Chem. Senses 35: 841–853, 2010
doi:10.1093/chemse/bjq092
Advance Access publication September 27, 2010

Gustofacial and Olfactofacial Responses in Human Adults

Romy Weiland[1], Heiner Ellgring[1] and Michael Macht[2]

[1]Department of Psychology, Biological Psychology, Clinical Psychology and Psychotherapy, University of Würzburg, Marcusstrasse 9-11, 97070 Würzburg, Germany and [2]Institute of Psychotherapy and Medical Psychology, University of Würzburg, Klinikstrasse 3, 97070 Würzburg, Germany

Correspondence to be sent to: Romy Weiland, Department of Psychology, Experimental Psychology, University of Mainz, Germany. e-mail: weilanr@uni-mainz.de

Accepted August 17, 2010

Abstract

Adults' facial reactions in response to tastes and odors were investigated in order to determine whether differential facial displays observed in newborns remain stable in adults who exhibit a greater voluntary facial control. Twenty-eight healthy nonsmokers (14 females) tasted solutions of PROP (bitter), NaCl (salty), citric acid (sour), sucrose (sweet), and glutamate (umami) differing in concentration (low, medium, and high) and smelled different odors (banana, cinnamon, clove, coffee, fish, and garlic). Their facial reactions were video recorded and analyzed using the Facial Action Coding System. Adults' facial reactions discriminated between stimuli with opponent valences. Unpleasant tastes and odors elicited negative displays (brow lower, upper lip raise, and lip corner depress). The pleasant sweet taste elicited positive displays (lip suck), whereas the pleasant odors did not. Unlike newborns, adults smiled with higher concentrations of some unpleasant tastes that can be regarded as serving communicative functions. Moreover, adults expressed negative displays with higher sweetness. Except for the "social" smile in response to unpleasant tastes, adults' facial reactions elicited by tastes and odors mostly correspond to those found in newborns. In conclusion, adults' facial reactions to tastes and odors appear to remain stable in their basic displays; however, some additional reactions might reflect socialization influences.

Key words: facial reactions, gustation, odor, olfaction, taste, taste concentration

Introduction

Facial reactions are a powerful source of information for studies on taste- and odor-elicited affect in humans. In newborns, tastes and odors have been found to elicit differential facial reactions which indicate newborns' ability to discriminate among different taste and odor stimuli (Steiner 1973, 1977, 1979; Rosenstein and Oster 1988, 1997; Soussignan et al. 1997) and among different taste concentrations (Ganchrow et al. 1983). Taste- and odor-elicited facial reactions, which have an innate basis and genetic origin, have been observed immediately after birth in newborns who received no prior postnatal nutrition. It is, however, unclear whether these specific facial displays remain stable during ontogeny. Acquired food preferences and aversions due to individual food experiences as well as higher voluntary facial control with increasing age (Ekman 1972; Rinn 1991; Ganchrow and Mennella 2003; Doty and Shah 2008) may both lead to changes in facial activity elicited by tastes and odors. The present study was designed to examine facial reactions to primary tastes differing in concentration and odors in healthy adults by using the Facial Action Coding System (FACS, Ekman and Friesen 1978) in order to investigate whether adults display similar taste- and odor-elicited facial reactions like newborns.

Studies on taste-elicited facial reactions have consistently demonstrated that newborns show expressions indicating pleasure in response to sweet tastes and expressions indicating displeasure in response to sour, bitter, and sometimes salty tastes (see review by Peiper 1963; Steiner 1973, 1977; Cowart 1981; Ganchrow et al. 1983; Rosenstein and Oster 1988, 1997; Steiner et al. 2001). Despite this consistent view regarding facial hedonics to tastes in general, researchers do not completely agree on the specific facial components elicited by the taste qualities observed in newborns. In response to the sweet taste, Steiner (1973, 1977, 1979) and Steiner et al. (2001) reported expressions of facial relaxation, smiling, lip wiping, and lip sucking. With increasing sweetness, more infants displayed these positive facial reactions (Ganchrow et al. 1983). Rosenstein and Oster (1988) confirmed facial relaxation elicited by the sweet taste but did not observe more smiling, lip sucking, and lip wiping. Umami tastes (mono-sodium glutamate) added to a soup produced the same—albeit less intense—positive lower-face components as did sweet tastes (Steiner 1987). Consistent facial responses to the bitter tastes included mouth opening, upper lip raising, and nose wrinkling (Steiner 1973, 1977, 1979; Rosenstein and Oster 1988). Likewise, Steiner (1973, 1977, 1979) observed lip corner depression and Rosenstein and Oster (1988) reported activity of upper face components, for example, brow and cheek raising and brow lowering, as most frequent additional responses to the bitter taste. With increasing bitterness, the percentage of infants displaying negative facial reactions increased (Ganchrow et al. 1983). The sour taste has been shown to consistently elicit lip pursing and nose wrinkling (Steiner 1973, 1977, 1979; Rosenstein and Oster 1988) and similar upper face reactions as observed to the bitter taste (Rosenstein and Oster 1988). The salty taste elicited facial responses with diffuse mouth and lip movements and occasionally negative upper- and mid-face actions, mouth gaping, and lip pursing (Rosenstein and Oster 1988). In sum, newborns responded differentially to sweet (vs. nonsweet stimuli, Rosenstein and Oster 1988), bitter, and sour tastes.

Studies on olfactofacial responses have demonstrated inconsistent evidence that newborns display specific facial reactions according to the hedonic odor valence appraised by adults (Steiner 1979; Soussignan et al. 1997). Observers (blind to stimuli) judged photographs of newborns displaying positive facial expressions, for example, smiling and sucking, in response to pleasant odors (banana, butter, and vanilla) as indicating attraction/indifference and negative facial expressions such as lip corner depression and lip pursing in response to unpleasant odors (fish and rotten eggs) as indicating rejection (Steiner 1977, 1979).

In contrast, Soussignan et al. (1997) who reinvestigated olfactofacial responses in 3-day-old infants controlling for methodological shortcomings in the studies by Steiner, found no evidence that odors classified by adults in terms of hedonic valence as pleasant (vanilla) or unpleasant (butyric acid) elicit facial reactions reflecting attraction or aversion. Butyric acid, however, elicited more facial reactions indicating disgust (nose wrinkling and upper lip raising) than vanillin, whereas vanillin did not elicit more smiling (lip corner pull) than butyric acid. Moreover, newborns did not respond differentially to the 4 different concentrations of butyric acid and vanillin. In sum, inconsistent olfactofacial evidence suggests that facial reactions in response to pleasant and unpleasant odors do not seem to be highly stereotyped (Schaal et al. 2000, 2002) and that newborns' hedonic experience to odors may be different from that of adults.

Newborns' facial responses convey communication signals about the hedonic value of stimuli (Steiner 1977; Rosenstein and Oster 1997). They are based on biologically adaptive functions that might facilitate ingestion of nutritious stimuli or block ingestion of harmful substances (Rosenstein and Oster 1997; Oster 2004). The subcortical origin of facial responses to tastes and odors was evidenced in anencephalic and hydranencephalic newborns, who displayed specific facial reactions a few hours after birth without prior postnatal ingestion before stimulus application (see Peiper 1963; Steiner 1973, 1977, 1979). Newborn's discriminative facial reactions were regarded as low-level reflex-like responses (Steiner 1977) reflecting a universal and innate behavior present at birth and thus independent from learning. Consequently, such prototypical facial reactions should be also present in adults. Indeed, several studies using observational systems have demonstrated that some taste-elicited (Perl et al. 1992; Steiner et al. 1993; Greimel et al. 2006) and odor-elicited facial reactions (Perl et al. 1992; Saku and Ellgring 1992; Steiner et al. 1993) in healthy adults are comparable with facial displays observed in newborns. However, adults showed a reaction that has never been observed in newborns, that is, smiling in response to the bitter taste (Greimel et al. 2006), which indicated an influence of display rules on their facial reactions to unpleasant tastes. These results were discussed in the light of the neurocultural view (Ekman 1972) suggesting that the social context such as the presence of the experimenter and the camera may have activated a socially accepted reaction, that is, a display rule to mask the internal negative state by a smile.

A direct comparison of results across adult studies in this field is difficult due to different research methods and research questions. Although some consistent facial displays have been found across adult studies (e.g., smiles to the sweet taste and to pleasant smells, brow lower to the bitter taste, and nose wrinkle to unpleasant smells), some of these studies described specific distinct facial displays in response to specific stimuli. For instance, in response to the bitter taste, Greimel et al. (2006) observed upper lip raise (AU 10) and jaw drop (AU 26), whereas Steiner et al. (1993) observed closing the eyes and pulling down the outer lip corners and the lower lip. Some studies (Saku and Ellgring 1992; Greimel et al. 2006) used the fine-grained FACS (Ekman and Friesen 1978) to analyze facial reactions, whereas other studies used self-developed notational systems (Perl et al. 1992; Steiner et al. 1993). Moreover, 3 of 4 studies addressed whether neurodegenerative and psychiatric disorders moderate adults' facial reactions in response to tastes and odors. However, these studies did not directly address the comparison of facial features between healthy adults and newborns and thus it remains open whether adults display similar facial reactions as observed in newborns.

In addition, the studies differed in the stimuli used. Some studies investigated facial reactions in one modality, either tastes (Greimel et al. 2006) or odors (Saku and Ellgring 1992), whereas other studies used both tastes and odors (Perl et al. 1992; Steiner et al. 1993). Because Greimel et al. (2006) did not use pure taste solutions, unlike in the newborn studies, and did not apply a variety of taste qualities, unlike Perl et al. (1992) and Steiner et al. (1993), it remains unclear, whether the full range of taste qualities elicits the same differential facial reactions in adults as it does in newborns. Therefore, our first objective was to examine whether qualitatively different tastes, that is, bitter, salty, sour, sweet and umami, and qualitatively different odors, that is, banana, cinnamon, clove, coffee, fish, and garlic, elicit specific facial reactions in adults using FACS to measure facial reactions. We expected specific taste- and odor-elicited facial reactions in adults, which are comparable with those in newborns, but also facial displays, for example, smiling to unpleasant stimuli, serving social-communicative purposes, which were not observed in newborns.

Taste concentration has also been demonstrated to increase specific facial reactions in newborns with a higher percentage of newborns displaying positive reactions with increasing sweetness and negative reactions with increasing bitterness (Ganchrow et al. 1983). Because salty, sour, and umami tastes were not applied in their study, it remains unclear if the newborns' facial reactions to these tastes are similarly affected by concentration. Based on this evidence, our second objective was to examine whether the frequency of adults showing facial reactions is affected by taste concentration using low, medium, and high concentrations. With increasing taste concentration, as was the case for newborns, we expected that more adults display positive reactions to pleasant tastes and negative reactions to unpleasant tastes.

Studies on taste-elicited facial reactions in children and adults have already suggested that unpleasant tastes generally evoke more facial displays than pleasant tastes (Looy and Weingarten 1992; Greimel et al. 2006; Zeinstra et al. 2009). Our third objective was to examine whether overall facial activity differs between unpleasant and pleasant tastes and odors in adults and whether overall taste-elicited facial activity is affected by taste concentration. Because there exist, in general, far more negative than positive facial displays, we expected a higher overall facial activity in adults in response to unpleasant stimuli compared with pleasant stimuli and a higher overall facial activity with increasing concentration for each taste quality.

Materials and methods

Participants

Twenty-eight healthy participants (14 female, 14 male) were recruited at the University of Würzburg to voluntarily take part in the study. They were mostly students (90%) with a mean age of 25 years (standard deviation [SD] = 3.4), ranging from 18 to 32 years. Participants had normal weight with a mean body mass index of 21.80 (SD = 3.1) for female participants and 22.89 (SD = 2.4) for male participants. Participants were native German speakers, nonsmokers, free from medications, free from colds, food allergies, nasal allergies, and olfactory or gustatory disorders at the moment of the test. They abstained from eating and drinking for at least 1.5 h prior to the experiment. The study was approved by the ethics commission of the German Psychological Association (DGPs).

Taste and odor stimuli

Taste stimuli were solutions of PROP (6-*n*-propylthiouracil) for bitter taste (Merck-VWR), NaCl for salty taste, citric acid for sour taste, sucrose for sweet taste (Adler Apotheke), and monosodium glutamate (MSG) for umami taste (Ajinomoto Foods). Each taste quality was applied in 3 different concentrations, that is, low, medium, and high. Taste concentration were solutions of 0.032 mM, 0.32 mM, and 3.20 M PROP; 0.01, 0.1, and 1.0 M NaCl; 0.01, 0.03, and 0.05 M citric acid; 0.10, 0.42, and 0.83 M sucrose; and 0.001, 0.05, and 0.1 glutamate. The choice of concentrations was determined according to criteria set up by Looy and Weingarten (1992), Bartoshuk et al. (1994), Hodson and Linden (2006), and Rousmans et al. (2000). Taste concentrations used in this study were all above the detection threshold for citric acid, NaCl, sucrose (0.0023, 0.01, 0.01 M; Birbaumer and Schmidt 1999), PROP (nontasters $>1.8 \times 10^{-4}$ mol/L PROP, supertasters $<3.2 \times 10^{-5}$ mol/L PROP, Drewnowski et al. 1997), and MSG (0.009 M; Lugaz et al. 2002). Evian mineral water (pH 7.2) served as the control taste (neutral taste). All solutions were dispensed in 5 mL distilled water and were administered at room temperature (20–22 °C). Before and after testing, taste solutions were stored in the refrigerator. Taste solutions were removed from the refrigerator at least 3 h prior to testing to ensure an up to room temperature warmth, which was measured by a thermometer immediately before testing. Each stimulus was presented once in a disposable cup of 20 mL maximum content. The stimuli were colorless to avoid that participants guessed the taste quality in the cups before actually tasting the stimulus.

Odor stimuli were pen-like odor dispensing devices of the "Sniffin' Sticks" test (Kobal et al. 1996). Sniffin' Sticks is a test of nasal chemosensory performance which consists of 3 tests of olfactory functions, that is, odor threshold, odor discrimination, and odor identification. In this study, only the odor identification test was used. It contains 16 common odors, which are presented in a randomized order by the use of felt-tip pens. Due to the high time costs of facial expression analysis by observational systems, we analyzed video recordings of only 6 of these 16 odors, that is, banana, cinnamon, clove, coffee, fish, and garlic. These odors were selected according to their perceived pleasantness with banana, cinnamon, and coffee representing the pleasant pole and with fish, garlic, and clove representing the unpleasant pole.

Procedure

Participants were individually tested and seated in a comfortable chair in a room with a constant temperature (22 °C) and received identical written and spoken instructions. They were told that the study examines taste and odor perception. No other details about the aims of the study were given. Participants were informed that the experiment would be continuously video recorded. They were, however, not told that their facial expressions would be analyzed specifically, in order to avoid exaggerated or moderated facial expressions. The video camera was placed in front of the participants at a distance of 2.5 m. The experimenter who was present in the room during the entire experiment was not visible to the participants but could watch their behavior online via closed circuit TV. All participants gave informed consent, including agreement to be recorded on video.

Taste presentation

For each of the 16 liquid solutions, participants were asked to rinse their mouth with mineral water prior to each liquid sample. Participants were requested to give the experimenter the verbal signal "Ready" each time when they had finished rinsing. Immediately after this signal, the experimenter measured 45 s with a stopwatch. Within this time period, participants were asked to relax. After this 45-s rest period, participants were told to taste the liquid, to keep it in the mouth for 5 s and then to swallow it. Immediately after swallowing, participants rated intensity and pleasantness of the solution and the perceived taste quality. Participants then rinsed their mouth with mineral water and were asked again to give the experimenter the signal (Ready). This experimental procedure of tasting was repeated identically with the 15 solutions.

Taste solutions were placed on a table in front of the participants in small cups numbered from 0 to 15. Mineral water (no. 0) was always presented as the first stimulus to make the participant familiar with the tasting procedure and to suppress some surprise effect. The initial water stimulus was not taken into account in the data analysis. Next, sweet, sour, salty, and umami solutions (no. 1–12) were presented in a pseudorandomized order. We used 4 different pseudorandomized taste orders, with 7 participants each receiving one taste order. Participants received the bitter taste (no. 13, 14, and 15) at the end due to its masking effect (Dallenbach JW and Dallenbach KM 1943; Leach and Noble 1986). For each taste quality, the concentration was applied in ascending order, first low, then medium, and lastly high concentration.

Odor presentation

The odors were placed on a table in front of the participants numbered from 1 to 16. For each of the 16 odors, participants were asked to give the experimenter the verbal signal "Ready". Immediately after this signal, the experimenter measured 30 s with a stopwatch. After this 30-s rest period, the experimenter told the participants to smell the odor (no. 1). Participants took the stick from the penholder, removed the cap, placed it about 2 cm in front of both nostrils, and smelled it for at least 5 s. After smelling, the participants put the stick back into the penholder. Participants rated intensity and pleasantness of the odor and identified the odor using a multiple-choice task with 4 odor descriptors. After the ratings, participants gave the experimenter the verbal signal "Ready." This experimental procedure of smelling was repeated identically with the 15 odors. The entire experiment lasted ~45 min.

Dependent variables

Participants were instructed to rate intensity, pleasantness, and perceived quality for each taste and odor stimulus. Intensity and pleasantness in response to each stimulus were rated on verbally anchored scales from 1 to 25, using a method of category scaling developed by Heller (1985): Five numerical subdivisions are assigned to each of the 5 verbal categories (with endpoints "very low intensity" and "very high intensity," "very unpleasant," and "very pleasant"). Participants are asked to first decide on a verbal category and then on the numerical gradation within the category. This scaling method allows participants to make a rough categorization in the first step and then fine grade their decision in the second step. For the identification of taste quality, participants had to decide for 1 of 6 possible tastes in a multiple-choice task (bitter, salty, sour, sweet, neutral, and miscellaneous). To identify odors, participants had to choose 1 of 4 odor descriptors in a multiple-choice task.

Facial expressions were analyzed from video recordings using the FACS (Ekman and Friesen 1978), an objective, standardized, and descriptive system for coding facial expressions based on the anatomy of facial movements. A visible facial movement is assigned to a single Action Unit (AU). Specific facial reactions refer to the frequency of each single AU. A parameter of overall facial activity was defined as the total number of AUs shown (multioccurrence of AUs from 1 to 40; cf. Ellgring 1989).

Two trained FACS coders, blind to stimulus condition, independently analyzed the videos in slow motion and frame by frame and coded the apex (moment of the most intense facial expression) of each facial expression. Facial reactions in response to tastes were separately assessed during 2 observation periods, that is, before swallowing (a) and after swallowing (b), to exclude facial activity due to swallowing. The observation period before swallowing (a) began when the cup was put down to chin level to ensure visibility of participants' entire face. This observation period ended when the participants had swallowed the liquid. The second observation period began after the participants had swallowed the liquid (b). The observation period for facial odor reactions began when the participant had placed the pen's tip 2 cm in front of both nostrils. Each observation period lasted up to a maximum of 4 s.

Interrater reliability (IR) of FACS coding was assessed by a second coder who independently scored the expressions of 7 randomly chosen participants. IR was determined by dividing the number of AUs agreed upon by the 2 coders by the total sum of AUs scored by each (cf. Ekman and Friesen 1978). Interrater reliabilities of IR = 0.82 and IR = 0.86 were achieved for reactions to taste and odor stimuli, respectively, and are regarded as good.

Statistical analysis

To explore whether various tastes and odors elicited specific facial reactions, the frequencies of single facial reactions, that is, Action Units, in response to all tastes versus odors were compared by Cochran's *Q*-tests in order to explore whether the frequency of facial reactions is uniformly distributed across all tastes and odors, respectively. McNemar-tests were carried out to explore differences of specific facial activity between tastes and odors.

To test whether taste concentration affects the number of adults showing specific facial reactions, the frequencies of single facial reactions, that is, Action Units, in response to each taste concentration were compared by Cochran's *Q*-tests for difference among proportions. McNemar-tests were carried out to explore differences between tastes with respect to frequencies of Action Units.

To test taste-elicited and odor-elicited overall facial activity, that is, the total number of facial reactions (AU 1–40), we used repeated measures analyses of variance (ANOVAs). For all ANOVAs, a Bonferroni correction was applied for single comparisons in case of significant main effects or significant interaction effects.

Manipulation check of subjective reactions to tastes and odors

Tastes

Perceived taste intensity of each taste quality significantly increased across concentrations—from low to medium, from low to high, and from medium to high (main effects of taste quality, $F_{4,104} = 27.57$, $P < 0.001$; taste concentration, $F_{2,52} = 280.86$, $P < 0.001$; taste quality × taste concentration interaction, $F_{8,208} = 14.69$, $P < 0.001$). This finding demonstrates that concentrations were successfully chosen within each taste quality. However, within each concentration, some tastes were not matched in perceived intensity (low levels: sour more intense than the other tastes, *P*s < 0.001; sweet more intense than bitter, salty, umami, *P*s < 0.05; medium levels: sour more intense than bitter, salty, umami, *P*s < 0.05; sweet more intense than umami, $P = 0.009$; high levels: umami less intense than the other tastes, $P \leq 0.002$, sweet less intense than salty, $P = 0.005$).

Taste pleasantness of bitter, salty, sour, and umami tastes, but not the pleasantness of sweet tastes, was reduced with increasing concentration (main effects of taste quality, $F_{4,104} = 27.07$, $P < 0.001$; taste concentration, $F_{2,52} = 41.29$, $P < 0.001$; taste quality × taste concentration interaction, $F_{8,208} = 9.18$, $P < 0.001$). Taste pleasantness declined across each concentration of the bitter and the salty taste—from low to medium, from low to high, and from medium to high (*Ps* ≤ 0.05). In response to the umami taste, adults rated the medium and the high concentration as less pleasant compared with the low concentration (*Ps* ≤ 0.001). The pleasantness of the sour taste significantly declined from medium to high concentration ($P = 0.042$).

Identification rates were significantly different among the 15 taste solutions ($\chi^2 = 1280.24$, $P < 0.001$). They were high for mineral water (100%) and for the medium and the high concentration of PROP (75%, 96%), NaCl (82%, 100%), citric acid (100%, 96%), and sucrose (96%, 96%). Low sour (89%) and low sweet (86%) concentrated solutions were also clearly recognized. Low bitter was recognized as bitter in 54% of the cases. Low salty was mostly perceived as bitter (39%) and as neutral (29%) rather than as salty (18%). The umami taste showed mixed perceived gustatory sensations for each concentration, mostly perceived as neutral in the low concentration (68%) or as salty in the medium (71%) and high concentration (50%). No gender differences were found for taste intensity ratings, $F_{1,26} = .332$, $P = 0.569$; taste pleasantness ratings, $F_{1,26} = 0.003$, $P = 0.958$; and taste identification rates (*P*s > 0.05).

Odors

Perceived odor intensity differed across odors, $F_{5,130} = 4.94$, $P = 0.001$. Garlic was rated as more intense than cinnamon and coffee (*Ps* ≤ 0.005). Odor stimuli were rated as differently pleasant, $F_{5,130} = 33.08$, $P < 0.001$. Banana, cinnamon and coffee were rated as more pleasant than garlic, fish and clove (*P*s ≤ 0.001).

Identification rates were similar among the 6 odors ($\chi^2 = 8.13$, $P > 0.05$). Participants correctly identified cinnamon, clove, and garlic in 89% of the cases. Coffee and fish were correctly identified by 93% of the participants and banana by 96% of the participants.

No gender differences were found for odor intensity ratings, $F_{1,26} = 0.002$, $P = 0.968$, odor pleasantness ratings, $F_{1,26} = 0.225$, $P = 0.639$, and odor identification rates (*P*s > 0.05).

Results

Specific facial reactions in response to tastes and odors

Tastes

In line with our fist objective, tastes elicited significantly different facial reactions in adults, which are comparable with those observed in newborns (Cochran's *Q*-tests). These displays were indicated by positive facial reactions to the sweet taste (lip suck, AU 28) and by negative facial reactions to the bitter, salty, sour, and umami taste (brow lower, AU 4; upper lip raise, AU 10; lip corner depress, AU 15). Moreover, smiling (cheek raise, AU 6; lip corner pull, AU 12) to unpleasant tastes (bitter, salty, and sour) was confirmed. Table 1 lists the numbers of facial reactions, that is, AUs, to each taste quality regardless of concentration and observation period.

The sweet taste elicited lip suck (AU 28) more frequently than the salty taste ($P = 0.002$) and the sour taste ($P = 0.031$). Unexpectedly, lip wipe (AU 37) and lip corner pull (AU 12), that is, an indicator of smiling, were displayed equally among taste qualities and thus were not frequent responses to the sweet taste.

The bitter, salty, and sour taste shared the same negative and positive facial reactions, as well as the typical surprise reaction. In response to the bitter, salty, and sour taste, adults displayed brow lower (AU 4, $P = 0.004$, $P = 0.039$), upper lip raise (AU 10, $P = 0.002$, $P < 0.001$, $P = 0.001$), and lip corner depress (AU 15, $P = 0.012$, $P = 0.001$, $P = 0.039$) more frequently when compared with the sweet taste. Furthermore, the bitter, salty, and sour taste elicited cheek raise (AU 6) more frequently than the sweet taste ($P = 0.065$, $P = 0.002$, $P = 0.003$). The higher frequency of cheek raise occurring together with lip corner pull (AU 12) indicated that adults smiled more often in response to these taste qualities when compared with the sweet taste. However, lip corner pull (AU 12) was equally displayed among these tastes. In addition, the bitter, salty, and sour taste elicited inner and outer brow raise (AU 1 + 2) more frequently than the sweet taste (AU 1, $P = 0.004$, $P = 0.001$, $P < 0.001$; AU 2, $P = 0.031$, $P = 0.001$, $P < 0.001$), which reflects a surprise expression.

Table 1 Frequencies of single facial reactions in response to the bitter, salty, sour, sweet, and umami taste

AU	Taste stimuli					
	Bitter	Salty	Sour	Sweet	Umami	*Q*-tests
AU 1: inner brow raise	13	15	16	4	12	***
AU 2: outer brow raise	10	15	16	4	6	***
AU 4: brow lower	28	26	24	19	25	**
AU 6: cheek raise	13	16	17	6	10	**
AU 7: lids tight	10	13	15	9	12	ns
AU 9: nose wrinkle	2	6	5	2	5	ns
AU 10: upper lip raise	24	26	24	11	19	***
AU 12: lip corner pull	17	19	23	21	16	**
AU 13: sharp lip pull	1	1	5	2	1	**
AU 14: dimpler	24	23	22	25	25	ns
AU 15: lip corner depress	15	19	14	6	12	***
AU 16: lower lip depress	10	8	8	4	8	ns
AU 17: chin raise	12	13	12	11	14	ns
AU 18: lip pucker	4	2	8	2	3	*
AU 19: tongue show	4	3	0	1	4	*
AU 20: lip stretch	2	5	2	1	1	*
AU 23: lip tight	3	4	12	3	2	***
AU 24: lip press	16	15	21	18	20	ns
AU 25: lips part	20	19	24	23	22	ns
AU 26: jaw drop	22	20	24	21	23	ns
AU 28: lip suck	6	0	4	10	6	*
AU 37: lip wipe	1	0	2	4	3	ns
AU 84: head shake	2	1	2	1	2	ns

The data represent the number of participants (maximum $N = 28$) who showed Action Units (AUs). AUs were only included if shown by ≥4 participants. Cochran's *Q*-tests comparing reactions to each of the 5 stimuli. ns, not significant.
$*P \leq 0.10$, $**P < 0.05$, $***P \leq 0.001$.

The sour taste elicited the most manifold facial pattern when compared with the other tastes. In response to the sour taste, adults displayed lip tight (AU 23) more frequently than to the bitter ($P = 0.004$), salty ($P = 0.021$), sweet ($P = 0.004$), and umami taste ($P = 0.002$). Additionally, the sour taste tended to elicit lip pucker (AU 18) more frequently than the salty taste and the sweet taste ($Ps = 0.070$). Lip press (AU 24) was more often elicited by the sour taste than by the salty taste ($P = 0.031$). The sour taste elicited outer brow raise (AU 2) and lip corner pull (AU 12) more frequently when compared with the umami taste ($P = 0.013$, $P = 0.016$).

The umami taste elicited more facial displays indicating a lower pleasantness than the sweet taste and more facial displays indicating a higher pleasantness than the salty taste. Compared with the sweet taste, the umami taste more often elicited inner brow raise (AU 1, $P = 0.021$) and tended to elicit upper lip raise (AU 10, $P = 0.057$) more frequently. In response to the umami taste, adults displayed outer brow raise (AU 2, $P = 0.022$) and upper lip raise (AU 10, $P = 0.016$) less frequently, lip corner depress (AU 15, $P = 0.065$) marginally less frequent, and lip suck (AU 28, $P = 0.031$) more frequently when compared with the salty taste.

Odors

As expected, different odors elicited different facial reactions (Cochran's *Q*-tests) with unpleasant odors (fish, garlic, and clove) evoking negative facial displays such as brow lower (AU 4), lids tight (AU 7), and upper lip raise (AU 10). In contrast, pleasant odors did not elicit positive facial reactions. Moreover, smiling (cheek raise, AU 6; lip corner pull, AU 12) to unpleasant odors, unlike to unpleasant tastes, was not confirmed. Table 2 displays the numbers of facial reactions, that is, AUs, to each odor.

In response to fish and garlic, adults displayed brow lower (AU 4), lids tight (AU 7), upper lip raise (AU 10), and lip corner depress (AU 15) more frequently when compared with banana and cinnamon ($Ps < 0.05$). Fish and garlic more often elicited brow lower (AU 4) and upper lip raise (AU 10) when compared with coffee ($Ps < 0.05$). Clove elicited brow lower (AU 4), lids tight (AU 7), and upper lip raise (AU 10) more frequently than banana and cinnamon. Also, adults

Table 2 Frequencies of single facial reactions in response to banana, cinnamon, clove, coffee, fish, and garlic odors

AU	Odor stimuli						
	Banana	Cinnamon	Clove	Coffee	Fish	Garlic	*Q*-tests
AU 1: inner brow raise	1	0	4	2	5	1	**
AU 2: outer brow raise	1	0	3	2	3	1	ns
AU 4: brow lower	3	2	13	6	16	14	***
AU 5: lid raise	3	2	0	1	3	0	ns
AU 6: cheek raise	0	0	2	0	2	2	ns
AU 7: lids tight	8	10	17	16	19	17	**
AU 9: nose wrinkle	1	1	2	0	4	3	ns
AU 10: upper lip raise	5	6	13	8	18	17	***
AU 12: lip corner pull	2	2	3	3	3	3	ns
AU 14: dimpler	3	2	2	6	3	6	ns
AU 15: lip corner depress	0	1	2	3	6	6	**
AU 17: chin raise	1	1	2	2	5	5	ns
AU 25: lips part	2	1	2	3	3	4	ns

The data represent the number of participants (maximum N = 28) who showed AUs. Total occurrence of AU 13, 16, 18, 84 = 0; AU 19, 24 = 1; AU 23 = 2; AU 20, 26, 38 = 5; AU 43 = 6. Cochran's *Q*-tests comparing reactions to each of the 6 stimuli. ns, not significant.
$^{**}P < 0.05$, $^{***}P \leq 0.001$.

displayed brow lower (AU 4) in response to clove more often than in response to coffee ($P < 0.05$). Coffee elicited lids tight (AU 7, $P = 0.039$) more often than banana. In conclusion, negative facial displays to the most unpleasant odors (garlic, fish) were all characterized by brow lower (AU 4), lids tight (AU 7), upper lip raise (AU 10), and lip corner depress (AU 15) when compared with the most pleasant odors (banana, cinnamon).

Specific facial reactions with increasing taste concentration

In general, with increasing concentration of the bitter, salty, sweet, and umami taste, but not of the sour taste, the frequency of adults showing specific facial reactions increased significantly (Cochran's *Q*-tests). The results confirmed our hypothesis that with increasing concentration of unpleasant tastes (bitter, salty, and umami, but not sour) more negative facial reactions, for example, brow lower and upper lip raise, occurred. Unlike newborns, adults showed negative facial displays (brow lower), but not the expected positive facial displays, in response to the pleasant sweet taste. Table 3 displays the number of adults displaying specific facial reactions, that is, AUs, to each of the taste qualities and its concentration.

With increasing concentration of the bitter, salty, sweet, and umami taste, more adults showed negative facial reactions indicating displeasure such as brow lower (AU 4) and upper lip raise (AU 10). Specifically, more adults displayed brow lower in response to the high concentration when compared with the low concentration of the bitter ($P = 0.007$), salty ($P = 0.021$), sweet ($P = 0.001$), and umami taste ($P = 0.002$). Moreover, the frequency of adults showing brow lower increased from low to medium umami concentration ($P = 0.002$). In response to the sweet taste, more adults displayed brow lower to the high concentration when compared with the medium concentration ($P = 0.021$). Upper lip raise increased with increasing bitterness, that is, from low to medium ($P < 0.001$), medium to high ($P = 0.070$), and low to high ($P < 0.001$). In response to the salty and umami taste, more adults expressed upper lip raise in response to the medium ($P < 0.001$, $P = 0.002$) and high concentration ($P < 0.001$, $P = 0.002$) when compared with the low concentration. Also, in response to the sweet taste, more adults tended to show upper lip raise to the high concentration when compared with the low concentration ($P = 0.070$).

With increasing concentration of the bitter and the salty tastes, further negative facial reactions were elicited. In particular, more adults displayed lip corner depress (AU 15) with increasing bitterness, that is, from low to high ($P = 0.012$) and medium to high ($P = 0.039$) and with increasing saltiness, that is, from low to medium ($P = 0.057$) and low to high ($P = 0.022$). Moreover, the frequency of adults showing chin raise (AU 17) and nose wrinkle (AU 9) increased from the low to the high concentration ($P = 0.039$, $P = 0.031$) of the salty taste. In addition, with increasing concentration of the bitter and the salty taste, more adults smiled. In particular, more adults displayed cheek raise (AU 6) and lip corner pull (AU 12) in response to the high concentration when compared with the low and medium concentration of the bitter taste (AU 6, $P < 0.001$, $P = 0.004$, AU 12, $P < 0.001$, $P = 0.006$) and salty taste (AU 6, $P < 0.001$, $P = 0.012$, AU 12, $P < 0.001$, $P = 0.012$). Here, display rules may have played a role (cf. Discussion).

Moreover, surprise reactions (AU 1 + 2) increased with increasing concentration of the bitter, salty, and umami taste. In response to the salty taste, more adults displayed brow raise (AU 1 + 2) to the high concentration when compared with the low (Ps < 0.001) and medium concentration ($P = 0.039$, $P = 0.012$). The bitter and the umami tastes also elicited inner brow raise more frequently when comparing high with low concentration (AU 1, Ps = 0.039).

In contrast to the increase of many facial reactions, there were 2 facial reactions, that is, dimpler (AU 14, pulling of the lip corners inward) and chin raise (AU 17, upward movement of the lower lip), whose frequency decreased with increasing concentration of some tastes. Less adults

Table 3 Single facial reactions in response to low, medium, and high concentrations of the bitter, salty, sour, sweet, and umami taste

	Bitter				Salty				Sour				Sweet				Umami			
	Low	Medium	High	*Q*-tests	Low	Medium	High	*Q*-tests	Low	Medium	High	*Q*-tests	Low	Medium	High	*Q*-tests	Low	Medium	High	*Q*-tests
AU 1	1	6	8	**	2	7	14	***	9	13	11	ns	1	2	4	ns	1	5	8	**
AU 2	1	4	7	*	2	5	14	***	8	11	10	ns	1	1	3	ns	1	2	5	*
AU 4	11	19	22	**	12	17	22	**	16	18	17	ns	5	10	18	***	7	20	20	***
AU 6	1	4	13	***	1	6	15	***	11	9	12	ns	1	4	4	ns	4	5	4	ns
AU 9	1	1	1	ns	0	3	6	**	3	1	2	ns	0	0	2	ns	0	3	5	**
AU 10	5	17	23	***	5	19	24	***	17	20	20	ns	2	6	8	*	3	16	15	**
AU 12	2	6	16	***	3	9	18	***	15	12	17	ns	15	13	13	ns	10	7	7	ns
AU 13	1	1	0	ns	1	0	0	ns	4	3	1	*	0	2	1	ns	1	1	1	ns
AU 14	19	16	11	**	20	12	14	**	16	16	15	ns	20	20	20	ns	21	17	14	*
AU 15	4	6	13	**	4	12	13	**	9	9	8	ns	2	3	5	ns	3	6	8	ns
AU 16	1	5	6	*	2	4	5	ns	3	3	6	ns	2	1	3	ns	3	4	5	ns
AU 17	3	7	8	ns	3	4	10	**	7	7	7	ns	8	2	6	*	6	7	7	ns
AU 19	1	1	3	ns	0	1	3	*	0	0	0	ns	0	0	1	ns	0	2	4	**
AU 23	0	1	2	ns	0	2	4	**	5	5	10	*	0	0	3	ns	0	2	0	ns
AU 24	9	11	9	ns	9	11	11	ns	13	18	13	*	14	12	15	ns	11	16	10	*
AU 25	14	13	12	ns	16	9	12	*	18	16	17	ns	16	16	15	ns	14	14	10	ns
AU 26	13	12	18	*	10	15	16	*	18	20	19	ns	12	15	14	ns	10	11	18	*
AU 28	2	2	3	ns	0	0	0	ns	3	3	2	ns	4	4	5	ns	3	1	3	*
AU 37	0	1	0	ns	1	1	0	ns	0	1	2	ns	2	1	2	ns	1	0	2	*

The data represent the number of participants (maximum $N = 28$) who showed AUs. AUs were only included if shown by ≥4 participants. Cochran's *Q*-tests comparing reactions among taste concentrations within each taste quality. ns, not significant.
*$P \leq 0.10$, **$P < 0.05$, ***$P \leq 0.001$.

displayed the dimpler in response to the bitter taste to the high concentration when compared with the low and medium concentration ($P = 0.039$, $P = 0.063$). In response to the salty taste, the number of adults showing the dimpler also decreased from low to medium concentration ($P = 0.008$). Thus, a lower frequency of the dimpler appears to be associated with a higher unpleasantness. Chin raise decreased from low to medium concentration of the sweet taste ($P = 0.039$) and thus less chin raise appears to be associated with higher pleasantness because chin raise decreased for the sweet taste but increased for the salty taste. Both Action Units seem incompatible on a functional muscular basis with those increasing with negative tastes.

To sum up, with increasing concentration more negative facial reactions, for example, brow lower and upper lip raise, were observed in response to the bitter, salty, sweet, and umami taste. The bitter and the salty tastes also elicited smiling with increasing concentration. In contrast, an increase of concentration of the sour taste had no impact on the frequency of facial reactions displayed.

Overall facial activity in response to tastes and odors

Tastes

A higher overall facial activity was expected with increasing concentration for each taste quality. This hypothesis was confirmed partly because overall facial activity increased with increasing concentration of bitter, salty, and umami tastes but not of sour and sweet tastes (Figure 1). The sour taste elicited the highest overall facial activity than all other tastes (*Ps* ≤ 0.001). ANOVA revealed main effects of taste quality, $F_{4,104} = 13.42$, $P < 0.001$; taste concentration, $F_{2,52} = 32.08$, $P < 0.001$; and a significant taste quality × taste concentration interaction, $F_{8,208} = 3.59$, $P < 0.01$.

In response to the bitter and the umami tastes, overall facial activity significantly increased from low to medium concentration ($P = 0.004$, $P = 0.009$) and from low to high concentration ($P = 0.001$, $P = 0.036$). In response to the salty taste, overall facial activity significantly increased across each concentration, that is, from low to medium ($P < 0.001$), from medium to high ($P < 0.001$), and from low

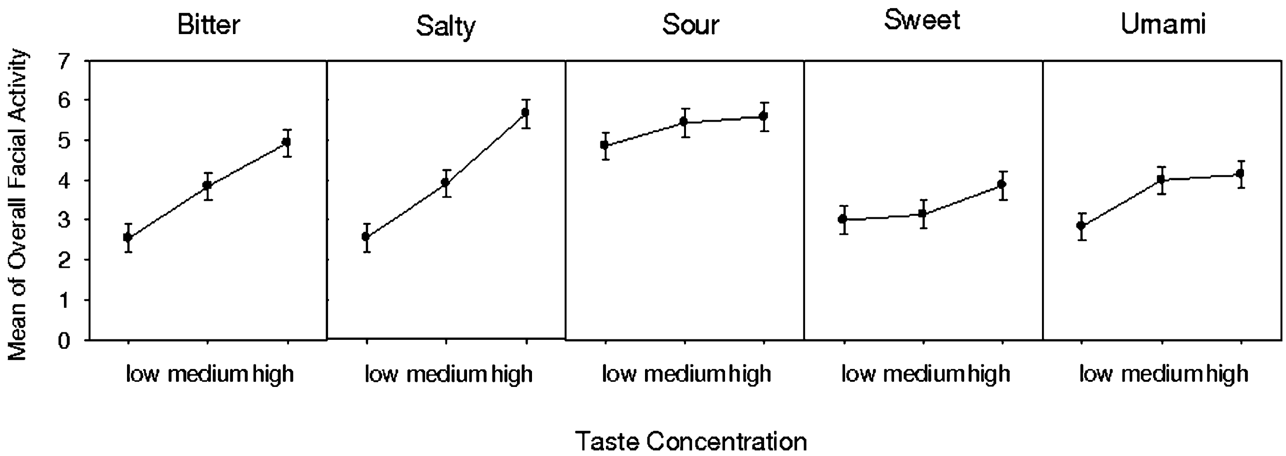

Figure 1 Overall facial activity (means ± SEM) for bitter, salty, sour, sweet, and umami tastes differing in concentration (low, medium, and high) (N = 28).

to high (P = 0.002). An increase of taste concentration of sour and sweet tastes did not affect overall facial activity (Ps > 0 .05).

In addition, the observation period affected overall facial activity, $F_{1,27}$ = 79.17, P < 0.001, and indicated that more facial reactions were displayed after swallowing (M = 5.38, standard error of the mean [SEM] = 0.13) than before swallowing (M = 2.67, SEM = 0.13).

Odors

In line with our hypothesis, overall facial activity differed across odors (main effect of odor $F_{5,130}$ = 7.30, P < 0.001) with adults displaying more facial reactions in response to unpleasant odors (garlic and fish) than to pleasant odors (banana and cinnamon) (Figure 2).

Post hoc tests indicated that fish and garlic elicited a higher overall facial activity when compared with banana (P = 0.003, P = 0.020) and cinnamon (P = 0.001, P = 0.011). Fish also elicited a higher overall facial activity than coffee (P < 0.05).

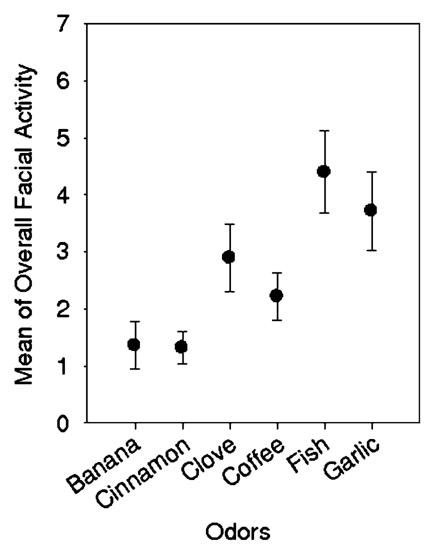

Figure 2 Overall facial activity (means ± SEM) for banana, cinnamon, clove, coffee, fish, and garlic odors (N = 28).

Discussion

The present experiment indicated: 1) adults' facial reactions in response to tastes and odors mostly correspond to those observed in newborns, except for smiling to unpleasant tastes. 2) The frequency of adults showing negative reactions to unpleasant tastes increased with taste concentration similar to newborns, which was not the case for positive reactions to pleasant tastes. 3) Unpleasant odors, but not unpleasant tastes, elicited a greater overall facial activity than pleasant odors, and higher concentrations of bitter, salty and umami tastes, but not of sour and sweet tastes, elicited a greater overall facial activity.

1) Adults displayed specific taste- and odor-elicited facial reactions, which are mostly comparable with those observed in newborns (Steiner 1973, 1977, 1979, 1987; Rosenstein and Oster 1988; Steiner et al. 2001) and adults (Perl et al. 1992; Steiner et al. 1993; Greimel et al. 2006). Adults' facial reactions to unpleasant tastes (bitter, salty, and sour) and odors (fish, garlic, and clove) were characterized by negative facial displays of brow lower (AU 4), upper lip raise (AU 10), and lip corner depress (AU 15). Corresponding with our adult sample, upper lip raise and brow lower have been found to be frequent reactions to unpleasant tastes and odors in newborns (Steiner 1973; Rosenstein and Oster 1988; Soussignan et al. 1997) and in adults (Saku and Ellgring 1992; Steiner et al. 1993; Greimel et al. 2006). Upper lip raise has often been associated with the prototypical disgust reaction (Darwin 1872; Izard 1971; Ekman and Friesen 1975; Vrana 1993; Rozin et al. 1994, 2000). Brow lower characterizes disgust expressions to unpleasant tastes as well (Horio 2003); it is, however, also associated with other negative emotions, for example, anger, or with cognitively demanding

tasks. Lip corner depress (AU 15), which has been related to disgust by Darwin (1872) distinguished unpleasant from pleasant stimuli in our adult sample, which corresponds to the findings by Steiner (1973) and Steiner et al. (1993). In sum, the negative facial reactions in response to unpleasant tastes and odors in adults can be regarded as avoidance reactions.

In contrast to newborns, adults displayed Duchenne smiles including cheek raise (AU 6) and lip corner pull (AU 12) to the unpleasant tastes (bitter, salty, and sour). This is consistent with the finding of smiles in adults in response to the bitter taste (Greimel et al. 2006). The facial display of smiling, which seems incompatible with the unpleasant subjective taste experience might serve social communicative functions (Ekman and Friesen 1982; Fridlund 1991). According to Ekman (1972), participants might have been embarrassed by their grimace or surprised by the highly aversive taste and thus masking their negative facial expressions by a display rule such as smiling. Likewise, according to the behavioral ecological view of Fridlund (1991), who argued that facial displays are social signals driven by social intents serving exclusively to communicate social motives, smiling serves as a signal, for example, to indicate that one can manage the aversive gustatory stimulus. Moreover, smiling may serve as a self-regulatory coping strategy, which enables individuals to distract themselves from threat. This was recently discussed as explanation of smiles during painful stimulation (Kunz et al. 2009) and negative emotional events (Keltner and Bonanno 1997; Ansfield 2007). In contrast, unpleasant odors have not elicited smiles, presumably due to the less invasive and less aversive nature of odors when compared with tastes. Taken together, facial responses are dependent from learning as indicated by smiles in response to unpleasant tastes, which may serve communicative or self-regulatory functions.

The comparable frequency of gapes and head shakes to unpleasant and pleasant tastes might also be affected by display rules, for example, the facial suppression of these components in response to unpleasant tastes. In contrast to our adult sample, gapes were found in response to the bitter, sour, and salty taste and head shakes in response to the bitter taste in newborns (Steiner et al. 2001) and children (Zeinstra et al. 2009). According to the definition of the gape as large amplitude lowering of the jaw accompanied by other facial reactions (Steiner et al. 2001), the gape corresponds to Action Unit 26 (jaw drop) and 27 (mouth stretch). Jaw drop was a frequently observed facial reaction in this adult sample and can be described as a frequently aftertaste movement after swallowing. In contrast, mouth stretch had never been observed in our sample. Because the intensity of facial reactions has not been investigated in this study, all jaw drops are referred to as gapes. Further studies could attend to the intensity of facial reactions, for example, gapes, as a larger mouth opening might accompany a more aversive taste.

Given the evidence that social context moderates facial expressiveness, it is necessary to address the question of whether gusto- and olfactofacial responses would be similar when obtained unobtrusively. Four studies directly tested the effect of social presence on taste-elicited (Brightman et al. 1975) and odor-elicited facial responses (Kraut 1982; Jäncke and Kaufmann 1994; Soussignan and Schaal 1996). These studies either supported Ekmans' neurocultural view from 1972 (Kraut 1982; Soussignan and Schaal 1996) or Fridlunds' behavioral ecological view from 1991 (Brightman et al. 1975; Jäncke and Kaufmann 1994). Our study, however, was not designed to examine whether facial responsiveness to tastes and odors varies as a function of social context. The method to study facial behavior here, that is, to record videos when the experimenter is present, was selected in order to stick to the method used in the existing studies. According to Fridlund (1991), facial reactions should also occur in solitary situations because people act as if other people are present (implicit friend) even when physically alone. In general, we assume that the social context has a minor impact on the core facial reactions elicited by tastes and odors, whereas the social smile to unpleasant tastes might be absent or less frequent when feeling as being alone. These assumptions, however, have to be proven in a further study on the influence of social presence on facial reactions.

Unexpectedly, the pleasant sweet taste and pleasant odors (banana, cinnamon, and coffee) evoked less positive facial displays. The sweet taste elicited lip suck (AU 28), which corresponds to findings in newborns (Steiner 1973, 1977, 1979) and in adults (Greimel et al. 2006). The low positive facial responsiveness to the sweet taste might be due to the fact that sugar diluted in water is simply not as pleasant as sugar containing foods for adults. In further studies, it would be more ecological valid to use real food stimuli instead of taste solutions. Likewise, adults have expressed few smiles to pleasant odors, which is consistent to findings in newborns (Soussignan et al. 1997). It might also be argued that the pleasantness of tastes and odors is more likely to be expressed through a general facial relaxation that indicates satisfaction rather than through various positive facial displays. In sum, adults' taste- and odor-elicited facial reactions mostly correspond to those observed in newborns in particular for the unpleasant stimuli. Thus, it appears that the gustofacial and olfactofacial responses remain quite stable over the life span, confirming Steiner's (1977) proposed reflex-like facial responses to tastes and odors. Moreover, smiling is exclusively displayed by adults to unpleasant tastes, which demonstrate influences of learning.

2) It has been shown that the frequency of adults displaying negative and positive facial reactions increased with increasing concentration of unpleasant tastes (bitter, salty, and umami). More adults displayed negative facial reactions such as upper lip raise (AU 10), brow lower (AU 4), and gapes (AU 26). With increasing bitterness and

saltiness, more adults displayed lip corner depress (AU 15), that is, the only negative facial reaction in adults, which was also observed in newborns with increasing bitterness (Ganchrow et al. 1983). The negative displays indicate that unpleasant tastes become more aversive with increasing concentration, which is consistent with the decreased pleasantness of these tastes. In addition, more adults have expressed the positive facial reaction of smiling (AU 6 + 12) with increasing bitterness and saltiness, which might serve social communicative (Ekman and Friesen 1982; Fridlund 1991) or self-regulatory functions (Ansfield 2007; Kunz et al. 2009).

Unexpectedly, with increasing sweetness, adults displayed the negative facial reaction of brow lower (AU 4) instead of positive facial reactions as observed in newborns (Ganchrow et al. 1983). Because pleasantness of the sweet taste remains stable with increasing concentration, brow lower may indicate a negative display associated with the high taste concentration rather than with taste pleasantness. The frequencies of adults showing specific facial reactions are unaffected by increasing sourness. This might be due to the fact that the sour taste elicits reflex-like facial responses such as lip tight (AU 23) and lip pucker (AU 18) based on its sensory properties, which may be independent of taste concentration.

3) Unpleasant odors (fish, garlic), but not unpleasant tastes, elicited more facial reactions than pleasant odors (banana, cinnamon) in our adult sample, which was not observed in newborns (Soussignan et al. 1997). Moreover, the sour taste has been found to elicit more facial reactions than the other tastes, which is inconsistent to the finding by Zeinstra et al. (2009). Facial reactions to the sour taste are strongly influenced in our sample by the high taste concentrations as indicated by subjective ratings. Furthermore, even when comparing taste qualities within each taste concentration, unpleasant tastes (except for the sour taste) did not elicit more facial reactions than pleasant tastes. Therefore, it can be concluded that overall facial activity in response to tastes seems to be much less affected by valence, whereas overall facial activity in response to odors is strongly affected by valence.

Moreover, adults' overall facial activity increased with increasing concentration of bitter, salty, and umami tastes but not of sour and sweet tastes. This reflects the subjective increase in experienced intensity and unpleasantness with increasing concentration of these tastes. It is, however, not clear, whether more intense and more pleasant tastes may also elicit more facial reactions in adults. In newborns, with increasing sweetness, more positive facial reactions were observed (Ganchrow et al. 1983), whereas positive facial reactions were not associated with higher subjective pleasantness in 5- to 13 year-old children (Zeinstra et al. 2009). Due to a general lower complexity of facial reactions to positive stimuli, we would expect no greater facial activity (Looy and Weingarten 1992; Greimel et al. 2006). Adults' overall facial activity is not enhanced with increasing concentration of sour and sweet tastes despite being rated as more intense but as equally pleasant with increasing concentration. Thus overall facial activity seems to be affected by pleasantness but not by intensity of tastes.

Conclusions

This is the first study that assessed facial reactions to both tastes and odors in healthy adults by using the FACS. Overall, adults' reactions mostly correspond to those observed in newborns supporting that taste- and odor-elicited facial displays remain quite stable over the life span. It could be shown, which facial reactions in response to tastes and odors are prototypically displayed by adults. This information might be used in consumer research that has recently begun to focus on facial reactions as a tool studying food pleasantness. It became evident that pure sugar solutions do not elicit positive facial displays. Prior individual food experiences and food-related attitudes might change the preference for sweet. Our further aim is to study facial behavior in patients with eating disorders, who might display aversive reactions to the sweet taste by anticipated weight gain.

The finding that adults smiled to unpleasant tastes can be either regarded as a display rule or as a social signal to others. Moreover, this is the first study indicating that taste concentration affects the frequency of adults showing facial reactions as it does in newborns. Future studies should aim to use equi-intense concentrations to examine the role of taste concentration on differential facial reactions. This study focused on the frequency of facial reactions (e.g., Steiner 1977; Soussignan et al. 1997) rather than on facial configurations (Rosenstein and Oster 1988). In future studies dynamic aspects of facial behavior should be addressed in order to investigate whether high taste concentrations elicit more rapid and longer lasting facial reactions compared with low concentrations or at which time negative and positive facial reactions occur during ambivalent responses. For that purpose, it may also be helpful to use facial electromyography (e.g., Vrana 1993), in addition to FACS.

Funding

This work was supported by the German Research Foundation (DFG) within the Research Training Group Emotions RTG 1253/1.

References

Ansfield ME. 2007. Smiling when distressed: when a smile is a frown turned upside down. Pers Soc Psychol Bull. 33:763–775.

Bartoshuk LM, Duffy VB, Miller IJ. 1994. PTC/PROP tasting: anatomy psychophysics and sex effects. Physiol Behav. 56:1165–1171.

Birbaumer N, Schmidt RF. 1999. Biologische psychologie. Berlin (Germany): Springer-Verlag.

Brightman VJ, Segal A, Werther P, Steiner JE. 1975. Ethologic study of facial expressions in response to taste stimuli. J Dent Res. 54:1–141.

Cowart BJ. 1981. Development of taste perception in humans: sensitivity and preference throughout the life span. Psychol Bull. 90:43–73.

Dallenbach JW, Dallenbach KM. 1943. The effects of bitter adaptation on sensitivity to the other taste qualities. Am J Physiol. 56:21–31.

Darwin C. 1872. The expression of the emotions in man and animals. London: John Murray.

Doty RL, Shah M. 2008. Taste and smell. In: Marshall MH, Janette BB, editors. Encyclopedia of infant and early childhood development. Oxford: Academic Press. p. 299–308.

Drewnowski A, Henderson SA, Shore AB, Barratt-Fornell A. 1997. Nontasters, tasters and supertasters of 6-n-propylthiouracil (PROP) and hedonic response to sweet. Physiol Behav. 62:649–655.

Ekman P. 1972. Universal and cultural differences in facial expressions of emotion. In: Cole J, editor. Nebraska symposium on motivation 1971. Lincoln (NE): University of Nebraska Press. p. 207–283.

Ekman P, Friesen WV. 1975. Unmasking the face: a guide to recognizing emotions from facial clues. Oxford: Prentice Hall.

Ekman P, Friesen WV. 1982. Felt, false and miserable smile. J Nonverbal Behav. 6:238–252.

Ekman P, Friesen WV. 1978. Facial Action Coding System: a technique for the measurement of facial movement. Palo Alto (CA): Consulting Psychologists Press.

Ellgring H. 1989. Nonverbal communication in depression. Cambridge: Cambridge University Press.

Fridlund AJ. 1991. Evolution and facial action in reflex social motive and paralanguage. Biol Psychol. 32:3–100.

Ganchrow JR, Mennella JA. 2003. The ontogeny of human flavor perception. In: Doty RL, editor. Handbook of olfaction and gustation. 2nd ed. New York: Marcel Dekker. p. 823–846.

Ganchrow JR, Steiner JE, Daher M. 1983. Neonatal facial expressions in response to different qualities and intensities of gustatory stimuli. Infant Behav Dev. 6:189–200.

Greimel E, Macht M, Krumhuber E, Ellgring H. 2006. Facial and affective reactions to tastes and their modulation by sadness and joy. Physiol Behav. 89:261–269.

Heller O. 1985. Hörfeldaudiometrie mit dem Verfahren der Kategorienunterteilung (KU). Psychol Beitrage. 27:478–493.

Hodson NA, Linden RWA. 2006. The effect of monosodium glutamate on parotid salivary flow in comparison to the response to representatives of the other four basic tastes. Physiol Behav. 89: 711–717.

Horio T. 2003. EMG activities of facial and chewing muscles of human adults in response to taste stimuli. Percept Mot Skills. 97:289–298.

Izard CE. 1971. The face of emotion. East Norwalk (CT): Appleton-Century-Crofts.

Jäncke L, Kaufmann N. 1994. Facial EMG responses to odors in solitude and with an audience. Chem Senses. 19:99–111.

Keltner D, Bonanno GA. 1997. A study of laughter and dissociation: distinct correlates of laughter and smiling during bereavement. J Pers Soc Psychol. 73:687–702.

Kobal G, Hummel T, Sekinger B, Barz S, Roscher S, Wolf S. 1996. "Sniffin' sticks": screening of olfactory performance. Rhinology. 34: 222–226.

Kraut RE. 1982. Social presence, facial feedback, and emotion. J Pers Soc Psychol. 42:853–863.

Kunz M, Prkachin K, Lautenbacher S. 2009. The smile of pain. Pain. 145:273–275.

Leach EJ, Noble AC. 1986. Comparison of bitterness of caffeine and quinine by a time intensity procedure. Chem Senses. 11:339–345.

Looy H, Weingarten HP. 1992. Facial expressions and genetic sensitivity to 6-n-propylthiouracil predict hedonic response to sweet. Physiol Behav. 52:75–82.

Lugaz O, Pillias A-M, Faurion A. 2002. A new specific Ageusia: some humans cannot taste L-glutamate. Chem Senses. 27:105–115.

Oster H. 2004. The repertoire of infant facial expressions: an ontogenic perspective. In: Nadel J, Muir D, editors. Emotional development: recent research advances. New York: Oxford University Press. p. 261–292.

Peiper A. 1963. Cerebral function in infancy and childhood. New York: Consultants Bureau.

Perl E, Shay U, Hamburger R, Steiner JE. 1992. Taste- and odor reactivity in elderly demented patients. Chem Senses. 17:779–794.

Rinn WE. 1991. Neuropsychology of facial expression. In: Feldman RS, Rimé B, editors. Fundamentals of nonverbal behavior. Cambridge (MA): Cambridge University Press. p. 3–30.

Rosenstein D, Oster H. 1988. Differential facial responses to four basic tastes in newborns. Child Dev. 59:1555–1568.

Rosenstein D, Oster H. 1997. Differential facial responses to four basic tastes in newborns. In: Ekman P, Rosenberg EL, editors. What the face reveals: basic and applied studies of spontaneous expression using the Facial Action Coding System (FACS). Oxford: Oxford University Press. p. 302–330.

Rousmans S, Robin O, Dittmar A, Vernet-Maury E. 2000. Autonomic nervous system responses associated with primary tastes. Chem Senses. 25: 709–718.

Rozin P, Haidt J, McCauley CR. 2000. Disgust. In: Lewis M, Haviland JM, editors. Handbook of emotions. New York: Guilford Press. p. 637–653.

Rozin P, Lowery L, Ebert R. 1994. Varieties of disgust faces and the structure of disgust. J Pers Soc Psychol. 66:870–881.

Saku M, Ellgring H. 1992. Emotional reactions to odours in Parkinson's disease: a clinical application of ethological methods. J Ethol. 10:47–52.

Schaal B, Marlier L, Soussignan R. 2000. Human foetuses learn odours from their pregnant mother's diet. Chem Senses. 25:729–737.

Schaal B, Soussignan R, Marlier L. 2002. Olfactory cognition at the start of life: the perinatal shaping of selective odor responsiveness. In: Rouby C, Schaal B, Dubois D, Gervais R, Holley A, editors. Olfaction taste and cognition. Cambridge: Cambridge University Press. p. 421–440.

Soussignan R, Schaal B. 1996. Children's facial responsiveness to odors: influences of hedonic valence of odor, gender, age, and social presence. Dev Psychol. 32:367–379.

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.

Steiner JE. 1973. The gusto-facial response observation on normal and anencephalic newborn infants. In: Bosma JF, editor. The fourth symposium on oral sensation and perception. Washington (DC): US Government Printing Office. p. 254–278.

Steiner JE. 1977. Facial expressions of the neonate infant indicating the hedonics of food-related chemical stimuli. In: Weiffenbach JM, editor. Taste and development—the genesis of sweet preference. Bethesda (MD): National Institutes of Health. p. 173–189.

Steiner JE. 1979. Human facial expressions in response to taste and smell stimulation. Adv Child Dev Behav. 13:257–295.

Steiner JE. 1987. What the neonate can tell us about umami. In: Kawamura Y, Kare MR, editors. Umami a basic taste. New York: Marcel Dekker. p. 97–124.

Steiner JE, Glaser D, Hawilo ME, Berridge KC. 2001. Comparative expression of hedonic impact: affective reactions to taste by human infants and other primates. Neurosci Biobehav Rev. 25:53–74.

Steiner JE, Lidar-Lifschitz D, Perl E. 1993. Taste and odor: reactivity in depressive disorders a multidisciplinary approach. Percept Mot Skills. 77:1331–1346.

Vrana SR. 1993. The psychophysiology of disgust: differentiating negative emotional contexts with facial EMG. Psychophysiology. 30:279–286.

Zeinstra GG, Koelen MA, Colindres D, Kok FJ, de Graaf C. 2009. Facial expressions in school-aged children are a good indicator of dislikes,' but not of likes'. Food Qual Pref. 20:620–624.