signals and ovarian function during sexual development. *J. Anim. Sci.* **67**, 1841-1847. (DOI:10.2527/jas1989.6771841x).

[200] Vandenbergh, JG. 1983 Pheromonal regulation of puberty. In *Pheromones and Reproduction in Mammals* (ed. JG Vandenbergh), pp. 95-112. New York, Academic Press.

[201] Stern, K, McClintock, MK. 1998 Regulation of ovulation by human pheromones. *Nature* **392**, 177-179. (DOI:10.1038/32408).

[202] Shinohara, K, Morofushi, M, Funabashi, T, Kimura, F. 2001 Axillary pheromones modulate pulsatile LH secretion in humans. *Neuroreport* **12**, 893-895.

[203] Preti, G, Wysocki, CJ, Barnhart, KT, Sondheimer, SJ, Leyden, JJ. 2003 Male axillary extracts contain pheromones that affect pulsatile secretion of luteinizing hormone and mood in women recipients. *Biol. Reprod.* **68**, 2107-2113. (DOI:10.1095/biolreprod.102.008268).

[204] Schank, J. 2006 Do human menstrual-cycle pheromones exist? *Human Nat.* **17**, 448-470. (DOI:10.1007/s12110-006-1006-y).

[205] Doty, RL. 2010 *The Great Pheromone Myth*, JHU Press.

[206] Doty, RL. 2014 Human pheromones: Do they exist? In *Neurobiology of Chemical Communication* (ed. C Mucignat-Caretta), pp. 535-560. Boca Raton, FL, CRC Press.

[207] de Lacy Costello, B, Amann, A, Al-Kateb, H, Flynn, C, Filipiak, W, Khalid, T, Osborne, D, Ratcliffe, NM. 2014 A review of the volatiles from the healthy human body. *J. Breath Res.* **8**, 014001. (DOI:10.1088/1752-7155/8/1/014001).

[208] Amann, A, de Lacy Costello, B, Miekisch, W, Schubert, J, Buszewski, B, Pleil, J, Ratcliffe, N, Risby, T. 2014 The human volatilome: volatile organic compounds (VOCs) in exhaled breath, skin emanations, urine, feces and saliva. *J. Breath Res.* **8**, 034001. (DOI:10.1088/1752-7155/8/3/034001).

[209] Dormont, L, Bessière, J-M, Cohuet, A. 2013 Human skin volatiles: a review. *J. Chem. Ecol.* **39**, 569-578. (DOI:10.1007/s10886-013-0286-z).

[210] Raw, GJ, Coward, SK, Brown, VM, Crump, DR. 2004 Exposure to air pollutants in English homes. *J. Exposure Sci. Environ. Epidemiol.* **14**, S85-S94.

[211] Hammond, CJ. 2013 Chemical composition of household malodours - an overview. *Flav. Fragr. J.* **28**, 251-261. (DOI:10.1002/ffj.3163).

[212] Williams, J, Stönner, C, Wicker, J, Krauter, N, Derstroff, B, Bourtsoukidis, E, Klüpfel, T, Kramer, S. 2016 Cinema audiences reproducibly vary the chemical composition of air during films, by broadcasting scene specific emissions on breath. *Sci. Rep.* **6**, 25464. (DOI:10.1038/srep25464).

[213] Roberts, CR, Misztal, P, Langford, B. 2020 Decoding the social volatilome by tracking rapid context-dependent odour change. *Phil. Trans. Roy. Soc. B.*

[214] Marr, JN, Gardner Jr, LE. 1965 Early olfactory experience and later social behavior in the rat: Preference, sexual responsiveness, and care of young. *J. Genet. Psychol.* **107**, 167-174. (DOI:10.1080/00221325.1965.10532774).

[215] Mainardi, D, Marsan, M, Pasquali, A. 1965 Causation of sexual preferences of the house mouse. The behaviour of mice reared by parents whose odour was artificially altered. *Atti Soc. It. Sci. Nat.* **104**, 325-338.

[216] Müller-Schwarze, D, Müller-Schwarze, C. 1971 Olfactory imprinting in a precocial mammal. *Nature* **229**, 55-56. (DOI:10.1038/229055a0).

[217] Fillion, TJ, Blass, EM. 1986 Infantile experience with suckling odors determines adult sexual behavior in male rats. *Science* **231**, 729-731. (DOI:10.1126/science.3945807).

[218] Beauchamp, GK, Mennella, JA. 1998 Sensitive periods in the development of human flavor perception and preference. *Ann. Nestle [Fr].* **56**, 19-31.

[219] Mennella, JA, Griffin, CE, Beauchamp, GK. 2004 Flavor programming during infancy. *Pediatrics* **113**, 840-845. (DOI:10.1542/peds.113.4.840).

[220] Mennella, JA, Castor, SM. 2012 Sensitive period in flavor learning: effects of duration of exposure to formula flavors on food likes during infancy. *Clin. Nutr.* **31**, 1022-1025. (DOI:10.1016/j.clnu.2012.05.005).

[221] Poncelet, J, Rinck, F, Bourgeat, F, Schaal, B, Rouby, C, Bensafi, M, Hummel, T. 2010 The effect of early experience on odor perception in humans: psychological and physiological correlates. *Behav. Brain Res.* **208**, 458-465. (DOI:10.1016/j.bbr.2009.12.011).

[222] Herz, RS, Inzlicht, M. 2002 Sex differences in response to physical and social factors involved in human mate selection - The importance of smell for women. *Evol. Hum. Behav.* **23**, 359-364. (DOI:10.1016/S1090-5138(02)00095-8).

[223] Sergeant, MJ, Davies, MN, Dickins, TE, Griffiths, MD. 2005 The self-reported importance of olfaction during human mate choice. *Sex. Evol. Gender* **7**, 199-213. (DOI:10.1080/14616660500173685).

[224] Havlicek, J, Saxton, TK, Roberts, SC, Jozifkova, E, Lhota, S, Valentova, J, Flegr, J. 2008 He sees, she smells? Male and female reports of sensory reliance in mate choice and non-mate choice contexts. *Pers. Indiv. Differ.* **45**, 564-569. (DOI:10.1016/j.paid.2008.06.019).

[225] Havlíček, J, Winternitz, J, Roberts, CR. 2020 MHC-associated odour preferences and human mate choice: near and far horizons. *Phil. Trans. Roy. Soc. B.*

[226] Jacob, S, McClintock, MK, Zelano, B, Ober, C. 2002 Paternally inherited HLA alleles are associated with women's choice of male odor. *Nat. Genet.* **30**, 175-179. (DOI:10.1038/ng830).

[227] Bereczkei, T, Gyuris, P, Weisfeld, GE. 2004 Sexual imprinting in human mate choice. *Proc. Biol. Sci.* **271**, 1129-1134. (DOI:10.1098/rspb.2003.2672).

[228] Westermarck, E. 1891 *The History of Human Marriage*. London, Macmillan & Co.

[229] Silverman, I, Bevc, I. 2005 Evolutionary origins and ontogenetic development of incest avoidance. In *Origins of the social mind: Evolutionary psychology and child development* (eds. B Ellis, D Bjorklund), pp. 292-313. New York, Guildford.

[230] Schneider, MA, Hendrix, L. 2000 Olfactory sexual inhibition and the Westermarck effect. *Human Nat.* **11**, 65-91. (DOI:10.1007/s12110-000-1003-5).

[231] Hudson, R, Distel, H. 1983 Nipple location by newborn rabbits: behavioural evidence for pheromonal guidance. *Behaviour*, 260-275.

[232] Ferdenzi, C, Mustonen, S, Tuorila, H, Schaal, B. 2008 Children's awareness and uses of odor cues in everyday life: A Finland - France comparison. *Chemosens. Percept.* **1**, 190-199. (DOI:10.1007/s12078-008-9020-6).

[233] Wathelet, O. 2012 «Le doudou de ma fille, ça pue tellement bon!»: Intimité familiale et jugements olfactifs. *Anthropol. Sociétés* **36**, 205-222. (DOI:10.7202/1014173ar).

[234] Saxton, TK, Nováková, LM, Jash, R, Šandová, A, Plotěná, D, Havlíček, J. 2014 Sex differences in olfactory behavior in Namibian and Czech children. *Chemosens. Percept.* **7**, 117-125. (DOI:10.1007/s12078-014-9172-5).

[235] Aubaile-Sallenave, F. 1997 Le monde traditionnel des odeurs et des saveurs chez le petit enfant maghrébin. *Enfance* **50**, 186-208.

[236] Nielsen, M, Haun, D, Kärtner, J, Legare, CH. 2017 The persistent sampling bias in developmental psychology: A call to action. *J. Exp. Child Psychol.* **162**, 31-38. (DOI:10.1016/j.jecp.2017.04.017).

[237] Stevenson, RJ. 2010 An initial evaluation of the functions of human olfaction. *Chem. Senses* **35**, 3-20. (DOI:10.1093/chemse/bjp083).