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Human Foetuses Learn Odours from their Pregnant Mother's Diet

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Abstract

Olfactory responsiveness was assessed in 24 neonates born to mothers who had or had not consumed anise flavour during pregnancy. Both groups of infants were followed-up for behavioural markers of attraction and aversion when exposed to anise odour and a control odour immediately after birth and on day 4. Infants born to anise-consuming mothers evinced a stable preference for anise odour over this period, whereas those born to anise non-consuming mothers displayed aversion or neutral responses. This study provides the first clear evidence that through their diet human mothers influence the hedonic polarity of their neonates' initial olfactory responses. The findings have potential implications for the early mother-to-infant transmission of chemosensory information relative to food and addictive products.

Introduction

During the embryonic or foetal stages, the environment constrains the perceptual information available to the growing brain and thus influences the behaviour of the newborn (Smotherman and Robinson, 1988; Lecanuet *et al.*, 1995; Gottlieb, 1997). In humans, for example, the way vocal and speech sounds are processed by the newborn depends on prenatal exposure to maternal voice or specific speech sequences (De Casper and Spence, 1986; Fifer and Moon, 1995). Whether this foetal ability is indicative of mechanisms specific to audition and language processing or of more general learning mechanisms applicable to a broad range of perceptual inputs remains unclear. We investigated whether the human foetus can acquire information from olfactory cues, which are involved in other psychobiological realms such as ingestive behaviour, emotional stability and early attachment (Schaal, 1988).

The ability to learn olfactory cues has been demonstrated in the foetuses of various mammals, such as rats (Pedersen and Blass, 1982; Smotherman, 1982; Smotherman and Robinson, 1987; Hepper, 1988; Molina *et al.*, 1995), rabbits (Bilkó *et al.*, 1994; Semke *et al.*, 1995) and sheep (Schaal *et al.*, 1995a). In these species, the introduction of odorants into the amnion either by direct infusion or maternal ingestion affects later infantile responses to the same stimuli. These studies in non-primate species highlight the fact that chemosensory information is part of the normal experience of the foetus. It is the aim of the present study to examine whether similar prenatal facilitative or inductive processes [in the sense of Gottlieb (Gottlieb, 1983)] might operate in the formation of the earliest selective responses to odours in human infants.

Taking advantage of the widespread use of anise flavour in the local Alsatian cuisine and of the fact that it is readily perceived by newborns immediately after birth (Stirnimann, 1936; Engen and Lipsitt, 1965), we studied odour-elicited responses in infants born to mothers who had regularly consumed anise flavoured sweets or drinks during late pregnancy and infants born to mothers who had not ingested such products during pregnancy.

Participants and methods

Participants

Two sub-groups of mothers were recruited on the basis of their habitual intake of anise flavoured foods or drinks, who were named thereafter anise-consuming (AC) and anise-non-consuming (nAC) mothers ($n = 24$, 12 per group). Both groups of mothers were comparable for parity (5/7 primi/multiparae per group) and age [AC, 27.7 ± 3.9 years; nAC, 30.5 ± 3.9 years; $t(24) = 1.66$, $P > 0.10$]. Infants were selected for the absence of medical complications during gestation and vaginal delivery (gestational age range, 37–42 weeks; 1 min Apgar score of ≥8). The infants born to AC mothers (8 girls, 4 boys) had an average birthweight of 3474 ± 443 g, while those born to nAC mothers (6 girls, 6 boys) had a mean birthweight of 3408 ± 376 g [$t(22) = 0.38$, $P =$

0.71]. Mothers signed informed consents before their own and their infant's participation.

Prenatal exposure

In the last two gestational weeks (i.e. 15 days before the expected term), AC mothers were offered commercially available anise flavoured sweets (Société Nouvelle des Pastilles de Vichy, Courbevoie, France), cookies (C. Miller, Strasbourg, France) and sirup (Teisseire, Grenoble, France) which they could ingest *ad libitum*, but without changing their customary intake rate. During this period, they were also asked to fill out a detailed record of their eating habits and of their actual consumption of anise flavoured foodstuffs. By decoding these records and using the quantitative informations provided by the fabricants on the flavour content of the different foodstuffs, we could precisely evaluate the amount of anise flavour consumed by each individual mother. The AC group consumed anise flavour on an average of 5.6 ± 3.5 days preceding delivery (due to the fact that most women delivered before the expected term of gestation), during which they ingested a daily average of ~121.2 ± 28.7 mg anethole. Over the same period, the group of nAC mothers ingested no food in which anethole constituted the dominant flavour. AC mothers ceased to consume anise flavour before the onset of labour (average time between last anise intake and delivery 13.4 ± 8.7 h) and did not ingest anise flavored food during the postnatal test period.

Postnatal stimuli

The newborns were tested with anethole, the pure anise flavour (Guenther, 1972) most abundantly used in the above sweets or sirup as indicated by the respective companies. The anethole was diluted to a subjective intensity corresponding to that of amniotic fluid. The final dilution step of anethole in paraffin oil, which represented the best match in subjective intensity with amniotic fluid, was 1.042%. The solvent, paraffin oil, was used as the control stimulus. Both anethole and paraffin oil were purchased from Aldrich (Saint-Quentin-Favallier, France).

Testing procedures

Both groups of infants were compared along several behavioural measures of immediate responsiveness: (i) oral and facial responses; (ii) approach to or withdrawl from the anise odorant (head orientation). To assess whether the arousing property of the prenatally experienced odorant has a longer lasting effect during early development, the infants were examined within the first 8 postnatal hours (mean age 2.9 ± 1.9 h, range 0.5–8 h) and in a follow-up test conducted on day 4 (mean age 87.3 ± 10.7 h, range 68–110 h). The day-of-birth test was run before the infants had had their first postnatal ingestive experience. The day 4 test was run while the infants were in a preprandial state [mean duration since last feed in AC infants 3.76 ± 2.04 h; in nAC infants 3.62 ± 1.23 h; $t(18) = 0.186$, $P = 0.85$].

Two tests were conducted on days 1 and 4. In the first test, the infants were sitting immobile in a reclining chair to be videotaped for odour-elicited oral and facial movements. They were recorded in an awake state [state 3 or 4 of Prechtl's classification (Prechtl, 1974)] while exposed to two successive 10 s presentation trials of cotton swabs impregnated with diluted anethole and with the control stimulus. The cotton swabs were mounted on 20 cm long sticks in order to avoid possible contamination with hand odours. Stimuli were held under the infants' noses (midline), at ambient temperature, in an order that was systematically counterbalanced between subjects and with a minimal inter-stimulus interval of 60 s.

In the second test a two-choice paradigm was used. The subjects sat in a semi-reclining seat facing a standardized visual scene in a dim light environment. They were exposed to two stimuli fastened to a device that allowed these to be presented symmetrically to each side of the infants' face (eccentricity, 20–70°) [for a detailed description, see (Schaal *et al.*, 1995b)]. The stimuli consisted of gauze pads (10 × 10 cm^2, 100% cotton; Hartmann, Châtenois, France) impregnated either with 1 ml of the 1.042% anethole dilution or with pure paraffin oil. After the stimuli were positioned at 1–2 cm from the possible trajectory of the infants' nose, the infants' heads were brought manually to a sagittal position and released after disappearance of tonic neck asymmetry. Head orientation responses were recorded during two 1 min trials between which the lateral position of the stimuli was reversed. The duration of orientation to each of the stimuli was summed across both trials of each test. In addition to the within-subject alternation of side of stimulus presentation, the relative position of the two stimuli was also systematically alternated between subjects.

Behavioural responses

The infants' oro-facial activity was scored in 11 subjects from the AC group (one subject was excluded from this analysis because of fussing during the test) and in the 12 nAC subjects on the day of birth. On the day 4 follow-up testing, each group comprised 10 subjects (the sample reduction was due to two mothers leaving earlier than day 4 and to two infants contracting neonatal jaundice). The video records of the oro-facial response test were analysed blind by a coder who performed at a level of reliability >70% (Facial Action Coding System final proficiency test). The responses were coded during the stimulus presentation period (10 s) and during an additional post-stimulus period (10 s). We used an anatomically based coding scheme of minimally distinguishable motions of the facial muscles [Facial Action Coding System, adult version (Ekman and Friesen, 1978) and infant version (H. Oster and D. Rosenstein, unpublished manuscript)]. In the light of previous studies which found that negative facial configurations were more discriminant than positive configurations in gauging odour-elicited hedonic responsiveness in newborns (Steiner, 1979; Soussignan *et al.*, 1997), the coding of the infants' responses focused on negative facial actions as defined in newborns, infants and children (Oster and Ekman, 1978; Ganchrow *et al.*, 1983; Rosenstein and Oster, 1988; Soussignan and Schaal, 1996; Camras *et al.*, 1998). Specifically, all facial configurations, including action units 4 (brow lowering), 9 (nose wrinkling), 10 (upper lip raising), 15 (lip corner depressing), 20 (lip stretching), 26 and 27 (gaping) and 51 and 52 (head turning), were systematically decoded and timed (Figure 1). Additional responses, such as sucking, licking, munching and chewing, subsumed under the generic term 'mouthing', were considered as expressing acceptance (Lipsitt, 1977; Rosenstein and Oster, 1988; Travers *et al.*, 1997). Each movement of distinct parts of the face (lower, middle and upper) was screened separately in slow motion and frame by frame to score the onset/offset points of each target action unit (accuracy ±0.04 s).

The video records of the two-odour choice test served to code the duration of head orientation to either stimulus. Twelve and 10 infants from each group were subjected to these tests on the day of birth and day 4, respectively (the reduction in group size being the same as above). The possible trajectory of 180° that the newborns' nose could scan in the test situation was divided into three bilateral angular sectors: a sector corresponding to the stimulus ('stimulus sector') and two sectors corresponding to the zones free of stimulus ('stimulus-free sectors', covering the 0–20° and 70–90° angles relative to the infant's sagittal plane). To be considered positively oriented towards a stimulus, subjects had to position their nose over one of the stimulus sectors, which required a minimal head turn of 20° from the midline in the direction of that stimulus. The time spent over the defined orientation sectors was independently recorded using Observer sofware (Noldus, The Netherlands; accuracy ±0.1 s) by two coders who were blind to the lateral position of the stimuli. One of the coders was uninvolved in the study and although both of them performed at a high level of reliability (r = 0.961 and 0.976 for duration of orientation to either stimuli), only the data of the fully blind coder were considered for statistical treatments. The total time oriented to each stimulus was obtained by adding the different orientation durations recorded across the two consecutive trials composing each test. The duration of orientation towards a given stimulus is reported as the mean proportion of time spent oriented towards that stimulus sector as a function of the total time of orientation to the two stimulus sectors and the two stimulus-free sectors.

Statistical analyses

To assess the differential effects of the odour stimuli on responsiveness in the oro-facial tests the frequencies of infants responding to either stimulus were compared using the Fisher exact probability test (for contrasts between the AC and nAC groups) and binomial tests were used for within-group comparisons of frequency of responding to the anise versus control stimuli. Treatment and stimulus effects on the duration of facial and mouthing actions in the oro-facial tests and on the relative duration of head orientation in the two-odour choice tests were analysed using two-way repeated analyses of variance (ANOVAs) on the data of the day-of-birth tests. Two independent factors were considered as potential determinants of differential responding of the infants, namely stimulus quality (anise odour versus control odour) and the exposure group (AC versus nAC). To assess main or interaction effects due to age, testing time (day of birth versus day 4) was entered as an additional factor in the ANOVA design for the data from the infants that could be followed up to day 4. t-tests for matched samples were used to assess the significance of differences between conditions revealed by interaction effects.

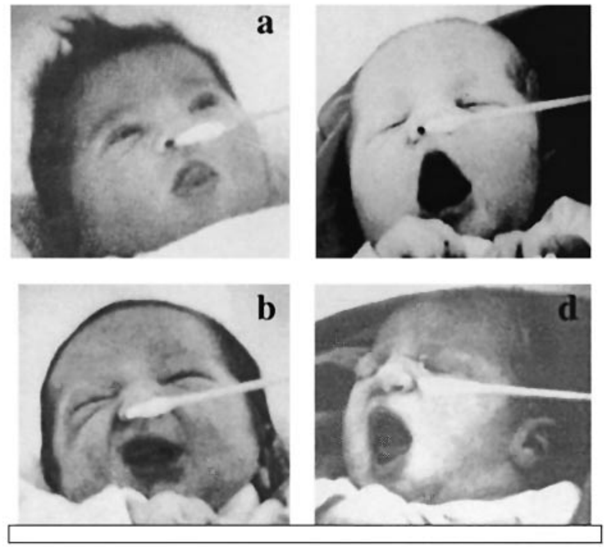

Figure 1 Representative examples of facial expressions of awake newborns exposed to 10 s anise odor stimuli. **(a)** Age at test, 3 h; facial behaviour displayed, repeated action units (AUs) 19 + 25 (tongue protruding, licking); latency from onset of stimulus presentation, 1.5 s. **(b)** Age, 8 h; AUs activated, 4 + 6 + 9 + 26 + 42 (respectively, brow lowering, cheek raising, nose wrinkling, gaping, upper eye lid lowering); latency from onset of stimulus, 5.1 s. **(c)** Age, 1.5 h; AUs activated, 27 + 43 (gaping, eyes closed); latency from onset of stimulus, 1.7 s. **(d)** Age, 0.5 h; AUs activated, 10 + 27 + 43 + 52 (upper lip raising, gaping, eyes closed, head turning); latency from onset of stimulus, 4.36 s. Infant (a) belongs to the anise-exposed group; infants (b)–(d) belong to the non-anise-exposed group.

Fisher exact probability tests were also used to compare the number of infants who spent longer oriented to stimulus A than to stimulus B and the number of infants who exhibited the reverse pattern in the two-choice odour tests. Individual infants were defined as orienting longer to one stimulus than to the other when they spent >50% of the total orientation time to both stimulus sectors turned towards

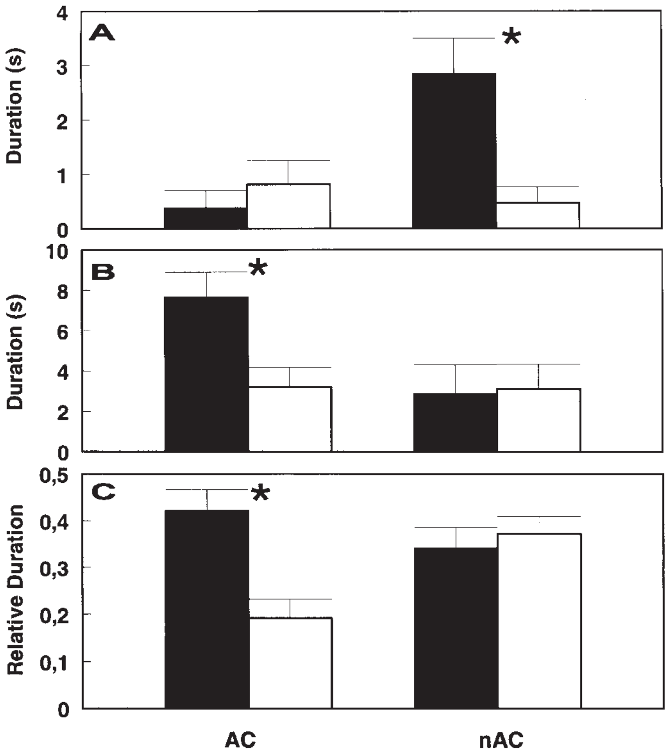

Figure 2 Mean duration of **(A)** negative facial configurations, of **(B)** mouthing activities and of **(C)** head orientation in response to the presentation of anise odor (solid bars) and the control stimulus (empty bars) to infants of an average age of 2.9 h born to anise-consuming (AC) or to non-anise-consuming (nAC) mothers (error bars show standard errors). Results in (A) and (B) derive from successive presentations of the two stimuli, while results in (C) derive from simultaneous presentation. $^*P < 0.01$.

that stimulus. All tests were two-tailed and the α level was set at 0.05.

Results

Odour responses on the day of birth

Infants born to nAC mothers more frequently displayed negative facial responses to anise odour than did those born to AC mothers (10/12 versus 2/11, respectively; $P < 0.01$, Fisher exact probability test). Also, more subjects in the nAC group expressed negative facial actions in response to the anise odour relative to the control stimulus (anise 10/12 versus control 3/12), while the AC infants showed a low frequency of negative facial expressions to either stimulus (anise 2/11 versus control 3/11; $P = 0.16$, binomial test). An ANOVA showed that infants born to nAC mothers exhibited a longer duration of negative facial responses to the anise odour than did infants born to AC mothers (Figure 2A) [two-way odour × exposure group ANOVA, odour main effect, $F(1,21) = 5.35$, $P = 0.031$; odour × group interaction, $F(1,21) = 11.19$, $P = 0.003$; matched sample t-tests on the duration of negative facial action to anise versus control stimuli: in the AC group $t(10) = 0.08$, $P = 0.45$; in the nAC group $t(11) = 3.81$, $P < 0.003$)].

The same analyses on mouthing actions revealed that infants born to AC mothers displayed these more frequently than infants born to nAC mothers (AC group 10/11 versus nAC group 4/12; $P < 0.01$, Fisher exact probability test). They also exhibited longer mouthing responses to the anise odour than infants born to nAC mothers (Figure 2B) [two-way odour × exposure group ANOVA, odour main effect, $F(1,21) = 5.81$, $P < 0.004$; odour × group interaction, $F(1,21) = 7.36$, $P < 0.02$; two sample t-test on duration of mouthing to the anise odour in the AC versus the nAC group: $t(21) = 2.48$, $P = 0.02$]. It may be noted that although the percentage of mouthing AC infants did not differ between the anise and the control odorant (anise 10/11 versus control 8/11), they mouthed significantly longer in response to the anise than to the control stimulus [matched sample t-tests on duration of mouthing to anise versus control stimuli: in the AC group $t(10) = 3.71$, $P = 0.004$; in the nAC group $t(11) = 0.22$, $P = 0.83$]. Finally, the infants of both groups mouthed equally to the control odour (AC group 8/11 versus nAC group 8/12). Thus, depending on whether or not their mothers ingested anise flavoured sweets or drinks during the last days of pregnancy, the infants in this study displayed differential facial and oral responses to a pure anise odour within the first hour following birth.

Further evidence for the effect of prenatal exposure to anise on early postnatal responding to anise odour was provided by the head orientation test. As shown in Figure 2C, the relative duration of head orientation to the two stimuli was significantly different in the two groups of newborns [two-way odour × group ANOVA, odour main effect, $F(1,22) = 5.13$, $P < 0.04$; odour × group interaction, $F(1,22) = 8.93$, $P < 0.01$). While the AC newborns oriented their head to the anise odour longer than to the control stimulus, the nAC infants did not show a differential duration of head orientation [matched sample t-tests: AC group $t(11) = 3.13$, $P < 0.01$; nAC group $t(11) = 0.66$, $P = 0.52$]. Finally, when considered individually, more AC subjects oriented for longer to the anise than to the control stimulus, whereas nAC subjects exhibited the reverse pattern ($P < 0.05$, Fisher exact probability test) (Figure 4).

Thus, at 3 h of age, the newborn infants of this study used previously gained odour information to make decisions supporting directional head motions. The polarity of head movements indicated that prenatal exposure to anise was linked to postnatal attraction to anise, whereas a majority of anise naïve infants showed either indifference to or avoidance of the anise odour (Figure 4). Because the local infant care routine ensured that newborns were minimally exposed to amniotic fluid odour after birth (i.e. within minutes after birth their skin was thoroughly wiped clean and dried and their oro-nasal passages cleared by aspiration) and because they were tested before any postnatal ingestion, these results indicate that the motivational value of an olfactory stimulus

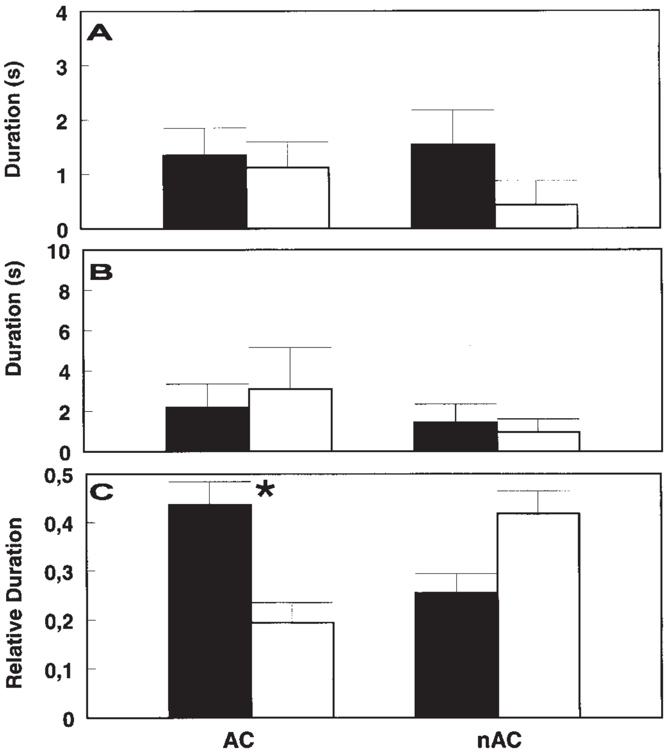

Figure 3 Mean duration of **(A)** negative facial configurations, of **(B)** mouthing activities and of **(C)** head orientation in response to the presentation of anise odor (solid bars) and the control stimulus (empty bars) to infants aged 4 days of mothers consuming anise (AC) or not (nAC) during gestation. Results in (A) and (B) derive from successive presentations of the two stimuli, while results in (C) derive from simultaneous presentation. *$P < 0.01$.

in the immediate postnatal environment can be strongly influenced by experience of that odorant in the late fetal environment.

Odour responses on day 4

To assess whether such prenatal odour priming can influence behaviour for a period longer than the first postnatal hour, the infants of both groups were administered the same oro-facial and two-choice tests on day 4. Although >80% of ingested anethole is eliminated within 8 h after intake (Caldwell and Sutton, 1988), it cannot be entirely ruled out that the infants born to AC mothers encountered traces of anise in her colostrum or milk between birth and the day 4 test. To assess this possibility we compared the responsiveness of breast- and bottle-fed infants (n = 6 and 4, respectively, in each group) to the anise odour along the three response criteria considered. The mode of feeding, and hence the putative re-exposure to the anise flavour carried in maternal milk, did not affect the behavioural outcomes noted on day 4 [$F(1,16) = 0.43$, 1.17 and 0.03 for duration of negative facial response, duration of mouthing and relative duration of head orientation, respectively; $P > 0.05$ in all cases]. This suggests that prenatal plus potential postnatal exposure to anise does not have a stronger effect than prenatal exposure alone on the expression of preference for anise on day 4.

Analyses of variance were then conducted on the three behavioural variables (negative facial actions, mouthing and duration of these responses) by considering stimulus and age as within-subject factors and the mother's exposure to anise in late pregnancy as a between-subject factor. On day 4, the frequency of infants displaying negative facial actions and mouthing in response to the odour of anise, as well as the durations of these responses, were no longer affected by whether or not the pregnant mothers consumed anise flavoured foods (Figure 3A,B). The number of infants responding by negative facial actions to anise was 5/10 in both groups and to the control odour 5/10 versus 1/10 in the nAC and AC groups, respectively. The number of infants mouthing to anise was 5/10 versus 3/10 in the AC and nAC groups, respectively, and to the control odour 3/10 in both groups. However, when the infants' relative head orientation was compared in the test pairing of the anise odour and the control odour (Figure 3C), infants born to AC mothers remained oriented to the anise odour for longer than to the control odour, while infants born to nAC mothers remained on average undifferentiated in their relative choice [three-way odour × group × age ANOVA, odour main effect, $F(1,18) = 3.18$, $P = 0.09$, age main effect, $F(1,18) = 0.16$, $P = 0.69$; odour × group interaction, $F(1,18) = 16.57$, $P < 0.001$; odour × age interaction, $F(1,18) = 1.83$, $P = 0.19$; matched sample t-tests between relative durations of head oriention to anise versus control: AC group $t(9) = 3.72$, $P < 0.005$; nAC group $t(9) = 2.06$, $P = 0.069$; two-sample t-test between duration of head turning to anise odour in AC versus nAC groups: $t(18) = 2.87$, $P = 0.01$]. Individual data corroborated this result, i.e. more infants from AC mothers oriented their head towards the anise stimulus for longer than towards the control and, conversely, more infants from nAC mothers remained oriented to the control for longer than to the anise stimulus ($P < 0.003$, Fisher exact probability test) (Figure 4). Finally, the stability of the general motivation to approach the anise stimulus was expressed by a positive correlation between duration of orientation towards anise at 3 h and at 4 days (Pearson's $r = 0.59$, $n = 20$, $P = 0.005$).

No correlation was found between maternal anise consumption expressed as the daily or total amount of anethole consumed within the last 15 days before term and the infants' response pattern to anise odour.

Discussion

These data show that behavioural effects attributable to prenatal experience with anise can still be demonstrated 4 days after exposure cessation. Interestingly, the multiple measures of infant response to anise odour appeared to follow different developmental pathways. While the head

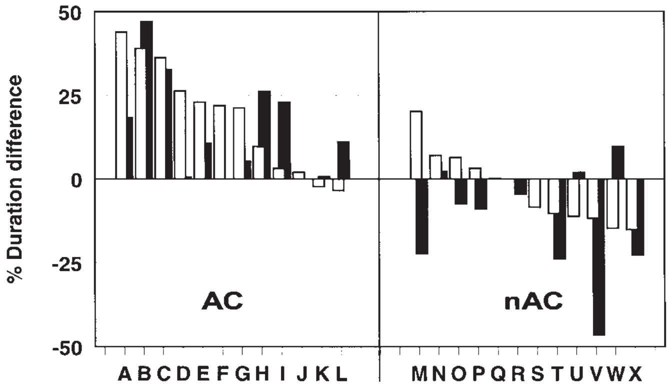

Figure 4 Percent difference in duration of head orientation to simultaneously presented anise and control odors for individual infants born to either anise-consuming (AC) or non-anise-consuming mothers (nAC) on the day of birth (empty bars; $n = 12$/group) and on day 4 (solid bars; $n = 10$/group). Values > 0 represent orientation towards the anise odour; letters on the abcissa designate individuals (subjects Q and R demonstrated close to 0 values in the day-of-birth test; subjects F, J, Q and S could not be followed up at the day 4 test).

turning response constituted a stable index of retention of the prenatal odour in the newborns of AC mothers, anise-related oral and facial responses shifted between the first postnatal hour and day 4 in both groups of infants. Such variable outcomes suggest that these different behavioural markers of an infant's propensities to display attraction/aversion are independently influenced by events occurring in the early postnatal environment. Neonatal head orientation is generally held as reflecting the coordinated output of a general mechanism expressing sensation seeking and recognition memory (Kuhl, 1985), whereas oral and facial responses are seen at this early age as reflecting the stimulus-bound operation of a selective hedonic monitor tied to ingestion (Lipsitt, 1977; Steiner, 1979; Soussignan *et al.*, 1997, 1999). This leads to the expectation that oro-facial responses would be more sensitive to the influence of recent ingestive experience and, hence, would show greater plasticity than head orientation. The present results are consistent with this view.

Implicit in the notion that the earliest oral and facial responses are influenced by earlier perceptual learning is that opportunities for such processes actually exist *in utero*. First, real-time ultrasonographic recordings clearly show that mouthing movements (i.e. mouth opening, sucking, tongue protrusion) commonly occur in the foetus, and with increasing frequency as gestation advances (van Woerden *et al.*, 1988; Horimoto *et al.*, 1989).

Second, the frequent mouthing activity to anise odour observed 3 h after birth in AC infants may be the result of an anise–mouthing contingency established within the days before birth. Such positive acquisition processes involving the chemical senses may be engaged in the foetus at each episode of ingestion by the pregnant mother in the following way: (i) when the mother consumes food, the amounts of various metabolites, including those with olfactory properties, increase in maternal and foetal plasma (Phelps *et al.*, 1981; Desage *et al.*, 1996) and are transferred to the amniotic fluid (Hauser *et al.*, 1985; Mennella, *et al.*, 1995; Schaal *et al.*, 1995c), with growing efficacy and rapidity as gestation advances (Dancis and Schneider, 1978); (ii) this metabolite flow induces functional changes in the foetus, specifically in terms of enhanced respiratory, swallowing and mouthing motions (Natale *et al.*, 1978; Patrick *et al.*, 1980, 1982; Luther *et al.*, 1984; Harper *et al.*, 1987); (iii) such fetal activities displace the amniotic fluid in the oro-nasal cavities with an age-related improvement in velocity (Badalian *et al.*, 1993), creating 'amniotic pulses' that are increasingly compatible with chemosensory stimulation; (iv) the concurrent operation of olfactory stimulation and in-flow of metabolites (namely glucose) may consolidate the reinforcing properties of a predominant odorant (Gold, 1986). The exposure of the rapidly developing brain to this cascade of events that recurs at each maternal meal might thus result in the establishment of a functional link between a chemosensory cue and foetal behavioural effectors. Such a functional link may support different behavioural outcomes either by boosting positive responses (e.g. appetitive head orientation or consummatory oral actions) or by inhibiting aversive responses (e.g. negative facial actions) to the odour and may thus explain the pattern of behaviour noted within hours after birth in the present study.

Following the above logic, infants from nAC mothers could not have attached any positive reinforcing value to the odour of anise and, accordingly, did not display increased appetitive head turning or consumatory mouthing movements in response to it at either age of testing. Nonetheless, at 3 h of age the anise odour evoked more negative facial actions in these infants than in infants born to AC mothers, a pattern of facial response that may be elicited by neophobia. The disappearance of these anise-linked negative facial motions at 4 days of age in the nAC group may be interpreted in terms of maturation or of attenuation of neophobia due to anise exposure in the previous test session. This interpretation raises the possibility of very rapid odour familiarization shortly after birth.

To our knowledge, this study represents the first evidence that oral and facial correlates of hedonic processing in the newborn infant can be influenced by prenatal chemosensory experience. Differential hedonic configurations of the newborns' oro-facial responses may be selectively activated to signal to the caretaker a hedonic discrepancy between an olfactory stimulus learned *in utero* and an olfactory cue encountered in the postnatal environment: while a perinatal olfactory match may elicit positive responses (e.g. increased mouthing and decreased negative facial action), conversely, an olfactory mismatch may elicit increased negative responses (decreased mouthing and increased negative facial actions). The infants' ability to reliably convert chemosensory inputs into visually expressive displays to which caretakers are extremely reactive may thus contribute to subtle regulatory processes in incipient nurturing responses [maternal responses to infant facial expressions (Robson, 1967; Huebner and Izard, 1988); reliable infant face reading by adults other than mothers (Ganchrow *et al.*, 1983; Rosenstein and Oster, 1988; Soussignan *et al.*, 1997, 1999)].

Further, the present study provides the first clear evidence from the newborn's point of view that the human foetus has the ability to detect and record odour information afforded by the pregnant mother through her diet. Previous suggestive attempts had only noted discriminative (Schaal and Orgeur, 1992) or reduced aversive (Hepper, 1995) responses of newborns to an aroma consumed by the pregnant mother. More specifically, within the first 4 days after birth infants not only recognize the individual signature of the amniotic fluid they inhaled during the last days before term (Marlier *et al.*, 1998; Schaal *et al.*, 1998), but can also perceptually extract an isolated olfactory facet from this whole amniotic mixture. Thus, selective perception and learning of odour information is possible near gestational term.

Finally, at the same time as it shapes olfactory perception and cognition, intra-uterine odour experience sets the motivational frame in which the oriented behaviour of the infant initially develops. Odour learning within the amnion becomes coupled with more or less plastic motor patterns. In the case of head orientation, the prenatally acquired odour–response link persists for *at least* the first 4 postnatal days. Thus, foetal olfaction fosters the acquisition of predictable sensory information upon which neonates can rely during a period when they encounter a variety of vital micro- and macro-transitions in the context of variable and unprecedented stimuli [e.g. the very first pre-ingestive and ingestive behaviours, transition from the colostral to the milk phase, acceptance of mother's milk despite qualitative changes due to day-to-day dietary fluctuations (Marlier *et al.*, 1997, 1998)].

Although the longer term recall of such odour preferences acquired *in utero* is not known in the human, several studies in other animals have demonstrated its persistence until weaning or adult age (Smotherman, 1982; Bilkó *et al.*, 1994). It can thus be expected that the acceptance at weaning of non-milk foods is influenced by their congruence with odour qualities resembling those encountered in the weeks or days before birth. More generally, this raises the possibility that a pregnant mother's intake during late gestation of flavour-rich foods, drinks or addictive substances, including alcohol and tobacco (Kandel *et al.*, 1994; Kirstein *et al.*, 1997), may have latent and deferred influences on the selective behaviour of the human offspring.

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