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Flavor learning and memory in utero as assessed through the changing pattern of olfactory responses from fetal to neonatal life

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ABSTRACT

Mammalian chemosensory experience begins in utero, where fetuses are exposed to odors and tastes from the mother's diet. Although the effects of prenatal flavor exposure in humans have been investigated postnatally in infant behaviors, longitudinal follow-up studies of fetal and neonatal responses are lacking. To address this, we compared fetal and neonatal facial reactions to specific odors by asking mothers to consume a single calorie-controlled encapsulated dose of powdered kale (n = 14) or a carrot (n = 18) before 4D ultrasound scans at 32 and 36 gestational weeks. Following the 36-week scan, mothers consumed the capsules daily for three consecutive weeks. Results indicated that neonates (mean age = 3.06 weeks) showed a decreased frequency of cry-face, and an increased frequency of laughter-face gestalts in response to the odor stimulus experienced prenatally, regardless of associated taste profile (bitter or non-bitter). These results suggest that repeated chemosensory experience in utero can reduce the aversive hedonic responses of fetuses and shape postnatal memory of the in utero experienced odor. This suggests that prenatal chemosensory mechanisms may have the potential to promote healthy eating habits after birth.

1. Introduction

Fetuses perceive the chemical environment through their developing gustatory and olfactory systems in the last three months of pregnancy (Sarnat & Flores-Sarnat, 2023; Schaal, 2015, pp. 307–337; Witt, 2020). This sensory capacity allows fetuses to experience and respond to flavor compounds transferred from the maternal diet to the amniotic fluid, affecting taste, odor and trigeminal chemesthesis (Schaal, 2023; Schaal et al., 2023). Prenatal flavor exposure, driven by maternal dietary intake, can guide fetuses in developing associative patterns, leading to flavor-mediated familiar percepts that are accessible after birth (Forestell & Mennella, 2015; Mellor, 2019; Schaal, 2005). Understanding how these early chemosensory experiences shape postnatal preferences is essential for explaining the earliest developmental origins of dietary behaviors and for establishing strategies to promote healthy eating habits (Ventura & Worobey, 2013).

One of the primary challenges in establishing healthy eating habits in children is their widespread aversion to bitter-tasting foods, such as green vegetables, which are essential for a balanced diet (Birch & Fisher, 1998). Many children show a strong dislike for bitter flavors, which is believed to be partly an innate survival mechanism evolved to protect against toxic plant compounds (Beauchamp & Mennella, 2011; Ventura & Mennella, 2011). Additionally, adverse responses to bitter taste have been linked to variations in the *TAS2R38* gene, which codes for bitter taste receptors and influences individual taste sensitivity (Duffy & Bartoshuk, 2000). Moreover, pregnant women often avoid bitter foods due to altered taste and smell sensitivity (Nordin et al., 2004; Peyrot des Gachons et al., 2011), leading to reduced fetal exposure to bitter tastants and, consequently, to a lack of opportunities to familiarize themselves with these flavors. Initial aversions to bitter flavors in human fetuses or neonates may arise from predisposed taste aversions, the novelty of unfamiliar chemical stimuli, or a combination of both (Forestell, 2017; Beauchamp & Mennella, 2011).

However, repeated exposure can attenuate these aversions in human infants or toddlers and increase the acceptance of novel flavors (e.g., de Wild et al., 2015; Johnson et al., 2021; Wagner et al., 2019). Previous

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research has used orofacial expressions to evaluate how repeated prenatal exposure affects postnatal chemosensory preferences. For example, Schaal et al. (2000) and Mennella et al. (2001) demonstrated that human infants exposed to specific flavors in utero, such as anise and carrot, showed more positive facial reactions to these flavors postnatally. These studies suggest that prenatal flavor exposure can increase familiarity with specific flavors and reduce neophobia (i.e., reluctance to approach new flavours or to try new foods; Blissett & Fogel, 2013), thereby enhancing postnatal food acceptance. More recently, Wagner et al. (2019) expanded these findings by showing that repeated prenatal exposure to the odors of often-disliked foods, such as green vegetables, can transform predisposed negative reactions into positive postnatal responses. While these studies have greatly advanced our understanding of how prenatal flavor exposure shapes postnatal preferences, they focus predominantly on postnatal outcomes and do not indicate whether, from the prenatal stage, fetuses exhibit differential responses as evidenced by facial reactions to specific flavors in utero or whether these responses only emerge in the postnatal period. None of the human studies to date have compared, systematically and longitudinally, reactions of fetuses and neonates of the same cohort to assess the development and transnatal continuity of chemosensory learning.

Studies with premature human infants indicate that chemosensory responses and facial muscular abilities are functional before full gestational term (Goubet et al., 2002; Schaal et al., 2004). This suggests that the capacity to react to distinct chemosensory stimuli might emerge in utero. Supporting this hypothesis, our previous study was the first to provide direct evidence of discriminative fetal facial responses to specific flavors (Ustun et al., 2022). Using frame-by-frame analysis of 4D ultrasound recordings, we found that fetuses exposed to carrot flavor exhibited more laughter-face gestalts, while those exposed to kale flavor showed more cry-face gestalts, demonstrating their ability for flavor discrimination. However, at that time, the long-term relationships between these prenatal facial responses and postnatal chemosensory preferences and hedonic reactions were not investigated.

The current study builds on our previous findings by longitudinally assessing both prenatal and postnatal facial responses within the same cohort, allowing us to investigate the transnatal continuity of chemosensory learning. By comparing fetal and neonatal responses to the same flavors, we aim to determine whether *repeated exposure* in utero establishes a chemosensory memory that influences postnatal responses. Thus, this study not only replicates previous research demonstrating positive postnatal responses to familiar flavors (e.g., Hepper, 1995; Mennella et al., 2001; Schaal et al., 2000; Wagner et al., 2019), but also introduces novel prenatal "baseline" responsiveness to establish a direct link between prenatal flavor familiarization and postnatal chemosensory outcomes.

Based on previous research, we hypothesize that: i) neonates will display more frequent laughter-face gestalts in response to the odor component of flavors repeatedly experienced in utero, and more frequent cry-face gestalts to the odor component of flavors that were not repeatedly experienced in utero; ii) repeated flavor exposure from the prenatal to postnatal period will result in an increase over time in the frequency of laughter-face gestalts and a decrease in the frequency of cry-face gestalts in response to the corresponding odor.

2. Methods

2.1. Ethics

This study was conducted in accordance with the Declaration of Helsinki, and ethical approval was granted by Durham University (PSYCH-2019-03-12T15_59_32-wvgf27). All participating mothers provided informed written consent for both themselves and their infants.

2.2. Participants

Initially, 99 participants from the prenatal cohort agreed to complete the postnatal stage. However, due to COVID-19 pandemic restrictions in the UK (March 2020–June 2021), many of them were unable to participate. Consequently, our group consisted of 35 participants who took part in the study from 32 gestational weeks (GW) until the first postnatal month. One infant was excluded because the mother did not meet the minimum required capsule consumption after 36 GW. Additionally, technical issues during recording led to the exclusion of data from two other participants. The final sample comprised 32 healthy infants (16 female, 16 male), with 14 exposed repeatedly to kale flavor and 18 to carrot flavor during the last trimester of pregnancy.

2.3. Design and procedure

Participants were involved in three experimental stages (Fig. 1.): 1) Fetal assessment with a single dose flavor stimulation at 32 and 36 GW; 2) Repeated flavor exposure from 36 GW for three consecutive weeks; 3) Neonatal assessment with odor stimulation during weeks 2–4 post-birth.

2.3.1. Single flavor stimulation in utero and fetal testing procedure

At 32- and 36 GW, mothers were randomly assigned to kale or carrot groups and their fetuses were exposed to a single calorie-controlled dose of kale or carrot powder, administered via a 400 mg capsule consumed by the mother 25 min before undergoing 4D ultrasound scans ($M = 25.18$, $SE = 1.02$). Prior to each scan, mothers completed the Perceived Stress Scale (PSS) and Hospital Anxiety and Depression Scale (HADS; Cohen et al., 1983; Zigmond & Snaith, 1983) and reported their frequency of bitter (e.g., kale, brassica vegetables) and non-bitter (e.g., carrot, potatoes) vegetable consumption in the week before each scan to control for potential covariates. They were instructed not to eat an hour before their appointments and to avoid consuming any foods or beverages containing kale or carrot on ultrasound scan days.

Each scan began with biometric assessments, including measurements of heartbeat, femur length, head circumference (HC), and gestational age to monitor fetal health and development. The fetal face and upper torso were then visualized and recorded using 4D ultrasound scans for offline coding of facial reactions to the flavors (see Ustun et al., 2022 for a detailed description of the procedure).

2.3.2. Repeated flavor exposure in utero

After the 36-GW scan, mothers consumed their allocated flavor capsule at least four times a week for three consecutive weeks. Participants documented intake using a checklist to monitor for any significant differences in number of capsules consumed. Capsules were taken daily between 10 a.m. and 3 p.m. On average, mothers consumed 14 capsules during this period (kale: $M = 12.79$, $SE = 0.45$, range 12–18; carrot: $M = 14.94$, $SE = 0.59$, range 12–21).

2.3.3. Postnatal stimulation and infant testing procedure

Neonatal assessments took place at the participants' homes in the first postnatal month, at an average age of 3.06 ± 0.15 weeks (range: 2–4 weeks). Before starting the test, we asked mothers to complete a set of questionnaires that included information about birth outcomes (birth weight, gestational age at birth), mental health status (using the PSS and HADS), vegetable consumption frequency (same as in the prenatal period), and the neonate's feeding type (breast, bottle, or mixed). These factors were assessed to identify potential covariates.

Kale and carrot powders from the capsules were used to create the odor stimuli. First, a cotton swab was moistened with still water; then dipped into either kale or carrot powder (~1 teaspoon) to ensure complete coverage of the cotton surface. A control stimulus was created using a water-moistened cotton swab only. Mothers were instructed to feed their babies 30 min before testing and avoid consuming kale or carrot, if breastfeeding. Testing took place in a quiet, distraction-free

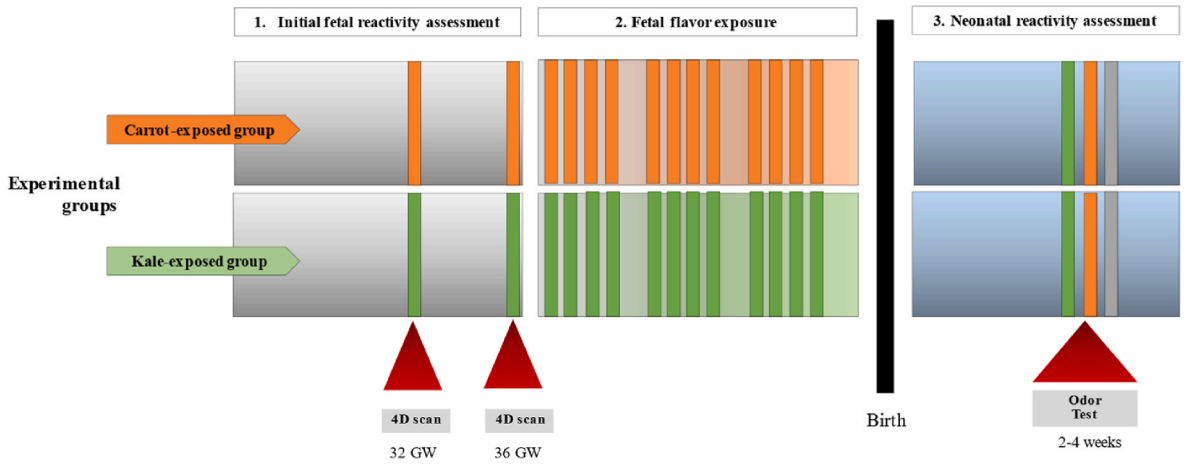

Fig. 1. Schema of the three-stages of the experimental design.

environment, with neonates in an awake, calm and active behavioral state (Prechtl, 1974).

The test session began with a baseline period of 20 s to establish a neutral starting point. The odor stimuli were presented in two sets, with each set including a presentation of kale, carrot, and a control stimulus (for 20 s each). The order of the stimuli presentation within each set was randomized. Each presentation was separated by a 60-s interval to minimize potential carry-over effects. Facial reactions were video recorded for offline coding.

Due to COVID-19 restrictions, some sessions (n = 10) were conducted online with parental assistance. These sessions followed the same procedures as in-person assessments to maintain consistency and ensure data quality was not compromised (see Supplemental Table S1 and Fig. S1).

2.4. Behavioral coding of fetal and neonatal facial responses

Facial expressions were analyzed using 17 discrete facial movements (i.e., FM1, 2, 4, 6, 9–12, 16, 18–20, 24–28) that are observable in both fetal and neonatal faces, ensuring consistency in coding across developmental stages (FACS, Ekman & Friesen, 1978; BABYFACS, Oster, 2006; FOMS, Reissland et al., 2016). These movements are associated with two main gestalts: the cry-face gestalt, defined as a prototypical facial expression indicating distress, and the laughter-face gestalt, characterized by a smiling expression (Oster, 2006; Reissland et al., 2016, see Ustun et al., 2022 for more details on the coding approach).

Five facial movements were coded specifically for the cry-face gestalt: FM1 (inner-brow raiser), FM4 (brow lowerer), FM10 (upper-lip raiser), FM16 (lower-lip depressor), and FM20 (lip stretch). Two facial movements were coded specifically for the Laughter-face gestalt: FM12 (lip-corner puller) and FM19 (tongue show). The remaining 10 facial movements could occur in either gestalt: FM2 (outer-brow raiser), FM6 (cheek raiser), FM9 (nose wrinkle), FM11 (nasolabial furrow), FM18 (lip pucker), FM24 (lip presser), FM25 (lips parting), FM26 (jaw drop), FM27 (mouth stretch), and FM28 (lip suck). For these common movements (e.g., FM25-lips parting), the final determination of the facial gestalt depends on the presence of other co-occurring facial movements. For example, when lips parting (FM25) co-occurs with upper-lip raiser (FM10), it is interpreted as a cry-face, whereas it is coded as laughter-face gestalt when it occurs together with lip-corner puller (FM12).

The primary coder (BUE), a certified FACS coder and trained Fetal Observable Movement System (FOMS) coder, analyzed all the ultrasound scans and the neonatal videos. Fetal and neonatal facial movements were coded frame-by-frame using offline video recordings in the Observer® (version 15XT, Noldus, Wageningen, NL). During the 4D ultrasound scans, the fetal face was not always visible due to fetal positioning (e.g., arms covering the face) or poor image quality. Therefore, “Start” and “Stop” codes were used to mark sections where the face was visible and of sufficient quality for coding. After the coding of the videos, the relative frequency of each facial gestalt per minute was calculated, accounting for the variability in video length due to face visibility.

During the postnatal assessments, odor stimuli were presented only when the neonate’s face was clearly visible (e.g., if infant moved their arms excessively, obstructing the view, the presentation was paused until they were calm again). As a result, the coding duration was standardized for all postnatal videos. For each stimulus, 30 s were coded, including 20 s during odor presentation and 10 s post-stimulus to capture any lasting effects, resulting in a total of 3 min of coding per video. Although the duration of odor stimulation was consistent across postnatal videos, the relative frequency of facial gestalts per minute was calculated to allow a comparable analysis of fetal and neonatal responses.

Inter-coder reliability was assessed by three independent reliability coders (one certified FACS coder, the creator of FOMS (NR), and two trained FACS and FOMS coders) on 15% of the dataset, with a Cohen’s kappa of 0.95 (range 0.93–0.96). Intra-coder reliability was assessed on 10% of the prenatal and postnatal datasets to ensure consistency of coding criteria over time, yielding Cohen’s kappa values of 0.97 and 0.98, respectively. All coders were blinded to flavor conditions for both fetal and neonatal videos. For the neonatal videos, a lab assistant, who was unaware of the study aims, changed the color of the kale and carrot powders to grey on the videos prior to coding to prevent any potential bias during coding.

2.5. Statistical analyses

The study used a mixed measures design with longitudinal sampling across two Prenatal Exposure groups (kale and carrot flavor) at three Time points (32 GW, 36 GW, and the first postnatal month) and included three Postnatal Odor Test Exposure conditions (kale, carrot, and control odor) in which two types of facial Gestalts were measured (cry-face and laughter-face). All dependent variables, specifically the frequency of facial gestalts per minute, were log-transformed for normalization and subsequently back-transformed for data presentation.

First, the Pearson chi-square test determined whether the infant sex ratio differed between the groups. Pearson correlations were used to examine associations between maternal variables (age, pre-pregnancy BMI, mental health scores from 32 GW to neonatal stage), fetal and birth variables (the head circumference at 20 GW, gestational age at birth, and birth weight), neonatal age at testing, flavor exposure

(maternal vegetable frequency consumption from 32 GW to neonatal stage, and the number of capsules consumed after 36 GW) and the dependent variables, namely fetal and neonatal facial gestalts. Feeding type (breastfeeding, bottle-feeding, mixed feeding) and postnatal testing method (in-person vs. online) were tested using one-way ANOVA to detect covariance effects. Variables which were significantly related to the dependent variables, or showed a significant difference between the groups, were included as covariates in further analyses.

To explore facial responses to postnatal test odors, 2 x 3 repeated measures ANCOVAs were conducted to examine the effects of Prenatal Exposure Groups (kale and carrot) and Postnatal Test Odor Conditions (kale, carrot, and control) on the relative frequency of the two different types of gestalts (cry-face and laughter-face) per minute. When significant interactions were identified, simple main effects analyses were conducted to explore differences between the Prenatal Exposure Groups within each Postnatal Test Odor condition.

Given that the participants were exclusively exposed to either kale or carrot prenatally, we focused on longitudinal comparisons of cry-face and laughter-face gestalts within each Prenatal Exposure Group (kale and carrot) across three time points (32 GW, 36 GW, and postnatal). This approach allowed us to track changes in reactions to the odor to which the neonates were prenatally exposed. Specifically, in the *Prenatal Kale Exposure Group*, we undertook a 2 x 3 repeated measures ANCOVA to compare cry-face and laughter-face gestalts in response to *kale odor* at 32 GW and 36 GW and postnatally. Similarly, in the *Prenatal Carrot Exposure Group*, we undertook a 2 x 3 repeated measures ANCOVA was used to compare cry-face and laughter-face gestalts to carrot odor across the same time points. When significant interactions effects were observed, simple main effects analyses were conducted to explore the effects of Time within each Gestalt condition with Bonferroni corrections applied to control for multiple comparisons between time periods.

Effect sizes were reported using partial eta-squared (η^2) values to indicate the magnitude of the observed effects. An alpha level of 0.05 was applied for all statistical analyses, which were conducted using the Statistical Package for Social Sciences (SPSS 28.0).

3. Results

3.1. Participants characteristics

All mother-infant dyads were White British and resided in Northeast England. The mothers were healthy, aged 18–40 years, with no known allergies, a pre-pregnancy body mass index (BMI) of 18.5–30, and no history of medication prescription, recreational drug use, smoking, e-cigarette use, or alcohol consumption during pregnancy. All infants were born healthy, with Apgar scores ≥8 at 1 min and ≥9 at 5 min, no known allergies, a birth weight of ≥2500 g, and no Neonatal Intensive Care Unit admissions (see Table 1 for participant details).

Table 1
Maternal-infant descriptive information.

	Prenatal kale Flavor Exposure (n = 14)	Prenatal carrot Flavor Exposure (n = 18)
Female/Male	n = 5/9	n = 11/7
Head-circumference at 20 GW (cm)*	173.74 (2.03)	164.19 (1.63)
Gestational age at birth (gestational weeks)	39.14 (0.40)	39.37 (0.35)
Birth weight (grams)	3246.86 (61.27)	3406.22 (111.29)
Infant age at test (weeks)	3.05 (0.23)	3.07 (0.20)
Maternal age (years)	30.50 (1.29)	32.33 (0.95)
Maternal pre-pregnancy BMI	25.75 (0.87)	25.99 (0.66)
Feeding type:		
Breast/Bottle/Mixed feeding	n = 5/5/4	n = 9/8/1
Maternal consumption of kale/carrot flavored capsules after the 36 GW scan	12.79 (0.45)	14.94 (0.59)

Note: Values are averages, and in parentheses, standard errors. *$p < .001$.

3.2. Covariates

Various covariates were initially examined, including infant sex, maternal age, pre-pregnancy BMI, gestational age at birth, birth weight, infant age at testing, feeding type (breast, bottle, mixed), and postnatal testing methods (in person vs. online) (see Table 1 and Supplemental Tables S1–3). These covariates did not significantly affect fetal and infant facial gestalts and were therefore excluded from further analyses. Maternal stress scores at the postnatal stage, the number of capsules consumed after 36 GW, and postnatal maternal consumption of kale and other bitter vegetables showed significant correlations with a few dependent variables, but sensitivity analyses revealed no substantial differences as covariates. Therefore, they were excluded from the main analyses (see Supplemental Tables 4–5). However, fetal head-circumference (HC) at 20 GW was significantly associated with most dependent variables (see Supplemental Table S3) and altered results in sensitivity analyses. Including HC as a covariate rendered the main effects of both Postnatal Test Odor Condition and Time non-significant, suggesting that these main effects were influenced by HC differences. In contrast, the interaction between Prenatal Exposure Groups and Postnatal Test Odor Conditions, as well as the interaction between Time and Prenatal Exposure Group, remained significant, indicating that group differences across Postnatal Odor Test Conditions and over time were not solely explained by HC. As a result, HC was retained as a covariate in subsequent analyses.

3.3. Facial responses to postnatal test odors

As depicted in Fig. 2, the cry-face gestalts were most frequent in the Prenatal kale Exposure Group during the carrot Postnatal Odor Test, while the Prenatal carrot Exposure Group showed more cry-face gestalts during the kale Postnatal Odor Test. Similarly, laughter-face gestalts were most often observed in the Prenatal carrot Exposure Group during the carrot Postnatal Odor Test, while the Prenatal kale Exposure Group showed more laughter-face gestalts during the kale Postnatal Odor Test.

This pattern of results was confirmed by the 2 x 3 repeated measures ANCOVA revealing a significant interaction between Prenatal Exposure Groups and Postnatal Odor Test Conditons was found for both cry-face ($F(2, 42) = 43.22$, $p < .001$, $\eta^2 = 0.67$) and laughter-face gestalts ($F(2, 42) = 11.18$, $p < .001$, $\eta^2 = 0.35$.). The main effects of the Prenatal Exposure Group and Postnatal Odor Test condition were not significant for either cry-face ($F(1, 21) = 0.94$, $p = .34$, $\eta^2 = 0.04$; $F(2, 42) = 2.17$, $p = .13$, $\eta^2 = 0.10$) or laughter-face gestalts ($F(1, 21) = 0.74$, $p = .40$, $\eta^2 = 0.34$; $F(2, 42) = 0.94$, $p = .40$, $\eta^2 = 0.04$).

Simple main effects tests on the interaction showed significantly more Cry-face Gestalts to carrot odor (M = 0.94. SE = 0.10) compared to kale odor (M = 0.19, SE = 0.07, p < .001) in the Prenatal kale Exposure Group, whereas the Prenatal carrot Exposure Group showed more cry-face gestalts to kale odor (M = 1.32, SE = 0.07) compared to carrot odor (M = −0.02, SE = 0.10, p < .001). There were also no significant differences between the groups when presented with the control odor (Prenatal kale Exposure Group, M = 0.46, SE = 0.16; Prenatal carrot Exposure Group, M = 0.71, SE = 0.16, p = .38). For laughter-face gestalts, the Prenatal kale Exposure group showed significantly more laughter-face gestalts to kale odor (M = 0.89, SE = 0.14) compared to carrot (M = 0.58, SE = 0.12, p < .005), whereas the Prenatal carrot Exposure Group showed more laughter-face gestalts to carrot odor (M = 1.20, SE = 0.12) than kale odor (M = 0.42, SE = 0.14, p < .005). There were no significant differences between the Prenatal kale Exposure Group (M = 0.37, SE = 0.17) and the Prenatal carrot Exposure Group (M = 0.71, SE = 0.17, p = .22) during the control odor presentation.

Fig. 3 illustrates examples of *cry-face gestalts exhibited by a neonate in the carrot Prenatal Exposure Group in response to the kale Odor Test and by a neonate in the kale Prenatal Exposure Group in response to carrot Odor Test.*

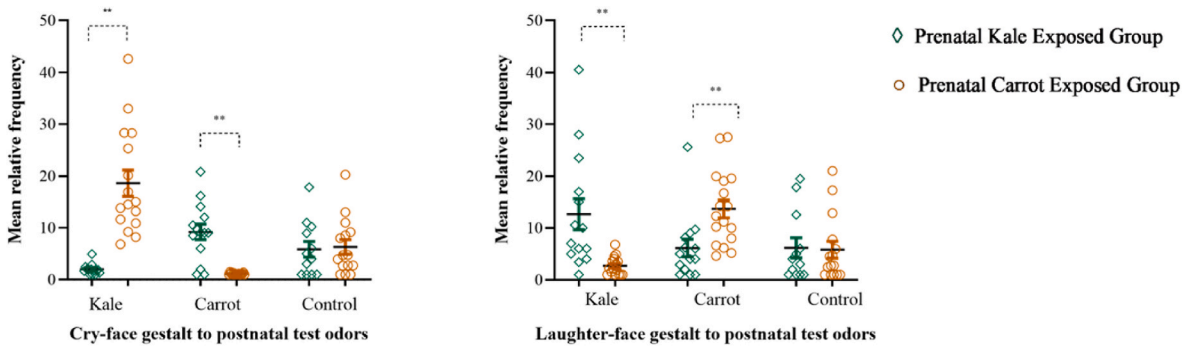

Fig. 2. Interaction effects of Prenatal Flavor Exposure Groups and Postnatal Odor Test Conditions (kale, carrot, control) and the mean relative frequency of cry-face and laughter-face gestalts per minute.
Note: Error bars represent 95% confidence intervals, $^{**}p < .001$.

Fig. 3. Examples of cry-face gestalts in response to non-prenatally exposed odors in two infants. Left: a cry-face gestalt in response to kale Odor displayed by a neonate (3 weeks and 3 days old) of the Prenatal carrot Exposure Group. Right: a cry-face gestalt in response to carrot Odor displayed by a neonate (3 weeks and 6 days old) of the Prenatal kale Exposure Group.
Note: The odor stimuli are presented in their natural colour for image presentation. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.4. Longitudinal facial responses to carrot and kale odors from fetus to neonate

Fig. 4 illustrates the longitidunal changes, showing an increase in laughter-face gestalts from the prenatal to the post-birth period in response to the odor stimuli repeatedly exposed to after 36 GW.

The 2 x 3 repeated measures ANCOVA on the frequency of facial responses of the group exposed to kale or carrot both revealed a significant Gestalt × Time interactions (kale Exposure Group: $F(2, 26) = 56.43$, $p < .001$, $\eta^2 = 0.81$; carrot Exposure Group: $F(2, 28) = 83.16$, $\eta^2 = 0.86$, $p < .001$). Simple main effects tests showed that although the main effects of Time were significant for both cry-face and laughter-face gestalts, the effects of Time were quite a lot bigger for laughter-face Gestalts (kale Exposure Group: $F(2,26) = 49.77$, $\eta^2 = 0.79$, $p < .001$; carrot Exposure Group: $F(2, 28) = 58.55$, $\eta^2 = 0.81$, $p < .001$) than for cry-face Gestalts (kale Exposure Group: $F(2, 26) = 18.33$, $\eta^2 = 0.59$, $p < .001$; carrot Exposure Group: $F(2, 28) = 8.78$, $\eta^2 = 0.39$, $p < .001$).

Post-hoc analyses with Bonferroni corrections also showed that for both the kale and carrot Exposure Groups, the cry-face Gestalts *decreased* significantly between the prenatal periods and post-birth (kale Exposure Group – 32 GW: $M = 0.47$, $SE = 0.06$; 36 GW: $M = 0.63$, $SE = 0.08$; Post-birth: $M = 0.26$, $SE = 0.05$, $ps \leq 0.001$); carrot Exposure Group – 32 GW: $M = 0.15$, $SE = 0.03$; 36 GW: $M = 0.22$, $SE = 0.05$; Post-birth: $M = 0.06$, $SE = 0.02$, $ps \leq 0.001$), whereas laughter-face Gestalts *increased* significantly (kale Exposure Group - 32 GW: $M = 0.02$, $SE = 0.01$; 36 GW: $M = 0.12$, $SE = 0.07$; Post-birth: $M = 0.94$, $SE = 0.11$, $ps \leq 0.001$; carrot Exposure Group - 32 GW: $M = 0.34$, $SE = 0.05$; 36 GW: $M = 0.38$, $SE = 0.08$; Post-birth: $M = 1.09$, $SE = 0.06$, $ps \leq 0.001$). No significant differences were found however between the two prenatal periods (32 GW and 36 GW) in the frequency of either cry-face or laughter-face gestalts ($p > .05$).

4. Discussion

The present study primarily investigated the impact of repeated flavor exposure to two different flavors (kale vs. carrot) from 36 Gestational weeks (GW) until birth on hedonic facial responses of newborns (cry-face vs. laughter-face gestalts). Fetal facial gestalts observed at 32 and 36 GW after a single flavor exposure through the mother's intake of kale or carrot capsules, served as the baseline for comparison. Consistent with previous research (Faas et al., 2015; Mennella et al., 2001; Schaal et al., 2000), the present study findings supported our hypothesis that neonates would react to the odors repeatedly experienced in utero with a higher frequency of laughter-face gestalts, while unfamiliar odors elicited a higher frequency of cry-face gestalts.

Our longitudinal analysis from 32 GW to one month postnatally demonstrated a significant increase in laughter-face and a decrease in cry-face gestalts in response to familiar odors. This transition suggests that repeated exposure facilitates familiarity and reduces aversive reactions, supporting the theory of transnatal chemosensory continuity

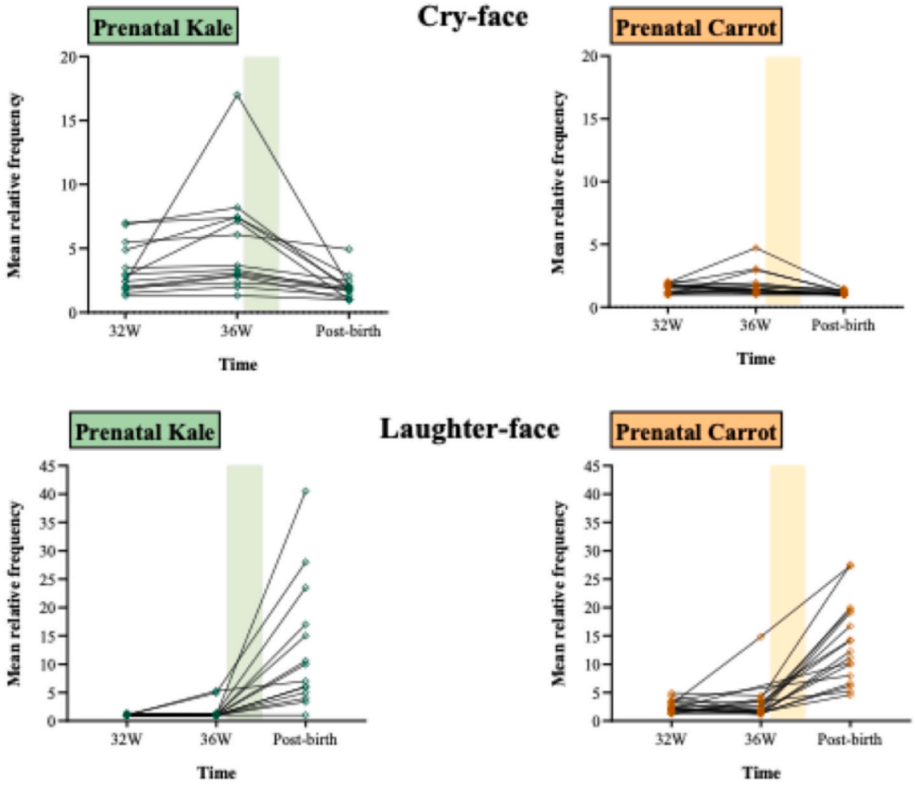

Fig. 4. Developmental trend of the relative frequency of facial responses per minute to the exposed flavor/odor from prenatal (32 and 36 GW) to post-birth periods as a function of repeated kale or carrot flavor exposure after 36 weeks gestation (green and orange vertical bars for the kale and carrot exposure groups, respectively). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

across sensory, perceptual, motor, and hedonic dimensions (André et al., 2018; Schaal, 2005, 2023). These findings echo the exposure effect, which posits that repeated exposure to a stimulus, even if initially disliked, can decrease negative responses and increase acceptance over time (Zajonc, 1968).

Previous postnatal studies have shown that early flavor exposure shapes later preferences (e.g., Aldridge et al., 2009; De Cosmi et al., 2017; Delaunay et al., 2010; Maier et al., 2007; Remy et al., 2013). For example, Delaunay et al. (2010) reports that week-old neonates' repeatedly exposed to an arbitrary odor while at breast develop a preference for it that can be detected after about 2 years. Likewise, Maier et al. (2007) found that 7-months-old infants developed preferences for flavors repeatedly experienced through breast milk, building robust chemosensory memories. Similarly, de Wild et al. (2015) showed that repeated vegetable exposure in 1.5–4 year-olds enhanced acceptance for those and similar-tasting vegetables. The present study, in line with previous ones (Mennella et al., 2001; Hepper et al., 2013) highlights that already such exposure to specific flavors can facilitate a shift from rejection to acceptance.

Facial gestalts are important indicators for understanding the rejection and acceptance for foods. However, the development of facial gestalts reflects complex interactions between exogenous and endogenous factors. Darwin (1872/1965) suggested that human facial expressions initially serve to regulate sensory input before developing into communicative functions. This concept extends to chemosensation, where facial muscle movements might reflect adaptive responses to unfamiliar or aversive stimuli (Steiner, 1979; Susskind et al., 2008). For instance, muscular actions like lip pressing (observed in cry-face gestalt) might limit exposure to "unwanted" flavors, while tongue show (as in laughter-face gestalt) may enhance chemosensory sampling by facilitating oral intake. This indicates an predisposed capacity of human fetuses and neonates to modulate chemosensory intake based on perceived qualities.

In utero, flavor exposure engages multiple chemosensory pathways, involving taste, chemesthesis and olfaction, the latter via both retro- and orthonasal routes (Schaal et al., 1995). The accumulation of taste- and odor-active molecules in the amniotic fluid, influenced by maternal diet and metabolism, enables the fetus to detect and respond through swallowing and pseudo respiration (e.g., De Snoo, 1935; Liley, 1972; Mistretta & Bradley, 1975; Piontelli et al., 2015; Ross & Nijland, 1998). Although taste-active molecules are also present in the amniotic fluid, current evidence predominantly supports the role of olfactory rather than gustatory cues in human fetal flavor detection (Schaal, 2005, 2023). Further research is necessary to clarify to the extent to which taste molecules directly influence fetal flavor perception. These fetal experiences contribute to the development of integrated chemosensory memories, affecting postnatal responses to flavors reviewed in Ganchrow & Mennella, 2003; Schaal, 2005, 2023; Spahn et al., 2019; Ustun et al., 2023).

In the present study, ortho-nasally administered stimuli are sufficient to elicit distinct facial responses in neonates, suggesting that in utero chemosensory experience recruits at least in part olfactory pathways. Further research should explore the distinct roles of gustatory and olfactory cues using targeted methodologies such as separating these chemosensory cues in postnatal tests or employing neuroimaging techniques in the postnatal period to deepen our understanding of fetal learning and its long-term effects on behavior.

4.1. *Strengths, limitations, and implications*

The primary strength of the current research lies in its longitudinal design, allowing direct comparisons of prenatal and postnatal responses within the same cohort, systematically assessing the development of facial responses to flavor exposure. Another significant strength is our rigorous methodological approach, which incorporates standardized assessments of facial movements and blinded coding procedures to

minimize potential biases. The use of the Fetal Observable Movements System(FOMS) and the Facial Action Coding System (FACS) provides high-resolution, objective measurements of chemosensory responses, and the high inter-coder and intra-coder reliability scores further demonstrate the robustness and reliability of our results. The homogeneity of the health characteristics of our sample also minimizes confounding variables, enhancing the internal validity of our findings.

However, the study does have limitations. The absence of a control group not exposed to specific flavors makes it challenging to fully disentangle developmental changes from the effects of repeated flavor exposure. If developmental changes alone were the primary driver, similar patterns would be expected across both facial gestalts. Instead, our results suggest a distinctive role for prenatal exposure in shaping postnatal hedonic responses (Mennella et al., 2001; Schaal et al., 2000; Wagner et al., 2019). To better understand the impacts of single versus repeated exposure, future studies should include a non-exposed control group.

Another limitation of our study was the small sample size. While our results align with previous studies that have used similar or even smaller cohorts (Hepper, 1995; Mennella et al., 2001; Schaal et al., 2000), our effect sizes should be interpreted with caution (Button et al., 2013). Further research with larger sample sizes is recommended to confirm our findings and provide more robust estimates of the effect sizes. The lack of maternal blinding to the conditions during the prenatal flavor exposure phase may have introduced biases. Considering the homogeneity of our sample and the use of a blinded coding procedure, it is unlikely that this affected the results at the coding stage. Implementing blinding techniques, such as over-encapsulation (commonly used in pharmacological studies, Wan et al., 2013), could help address this concern in future research.

Another consideration is the variability in the time elapsed between birth and neonatal testing, which may have contributed to interindividual differences in postnatal flavor experiences (Mennella et al., 2009; Ventura et al., 2021). Although we found no significant differences of outcome variables between feeding types (breastfeeding, bottle feeding, or a combination of both), we did not collect detailed information on the specific type of formula consumed by bottle-fed infants. The inclusion of casein hydrolyzed-based formulas, known for their bitter taste, might extend the knowledge of perinatal exposure to bitter flavors (Alim et al., 2020). Future research should consider these factors to capture a broader range of chemosensory exposures and might benefit from conducting immediate postnatal assessments followed by multiple testing points to minimize variability.

Finally, the lack of diversity in our sample, consisting exclusively of White British mothers, limits the generalizability of our findings. This homogeneity restricted our ability to explore how different cultural dietary practices might influence fetal receptivity to a wider array of flavors. Future research should investigate fetal and neonatal responses to bitter flavors in populations with a dietary emphasis on such flavors, potentially revealing significant cultural influences on flavor preference development (Rozin & Rozin, 1981).

5. Conclusion

This study introduces a novel prenatal "baseline" for assessing chemosensory familiarization and its continuity after birth, significantly adding to the existing literature by establishing a direct link between fetal reactions and postnatal outcomes after calibrated chemosensory stimulation. By highlighting the impact of repeated prenatal flavor exposure on neonatal chemosensory responses, our research emphasizes the importance of early chemosensory experiences and the formation of flavor-specific memories in utero, which shape postnatal preferences. This work deepens our understanding of the interconnected development of perception, action, emotion, and memory during human ontogeny (AboEllail & Hata, 2017; Ceriani et al., 2015; Gustafsson et al., 2022; Hepper, 1996; Schaal, 2023; Soussignan & Schaal, 2005). The broader implications of this research for sensory science and developmental psychobiology suggest that prenatal chemosensory interventions could be strategically used to promote healthy eating behaviors, reduce aversive responses to bitter foods, and potentially increase the acceptance of bitter, green vegetables during weaning and beyond (Johnson et al., 2021).

CRediT authorship contribution statement

Beyza Ustun-Elayan: Writing – original draft, Visualization, Methodology, Funding acquisition, Conceptualization. **Jacqueline Blissett:** Writing – review & editing, Methodology, Conceptualization. **Judith Covey:** Writing – review & editing, Conceptualization. **Benoist Schaal:** Writing – review & editing, Methodology, Conceptualization. **Nadja Reissland:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Ethical statement

This study was conducted in accordance with the Declaration of Helsinki, and ethical permission was granted by Durham University (PSYCH-2019-03-12T15_59_32-wvgf27). All participating mothers provided informed written consent for both themselves and their infants

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.appet.2025.107891.

Data availability

Data are made available in Appendix A.

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