ELSEVIER

Available online at www.sciencedirect.com

SCIENCE DIRECT®

Behavioural Brain Research 154 (2004) 261–271

BEHAVIOURAL BRAIN RESEARCH

www.elsevier.com/locate/bbr

Research report

Facial responses to four basic tastes in newborn rhesus macaques (*Macaca mulatta*) and chimpanzees (*Pan troglodytes*)

Ari Ueno[a,*], Yoshikazu Ueno[b], Masaki Tomonaga[c]

[a] *Section of Social Behavior, Primate Research Institute, Kyoto University, Kanrin 41, Inuyama, Aichi 484-8506, Japan*
[b] *Center for Human Evolution Modeling Research, Primate Research Institute, Kyoto University, Kanrin 41, Inuyama, Aichi 484-8506, Japan*
[c] *Section of Language and Intelligence, Primate Research Institute, Kyoto University, Kanrin 41, Inuyama, Aichi 484-8506, Japan*

Received 11 December 2003; received in revised form 16 February 2004; accepted 18 February 2004

Abstract

Newborn humans are known to show specific facial expressions in response to various kinds of taste stimuli and are presumed to be able to discriminate those kinds of tastes from just after birth. As the closest relatives to humans, the taste reactivity (threshold, preference and taste-elicited facial expression) of non-human primates has long been of great interest. To date, however, there have been few investigations in newborn non-human primates. In the present study, we investigated the facial expressions elicited in response to four basic taste stimuli, sweet, salty, sour and bitter, in the newborns of two non-human primate species, rhesus macaques and chimpanzees. The taste-elicited facial expressions were compared among the kinds of taste stimuli and between the two species. Rhesus macaques of less than 7 days old showed different patterns of facial expressions for water/sweet than for bitter, and chimpanzees less than 30 days old did so for sweet and bitter. The differences between these two species were evident in the presence and absence of certain facial expressions and the emerging patterns of certain components for each stimulus. In particular, chimpanzee response patterns to the bitter stimulus resembled to those of humans rather than rhesus macaques. Overall, rhesus macaques and chimpanzees responded differently to the same kinds of tastes, presumably reflecting differences in their evolutionary backgrounds.

Keywords: Four basic tastes; Taste-elicited facial expressions; Newborns; Rhesus macaques; Chimpanzees

1. Introduction

In humans, the newborn is known to be able discriminate the four basic taste stimuli (sweet, salty, sour and bitter), and is thus supposed to perceive them differently (for review, [5,12]). Several studies have reported that newborns showed specific patterns of facial expressions for sweet, sour and bitter solutions from just after birth (e.g. [19,24]). Newborns typically show relaxed and positive responses for sweet and negative responses for bitter. Such taste-elicited facial expression in newborns can work as communicative signals indicating their attitudes/motivation toward tastes [19]. These are thought to be fundamentally controlled by the brainstem but also partly by the forebrain [2,23,24].

As one of the reflections of affective impacts, facial expressions have long attracted our attention as Darwin duly noted [4]. It has been argued that certain taste-elicited facial expressions are not merely reflexes to stimuli but reflect instead the affective impact of stimuli [2,27]. When taste stimuli are infused into the mouth, human newborns are considered to express positive affective (so called hedonic) responses to sweet and negative affective (aversive) responses to bitter. Affective impact deriving from food tastes is one of the essential elements which contributes to the acquisition of food selection (e.g. [7,20]). The positive affective impact of a food taste can enhance its acceptance, working as a sensory reward. Conversely, the negative affective impact of a food taste can lead food rejection, working as an aversive stimulus. Exploring facial expressions, namely affective responses, to taste stimuli seems to be a fundamental component to comprehending food selection habits in humans and also in other animal species.

To shed light on the evolutionary foundation of taste-elicited facial expressions seen in humans, non-human primates have also been tested [25–27]. In total, 67 individuals of 13 non-human primate species (all adults or juveniles except for three individuals of *Callithrix jacchus*

---

[*] Corresponding author. Tel.: +81-568-63-0546; fax: +81-568-63-0564.
E-mail address: ueno@pri.kyoto-u.ac.jp (A. Ueno).

0166-4328/$ – see front matter © 2004 Elsevier B.V. All rights reserved.
doi:10.1016/j.bbr.2004.02.014

and *Saguinus oedipus* that were several-days-old) have been tested and they showed differential facial expressions for sweet and bitter stimuli. Comparing the taste-elicited facial expressions across primate species, including humans, Steiner et al. [27] suggested the existence of phylogenic differences in the kinds of facial expressions across primate species. Furthermore, they concluded that certain facial expressions observed in non-human primates reflected the affective impact of taste stimuli rather than being merely reflexive responses, and this is also the case in humans. As they noted, however, it was not certain whether their results were entirely species specific or whether reactions reflected the precedent food experience of each subject, since the majority of subjects were adults that differed in their captive environment and food experiences. To determine species specific taste-elicited facial expressions, investigations in newborns are essential.

In the present study, we investigate the facial expressions of newborns elicited in response to four basic taste stimuli (sweet, salty, sour and bitter) in two non-human primate species, the rhesus macaque (*Macaca mulatta*) and chimpanzee (*Pan troglodytes*). Comparing the facial expressions elicited by the different kinds of taste stimuli in each species, we discuss the following three points. (1) Do they perceive the different kinds of taste stimuli from an early stage of life? (2) Do they innately show different kinds of facial expressions, presumably constrained by phylogeny, as reported in adults [27]? (3) Do the two species differ in the emerging patterns of facial expressions, apparently contributing to their own food selection habits?

2. Materials and methods

2.1. Subjects

Three rhesus macaques within 3–7 days of birth, and four chimpanzees within 0–30 days of birth were tested at the Primate Research Institute, Kyoto University (Table 1). All rhesus macaques and three of the four chimpanzees (C1, C3 and C4) were nursed by their biological mothers and, except for C1, had been fed with maternal milk until tests were conducted. One chimpanzee, C1, was tested just after birth, before its first post-natal feeding. The chimpanzee, C2, was nursed by a human care-taker and fed with artificial milk for human babies eight times a day at approximately 3 h intervals. Thus, all subjects, except for C2, had tasted only maternal milk or had never experienced any tastes before the present tests postnatally. Although C2 also experienced the taste reactivity test within a day of birth, she was hypothermic during the testing and showed few facial expressions in response to any kind of stimuli due to drowsiness. Thus, we excluded that data from analysis and C2 was re-tested at 5 days old by which time, apart from the initial test, she had only tasted artificial milk.

Table 1
Subject of the present study

	Sex	Date of birth	Study period (age in days)	Weight (g) in the study period
Rhesus macaques				
R1	Female	24 April 2001	4	466
R2	Female	11 June 2001	7	522
R3	Female	25 June 2001	7	550
Chimpanzees				
C1	Female	19 June 2000	0	1640
C2	Female	15 May 2003	5	1570
C3	Female	9 August 2000	12–15	1810[a]
C4	Male	24 April 2000	24–30	2360[b]

[a] The body weight of subject C3 was measured on day 1, and was 2360 g at 33 days.

[b] The body weight of subject C4 was measured at day 25.

All rhesus macaques and two chimpanzees (C3 and C4) were tested at least 5 min after suckling, because the intervals between the tests and the precedent suckling could not be controlled. The chimpanzee, C2 (which was nursed by humans), however, was tested 3 h after its last suckling. Care and use of rhesus monkeys and chimpanzees adhered to the "Guide for the Care and Use of Laboratory Primates of the Primate Research Institute" (2002).

2.2. Stimuli

Sweet, salty, sour and bitter tastes were prepared in liquid solution diluted with distilled water into the following concentrations: 0.73 M sucrose, 0.73 M NaCl, 0.12 M citric acid, and 0.003 M quinine HCl. Each concentration was determined as being strong enough to elicit a newborn's facial expressions following the example of a previous study on human newborns [19]. Each kind of taste stimulus was tested once for each subject. Other than these four tastes, we also used distilled water as a control stimulus. Each stimulus of 0.2 ml was infused by syringe into the subject's mouth.

2.3. Procedure

All three rhesus macaques and one chimpanzee (C2) were tested while being held by a human experimenter and sitting upright. The other chimpanzees (C1, C3 and C4) were tested while being held by their anesthetized/awakening mothers, lying on their backs. Due to these differences in experimental conditions, some parts of the experimental procedure differed between the subjects as outlined below.

For the three rhesus macaques and the chimpanzees C1 and C2, the tests for all stimuli were conducted sequentially with 30 s ∼5 min intervals between stimuli. The testing order of taste stimuli was: control stimulus, then sweet, salty, sour, and finally bitter. Having observed any responses, before the presentation of the next stimulus, 0.2 ml of distilled water was infused into each subject's mouth to rinse it. For C3 and C4, the tests had to be performed as part of a series of experiments on behavioral and cognitive development [8,11,13–15,17,22,28]. Only one kind of taste stimulus was tested a day, and the tests for all taste stimuli were completed within 4 days for C3 and 7 days for C4. In each test, the control stimulus of 0.2 ml of distilled water was first infused, followed by one kind of taste stimulus. The taste stimuli were tested in the order of sweet, bitter, salty and sour for C3, and sweet, salty, sour and bitter for C4. For all subjects, facial expressions were recorded for 30 s immediately after the infusion of a stimulus with a hand-held video camera (SONY, CCD-MC100).

2.4. *Data analysis*

From the video records, we described all movements of the middle (cheek and nose) and upper (eyes and forehead) parts of the subject's face, and around the mouth (upper and lower lips, lip corners, upper and lower jaws). Based on the manner of coding and categorization of movement in a previous study [27], we classified the observed movements into 16 components. The components, which were apparently identical to what Steiner et al. [27] had classified, were labeled in the same manner.

Viewing videotapes at frame-by-frame speed, and occasionally at actual speed, an observer scored the components listed in Table 2. A component observed once in a trial was awarded one point. To reflect the duration and frequency of an observed component into the score, one more point was added to each component whenever it lasted for more than 2 s or was repeated at more than 2 s intervals [2,3,27]. Thus, the maximum attainable score for a component was 15 in a trial, which was obtained only when it lasted throughout the 30 s of observation. A component repeated within 2 s was considered a part of the same series of the component, unless the series was interrupted by other components.

We obtained 35 test trials in total (1 trial × 5 kinds of stimuli × 7 individuals). In each of C3 and C4 trials, an infusion of control stimulus was randomly extracted for analysis. One observer evaluated all 35 trials. To check for inter-observer reliability, another observer, familiar with rhesus macaques and chimpanzees, also evaluated 14% of the data (five trials) independently without knowing the stimulus used in each trial. The inter-observer reliability was $k = 0.80$ (Kappa coefficient) and $r_s = +0.73$ (Spearman rank correlation, $N = 16$ components × 5 trials = 80).

To assess the similarity among the components by means of their emergence, we performed hierarchical cluster analysis of the response profiles for each species, using the statistical package STATISTICA, 99 edition. Pearson correlation coefficients among the components were calculated across the trials, on the basis of respective scores. Inter-cluster distance was measured using those coefficients and then the cluster analysis was processed according to the Ward method.

3. Results

In rhesus macaques, 3 (Eye squinch, ES; Nose wrinkle, NW; Lip pursing, LP) of the 16 components were never observed irrespective of the stimulus (Table 3). In chimpanzees, 5 (Gape, G; Frown, Fr; Tongue exposure, TE; Forehead wrinkle, FW; Lateral tongue protrusion, lTP) components were never observed. In the following, only those components observed at least once within a species were analyzed (thus, 13 components for rhesus macaques and 11 components for chimpanzees).

3.1. *Taste-elicited facial expressions in newborn rhesus macaques*

The average scores of each component for each stimulus are presented in Fig. 1. In rhesus macaques (Fig. 1a), the scores of only one component, 'Tongue exposure (TE)'

Table 2
Definition of the components evaluated in this study

Components	Definition
Eye squinch (ES)*	Narrow or closed eyes with wrinkling around the eyes
Nose wrinkle (NW)*	Having horizontal wrinkles across the nose
Frown (Fr)*	Pulling lip corners downwards without opening mouth
Gape (G)*	Pulling lip corners horizontally or downwards with open mouth with jaw lowered
Grimace (Gr)*	Pulling lip corners horizontally or upwards with tense outward lip retraction
Corner elevation of lips (CE)*	Pulling lip corners upwards without retracting the lips outwards
Tongue protrusion (TP)*	Putting tongue between lips along the midline and pulling it back inside mouth within a second
Lip pursing (LP)*	Pursing closed lips with wrinkling around them for more than a second
Moving closed mouth (MM)*	Moving closed mouth and lips up and down or from side to side
Forehead wrinkle (FW)	Horizontal wrinkles on middle of the forehead
Lateral tongue protrusion (lTP)	Extending the tongue sideways along the lateral part of lips
Mouth open (MO)	Open mouth for more than a second, without pulling lip corners or retracting lips outwards
Mouth protrusion (MP)	Protruding open mouth forward for more than a second
Slightly open mouth (SO)	Opening mouth without pulling lip corners or retracting lips outwards, then closing mouth within a second
Tongue exposure (TE)	Opening mouth with jaw lowered and tongue spread downward outside of the mouth
Tongue holding (TH)	Putting the tongue between the lips along the midline for more than a second

Note. Classification of the components followed the example of Steiner et al. [27]. Those components identical to what Steiner et al. [27] evaluated were labeled the same and are marked with an asterisk. Steiner et al. [27] classified: ES, NW, Fr, G and Gr as aversive; CE and TP as hedonic; LP as a sensory-based reflex; and MM as reflecting a neutral or evaluative response.

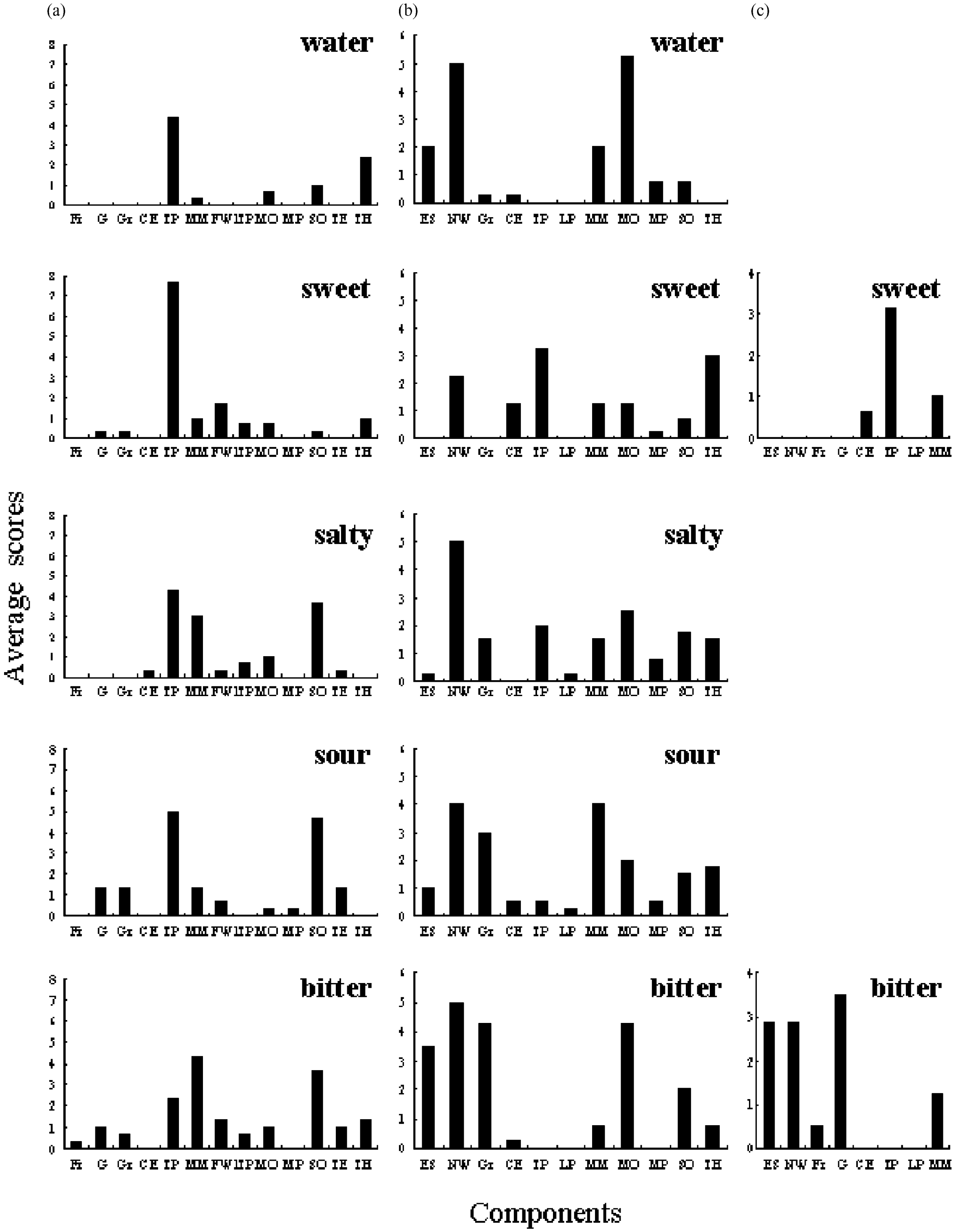

Fig. 1. The average scores of each component for each stimulus across subjects in each species. (a) Rhesus macaque; (b) chimpanzee; (c) human (quoted from Steiner et al. [27]).

Table 3
Emergence of the components in each individual

Components	Rhesus macaque			Chimpanzee			
	R1	R2	R3	C1	C2	C3	C4
Eye squinch (ES)				•		•	•
Nose wrinkle (NW)				•	•	•	•
Frown (Fr)	•						
Gape (G)	•	•	•				
Grimace (Gr)	•	•	•	•	•	•	•
Corner elevation of lips (CE)		•			•	•	•
Tongue protrusion (TP)	•	•	•	•	•	•	•
Lip pursing (LP)				•		•	
Moving closed mouth (MM)	•	•	•	•	•	•	•
Forehead wrinkle (FW)		•	•				
Lateral tongue protrusion (lTP)		•		•			
Mouth open (MO)	•	•	•	•	•	•	•
Mouth protrusion (MP)		•		•	•	•	
Slightly open mouth (SO)	•	•	•	•	•	•	•
Tongue exposure (TE)	•	•	•				
Tongue holding (TH)		•	•	•	•	•	•

Note. Irrespective of test stimulus, components observed at least once are marked with (•).

(Fig. 2a), differed significantly in response to the various stimuli (Friedman's χ^2 *r*-test: χ^2 $(4, N = 3) = 9.6$, $P < 0.05$). 'Tongue exposure (TE)' was observed in two of the three subjects for the bitter stimuli and in all three subjects for sour stimuli, but never for water or sweet stimuli (see Appendix A for the respective scores of each subject). When we consider a combination of the components elicited in response to each taste, 'Tongue protrusion (TP)' and 'Slightly open mouth (SO)' were elicited together in all individuals for salty, and 'Moving closed mouth (MM)' and 'Slightly open mouth (SO)' were elicited together for bitter stimuli. For other stimuli, only one component was elicited in all individuals: 'Tongue protrusion (TP)' for water and sweet, and 'Tongue exposure (TE)' for sour stimuli.

Cluster trees assessing the similarity among components are presented in Fig. 3. In rhesus macaques, hierarchical cluster analysis resulted in three major clusters, when divided at the points at which nod–nod distances are relatively long (Fig. 3a). Cluster I consisted of six components: Grimace, Gr; Gape, G; Frown, Fr; Lateral tongue protrusion, lTP; Slightly open mouth, SO; Moving closed mouth, MM. Cluster II consisted of four components: Tongue exposure, TE; Mouth protrusion, MP; Tongue protrusion, TP; Forehead wrinkle, FW. Cluster III consisted of three components: Corner elevation of lips, CE; Mouth open, MO; Tongue holding, TH.

The average scores of all components elicited in response to each kind of stimuli were calculated for each cluster, and in rhesus macaques (Fig. 4a), comparison of clustered components among the kinds of stimuli revealed that only in cluster I did the scores of each component differ significantly according to the kinds of stimuli (Friedman's χ^2 *r*-test: χ^2 $(4, N = 18) = 14.0$, $P < 0.01$). When we compared the scores of the components of cluster I over all possible dyads pairing two kinds of stimuli, the scores differed significantly from each other in the water-bitter and sweet-bitter dyads

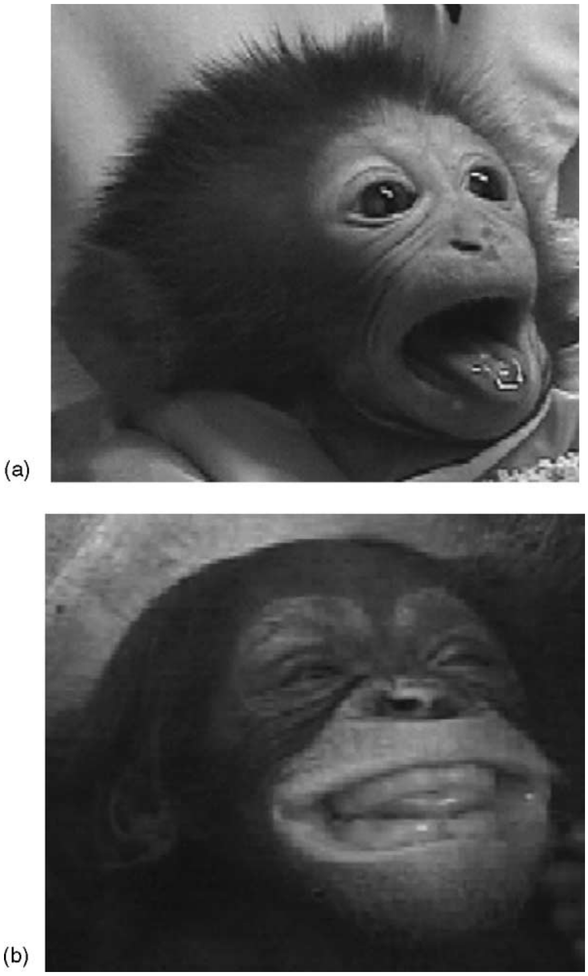

Fig. 2. Characteristic facial expressions in the respective species. (a) 'Tongue exposure' in a rhesus macaque for a sour stimulus, (b) 'Grimace,' 'Eye squinch' and 'Nose wrinkle' in a chimpanzee for a bitter stimulus.

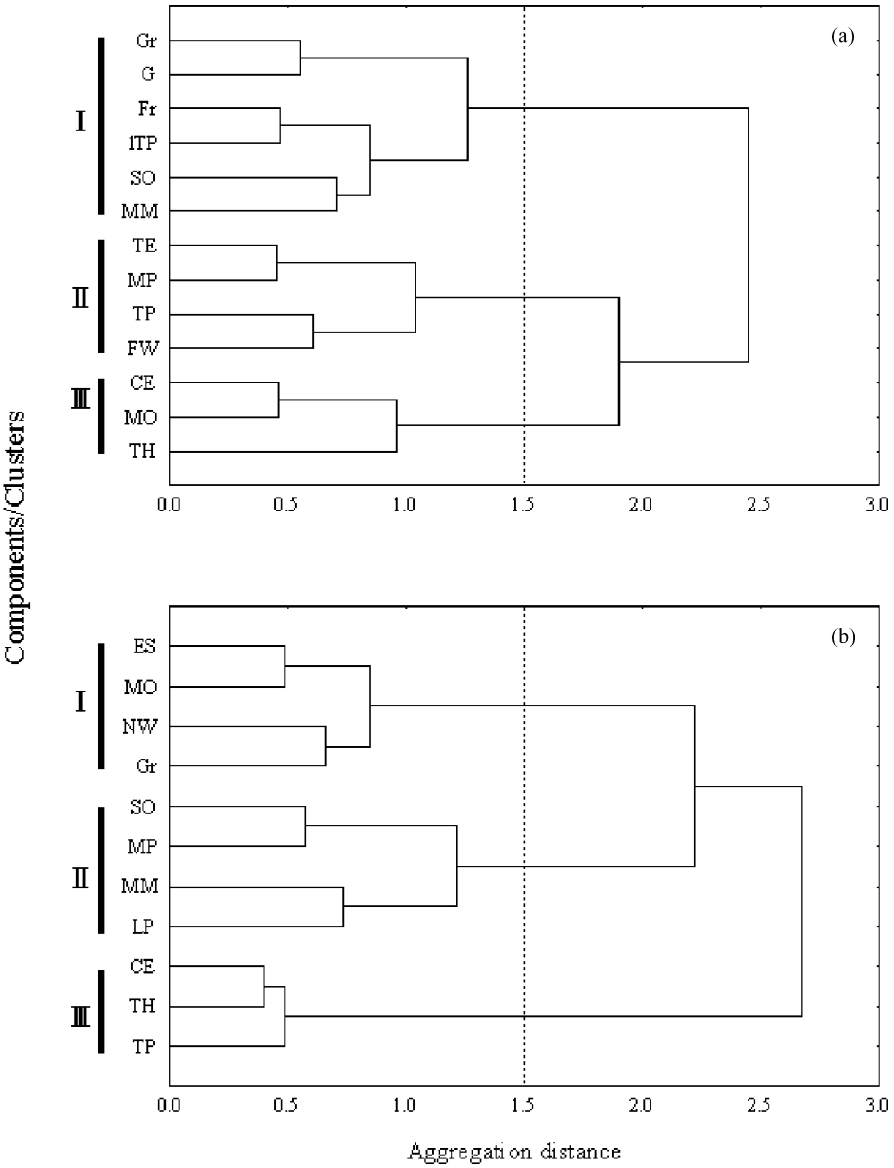

Fig. 3. Cluster trees of the components observed in (a) rhesus macaque or (b) chimpanzee. Inter-cluster distance was measured on the basis of the score of each component across trials. Three major clusters were recognizable in both rhesus macaque and chimpanzee analyses, when divided at the points at which nod–nod distances were relatively long.

(Wilcoxon signed rank test with Sequential Bonferroni correction: $P < 0.05$ for each dyad). Thus, the components allocated into cluster I occurred more often in response to bitter stimuli than to water or sweet stimuli. The scores of components allocated into clusters II and III did not differ according to the kinds of stimuli (Friedman's χ^2 r-test: χ^2 $(4, N = 12) = 6.0$, $P = 0.20$ for cluster II, χ^2 $(4, N = 9) = 1.6$, $P = 0.81$ for cluster III).

3.2. Taste-elicited facial expressions in newborn chimpanzees

The average scores of each component for each stimulus are presented in Fig. 1b. In chimpanzees, the scores of only one component, 'Grimace (Gr)' (Fig. 2b), differed significantly depending on the kinds of stimuli (Friedman's χ^2 r-test: χ^2 $(4, N = 4) = 12.1$, $P < 0.05$). 'Grimace (Gr)' was observed in response to sour stimuli in three of the four subjects and to bitter stimuli in all four subjects, but was never observed in response to sweet stimuli (see Appendix A for the respective scores of each subject). When we consider a combination of the components elicited in response to each taste, Moving closed mouth (MM)' and 'Mouth open (MO)' were elicited together in all individuals for salty, 'Nose wrinkle (NW)' and 'Mouth open (MO)' were elicited together for sour, and 'Nose wrinkle (NW),' 'Grimace (Gr)' and Mouth open (MO)' were elicited together for bitter stimuli. For other stimuli, only one component was elicited in all

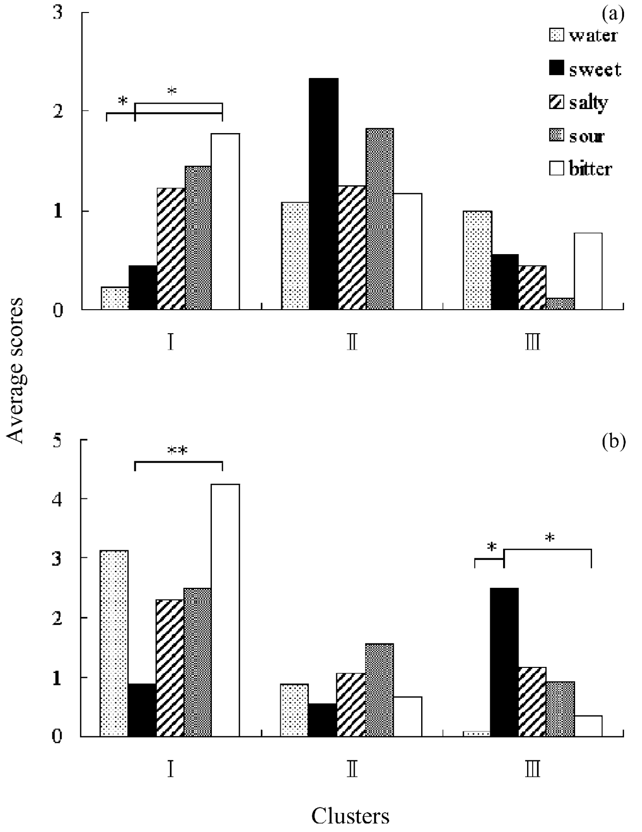

Fig. 4. The average scores of the clustered components for each stimulus in each species. (a) Rhesus macaque; (b) chimpanzee. $^{*}P < 0.05$, $^{**}P < 0.01$.

individuals: ‘Mouth open (MO),’ which was a component observed for all tastes tested, for water and sweet stimuli.

Hierarchical cluster analysis of the response profiles revealed three major clusters when divided at the points at which nod–nod distances were relatively long (Fig. 3b). Cluster I consisted of four components: Eye squinch, ES; Mouth open, MO; Nose wrinkle, NW; Grimace, Gr. Cluster II consisted of four components: Slightly open mouth, SO; Mouth protrusion, MP; Moving closed mouth, MM; Lip pursing, LP. Cluster III consisted of three components: Corner elevation of lips, CE; Tongue holding, TH; Tongue protrusion, TP.

The average scores of clustered components for each stimulus are presented in Fig. 4b. When we compared the scores of clustered components according to the kinds of stimuli, the scores differed significantly in clusters I and III (Friedman’s χ^2 r-test: χ^2 $(4, N = 16) = 22.7$, $P < 0.01$ for cluster I, χ^2 $(4, N = 12) = 12.6$, $P < 0.05$ for cluster III). We further compared the scores of components allocated into clusters I and III in all possible dyads pairing two kinds of stimuli. The scores significantly differed from each other in the sweet-bitter dyads for cluster I (Wilcoxon signed rank test with Sequential Bonferroni correction: $P < 0.01$), and in the sweet-water and sweet-bitter dyads for cluster III (Wilcoxon signed rank test with Sequential Bonferroni correction: $P < 0.05$ for each dyad). The components allocated into cluster I occurred more often in response to bitter than to sweet stimuli. The components allocated into cluster III occurred more often in response to sweet than to water or bitter stimuli. The scores of components clustered into II did not differ according to the kinds of stimuli (Friedman’s χ^2 r-test: χ^2 $(4, N = 16) = 6.0$, $P = 0.20$).

3.3. Comparison with human newborns

To highlight the comparison between newborn rhesus macaques and chimpanzees, data on human newborns ($N = 8$) were obtained from Steiner et al. [27] and analyzed in the same way as rhesus macaque and chimpanzee data. The appropriate data were available only for sweet and bitter stimuli (Fig. 1c).

In human newborns, ‘Frown (Fr),’ ‘Gape (G),’ ‘Eye squinch (ES)’ and ‘Nose wrinkle (NW)’ were often elicited in response to bitter stimuli but never to sweet. Conversely, ‘Corner elevation of lips (CE)’ and ‘Tongue protrusion (TP)’ were often elicited in response to sweet stimuli but not to bitter. In chimpanzee newborns, ‘Eye squinch (ES)’ was elicited in response to bitter stimuli but not to sweet. ‘Tongue protrusion (TP),’ which was elicited in response to sweet stimuli, never occurred for bitter stimuli. In newborns of rhesus macaque, ‘Frown (Fr)’ was elicited, albeit rarely, in response to bitter stimuli but never to sweet. ‘Tongue protrusion (TP),’ which was elicited in response to sweet stimuli, was also elicited to bitter.

4. Discussion

Considering the differences in taste-elicited facial expressions, both rhesus macaques and chimpanzees were assumed to perceive at least sweet and bitter stimuli differently from an early stage of life. However, the emerging patterns of facial expressions seemed to differ greatly between the two species. Chimpanzee newborns resembled to human newborns more than the newborns of rhesus macaque. In the following sections, we discuss our findings in detail, and provide possible explanations for why these species differences occurred.

4.1. Responses to taste stimuli in newborn rhesus macaques and chimpanzees

The majority of newborn rhesus macaques showed ‘Tongue exposure’ for bitter stimuli, but not one showed it for water or sweet stimuli. The emerging patterns of components allocated into cluster I by hierarchical cluster analysis differed significantly for the comparison between water and bitter stimuli, and for that between sweet and bitter stimuli. Thus, newborn rhesus macaques of less than 7 days were assumed to perceive water and sweet differently from bitter. For salty and sour stimuli, ‘Tongue exposure’ was observed to some extent, and the emerging patterns of components allocated into each cluster were between those for water, sweet and bitter stimuli. The responses to salty and sour stimuli then, seemed to be intermediate.

All of the newborn chimpanzees showed ‘Grimace’ in response to bitter stimuli, but never showed it for sweet stimuli. The emerging patterns of components allocated into cluster I by hierarchical cluster analysis differed significantly for the comparison between sweet and bitter stimuli. Likewise, those of cluster III differed significantly for the comparison between sweet and water, and for that between sweet and bitter. For water, the emerging patterns of components allocated into clusters I and III were similar to those for bitter stimuli. The ‘Grimace,’ however, which was unanimously observed in response to bitter stimuli, was scarcely observed for water. Thus, chimpanzee newborns of less than 30 days were assumed to perceive water, sweet and bitter tastes differently from each other. For salty and sour stimuli, the emerging patterns of components allocated into each cluster were between those for sweet and bitter, and the ‘Grimace’ was observed to some extent. As for chimpanzees then, the overall response patterns to salty and sour stimuli seemed to be between those for sweet and bitter.

In both newborn rhesus macaques and chimpanzees, responses to sweet and bitter were the most readily distinguishable among the four basic tastes. In human newborns, it is also known that the response patterns of facial expressions to salty and sour stimuli tend to fall between those of sweet and bitter stimuli [19,27]. From the view point of reactivity to each kind of taste stimuli, newborns of rhesus macaque, chimpanzee and human seemed to show a similar tendency by means of the facial expressions elicited.

4.2. Comparison between newborn rhesus macaques and chimpanzees

‘Eye squinch (ES),’ ‘Nose wrinkle (NW)’ and ‘Lip pursing (LP)’ were observed in newborn chimpanzees but never in newborn rhesus macaques. Such differences between the two species have also been reported in adult individuals [27]. Human newborns have been also reported to show ‘Eye squinch (ES),’ ‘Nose wrinkle (NW)’ and ‘Lip pursing (LP)’ in response to taste stimuli [19,27]. As Steiner et al. [27] suggested, based mainly on the results of adults from several primate species, this might be due to phylogenic constraints, leading to physical differences (e.g. patterns of facial musculature). Some other components, such as ‘Gape (G)’ and ‘Frown (Fr),’ which were observed only in rhesus macaques in the present study, but have been reported to occur in adult chimpanzees [27]. Such discrepancies between the two studies possibly result from differences in the experimental protocol/conditions, or in the ages of subjects tested. The subjects of the present study were relatively young, ranging from 0 to 30 days after birth. It is possible that the repertoire of facial expressions changes as animals develop. As macaques are estimated to mature almost twice as fast as chimpanzees when comparing comparative physical development (e.g. dental development) [18], the newborn rhesus macaques and chimpanzees tested in this study could be considered to be almost parallel in their developmental stages, even though they differed in chronological age. To further determine the presence or absence of specific taste-elicited facial expressions, accumulation of more data with more subjects across a variety of ages and species is needed.

The composition of the components, which were clustered and assumed to reflect the differences among the kinds of stimuli tested, differed between newborn rhesus macaques and chimpanzees. In newborn rhesus macaques, the components of cluster I (‘Grimace,’ ‘Gape,’ ‘Frown,’ ‘Lateral tongue protrusion,’ ‘Slightly open mouth’ and ‘Moving closed mouth’) contributed, as a whole, to distinguishing the kinds of stimuli tested. In newborn chimpanzees, the components of cluster I (‘Eye squinch,’ ‘Mouth open,’ ‘Nose wrinkle’ and ‘Grimace’) and III (‘Corner elevation of lips,’ ‘Tongue holding’ and ‘Tongue protrusion’) contributed. These results suggest that newborn rhesus macaques and chimpanzees responded differently to the same kind of stimuli.

Certain facial expressions evaluated in this study have been considered to reflect the affective impacts of taste stimuli in previous studies [2,27]. In the present study, the components, which have been regarded as affective (aversive or hedonic) responses, tended to be grouped into clusters which contributed to distinguishing the kinds of stimuli tested. Those components classified as aversive responses (‘Eye squinch,’ ‘Nose wrinkle,’ ‘Frown,’ ‘Gape’ and ‘Grimace’) were all allocated into cluster I in newborn rhesus macaques and chimpanzees. Those components classified as hedonic responses (‘Corner elevation of lips’ and ‘Tongue protrusion’) were all allocated into cluster III in newborn chimpanzees. In particular, the emerging patterns of facial expressions in chimpanzee newborns resembled those of human newborns. As for human newborns, in chimpanzee newborns, ‘Eye squinch’ was elicited in response to bitter stimuli but never to sweet and ‘Tongue protrusion’ occurred in response to sweet stimuli, but never to bitter. In newborn rhesus macaques, ‘Frown’ was elicited only in response to bitter stimuli, as is the case in human newborns but ‘Tongue protrusion’ occurred in response to both sweet and bitter stimuli.

These response patterns evident in individuals from such an early stage of life were inferred to be innate. So what did the species differences mean? Thresholds for each taste are supposed to differ between rhesus macaques and chimpanzees (e.g. the detective threshold for quinine HCl is approximately four times higher in rhesus macaques than in chimpanzees), and the concentrations of stimuli used in the present study were much higher than the supposed thresholds [9,10,21]. It is possible that the responses to such highly concentrated tastes differed between the two species, resulting in the differing response patterns. Alternatively, rhesus macaques possibly differed in the manner in which they perceive each kind of taste, especially bitter, from chimpanzees (and humans). Differential responses to various kinds of tastes have been generally considered to be adaptive in assessing the nutritional content or presence of toxic compounds contained in potential foods (e.g. [6,7]). Chimpanzees are assumed to include far fewer extremely bitter tasting foods in their food repertoire than macaques do [16]. In regard to evolutionary background, the ancestors of rhesus macaques differed markedly in their habitat and diet from those of chimpanzees and humans [1]. Cercopithecoids presumably had a folivorous diet, whereas hominids were frugivorous. It might be more advantageous for cercopithecoids to become tolerate (or less sensitive) for bitter taste in adapting to their diet, than for hominids. Chimpanzees and humans are known to share a similar rejection threshold for bitter stimuli, which differs from that of rhesus macaques [29]. In adapting to their own habitat and diet, the manner in which they perceive various tastes presumably differentiated between the two lineages. Rhesus macaques may perceive the affective impacts of bitter taste differently from chimpanzees and humans. Chimpanzees and humans possibly share a similar manner to perceive them, reflecting their rather common evolutionary backgrounds.

Acknowledgements

This research was funded by a Grant-in Aid for Scientific Research from the Ministry of Education, Culture, Sports, Science and Technology, Japan (no. 12002009 to T. Matsuzawa, no. 10CE2005 to O. Takenaka and 21st Century COE Program (A14). We wish to thank Dr. T. Matsuzawa, Dr. M. Tanaka, H. Kuwahata and all our colleagues who participated in the research project on behavioral and cognitive development of infant chimpanzees, for their support of this research. We also extend our thanks to Drs. A. Mori and M.A. Huffman for their valuable advice. Thanks are also due to N. Maeda and K. Kumazaki for their daily care, and to A. Kato, J. Suzuki, S. Goto, C. Hashimoto, and K. Matsubayashi for their veterinary treatment of the animals.

Appendix A

The scores of each component observed for each stimulus in each subject

	Subject/stimuli																			
	R1					R2					R3					C1				
	Wa	Sw	Sa	So	Bi	Wa	Sw	Sa	So	Bi	Wa	Sw	Sa	So	Bi	Wa	Sw	Sa	So	Bi
ES	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	5
NW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	3	3	1	4
Fr	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
G	0	0	0	1	2	0	0	0	0	1	0	1	0	3	0	0	0	0	0	0
Gr	0	1	0	0	0	0	0	0	1	0	0	0	0	3	2	0	0	0	0	2
CE	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
TP	3	4	1	0	1	9	13	9	13	6	1	6	3	2	0	0	0	0	1	0
LP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
MM	1	3	6	0	6	0	0	3	0	6	0	0	0	4	1	3	3	1	2	2
FW	0	0	0	2	1	0	5	1	0	3	0	0	0	0	0	0	0	0	0	0
lTP	0	0	0	0	2	0	0	0	0	0	0	2	2	0	0	0	0	0	0	0
MO	0	2	0	1	0	2	0	3	0	0	0	0	0	0	3	2	1	2	2	5
MP	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0
SO	3	0	4	11	8	0	0	4	0	2	0	1	3	3	1	0	0	1	2	6
TE	0	0	0	1	1	0	0	1	2	2	0	0	0	1	0	0	0	0	0	0
TH	0	0	0	0	0	6	1	0	0	0	1	2	0	0	4	0	0	0	1	0

	C2					C3					C4				
	Wa	Sw	Sa	So	Bi	Wa	Sw	Sa	So	Bi	Wa	Sw	Sa	So	Bi
ES	0	0	0	0	0	5	0	0	2	4	0	0	1	2	5
NW	0	6	0	1	6	6	0	2	9	4	6	0	15	5	6
Fr	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
G	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Appendix A (*Continued*)

	Subject/stimuli																			
	R1					R2					R3					C1				
	Wa	Sw	Sa	So	Bi	Wa	Sw	Sa	So	Bi	Wa	Sw	Sa	So	Bi	Wa	Sw	Sa	So	Bi
Gr	0	0	0	1	4	1	0	4	5	4	0	0	2	6	7					
CE	0	1	0	0	1	0	2	0	1	0	1	2	0	1	0					
TP	0	0	2	0	0	0	2	2	0	0	0	11	4	1	0					
LP	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0					
MM	3	2	2	8	1	0	0	1	6	0	2	0	2	0	0					
FW	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0					
lTP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0					
MO	3	2	1	1	6	14	1	6	2	2	2	1	1	3	4					
MP	1	1	2	1	0	2	0	0	0	0	0	0	0	0	0					
SO	3	1	6	4	1	0	2	0	0	0	0	0	0	0	1					
TE	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0					
TH	0	0	1	0	0	0	7	2	0	0	0	5	3	6	3					

The components are arranged in order of aversive, hedonic and the other responses according to the classification by Steiner et al. [27], and then the other components defined in this study. Wa: water: Sw: sweet; Sa: salty; So: sour; Bi: bitter.

References

[1] Anderw P, Aiello L. An evolutionary model for feeding and positional behavior. In: Chivers DJ, Wood BA, Bilsborough A, editors. Food acquisition and processing in primates. London: Plenum Press; 1984. p. 429–66.

[2] Berridge KC. Taste reactivity: measuring hedonic impact in human infants and animals. Neurosci Biobehav Rev 2000;24:173–98.

[3] Berridge KC, Grill HJ. Isohedonic tastes support a two-dimensional hypothesis of palatability. Appetite 1984;5:221–31.

[4] Darwin C. The expression of the emotions in man and animals. New York: AMS Press; 1872.

[5] Ganchrow JR. Ontogeny of human taste perception. In: Doty RL, editor. Handbook of olfaction and gustation. New York: Marcel Dekker; 1995. p. 715–29.

[6] Hladik CM, Pasquet P, Simmen B. New perspectives on taste and primate evolution: the dichotomy in gustatory coding for perception of beneficient versus noxious substances as supported by correlations among human thresholds. Am J Phys Anthropol 2002;117: 342–8.

[7] Hladik CM, Simmen B. Taste perception and feeding behavior in nonhuman primates and human populations. Evol Anthropol 1996;5:58–71.

[8] Hayashi M, Matsuzawa T. Cognitive development in object manipulation by infant chimpanzees. Anim Cogn 2003;6:225–33.

[9] Hellekant G, Danilova V, Ninomiya Y. Primate sense of taste: behavioral and single choda tympani and glossopharyngeal nerve fiber recordinhs in the rhesus monkeys *Macaca mulatta*. J Neurophysiol 1997;77:978–93.

[10] Hellekant G, Ninomiya Y. Bitter taste in single chorda tympani taste fibers from chimpanzee. Physiol Behav 1994;56:1185–8.

[11] Hirata S, Celli M. Role of mothers in the acquisition of tool use behaviours by captive infant chimpanzees. Anim Cogn 2003;6:235–44.

[12] Mennella JA, Beauchamp GK. The ontogeny of human flavor perception. In: Beauchamp GK, Bartoshuk L, editors. Tasting and smelling. San Diego: Academic Press; 1997. p. 199–221.

[13] Matsuzawa T. Chimpanzee Ai and her son Ayumu: an episode of education by master-apprenticeship. In: Bekoff M, Allen C, Burghart G, editors. The cognitive animal. Cambridge: MIT press; 2002. p. 189–95.

[14] Matsuzawa T. The Ai project: historical and ecological contexts. Anim Cogn 2003;6:199–211.

[15] Myowa-Yamakoshi M, Tomonaga M, Tanaka M, Matsuzawa T. Preference for human direct gaze in infant chimpanzees (*Pan troglodytes*). Cognition 2003;89:113–24.

[16] Nishida T, Ohigashi H, Koshimizu K. Tastes of chimpanzee plant foods. Curr Anthropol 2000;41:431–8.

[17] Okamoto S, Tomonaga M, Ishii K, Kawai N, Tanaka M, Matsuzawa T. An infant chimpanzee (*Pan troglodytes*) follows human gaze. Anim Cogn 2001;5:107–14.

[18] Parker ST, Mckinnet ML. Origins of intelligence. Maryland: The Johns Hopkins University Press; 1999. p. 215–32.

[19] Rosenstein D, Oster H. Differential facial responses to four basic tastes in newborns. Child Dev 1988;59:1555–68.

[20] Rozin P. The socio-cultural context of eating and food choice. In: Meiselman HL, MacFie HJH, editors. Food choice, acceptance and consumption. London: Blackie Academic; 1996. p. 83–104.

[21] Simmen B, Hladik CM. Sweet and bitter taste discrimination in primates: scaling effects across species. Folia Primatol 1998;69:129–38.

[22] Sousa C, Okamoto S, Matsuzawa T. Behavioral development in a matching-to-sample task and token use by an infant chimpanzee reared by his mother. Anim Cogn 2003;6:259–67.

[23] Steiner JE. Innate discriminative human facial expression to taste and smell stimulation. Ann NY Acad Sci 1974;237:229–33.

[24] Steiner JE. Human facial expressions in response to taste and smell stimulation. In: Reese HW, Lipsitt LP, editors. Advances in child development and behavior. Tokyo: Academic Press; 1979. p. 257–95.

[25] Steiner JE, Glaser D. Differential behavioral responses to taste stimuli in non-human primates. J Hum Evol 1984;13:709–23.

[26] Steiner JE, Glaser D. Taste-induced facial expressions in apes and humans. Hum Evol 1995;10:97–105.

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

[28] Tomonaga M, Myowa-Yamakoshi M, Mizuno Y, Okamoto S, Yamaguchi KM, Kosugi D, Bard KA, Tanaka M, Matsuzawa T (2004). Development of social cognition in infant chimpanzees (*Pan troglodytes*): face recognition, smiling, gaze and the lack of triadic interactions. J Psychol Res 2004;in press.

[29] Ueno Y. How do we eat?: Hypothesis of foraging strategy from the viewpoint of gustation in primates. In: Matsuzawa T, editor. Primate origins of human cognition and behavior. Tokyo: Springer; 2001. p. 104–11.