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Comparative expression of hedonic impact: affective reactions to taste by human infants and other primates

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Abstract

This study examines behavioral affective reactions elicited by tastes from eight newborn human infants, and from 27 other infant or adult primates. Non-human primates belonged to 11 species: three great apes (chimpanzee, orangutan, gorilla), three Old World monkeys (rhesus monkey, greater spot-nosed monkey, and red-capped mangabey), four New World monkeys (golden-handed tamarin, cotton-top tamarin, white tufted-ear marmoset, and Humboldt's night monkey), and one lemur (mongoose lemur). The taste of sucrose elicited homologous positive hedonic patterns of facial affective reactions from humans and other primates, whereas quinine elicited homologous aversive or negative affective patterns. The degree of similarity between human and other primate affective reaction patterns appeared to be strongly indicative of their phylogenetic relatedness. For example, affective reaction patterns of human infants and great apes were more similar to each other than either were to Old World monkeys or New World monkeys. Certain affective reaction components were found to be shared by humans and all primates, whereas other components were restricted to particular taxonomic groups. Finally, allometric timing parameters for the duration of components indicated that the 'same' affective reaction could have different durations in species of different size. These results show that both positive/negative valence and intensity of affective reaction may be quantitatively assessed in human and non-human primates, and indicate that taste-elicited affective reaction patterns of human infants are related systematically to those of other primate species. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Measurement of the positive or negative valence and intensity of affective reaction to a stimulus is an important goal both for psychology and affective neuroscience. The study of affective reaction in human psychology and human affective neuroscience has focused primarily on studies of subjective ratings of pleasantness or unpleasantness by human adults based on verbal reports or rating scales [18,30,41,60,67,77,113,115,117]. Yet creatures that cannot speak, animals and human infants, may have affective reactions too, and it is important to be able to measure them [6,37,40,65,68,81,116].

Measurement of the intensity of positive hedonic or affective reactions to stimuli, in particular, has been rare in studies of infants or of non-human animals. Some negative affective reactions are generally accepted to be recognizable in human

infants, such as crying, distress vocalizations, or physiological reactions, but there have been relatively few measures of the intensity of positive (hedonic) affective reactions to stimuli [11,45,50,54]. The study of affective neuroscience using animals has also tended to focus on negative affective reactions involved in fear and stress, such as startle or freezing reactions [31,42,70] more than on positive affective reactions.

1.1. Facial affective reactions to positive and negative gustatory stimuli

Positive and negative affective reactions both are important, and objective measures for both affective categories have been identified in the reactions to taste of human infants and other animals [11,22,23,45,50,54,79,103,108]. Affective facial reactions are a good source of potential information for studies of the affective valence of reactions to stimuli for both humans [36,39,64,66,98,99] and other animals [1,11,25,34,90,91,108]. Taste is an especially powerful stimulus domain for eliciting affective reactions,

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including positive affective reactions, because food is a basic biological commodity, and because gustatory stimuli can elicit either positive or negative affective valence [4,88,96,97,114].

Even newborn human infants respond with appropriate facial reactions to pleasant and unpleasant taste stimuli [45,50,65,75,95,103,105]. As described originally by Steiner and replicated by others, positive affective reactions are typically elicited from human newborns by sweet tastes, whereas negative affective reactions are elicited by bitter tastes (even within hours of birth, before the infants have had their first postnatal meal) [105,106]. In other animal species too, ranging from primates to rodents to birds, positive affective reactions are often elicited by sweet tastes, whereas negative affective reactions are typically elicited by bitter tastes [5,20,49,56,107,108].

1.2. Measuring intensity as well as valence of affective reactions

Although a number of studies have described those types of facial reaction that are typically elicited by positive or negative tastes from human infants, there is little precise information about the quantitative affective intensity of reaction. Steiner's original study of human infants and similar early studies focused on description of qualitative components. In a move toward quantification, Ganchrow, Steiner, and Daher [50] measured the percentage of infants who emitted reactions to particular tastes, and showed that the percentage grew as the concentration of the taste solution was increased. Similarly, Rosenstein and Oster [95] reported the percentage of infants who emitted particular facial action units to several taste stimuli. Crystal and Bernstein used a modification of the Ganchrow et al. procedure to measure affective reactions by human infants to a highly salty taste, and reported that infants who had been prenatally exposed to possible physiological induction of a sodium appetite (due to intense maternal morning sickness) subsequently showed a less negative affective reaction to salt than did normal infants [28].

Measurement of incidence, or percentage-of-individuals showing an affective reaction, provides some quantification but is not a precise measure of affective intensity. Incidence measures allow discrimination between an individual who does not emit a response at all, and those who emit the response at least once. But incidence measures do not discriminate at all between an individual who shows a response only once during a sampling period vs an individual who shows the response many times, even though the latter may reflect much greater intensity of affective impact.

More precise slow-motion videoanalysis methods for quantifying the actual number of affective reactions elicited by a taste stimulus were developed over two decades ago for behavioral neuroscience studies of taste reactivity in rodents [53–56]. Time-bin scoring methods were incorporated for combining together different taste reactivity components

belonging to the same affective category, in order to obtain positive vs negative 'affective profiles' for readouts of the valence and intensity of an affective reaction [14,15,54]. Affective profiles depict the number of each type of reaction elicited by a particular taste stimulus, balancing the contribution of frequent and rare components, and classifying each reaction according to affective category: positive (hedonic), neutral, or negative (aversive). Time-bin scoring methods also allow calculation of total numbers of positive vs negative affective reactions, while assuring that frequent reaction components do not swamp out the quantitative information provided by rare components [11,15]. Such quantitative scoring procedures for taste-elicited reactions have been used routinely in affective neuroscience studies aimed at identifying the brain substrates and physiological and associative controls of positive or negative affective reactions by rodents [3,8,11–13,16,17,19,27,32,43,44,48,54,58,82,83,85–87,94,104], but have not generally been applied to studies of affective reactions of human infants or other primates.

1.3. Classifying reactions as sensory vs affective

It is sometimes difficult to know whether a reaction to a stimulus should be classified as affective, reflecting an underlying evaluation of the stimulus as positive or negative, or instead classified as a simpler sensory reflex to the stimulus. This issue is especially important regarding studies of animals, where recognition of affective responses may not seem as intuitive as for humans. Above all, affective reactions are defined by possessing positive vs negative valence. When multiple affective reaction components are observed to have similar valence, then to decide whether all reflect the same affective state or 'liking' evaluation it is also important to consider the pattern among components of the reaction, and the pattern of change caused by stimulus alterations and by non-sensory manipulations [11]. Several criteria for evaluating whether behavioral reactions reflect a particular affective/motivational state have been suggested over the decades [61,76]. For classifying taste-elicited affective reactions in particular, for example, Berridge suggested three criteria for use in determining whether a pattern of reactions should be classified as reflecting the same affective evaluation (e.g. positive taste affect vs negative taste affect) [11]. These criteria are: (1) shared stimulus; (2) temporal association; and (3) shared outcome [11].

Shared stimulus means that positive reactions tend to be elicited together by the same stimulus [11,61,76]. If a stimulus is truly positive in affective valence, for example, then it ought to be able to elicit all the positive affective reactions relevant to its modality. And other positive taste stimuli ought to be able to elicit the same group of positive affective reactions. Negative affective reactions should also be elicited together by the same stimulus, and if a different stimulus is found to elicit one negative reaction then it ought to elicit the other negative reactions too. By contrast,

if a single stimulus uniquely elicits a particular reaction then the reaction is more likely to be a sensory reflex, unique to the sensory properties of that stimulus (e.g. sweet, sour, salt, bitter, etc.) rather than an affective reaction.

Temporal association means that affective reactions belonging to one valence category ought to cluster together in time and in sequence [11,14,61]. If a positive affective state is the cause of a reaction, then the same state ought to elicit other positive reactions at the same time. Thus the occurrence of individual reactions should not be randomly ordered, but should be sequentially clustered so that mostly positive reactions occur when a positive affective state dominates, and mostly negative reactions occur when a negative affective state dominates. Temporal association can be detected by measuring the transitions among components in a temporal stream of reaction to a stimulus. Even when a taste of mixed palatability elicits an ambivalent affective reaction comprising both positive and negative components, the components belonging to the same category tend most often to sequentially follow one another [14,54].

Shared outcome means that changes in the affective value of a stimulus should be reflected equivalently by all the behavioral reactions belonging to an affective category [11]. For example, if the positive hedonic impact of a stimulus is reduced, either by changing the taste itself, or by reducing the relevant physiological appetite state [8,13,21,23], or by training a learned aversion for the taste [51,55], or by neural or pharmacological disruption of hedonic processing [9,27,57,84], then positive hedonic reactions to the stimulus should all diminish together as a group, whereas all reactions that reflect a negative affective state should either not diminish or should increase [11,76]. Other criteria can be suggested for recognizing an affective reaction, but these give a basis on which to begin to evaluate objectively the affective status of an observed behavioral reaction, and were the criteria we used in this study of human infants and non-human primates.

1.4. How to recognize whether different species emit the same affective reaction

Determining whether two species have emitted the same behavioral affective reaction can be difficult, because even the same movement may not be identical for different species if they have strikingly different head or body shapes, body sizes, patterns of facial musculature, etc. By ‘same’ we mean that the affective reactions are likely to be homologous, preserved as a shared trait in different species that descended from a common ancestor. Homologous behavioral traits are more likely to reflect similar psychological processes, and be mediated by similar neural substrates, than analogous traits which are similar but which spring from separate sources or have different mechanisms. Hence homology is an important issue if one wishes to know whether affective reactions are essentially similar in humans and non-human species. The form or shape of a

behavioral reaction is the most relevant criterion for determining if reactions are similar in different species, but timing is also important, especially when comparing species that are markedly different in physical size. An important timing rule that often applies across species is allometry, that is, the logarithmic scaling of behavioral rate or duration to species size [101]. Behavioral components that share similar underlying timing rules have a stronger evidential basis for being considered to be homologous or the ‘same’ across species than components that do not [1,90,101].

1.5. Cross-species human/primate similarity in the pattern of affective reaction

Since Darwin’s original work [29], a number of investigators have noted that human emotional or affective expressions may bear certain similarities to those of non-human primates [1,25,90,108]. Regarding taste-elicited affective reactions in particular, Steiner and Glaser noted that human infants and great apes shared several similarities [108]. For example, bitter tastes often elicited a gape, whereas sweet tastes elicited a lip smacking and finger sucking, from most subjects regardless of species. Steiner and Glaser also carried out a semi-quantification of these reaction patterns, reporting which reactions were most frequent to a particular gustatory stimuli [107,108]. But it would be useful to have a more objective analysis. In particular, it would be useful to know precisely which components of affective reaction are similar across particular species, vs which components are different.

The purpose of this study was to address these issues. By applying quantitative taste reactivity scoring techniques to newborn human infants, we measured the intensity and valence of affective reaction elicited from an infant by a particular taste on its first experience (as well as to measure inter-individual differences across human infants). We further applied the same quantitative scoring technique to the taste-elicited affective reactions of 11 other primate species in order to assess the valence and intensity, and to compare their component patterns to those of humans.

2. Methods

2.1. Subjects and behavioral testing

Newborn human infants ($n = 8$) were tested for taste reactivity at the Hadassah University Hospitals in Jerusalem within 3–10 h after birth. All infants were tested with taste stimuli before they had their first post-natal meal. Sweet, water, sour, and bitter tastes were administered in liquid solution: 0.3 M sucrose, distilled water, 0.025 M citric acid, and 7×10^{-6} M quinine HCl. Approximately 3 ml was infused by dropper into the infant’s mouth, and facial reactions were videotaped for later analysis [108]. The taste solutions were delivered in counter-balanced order. Water rinses were given after each solution, and were followed by

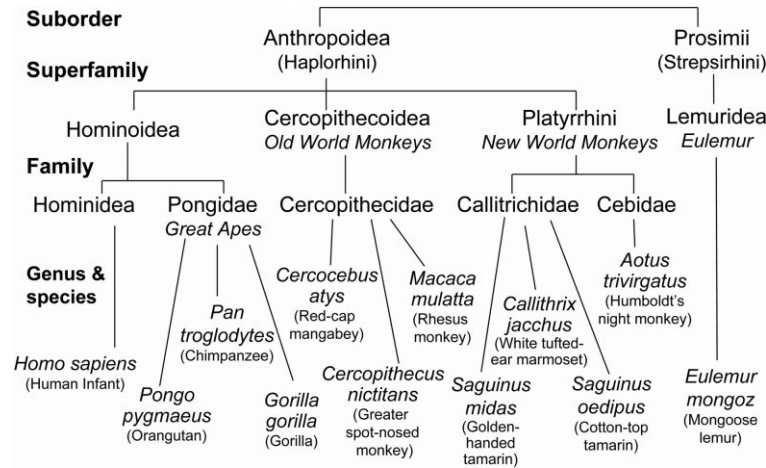


Fig. 1. Taxonomic relationships of human and other primate species used in this study.

a 1-min pause before the next taste solution. Videotapes were subsequently scored for microstructural components in a slow-motion analysis, as described below.

Videotaped taste-elicited reactions of non-human primates ($n = 27$ infants or adults from 11 species; Fig. 1) obtained at the Institute of Anthropology and at the Zoological Garden in Zurich, which have been previously described briefly by Steiner and Glaser [107], were rescored using a detailed quantitative analysis procedure identical to that used for the human infants. Non-human primate subjects included 10 great apes, five Old World monkeys (from Asia or Africa), 10 New World monkeys (from South or Central America), and two prosimians (from Madagascar). The 10 African or Asian great apes were: *Pan troglodytes* (common name: chimpanzee, $n =$ two adults), *Gorilla gorilla* (common name: gorilla, $n =$ one adult), and *Pongo pygmaeus* (common name: orangutan, $n =$ six adults, one infant). The five Old World monkeys were: *Macaca mulatta* (common name: rhesus monkey, $n =$ three adults), *Cercocebus atys* (common name: red-capped mangabey, $n =$ one adult), and *Cercopithecus nictitans stampflii* (common name: greater spot-nosed monkey, $n =$ one adult). The 10 New World monkeys were: *Saguinus midas niger* (common name: golden-handed tamarin, two adults, one infant), *Saguinus oedipus* (common name: cotton-top tamarin, $n =$ two infants), *Callithrix jacchus* (common name: white tufted-ear marmoset, $n =$ two adults, one infant), and *Aotus trivirgatus* (common name: Humboldt's night monkey, two adult). Finally, two members of a strepsirhine (Prosimii) species were also included: *Eulemur mongoz mongoz* (common name: mongoose lemur, $n =$ two adults).

Adult primates were presented with hand-held plastic beakers of approximately 50 ml of 0.03 M sucrose, 0.1 M NaCl, 0.025 M citric acid, or 0.00007 M quinine HCl, and were allowed to sample the taste solution voluntarily as they chose. Each adult primate tasted every solution at least once. Infant monkeys and apes were administered sucrose or quinine by dropper, using a procedure similar to that

described above for newborn human infants. Primate facial reactions were videotaped for subsequent slow-motion analysis, just as for human infants.

2.2. Scoring scheme for affective reaction components

No single scoring system currently available for facial components covered the full range of reactions observed across both human and non-human primate species. We therefore selected and combined behavioral components from several previous coding systems. From Andrew's description of primate components, we took lip movements such as zygomatic retraction of lip corners back and upwards. These included mouth corner elevation (in which the two corners of the mouth are raised simultaneously by the zygomatic muscle, lasting up to several seconds). A special variant of lip-corner elevation was the 'Duchenne smile' (in which the elevation of the lip corner produced by the zygomatic major muscle is accompanied by orbicularis oculi action that simultaneously raises the cheek, typically lasting 500–1500 ms). Conversely, frown or mouth corner depression produced an opposite pattern (simultaneous lowering of the two corners of the mouth by platysma retraction and the triangularis and zygomatic muscle, lasting up to several seconds). Eyebrow movements such as raising by m. frontalis and lowering by m. depressor supercilii muscles were also scored [1].

From the FACS coding scheme of Ekman and colleagues for human facial expression [38,39,95] we took several lip and middle face components such as large-amplitude zygomatic retraction into full-blown smiling (AU 12), and cheek raising (AU 6), which were sometimes combined into the 'Duchenne smile' pattern (simultaneous elevation of the corners of the mouth combined with crinkling of the corners of the eyes [33]). Nose wrinkle involved levator labii superioris compression of either side of the bridge of the nose, and zygomatic minor deepening of the nasolabial furrow, lasting 300 ms–2 s, and included FACS components nose

wrinkling (AU9), nasolabial furrow deepener (AU11) and upper lip raiser (AU 10). Brow furrow involved corrugator compression across the forehead and brow, lasting up to 5 s. A lip and mouth pattern was lip puckering (A 12) or pursing movements of the lips, often lasting 3–5 s [38,39,95].

From the taste reactivity coding scheme developed for human infants by Steiner [105], we took lip smacking (brief compression of the lips together followed immediately by their rapid and large amplitude opening and slight dropping of the jaw, often repeated, each cycle lasting up to 2 s), finger licking or sucking (drawing of the hand or paw up to the mouth, sometimes inserting it in the mouth, and directing the lick or suck movements specifically to the finger or paw); eye squinch (closing of the eyes and visible compression of the orbicularis oculi muscles above and below the eye, sometimes also accompanied by compression at the lateral corner of the eye, lasting 300 ms–5 s); and grimace (tense retraction of the lips away on all sides of the mouth, exposing the gums or teeth, often accompanied by deepening of the nasolabial furrow, lasting 500 ms–2 s); and spitting [105].

Finally from the taste reactivity coding scheme developed for taste-elicited reactions of rodents by Grill and Norgren [56], we took rhythmic tongue protrusion (extension of the tongue outwards along the midline, and sometimes upwards, past the outer edge of the lips, often simultaneously accompanied by slight dropping of the jaw; tongue protrusion is followed immediately by retraction of the tongue and closure of the jaw, and the cycle is repeated rhythmically again and again, each cycle lasting 300–1200 ms) and lateral non-rhythmic tongue protrusion, which were sweeping extensions of the tongue sideways along the lateral border of the mouth and along the lips on one side of the mouth. Gape was a large-amplitude lowering of the jaw accompanied by slight retraction of the lips and downwards pulling of the corners of the mouth, often forming a triangular shaped mouth opening, which lasted 200 ms–3 s depending on the species); and rhythmic or low-amplitude repetitive mouth movements (low-amplitude working of the lips and jaw around the taste, without much visible opening of the mouth or recruitment of other facial movements. A number of non-facial reactions were also measured, including headshake (rapid and often violent movements of the entire head from side to side); hand or paw flail (rapid shaking of both hands or paws together, side to side, or up and down, or combined); and hand or paw treading (pushing outwards in front of the body and sometimes upwards away from the face, alternating pushes of the left and right limb, retracting one while pushing the other, each cycle lasting 200 ms–2 s).

2.3. Videoanalysis and time-bin scoring procedure (for balancing component scores)

Videotapes were scored at speeds ranging from frame-by-frame to 1/10 actual speed, depending on the temporal density of facial reactions, by two independent observers, whose agreement across components ranged between 75 and 95%.

Some components (e.g. tongue protrusions to sucrose) occurred much more frequently than others (e.g. elevation of the mouth corners or ‘smiles’ to sucrose). In order to balance the scores of frequent and rare components within hedonic and aversive categories, a ‘time bin’ scoring system was used, in which the criterion for scoring a ‘unit’ was calibrated to its frequency [11,15]. Each occurrence was counted for rare or discrete-event components: corner elevation of lip and mouth, frown, gape, head shake, and arm flail. Two-second time bins were used to score frequent or sustained components: rhythmic tongue protrusion, smack, mouth movements, eye squinch, and nose wrinkle. The first occurrence of a frequent or sustained component was counted, but to be counted after that the component had to be repeated for longer than 2 s, or had to recur after a 2-s pause. This procedure produced scores that were more comparable across all response categories, and allowed ‘rare’ components to contribute as much to total positive hedonic category and aversive category scores as frequent components (for discussion see [11]).

2.4. Identifying components that are the ‘same’: allometric timing constancy and affective transition analysis

Many movement patterns that are essentially the ‘same’ across species show a lawful timing relationship to body mass. This relationship has been called ‘allometric’ [101]. In its most usual form, movements are performed by species of small body mass much faster than the ‘same’ movements when performed by larger species [7,101]. Allometric relationships are often expressed in equation form, as $y = a \times x^b$, where y is the behavioral timing dependent variable, x is body mass, and a and b are computed constants that describe the relationship.

We performed an allometric analysis to examine whether morphologically similar components were generated by the ‘same’ allometric timing rule. Microcomponent duration was measured by counting the number of video frames spanned during the duration of the microcomponent while advancing the videotape frame-by-frame. Each video frame spanned 1/30 s (33 ms), which was therefore the limit of temporal resolution. The duration of rhythmic tongue protrusions, which are emitted in repetition, the duration of the protrusion cycle was measured (e.g. from the moment of maximal extension of one tongue protrusion, through retraction and re-extension, until the maximal extension of the next protrusion). For gapes the duration of the visible movement pattern was measured (from the first beginning of jaw opening, through maximal mouth opening and subsequent closing, until movement of the jaw and mouth ceased). A non-linear regression analysis was performed based on the 2-factor power equation, $y = a \times x^b$.

Sequential transitions among components elicited from human infants were also tabulated, in order to identify the frequency with which particular pairs of components occurred in sequence. The purpose of this sequential analysis was to

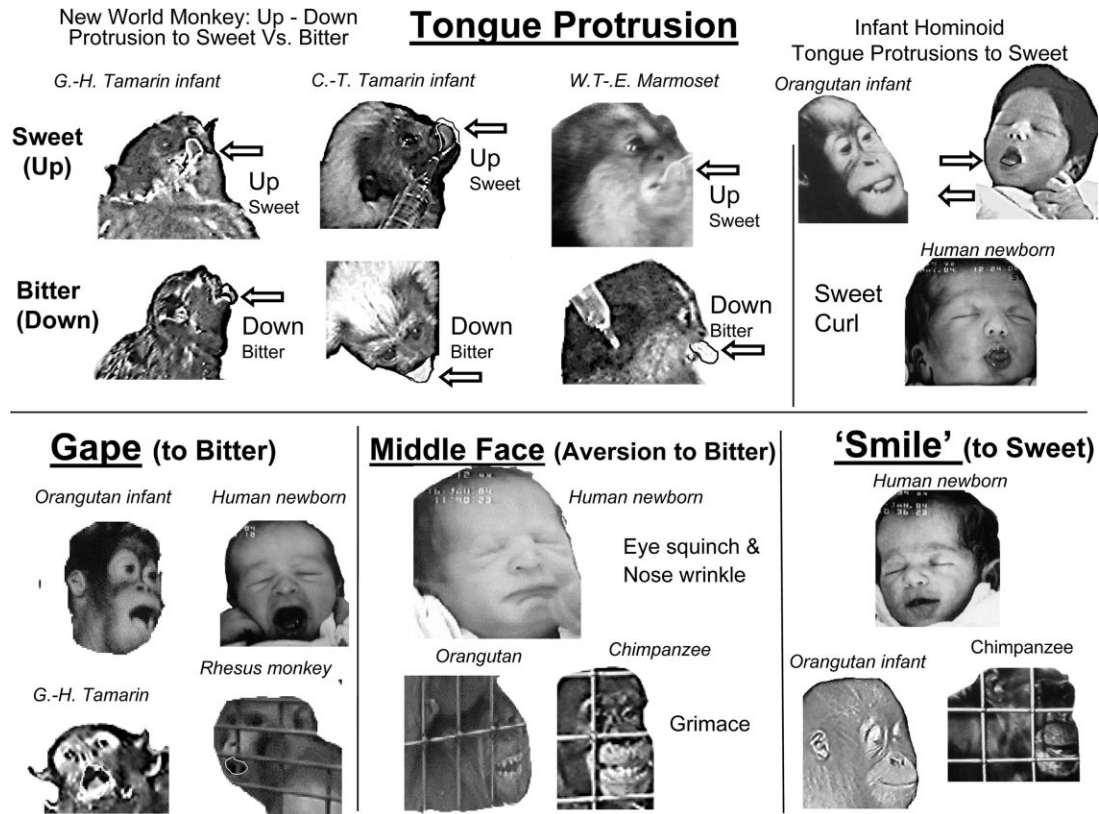


Fig. 2. Examples of positive hedonic and aversive components of facial expression to taste. Top: 'Universal components' were emitted by essentially all primate species. These included positive hedonic patterns of tongue protrusions and aversive patterns of gapes. Tongue protrusions were emitted to the sweet taste of sucrose by all by all primate species, including newborn humans (who occasionally curled the tongue into a U-shape). The tongue is highlighted along its lateral and distal border to aid visibility. Aversive gapes also were emitted by most primates, including human infants, great apes, and Old World and New World monkeys, to bitter quinine (and sometimes sour or salty tastes). Several other components were limited to particular family or superfamily groups. For humans and great apes, these included 'middle face' aversive components, such as 'wrinkle' of the nose and nasolabial fold, or periorbicular 'squinch' of the eye corners, or lip retraction 'grimace' to bitter. A hominoid-specific hedonic expression involved relaxation of the middle face and occasional elevation of the mouth corners to sweet, producing a 'smile-like' pattern. Only humans combined that microcomponent with a crinkling of the eye corners and elevation of the cheeks to create a full-fledged Duchenne smile (and even humans did so only rarely). A videomovie of examples of human infant and primate affective reactions are available at a web site:<http://www-personal.umich.edu/~berridge/>.

assess whether components classified as affectively positive tended to follow other affectively positive components, and conversely, whether negative components tended to follow each other [14,54]. This analysis was performed on the data for human infants, but not for the other primate species because sequential transition analysis requires observation of at least hundreds of sequential transitions, and only the human infant data set met the minimum size requirement. However, allometric timing analyses of microcomponent duration were performed on the data for all species.

3. Results

3.1. Human infant expressions to sweet, water, sour, and bitter tastes

3.1.1. Sweet

Sucrose elicited a distinct set of components from human infants (Figs. 2 and 3). Rhythmic tongue protrusions were

the most numerous component, followed in order of decreasing number by lip smacks, lip and finger sucking, and occasional elevation of the mouth corners into a pattern that resembled a smile. Rhythmic and complex mouth movements were also elicited in moderate number by sucrose. We will refer below to this constellation of rhythmic tongue protrusion combined with lip smack, sucking, and 'smile' or elevation of mouth corners as a positive 'hedonic pattern'. Conversely, we will refer to the bitter-typical constellation of gape, nose wrinkle, frown, grimace, head shake, and arm flail as an 'aversive pattern'.

Most human newborns emitted tongue protrusion, lip smack, finger sucks, and lip corner elevation components to sucrose as an entire positive hedonic reaction pattern (Fig. 4). Lip smacks and rhythmic tongue protrusions were each elicited by sucrose from seven infants out of eight. Finger sucks and elevation of mouth corners were each elicited from five out of seven human infants. In terms of absolute number, rhythmic tongue protrusions were the most frequent

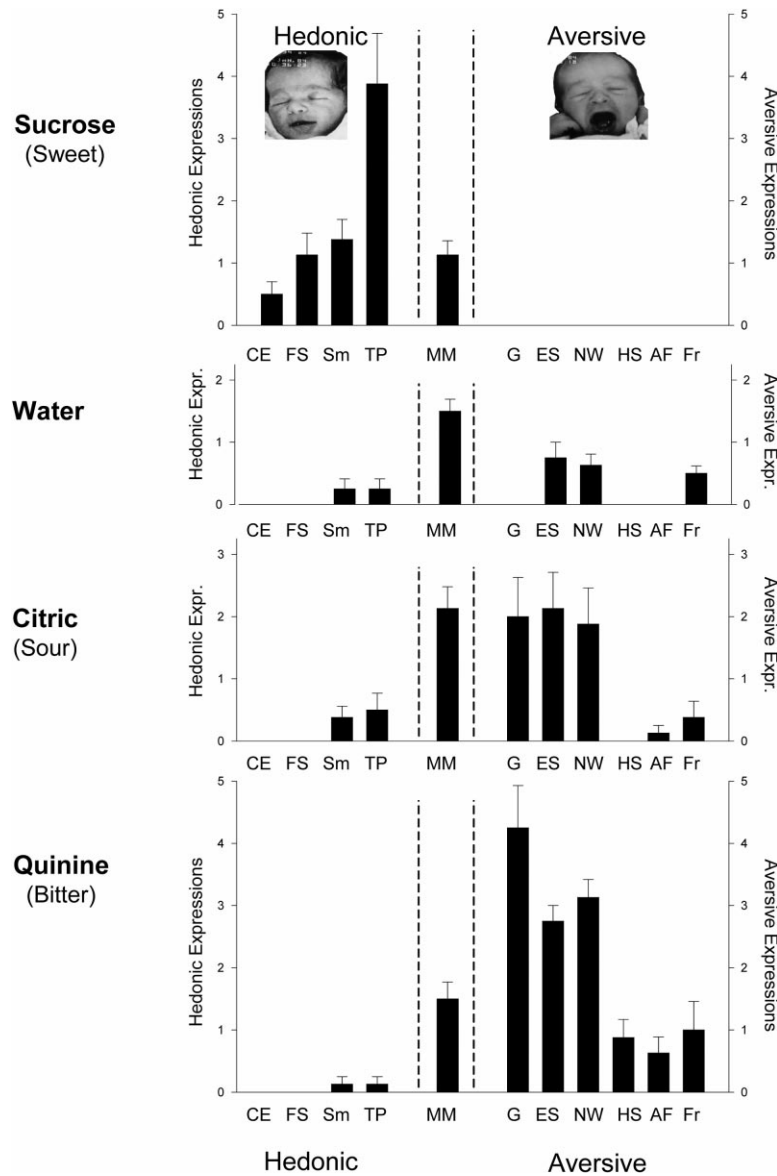


Fig. 3. Reactions by individual newborn human infants to sweet, water, sour, and bitter tastes. Bars show the number (mean + SEM) of positive hedonic and aversive reaction components elicited by each taste from an identified infant. Positive hedonic components are: CE, corner elevation of the mouths and lips (includes but not restricted to Duchenne smile); FS, finger suck; Sm, smacks of mouth and lips; TP, tongue protrusion. Neutral component is MM, mouth movements, irregular and involving the lips. Aversive components are: G, gape; ES, eye squinch; NW, nose wrinkle; HS, head shake; AF, arm flail; Fr, frown (corner depression of mouth and lips).

reaction to sucrose (even though this component was scored in 2-s bins, reducing its score relative to lip smacks and elevation of mouth corners, which were scored each time they occurred), and were emitted by every infant. Most positive hedonic components other than tongue protrusions were emitted in roughly equal numbers (Fig. 4). Rhythmic mouth movement did not share the same relation to the hedonic pattern, as it was also elicited as a component by all the other taste stimuli below, and so we classified it as a ‘neutral reaction’.

3.1.2. Water

The taste of water elicited few affective components

of either category, positive hedonic or aversive, from human infants. Slightly more aversive eye squinch, nose wrinkle, and frown (depression of mouth corners) components were elicited than positive hedonic tongue protrusions or lip smacks, but the difference was not significant. Neutral mouth movements were the most numerous reaction to water. The taste of water thus appeared to be of relatively neutral palatability, with perhaps a slightly aversive tinge (although it might appear surprising to suggest that water might be an aversive stimulus, the taste of pure water has probably not been an evolutionarily common stimulus for newborn human infants).

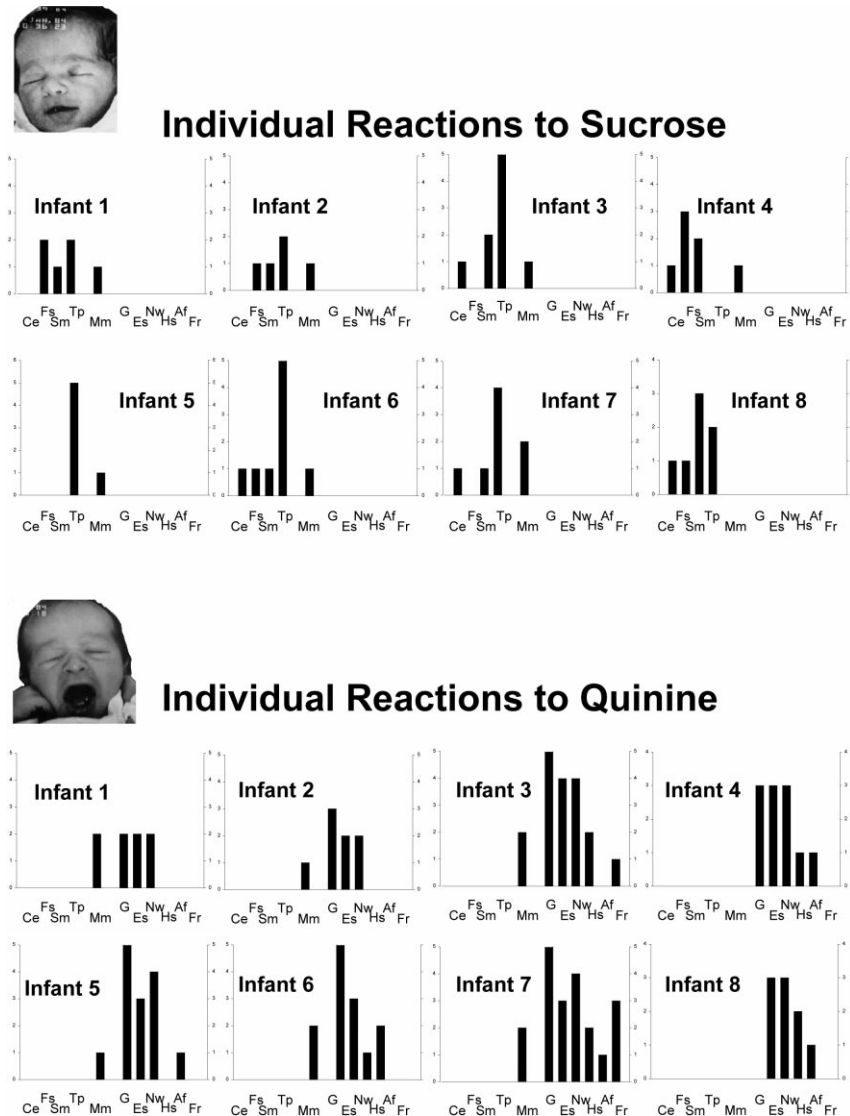


Fig. 4. Individual human infant components. Inter-individual variation in component profiles is shown by the response of identified individual infants to sucrose (top) and quinine (bottom). Labels as in Fig. 3.

3.1.3. Sour

Citric acid elicited moderate numbers of aversive gape, eye squinch, and nose wrinkle components, and a few arm flail and frown components from human newborns. An occasional positive hedonic tongue protrusion and lip smack components were also elicited. Neutral mouth movements were frequent. Thus sour citric acid appeared to have a moderate but mostly aversive palatability, eliciting mixed reactions.

3.1.4. Bitter

Quinine elicited the greatest numbers of aversive gapes, eye squinch, nose wrinkle, head shake, arm flail, and frown components from human infants (Fig. 3). Neutral mouth movements were also elicited in moderate numbers. No positive hedonic components at all were elicited by quinine. Thus quinine appeared to elicit the most pure and strongly

aversive affect of any of the taste stimuli. Gapes, eye squinch, nose wrinkle, head shake, arm flail, and frown components all shared the same 'best stimulus' of quinine. Nose wrinkle and eye squinch components were elicited from all human newborns, and gapes were elicited from seven out of eight infants (Fig. 4). Headshake and arm flail components were elicited from four infants, and 'frowns' or depression of the mouth corners was elicited from two infants. In terms of absolute number of components, most infants emitted gapes as the most numerous component, followed closely by eye squinch and nose wrinkle components, and more distantly by the other aversive components.

3.2. Sequential transitions among human infant components

For each human infant, scored transcript of reactions to

Table 1

Sequential transitions among taste-elicited components of human infants. The number of times a scored component (vertical labels) followed a previous component (horizontal labels) is shown in this table. Scores for sucrose, water, citric acid, and quinine have been combined together. Despite the ‘mixing’ of tastes and reaction patterns, components classified as belonging to the ‘positive hedonic reaction pattern’ category typically follow other components from the same hedonic category. Conversely, components classified as belonging to the ‘aversive reaction pattern’ category typically follow other aversive components. The occurrence of components from the same affective category in close sequential proximity to each other suggests that components belonging to one affective category are activated together by a taste as a coordinated affective reaction. Labels as in Fig. 3

Subsequent component	Antecedent Component										
	CE	FS	Sm	TP	MM	G	ES	NW	HS	AF	Fr
CE	10		15	15							
FS			11	29	10						
Sm	56	9	14	38	4					2	
TP	5	12	96	164	51						
MM		8	11	82	97	23	18	20		1	6
G					38	114	71	45	22	19	4
ES					16	63	7	104			
NW				8	21	12	89	16	10		
HS						16	20			9	
AF					9	14	5		12	4	
Fr					7	4					6

the four tastes were tabulated for the number of transitions between each possible pair of behavioral components. The results were collapsed across the tastes and put in table form (Table 1). Sequential transitions were not distributed evenly, but instead were restricted almost entirely to within-category pairs of affective components (Chi-square (100) = 2768, $P < 0.001$). Positive hedonic components (CE, corner elevation of the mouth; FS, finger suck; Sm, lip smack; TP, rhythmic tongue protrusion) tended to follow other hedonic components in 85% of hedonic component emissions. In approximately 14% of positive hedonic component emissions, a hedonic component followed the ‘neutral’ component of rhythmic or irregular mouth movement (MM). Positive hedonic reactions followed an aversive reaction in only 1% of transitions.

Conversely, aversive components (G, gape; ES, eye squinch; NW, nose wrinkle; HS, head shake; AF, arm flail; Fr, frown) tended to follow other aversive components almost exclusively. An aversive component followed another aversive component in 90% of all aversive occurrences. An aversive component followed a ‘neutral’ mouth movements in approximately 9% of transitions, and followed a hedonic component in only 1% of aversive component occurrences.

Thus most sequential transitions were ‘within affective category’ even when transition data were combined across all tastes (including citric acid and water tastes that elicited both positive and negative components). This appeared to support a ‘temporal contiguity’ criterion for classification of most components as belonging to either positive hedonic or aversive categories. ‘Neutral’ mouth movements served as the most common component to bridge between affective categories.

Direct alternation between components of different affective categories was extremely rare.

3.3. Positive vs negative categories of affective components

Based on the evidence above that most components could be assigned to affective categories, a combined ‘positive hedonic score’ was made by adding together scores for smile, lip smack, and rhythmic tongue protrusion components elicited from newborn human infants by each taste (Fig. 5). An aversive category score for each taste was made by adding together gape, headshake, eye squinch, nose wrinkle, arm flail, and frown.

Positive hedonic components as a group declined across

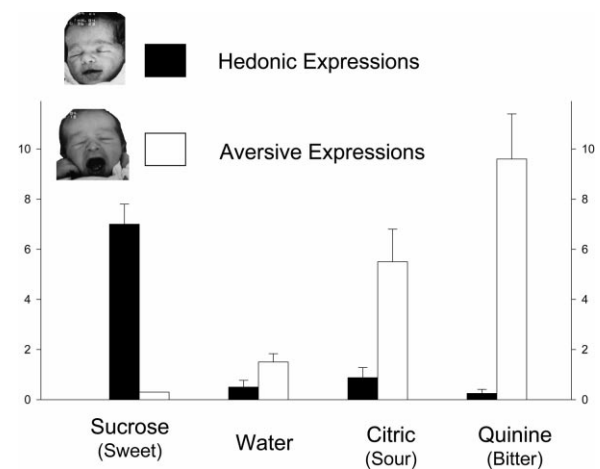


Fig. 5. Averaged positive hedonic and aversive category scores elicited from newborn human infants by each taste (mean + SEM for components averaged within each affective category).

sweet, water, sour, and, bitter taste stimuli ($F(3,31) = 50.5$, $P < 0.001$; within-subjects ANOVA). More positive hedonic reactions were elicited by sucrose than by either water, citric acid, or quinine ($P < 0.05$ in each case; Bonferroni post hoc tests). Each component within the positive hedonic category followed essentially the same pattern of decrement from sweet, water, sour, to bitter as the larger category. Positive hedonic tongue protrusions ($F(3,31) = 19.15$, $P < 0.001$), lip smacks ($F(3,31) = 7.41$, $P < 0.001$), finger sucks ($F(3,31) = 10.31$, $P < 0.001$), and lip corner elevation ($F(3,31) = 7.00$, $P < 0.002$), each changed significantly and in the same direction across the four taste stimuli ($P < 0.05$ in each comparison of sucrose to the other tastes).

The aversive category, as an entire group, also changed reciprocally to the positive category across the four taste stimuli ($F(3,31) = 21.8$, $P < 0.001$; Figs. 3 and 5). Combined aversive components were elicited more strongly by bitter quinine than by water, citric acid, or sucrose ($P < 0.05$ in each case). The sour taste of citric acid elicited an intermediate number of aversive reactions that was greater than for sucrose but smaller than for quinine ($P < 0.05$ for each comparison). Nearly every aversive component also changed together in ways similar to the larger affective category across the four tastes. Gapes ($F(3,31) = 13.46$, $P < 0.001$), eye squinches ($F(3,31) = 11.8$, $P < 0.001$), nose wrinkles ($F(3,31) = 13.93$, $P < 0.001$), and head shakes ($F(3,31) = 8.79$, $P < 0.01$) each varied significantly across the four tastes. Nearly significant changes in the same direction were also found for arm flails ($F(3,31) = 2.61$, $P = 0.079$) and frowns ($F(3,32) = 2.78$, $P = 0.066$). For gapes, eye squinches, and nose wrinkles, and head shakes, more of each component was elicited by bitter quinine than by sucrose or by water ($P < 0.05$ in each case). For gapes, eye squinches and nose wrinkles, citric acid elicited an intermediate response that was also greater than elicited by sucrose ($P < 0.05$ in each case).

It appears that most human infant components within the aversive category share an identical fate as the taste stimulus is changed, growing from sweet to sour, and from sour to bitter. Conversely, components within the positive hedonic category all share the opposite fate, diminishing from sweet to bitter. This supports the assignment of these components to positive/negative affective categories based on the criterion of shared outcome [11]. Most components we studied could be assigned to an affective category, except for two. Mouth movements as a component did not appear to belong to either the positive hedonic or aversive affective category, because the number of mouth movements was only marginally different across the four tastes ($F(3,31) = 2.78$, $P = 0.07$). It therefore failed to meet the shared outcome criterion for affective assignment in either the positive hedonic or aversive category, and instead was considered to be relatively 'neutral' in affective tone. One last facial component, lip pursing, was noted to appear only to the sour taste of citric acid and even then only on 50% of trials. This coincides with the report of Rosenstein and Oster that infants emit lip pursing only to a sour taste [95].

Because pursing of the lips seems to occur only to citric acid, it may better be regarded as a sensory reaction to the sour sensory properties of citric acid instead of as an affective reaction.

3.4. Comparison of components across primate species

3.4.1. Universal components: tongue protrusion, gape, and headshake

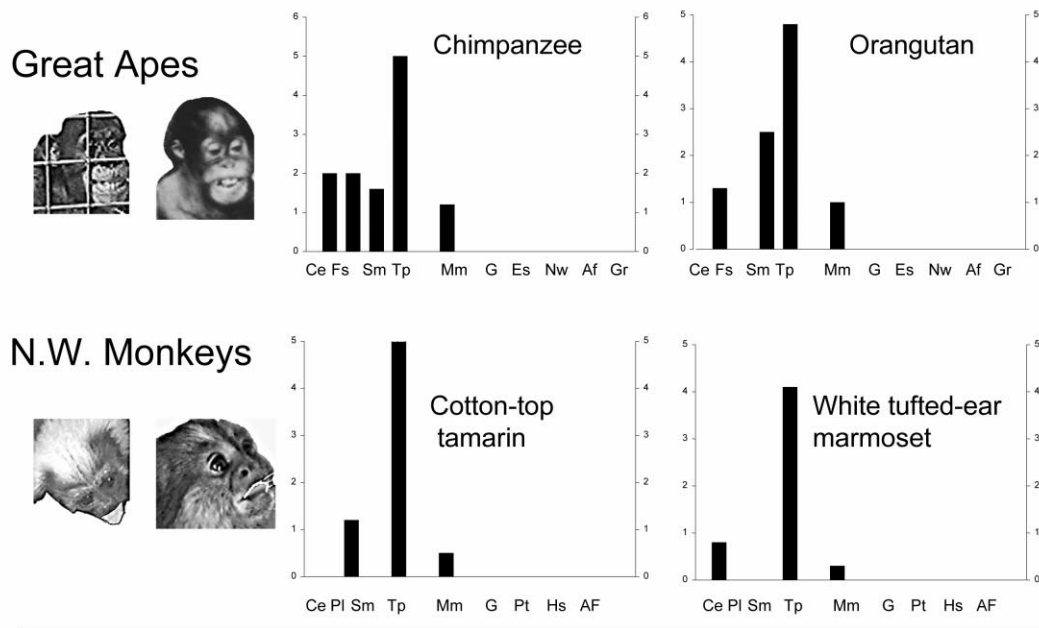
Several components were observed in primate species from every family group, and so can be considered to be essentially universal across our primate sample.

3.4.1.1. Tongue protrusion Rhythmic tongue protrusions were elicited by sucrose from every species of primate studied here (Figs. 2 and 6). We constructed a 'taxonomic tree of behavioral components' on the basis of whether different species shared this and each other particular behavioral component (Fig. 7). This type of behavioral taxonomy was first described, as far as we know, in a classic comparative behavioral study by the ethologist Konrad Lorenz [71] that traced the relatedness of waterfowl species based on the structure of their behavioral patterns. It was apparent from our behavioral taxonomic tree that rhythmic tongue protrusions to sweetness were a universal hedonic component shared by all the primate species tested in this study (Fig. 7). Tongue protrusions emitted by non-human primates were similar to those of human infants in each case, in that protrusion was oriented along the midline, and extended beyond the lips, lasting for 200 ms–1 s in duration (see below). The extent of protrusion beyond the lips, varied, however, from species to species. New World monkeys often protruded the tongue far enough to touch the nose, whereas great apes and Old World monkeys protruded just slightly past the lips.

3.4.1.2. Gape Gapes were elicited by quinine from nearly all primates (Figs. 2 and 6), including species from great ape, Old World monkey, and New World monkey groups (Fig. 7). In each of these species, a gape consisted of a rapid, large opening of the mouth accompanied by depression of the jaw, retraction of the lip corners to form a triangular mouth opening, and depressed extension of the tongue within the mouth, lasting 300 ms–2 s in duration depending on species (Figs. 3 and 4; $P < 0.01$ for all superfamily groups, Mann–Whitney U). Gapes were not observed in two of the Old World monkey species (Fig. 7), but these monkeys typically tasted the quinine solution for less than 1 s, before turning away and walking away from the experimenter.

3.4.1.3. Headshake Headshakes to quinine also were nearly universal across primates, appearing in seven of the species, including human, orangutan, and New World monkeys (Fig. 7). The adult Old World monkeys did not show head shakes, but again limited their voluntary exposure to quinine

Primate components to sucrose (4 species)



Primate components to quinine

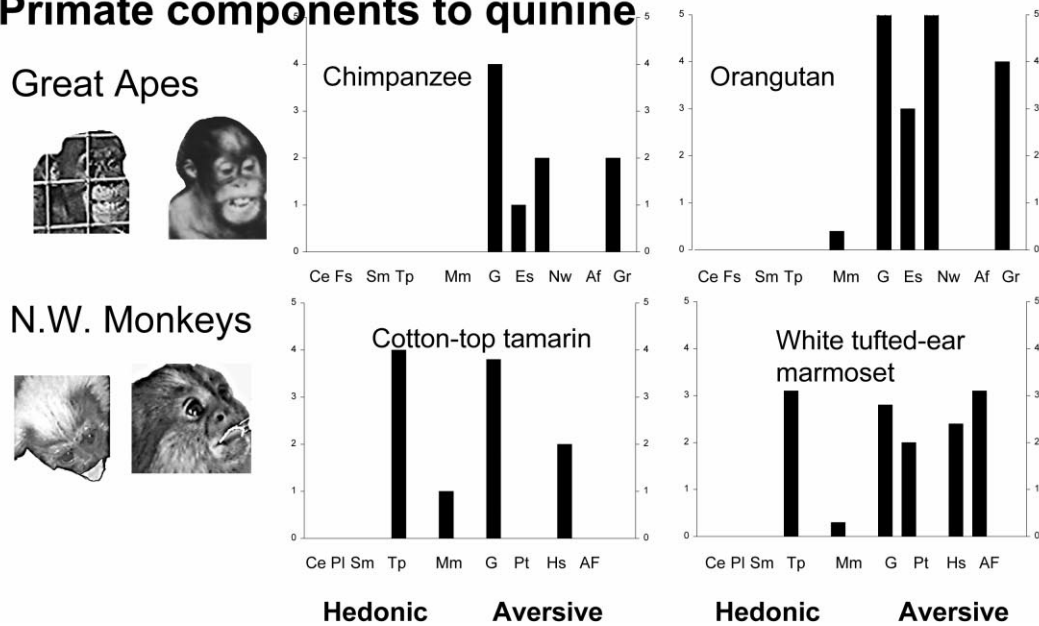


Fig. 6. Component scores for other primates (four species). Mean number of each component elicited by sucrose (top) or by quinine (bottom) from two species of great apes (chimpanzee and orangutan) and from two species of New World monkey (cotton-top tamarin and white tufted-ear marmoset) are shown. Positive hedonic lip and middle face components (e.g. elevation of mouth corners, lip smack) to sucrose were restricted primarily to great apes. Great apes also emitted middle-face aversive components (e.g. grimace, eye squinch). The taste-elicited components of New World monkey, by contrast, were dominated by tongue protrusions and by mouth, head, and limb components (gape, headshake, paw tread and arm flail). Each species, however, showed a distinct cluster of positive hedonic reaction components elicited by sucrose, and a very different pattern of aversive reaction components elicited by quinine. Symbols are: CE, corner elevation of the mouth and lips ('smile' pattern); FS, finger sucking; PL, paw licking; Sm, Smacking of the lips; TP, rhythmic tongue protrusion; Mm, irregular mouth movements; G, gape; ES, eye squinching; NW, nose wrinkle; AF, arm flail; Gr, grimace of lip and middle-face; Pt, paw treading; Hs, head shake.

to at most a second or two. Similarly, the adult chimpanzees and gorilla did not show headshakes, but dribbled the quinine out of their mouths. Among the orangutans, more energetic headshakes (and gapes) were elicited from the

infant than from adults. It is possible that further observations of Old World monkeys, chimpanzees or gorillas, especially of infants, might reveal headshakes to quinine.

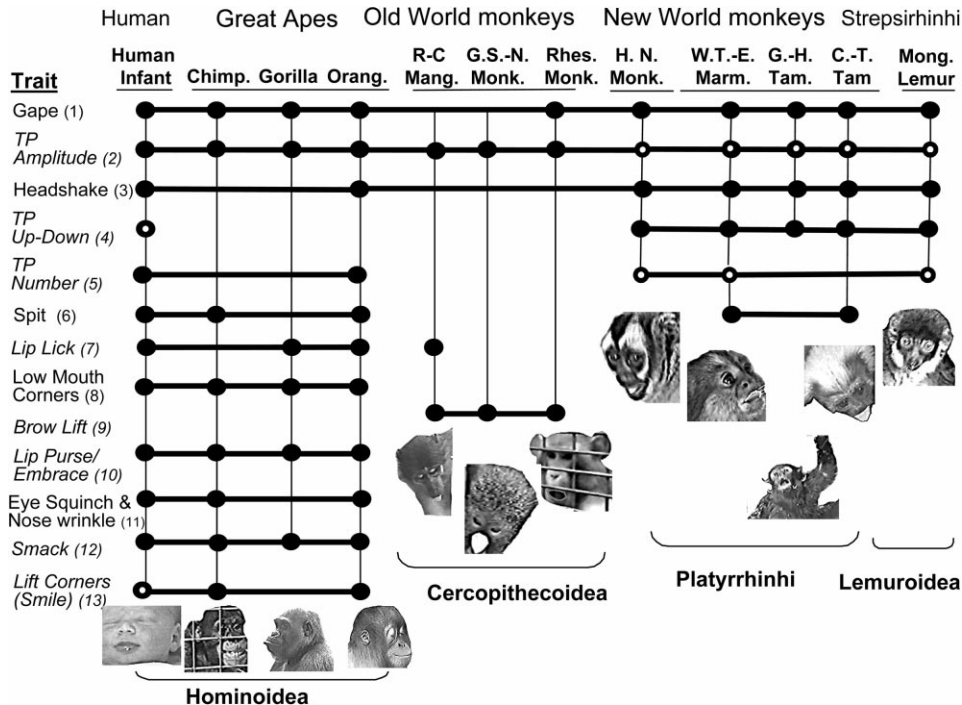


Fig. 7. Behavioral taxonomy of primate species based on whether they shared or did not share particular components of taste-elicited affective reaction. Each species is represented by a vertical line (full names in Fig. 1). Solid dots along a species' vertical line indicate possession of facial trait listed at left of dot. Horizontal lines connect species within a superfamily group if they shared a morphologically similar component. Superfamily groups are connected horizontally wherever a trait variant was shared across more than two families. Components are listed from top to bottom in order of descending frequency, as they were observed among species (positive hedonic traits to sucrose are in italics; aversive traits to quinine are in regular font). Components in descending order are: (1) aversive gapes to quinine, citric acid or NaCl; (2) tongue protrusions of larger amplitude (maximal extension) to sucrose than to quinine; (3) headshake to quinine; (4) tongue up/down coding: upward trajectory or terminal flip of tongue protrusion to sucrose, vs downward or flat trajectory to quinine; (5) greater frequency of tongue protrusions to sucrose than to quinine; (6) active spitting of quinine, citric acid, or NaCl; (7) licking of lips with lateral tongue movement to sucrose; (8) downward retraction of mouth corners to quinine; (9) brow elevation to sucrose; (10) complex pursing or sucking movements of the lips around the sucrose-containing object; (11) middle-face compression of the corners of the eyes and forehead muscles into a 'squint', and of the nose and nasolabial furrow into a 'wrinkle' to quinine; (12) lip smacking (compression of lips followed by sudden opening) to sucrose; and (13) relaxed elevation of the corners of the mouth to sucrose ('smile'). Open dots denote species-specific variations of a particular component, such as the reversal of proportion of tongue protrusions to bitter vs sweet in strepsirhine lemur and New World monkeys compared to other primates, or the U-curl variation of tongue shape shown by human infants to sucrose.

3.5. Special components restricted to taxonomic groups

3.5.1. Smile, frown, lip smack, lip purse, eye squinch, and nose wrinkle by human and great apes

Complex movements of the lips or mouth and movements involving the musculature of the middle face were seen only among hominoid species, namely, humans, chimpanzees, gorilla, and orangutans (Figs. 6 and 7). Hominoid-specific expressions involving the lips and middle face may reflect special development in facial musculature shared only by great apes and humans, such as of the triangularis, buccinator, zygomatic, levator labii, orbicularis oris, and orbicularis oculi muscles [63].

Lip smacks to sucrose and on occasion to other tastes were observed in each of the hominoid apes and humans, but not in any of the other non-hominoid primate species (Figs. 6 and 7). Lip pursing to sour was similarly unique to hominoid species. Hominoids also occasionally showed a 'smile' component to sucrose or 'frown' to quinine (component 13 in Fig. 7), while no other primate ever did. The

gorilla was observed to show depression of the mouth corners to quinine, but not elevation to sucrose. Elevation of mouth corners into a smile-like pattern was seen occasionally in orangutan and chimpanzee, but typically was not accompanied by elevation of the cheeks (Fig. 6). Unique hominoid components of facial expression to sucrose also included positive hedonic reactions such as relaxation of the corners of the mouth, and a series of richly-patterned rhythmic sucking movements by the lips (components 7, 10, and 12 in Fig. 7).

Only human infants showed the combined rapid elevation of the cheeks and corners of the mouth that could be unambiguously classed as a 'flashbulb smile' (because the sudden pattern seemed to 'light-up' the infant's face), sometimes accompanied by cheek elevation (i.e. a Duchenne-type smile pattern [75]), appearing as a rapid (200 ms) transition from relaxed mouth corners to maximum elevation of mouth corners (sustained for 500 ms–2 s). Full Duchenne smiles were shown only by human infants, only to sweet tastes, and even then only rarely (Figs. 2 and 3).

The great apes were similar to humans in emitting several complex movements of the middle face, such as nose wrinkle and eye squinch, in response to quinine and sometimes to citric acid. These components often occurred in close temporal association, in orangutan, chimpanzee, and human infant, suggesting that they were related forms.

3.5.1.1. Grimace by great apes A facial pattern we called grimace, involving the lips and middle face, was evoked by quinine only from great apes, such as chimpanzee, gorilla, and orangutan (Figs. 2, 6, and 7). Grimace was characterized by retraction of the mouth corners together with retraction of the lips away from the teeth, and contraction of middle face muscles (Fig. 2). The corners of the mouth as well as the upper and lower lips were retracted away from the teeth in most grimaces, producing a distinctive ‘bare toothed’ appearance. At the same time, muscles of the nasolabial fold and upper medial cheek often appeared drawn upwards slightly, toward the nose, giving an impression of middle face involvement. Grimace was different from frown in that there was retraction of the lips all around the mouth in addition to retraction of the mouth corners, and was different from eye squinch and nose wrinkle in that there was milder contraction of middle face muscles.

New World and Old World monkey superfamily groups showed their own distinctive microcomponent patterns of facial expression (Figs. 6 and 7). For example, all the platyrrhine (New World) monkeys and the strepsirhine lemur produced tongue protrusions to bitter quinine as well as to sucrose, and actually emitted more protrusions to quinine than to sucrose, whereas all other primates produced tongue protrusions primarily to sucrose but not to quinine ($P < 0.002$, Mann–Whitney; Fig. 7). Additionally, New World platyrrhine monkeys, which emitted tongue protrusions to all tastes, coded the sweet/bitter difference in a distinct fashion by the shape of their tongue trajectories (Figs. 2 and 7). Sucrose elicited a tongue trajectory that often terminated in an upward flip toward the nose whereas quinine elicited a downward trajectory toward the chin ($P < 0.001$, Chi-square test). The strepsirhine lemur also shared the up/down tongue coding of bitter vs sweet. No other primate shared this up/down particular pattern of tongue trajectory to discriminate between sweet or bitter tastes. Human infants, however, did occasionally elevate the lateral edges of the tongue, forming a U-shaped curl, in tongue protrusions to sucrose (Fig. 3), whereas bitter and other tastes evoked only the downward tongue depression into the floor of the mouth associated with gapes (traits 2 and 5 in Fig. 4). A separate family-specific hedonic reaction was found for cercopithecoïd (Old World) monkeys, in which all tested species showed a distinctive brow elevation (300–1500 ms duration) emitted irregularly to sucrose, but never to quinine (Fig. 7).

The number of positive hedonic vs aversive components emitted by each species varied appropriately across the

tastes similar to human infant components. For example, Fig. 6 shows quantified mean component scores elicited from four non-human primate species. The reactions of two great ape species (chimpanzee and orangutan) and two New World monkey species (white tufted-ear marmoset and cotton-top tamarin) were selected as examples for depiction of differences in response to sucrose vs quinine. Differences and similarities across species both can be seen in the pattern of reaction components. The great apes show middle face components in response to both sucrose (e.g. lip smacks and mouth corner elevation) and quinine (e.g. grimace and nose wrinkle), whereas the New World monkeys lack those components, and show a greater dominance of tongue protrusions in component profiles elicited by both tastes (Fig. 6). In all cases, however, a distinct positive hedonic pattern or constellation of components was elicited as a group by sucrose for each species (Fig. 6). Conversely, a distinctively different aversive pattern of components was elicited as a group by quinine. For all species, the positive hedonic pattern to sucrose included tongue protrusions, and the aversive pattern to quinine included gapes and headshakes. In other respects, the pattern of components contained within hedonic/aversive patterns varied systematically across species, with components becoming less shared as phylogenetic distance increased (Fig. 7).

3.6. Timing parameters of primate components

Certain components, such as tongue protrusions, appeared similar in form across all the species we examined. However, the duration of such components was quite different between species, raising the question of whether the component should be considered the ‘same’ or not. Our analysis of microcomponent timing focused on the component that was most stereotyped in duration, rhythmic tongue protrusion. The rhythmic cycles were highly stable within a single individual. The cycle duration of successive rhythmic protrusions was timed by counting the number of video frames between the emergence of the tongue past the lips that began one cycle and the beginning of the next protrusion that marked the next cycle’s beginning. Mean durations were obtained for each individual, and used to calculate the relation between component duration and mean body weight of the species.

3.6.1. Adult allometry

First, we selected data from adults only [gorilla, chimpanzee, rhesus and mangabey Old World monkeys, marmoset and golden-handed tamarin New World monkeys, and lemur; Fig. 8(a)] and performed a non-linear regression analysis using an allometric two-factor power equation ($y = ax^b$) [101]. A strong direct relation was found between the cycle duration of tongue protrusion movements and a species average adult body weight (regression ANOVA $F(1,17) = 259$, $P < 0.001$; Fig. 8). Plotting component

duration in ms as y , and body weight in kg as x , the allometric equation $y = a \times x^b$, predicted duration from body mass with equation constants of $a = 0.21$ and $b = 0.37$, and with a correlation value of $r^2 = 0.94$.

3.6.2. Infant allometry

In a separate allometric analysis, data from infants (human, orangutan, marmoset, and cotton-top tamarin) were selected for a similar analysis [Fig. 8(b) and (c)]. When the infant's own small body weight was used as the x -value, there was a direct relationship between body weight

and the cycle duration of tongue protrusions [$F(1,11) = 66.2$, $P < 0.001$; Fig. 8(b)]. Infant component duration increased with body weight with a slope similar to that of adults: $b = 0.34$ for the allometric equation $y = a \times x^b$, and $r^2 = 0.86$. Thus the rate of increase (b constant) was similar for both infants and adults. However, the value of the a constant for infants ($a = 0.83$) was much larger than for adults, indicating that body weight had to be multiplied by a larger constant to predict behavior timing. In other words, infants appeared much slower than adults, kilogram for kilogram, in the duration of their components.

We noted, however, that infants and adults of the same species had similar absolute durations for component movements in the two species where both adult and infant data were available. For example, tongue protrusion cycles for adult orangutans were between 780 and 940 ms, and the average cycle duration for the infant orangutan was 880–920 ms. Similarly, average cycle durations for adult white tufted-ear marmosets were between 210 and 230 ms, and the average duration for the infant marmoset was 240 ms. These observations suggested that infants and adults of the same species were both following the same underlying timing rule. If so, then the allometric equation values for infants would be more similar to those of adults if the infant equation was calculated using observed infant durations as the y -value using average adult weight for the species as the x -value, rather than actual infant weights.

We therefore replotted the allometric relationship for infant timing but plotting the horizontal axis using their species' average adult body weight [Fig. 8(c)] [35]. The results confirmed our expectation that infants obeyed the 'adult allometry law', and that their equation parameters were similar to adults' when plotted as a function of species' adult size. Again, a direct relation was found between movement timing and average species weight [$F(1,11) = 88.3$, $P < 0.001$; Fig. 8(c)]. Infant tongue protrusion duration increased with species adult body weight following the allometric equation ($y = a \times x^b$), with a correlation value of $r^2 = 0.89$. Similarly the a and b constants for the ($y = a \times x^b$) equation remained essentially equivalent to those of adults: $a = 0.29$ and

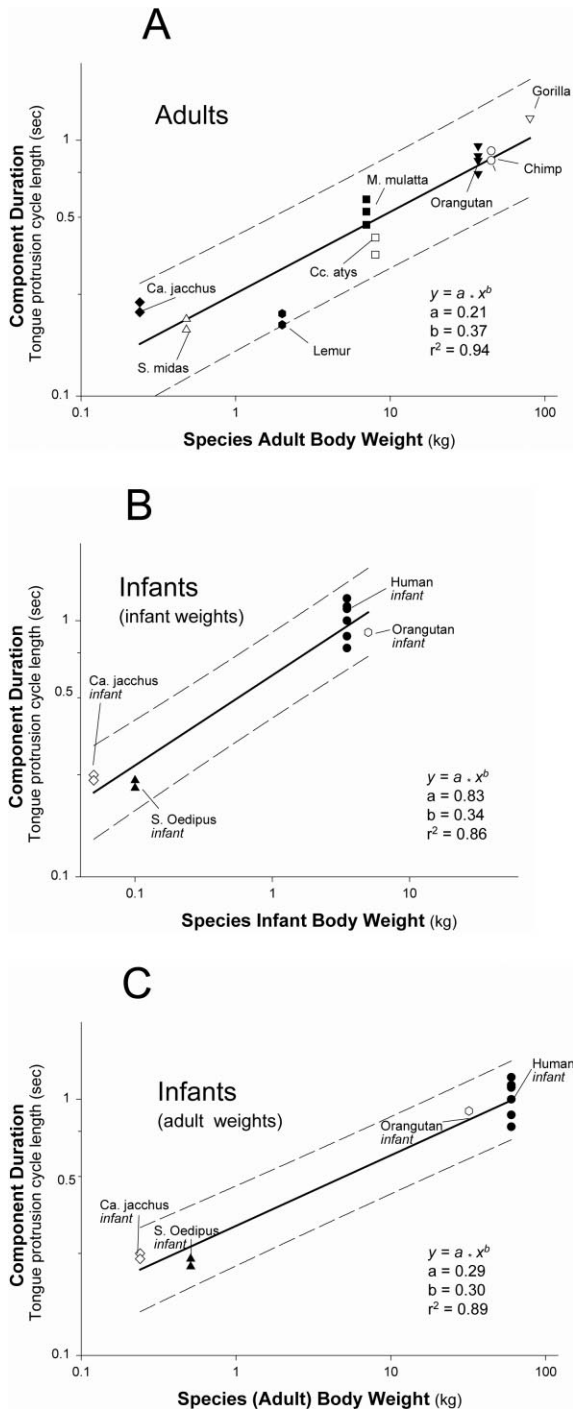


Fig. 8. (a) Adult allometric relation between timing of component duration and body weight (adult primates only). Labeled points show the observed cycle length (in s) of tongue protrusions that were elicited by sucrose plotted along the vertical axis (logarithmic scale). Identical point symbols denote individuals of the same species and age group. Horizontal axis shows average adult body weight of each species (in kg from [35]; logarithmic scale). Solid line shows calculated regression of the allometric relation, where cycle duration = $a(\text{body weight})^b$. Dashed lines denote 95% confidence prediction interval. (b) Infant allometric relation between timing of component duration and body weight (infant humans and other primates only). In this analysis, the infant allometric relation was calculated using infant weight for the x -value and for plotting along the horizontal axis. (c) Infant allometric relation between timing of facial expression and body weight (infant humans and other primates only). In this re-analysis, the infant allometric relation was recalculated using species' adult weight for the x -value, and for plotting along the horizontal axis.

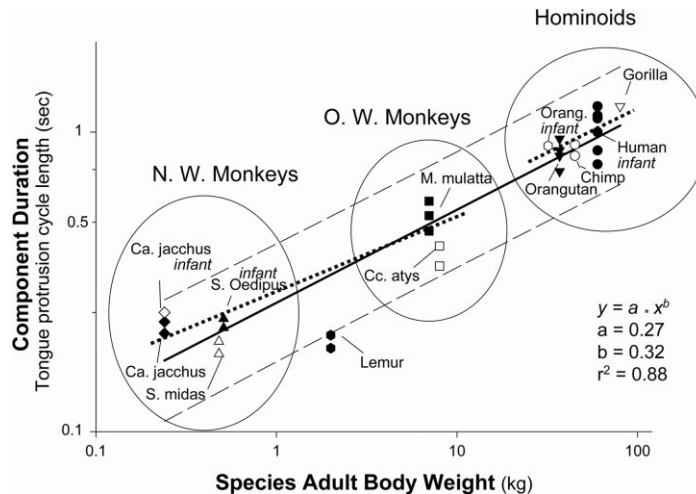


Fig. 9. Total allometric relation: all ages and species combined (based on species' average adult weight). Circles group together species belonging to the Hominoid (humans and great apes), or Old World monkey, or New superfamily groups. Solid line depicts predicted allometric relation based on the equation derived from *all* species and ages combined (duration = $a \times (\text{body weight})^b$). Dashed lines depict 95% confidence interval. Calculated values for a and b constants based on the total combined analysis and for r^2 correlation between duration and adult species weight are shown at right. Dotted lines show separate allometric relationships calculated for subgroups: (humans and apes) vs (Old and New World monkeys). Calculated values for subgroups are given in the text.

$b = 0.30$. Thus component timing for both infants and adults appears to be scaled allometrically to the average adult weight of the species, and both follow the same allometric relation based on that weight.

3.6.3. Overall allometry

Since adults and infants showed similar allometric functions based on average adult species weight, we combined all individuals together for a further allometric analysis (Fig. 9). This increased the number of observations sufficiently so that separate analyses could be run independently on taxonomic subgroups, in order to test whether similar relations held for more closely related subgroups with more similar body weights. An analysis was carried out on the combined hominoid species (humans and great apes) and a separate analysis was carried out on the combined cercopithecoïd and platyrrhine species (Old World and New World monkeys). For humans and great apes considered alone, the values of the allometric equation $y = a \times x^b$ were $a = 0.26$ and $b = 0.33$ ($r^2 = 0.82$). For Old World and New World monkeys considered alone, the allometric constants were $a = 0.26$ and $b = 0.21$ ($r^2 = 0.94$). Finally, when all primate species (humans, great apes, Old World monkeys, New World monkeys, lemur) were considered together, a strong direct relationship existed between component duration and average species adult weight ($F(1,27) = 404.8$, $P < 0.001$). The final allometric constants for the equation $y = a \times x^b$, when *all* primate species and ages were included, were $a = 0.27$, and $b = 0.32$ ($r^2 = 0.89$) (Fig. 9).

Thus large-bodied primate species tended to have longer component durations than did smaller species. The allometric relationship was robust. The timing appears determined by the

average species size and not an individual's own size, as indicated by the constancy of timing across infant and adults of the same species. In other words, infants and adults follow the same species-specific timing rule. The species-specific timing rule obeys allometric predictions in every case (Fig. 9). Human infants emitted rhythmic tongue protrusions at a rate of roughly 1/s ($x + \text{SEM} = 1.03 \text{ Hz} + 0.07$; Fig. 5). The cycle rate for chimpanzees ($1.15 + 0.05$) and orangutans ($1.17 + 0.02$ observed $x + \text{SEM}$) appeared to be just slightly faster than humans, which corresponds to their slightly smaller adult size. Gorilla tongue protrusion cycles were just slightly slower ($0.82 + 0.06$) than the human cycle ($F(3,16) = 5.12$, $P < 0.02$), corresponding to their larger size. New World monkeys, by contrast, had cycles that were uniformly four to five times faster than humans ($F(3,14) = 374.72$, $P < 0.001$). The New World monkey species studied here weigh between 250 and 500 g as adults and had cycles ranging from 4.1 to 5.4 Hz (Fig. 9).

A similar allometric relationship between microcomponent timing and body weight was observed for gapes (elicited by bitter and sour tastes), whose duration for each species tended to quite similar to its tongue protrusion cycle. For example, a human infant gape to quinine lasted $1.20 + 0.18$ s (whereas spontaneous yawns lasted 3–6 s), and the gapes of New World monkeys ranged between 0.2 and 0.3 s in duration (both infants and adults). In each case, the duration of gapes obeyed the allometric timing relationship between speed and body mass. Thus although a 'slow' human infant and a 'fast' New World monkey appear to be operating at different speeds when they emit a gape (or a tongue protrusion, etc.), in an allometric sense they are both doing the same thing.

4. Discussion

Our results indicate that quantitative taste reactivity scoring procedures can be used to measure both the affective valence and the affective intensity of taste-elicited reactions elicited from human infants or from non-human primates. Affective component profiles, or combined affective totals based on time-bin scoring procedures, provide a sensitive readout of the affective intensity of reactions for positive (hedonic) affective reactions as well as negative (aversive) affective reactions. Individual variation in the profiles of taste-elicited affective reaction components can be compared across different infants. And affective reactions may be compared objectively across species, in terms of the pattern of components that constitute a species' affective reaction to a taste stimulus, in terms of the microcomponent timing of a particular affective reaction component, and in terms of the relative valence of stimuli.

4.1. Cross-species comparison of affective reactions

The pattern of affective reaction components changed in a graded fashion across primate species. From human infants to great apes to other family groups, the pattern changed across species both in terms of the type of components constituting an affective reaction (e.g. whether it included smile, tongue protrusion, grimace, gape, etc.) and in terms of the microstructure of particular components (e.g. the shape and duration of a tongue protrusion).

Two determinants of systematic variation were identified. The first was the degree of phylogenetic relatedness between species. The evolutionary relationship among species was relevant to determining which components were used in an affective reaction. Phylogenetic relatedness was so important a determinant of component type that a 'behavioral taxonomic tree' could be constructed on the basis of whether a particular type of component was displayed by a species. The behavioral component-based tree essentially mirrors the actual phylogenetic relationships among the species (Fig. 7), reminiscent of classic ethological comparative studies [71].

4.2. Special hominoid affective reactions: human infants and great apes

Our behavioral taxonomy indicated that the affective facial reaction patterns of humans were strikingly similar to those of great apes in terms of their shared components. Human infants and great apes shared more components in common with each other than either shared with the other species (and humans and great apes were about as similar to each other as Old World monkey species were to each other, or as similar as New World monkeys were to each other). Humans and great apes belong to the same superfamily group (Hominoidea) and are believed on the basis of DNA and fossil evidence to have shared a common ancestor within approximately the last 10–20 million years [109]. By

contrast, hominoid ancestors are believed to have diverged from those of Old World monkeys much earlier, on the order of 20–40 million years ago, and ancestors of Old World monkeys diverged from those of New World monkeys even earlier, between 35 and 60 million years ago [2].

4.3. Species-typical components vs universal components

The taxonomic influence on component types meant that certain affective reaction components were shared only by primate species within a particular Hominoidea, Cercopithecoidea, or Platyrrhini phylogenetic groups. For example, only human infants and great apes (Hominoidea) displayed 'smiles', that is, elevation of the corners of the lips and mouth, in response to sucrose, and only human infants displayed a full-blown Duchenne smile, in which the mouth and lip movement was accompanied by crinkling of the eye corners. However, other affective reaction components appeared to be relatively universal, being shared by members of all primate species that were tested. Among universal affective reactions were positive hedonic components such as rhythmic tongue protrusions, which were elicited by sucrose from human infants and from great ape, Old World monkey, New World monkey, and Eulemur species. Certain aversive reactions were also universal, such as gapes, which were elicited by quinine and citric acid from primate species of all superfamily groups, from humans through New World monkeys. The universality of such positive hedonic and aversive taste-elicited components across species is supported by observations of similar affective taste reactivity components in non-primate animals. For example, rodents such as rats emit positive hedonic patterns of rhythmic tongue protrusions, etc., to sucrose, vs aversive patterns of gapes, head shakes, arm (paw) flails, etc., to quinine [9,20,56], carnivore domestic cats emit tongue protrusion "lip licks" to preferred foods [112], and even avian chicks emit distinctive gapes to bitter tastes [49]. Such widespread occurrence raises the possibility that certain affective reaction components to taste may have arisen very early in mammalian evolution (or even earlier vertebrate evolution).

4.4. Relationship of natural diet to positive affective reaction to sweetness

It is striking that positive hedonic reactions were observed to sucrose for all primates studied here, regardless of their natural diet. This is consistent with reports that most primate species that have been tested for taste preferences tend to prefer sweet tastes such as sugars, and to reject bitter tastes, such as quinine [5,69,92,93,110]. For the primates studied here, some species have a natural diet in the wild composed largely of fruits (e.g. orangutans). However, other of our primate species are primarily folivorous in the wild (e.g. gorillas) or even insectivorous (e.g. cotton-top tamarin). Still, virtually all have been reported to eat fruits in the wild at least on occasion, and all the subjects here had

the opportunity to eat fruits in captivity while living at the zoo. Exposure to sweet fruits in the captive diet may provide one possible explanation for the unanimous positive reaction to sweetness we observed, by facilitating a learned taste preference conditioned by the sensory qualities of sugars themselves or by their post-ingestive consequences [52,102].

An alternative possibility is that similar positive reactions to sucrose might be shown by wild conspecifics of all our primate species—even those that have not eaten fruits. If so, then a tendency for sweetness to elicit positive affective reactions might have evolved early in fruit-eating ancestors of primates, and simply persisted even after subsequent diet specializations by some species into alternative foods such as leaves, insects, etc. In that case, the taste of sucrose may simply trigger a pre-adapted tendency to respond with positive reaction to sweetness, which might ordinarily never be triggered in the natural lives of some leaf-eating or insect-eating species. Yet another alternative explanation for sweetness preference might derive from exposure to natural sugars in the taste of milk during suckling in early life of infant primates (although against this explanation it should be noted that some species, such as cats, are suckled in infancy but do not show preferences for sweet tastes in adulthood [5]).

In general, it can be noted that preference for sweetness has been found to be widespread for many mammalian species (though not all) in which the natural adult diet is not sweet [59,69,78,93,97]. Thus the question of why sweet tastes should be generally pleasant for eaters of non-fruit diets is not restricted to primates [5]. But regarding primates specifically, it would be of interest in the future for studies to examine further the relative influence on affective reactions to sweetness of natural diet (for example, to see whether specialization of certain species to a diet of bitter leaves reverses affective reactions to quinine and sucrose) and of captivity diet (for example, to see whether inclusion of fruits or other sweet foods specifically enhances subsequent affective reactions to the taste of sucrose).

4.5. Component microstructure: shape and duration

Microstructural aspects of component shape were also influenced by taxonomic relatedness, at least to a degree. For example, New World monkeys in the present study altered the shape and trajectories of their rhythmic tongue protrusions in response to pleasant vs unpleasant tastes. Sucrose elicited upwards protrusions of the tip of the tongue, sometimes extending up sufficiently to touch the nose, whereas quinine elicited downwards projections, parallel to the surface of the lower lip and chin. All species of New World monkey showed this modulation of tongue protrusion shape, but no Old World monkey, great ape, or human ever did.

4.6. Component duration: allometry and species body size

The strongest determinant of component microstructure, regarding duration, was an allometric rule based on the average adult body size of the species. Allometric control of behavioral duration applies to many aspects of movement, from heartbeat to walking cycle [101]. For taste-elicited affective reactions, allometry was most evident for components that were temporally stereotyped such as gape duration and the cycle duration of rhythmic tongue protrusions. Allometry implies that species may follow similar generative rules in producing the same behavioral component, even when the final outputs appears different in timing to a casual observer. When allometry is taken into account, the timing relationship was seen to reflect the same generative rule for all the primates we examined, including humans.

The allometric rule was that movement duration corresponds to body size, but duration increases less dramatically than body size as both rise because the exponent b -value was less than 1.0 in the allometric equation, $\text{duration} = a(\text{body weight})^b$. An exponential value close to 0.3 means that movement duration (in s) does not double with a doubling of body weight (in kg), but rather requires a much greater increase in the absolute body weight of the species. For example, the tongue protrusion cycle lengths of a human infant or a gorilla last about 1 s, twice the half-second duration of protrusions by an Old World rhesus monkey (*Macaca mulatta*), but even human and gorilla adults weigh nearly ten times more than those monkeys.

Although the duration and shape of facial expression components could be influenced in principle by the physics of anatomy (i.e. from body size, as the size of a clock pendulum determines its speed), it was clear from our comparison of infants and adults from the same species, that the allometric relationship was centrally programmed. That is, the most important source for the allometric timing rule appeared to be a species' brain, rather than the actual body. This was indicated by the observation that infants follow the timing rule appropriate to the average adult weight for their species, rather than to their own much lesser infant body weight. Similar pre-programming of adult timing parameters has been found in other types of stereotyped movement made by young rodent pups [26]. The crucial factor for allometric timing could not have been actual brain weight, any more than actual body weight, since infants would have had much smaller brain weights than adults of the same species, just as they had smaller body weights than adults. Instead the difference must lie in the detailed synaptic connectivity and neuronal processing within neural circuits that code movement timing.

Why should the brain of infant mammals be programmed in advance to follow adult-like timing parameters? The reason may be because the importance of well-coordinated movement is highest for adults, who have no caregivers to protect them from the consequences of clumsiness, and so

evolution has favored the selection of timing parameters that ensure competent adult movement. The central pattern generators that code these species-specific timing parameters are likely to lie in hindbrain motor nuclei and the brainstem reticular formation, since it has been demonstrated that both anencephalic human infants [105] and decerebrate rodents [57] have normal patterns of taste-elicited movements. The affective valence and affective intensity of reaction patterns, however, are also controlled hierarchically by neural circuits in the forebrain [27,54,86,100].

Behavioral homology is always difficult to infer with absolute certainty (pessimists might say impossible). But homology can be inferred with graded certainty, as the comparative primate psychologist William A. Mason has pointed out [74]. Mason suggested that confidence in homology grows with: (a) the number of related species that can be seen to share the trait (with highest sharing among the most closely related species); (b) the number of specific similarities that can be observed regarding the trait; and (c) the number of levels of organization (e.g. behavioral vs neural) at which similarity occurs [74]. Sharing an allometric timing rule for generating an affective reaction is not by itself proof that the affective reaction is the same homologous reaction in humans and other primates. But it adds an additional specific similarity, and perhaps even another level (within levels of behavioral organization) of similarity (also raising the possibility of similar neural substrates). Taken together with the similarities of movement patterns, component groupings, and shared outcome across different tastes, shared allometry gives further confidence that these are the 'same' homologous affective reactions in humans and other primate species.

4.7. *Affective nature of reaction patterns*

Tastes such as sweet, bitter, sour, and salt differ in both their sensory properties and their affective properties, and so it is important to distinguish whether the reaction patterns we observed reflected a response to pleasant/unpleasant affect or to sensation. Several observations support the conclusion that these components were constituents of affective reaction patterns and not sensory reflexes (except for mouth movements and lip pursing, which belonged to neither positive hedonic or aversive category). All components belonging to an affective category were elicited best by the same prototypical stimulus (positive hedonic = sweet; aversive = bitter), but were also elicited together in lesser numbers by other intermediate stimuli (water, citric acid). Even when positive hedonic and aversive reaction patterns were elicited together by a 'mixed affect stimulus', such as sour citric acid, components belonging to the positive hedonic category tended to follow one another sequentially, whereas components belonging to the aversive category tended to follow other aversive components.

Finally, shifts in the magnitude of one hedonic component, caused by changing the taste stimulus, were accompanied by similar shifts in the magnitude of other hedonic components. Conversely, these changes were accompanied by reciprocal shifts in the opposite direction in the magnitude of most aversive components.

An even stronger case for affective classification could be made if shifts in the affective pattern of taste-elicited responses were produced by changes in the infants' physiological state (e.g. deprivation vs satiety) or psychological state (e.g. via conditioning of a taste preference or aversion). We did not attempt to manipulate the physiological or psychological states of the infants in this study. However, a classification of facial reactions as affective in nature based on the criterion of shared outcome after physiological manipulation [11] is supported by the report of Crystal and Bernstein that a concentrated salty taste elicits fewer aversive components from human infants of mothers who may have experienced physiological sodium depletion during gestation than from infants who were never sodium deprived [28]. In that case, negative affective reactions were different across infants, even though the taste stimulus was identical for all infants, as a consequence of the palatability-relevant physiological manipulation.

For all of these reasons, we conclude that the pattern of components we have described reflect the positive hedonic impact or aversive impact of a taste for human infants and other primate species, rather than being a simple reflexive response to the sensory properties of a taste. This affective interpretation is consistent with one that has been applied to the taste-elicited behavioral reactions of other mammalian species, for which the evidence for 'affective tracking' is more clear [11]. The only exceptions to our affective classification were two components, irregular mouth movements and lip pursing. Irregular mouth movements were emitted to virtually *all* tastes and appeared to reflect a 'neutral' or evaluative response, rather than a positive hedonic or aversive reaction. That is, the response cannot be unambiguously assigned to either affective category, although it may sometimes accompany reactions that are strongly affective. It is possible that 'neutral' responses serve a function related to affect, such as to further evaluate the taste stimulus for affective classification (by exposing it to a larger tongue/mouth region) without being affective reactions themselves, or else might serve a purpose that is entirely non-affective, such as to facilitate the movements used in ingestion. In any case, the classification of irregular mouth movements as neutral is consistent with a similar classification accorded to rhythmic mouth movements by studies of rodent taste reactivity [16,54]. Lip pursing, conversely, was elicited from human infants and great apes only by sour citric acid, and not by any other taste stimulus. Lip pursing was not associated with either positive hedonic or aversive constellations of other

components, which supports the suggestion of Rosenstein and Oster that it may be a sensory-based reflex to a specific sensation of sourness [79,95].

Taste and smells may be especially useful stimuli modalities for assessing affective impact in human infants and other primates. Although thermal, acoustic, and tactile stimulation also induce differential behavioral responses in newborn infants, none of these other sensory modalities may have the clear bipolar affective organization of positive/negative behavioral patterns evoked by pleasant vs unpleasant gustatory and olfactory stimuli.

4.8. Are primate affective facial reactions to taste social signals?

Do affective facial reactions to taste serve to convey emotional information to conspecifics for all primate species that display affective reactions? The answer is unknown. Emotional expressions among non-human primates often have been documented in social situations, and several authors have suggested that emotional facial expressions do serve primarily to communicate social dispositions and intentions for non-human primates [1,25,62,111], as they do for humans [46,47,66,72]. The term “signal” is sometimes taken to mean a referential act performed in order to convey information to another individual. If affective displays were viewed as signals in that strongly informational sense, it might be difficult to imagine why a primate would emit a display unless a perceptive observer were present. However, another view is that animal signals are typically motivational, emitted in direct response to a specific motivational state, even when also referential [73]. The question here is whether the affective reactions displayed by any particular non-human primate species should be regarded as purely motivational or as motivational plus referential.

All of our primates displayed affective facial reactions. Those reactions contain affective valence information that potentially could be detected and used by conspecific observers. But use as a social signal requires conspecifics to have a perceiver system for detecting and decoding the information in a display. As Owings and Morton describe in a recent analysis of signal evolution, display systems and perceiver systems may evolve independently, because each may be subject to its own selection factors [80]. Perceiver systems for facial expressions are well developed in humans, for whom the mere visual recognition of facial expressions for emotion, such as disgust, is reported to trigger distinct circuits in a human observer’s brain [89]. It is simply not yet clear whether perceiver systems for affective facial expressions to taste also exist in non-human primates, and if so then whether in all our species or merely in some species (e.g. certain great apes?).

An explanatory alternative to social communication for the evolution of affective displays comes from a source as old as Darwin’s original ‘principle of serviceable habits’

[29], which suggested that useful reactions might have become stereotyped and expressive without ever being used for social communication. Regarding taste reactivity, the movement patterns involved in hedonic tongue protrusions, etc., generally serve to promote increased sensory exposure of taste buds to the pleasant stimulus, and to facilitate ingestion (although taste reactivity patterns track affective evaluation and not the decision to ingest under conditions where the two diverge [11]). Conversely, aversive gapes, head shakes, etc., tend to eliminate a noxious stimulus from the mouth. Positive and negative reactions programmed at the level of the brainstem may have originally been selected for these purposes in the service of a basic affective evaluation of the stimulus, independent of their potential communicative role. If the reactions evolved in that way, then the further evolution in any species (e.g. humans) of perceiver systems to decode the affective information potentially available would convert the affective displays into true affective signals—but only in species that evolved the appropriate perceiver systems. The universal sharing of certain components patterns (e.g. hedonic tongue protrusions, aversive gapes) by all primate species, and by some non-primates, and even by some non-mammals for components such as gapes, makes this alternative at least worth considering. In any case, the ubiquitous sharing of certain affective reaction components by all the primate species studied here suggests that those components appeared quite early in evolution, and before the divergence of primate taxonomic groups.

4.9. Caveats and future directions

Although this study examined more primate species in its comparison to humans, and in more detail, than any previous study we know, the data set remains smaller than could be wished. It would be of interest to examine still more primate species, especially those that have more highly specialized diets (e.g. a preference for bitter leaves). Future studies are needed also to expand the data set for the species that were included here, as a larger data set would allow application of quantitative techniques of systematic comparison for analyzing cross-species relationships, in order to confirm our conclusion that the degree of behavioral similarity across species parallels their taxonomic relatedness. Finally, it would be of great interest to compare infant and adult affective reactions more explicitly within the same species, especially for the great ape species. We had the impression that tastes elicited stronger affective reactions from infants than adults, especially from our infant orangutan compared to older juvenile or adult orangutans. While suggestive, this is not enough evidence to conclude whether infants have more pronounced affective reactions than adults, since direct infant vs adult comparisons could be made only for a few orangutan and New World monkey individuals. The issue would be especially interesting to pursue in other great apes. Would infant chimpanzees or

infant gorillas show stronger affective reactions than their adult conspecifics (as seems to be the case for human infants vs adults)? That is a question that only future research can answer.

5. Conclusion

Affective reaction patterns of human infants to taste are unique, compared to other primates. However, human affective patterns appear to be related systematically to those of other primate species. No two species of primate have exactly identical sets of behavioral components to sensory pleasure or displeasure, but the difference among them is merely quantitative and graded rather than categorical. Humans are at least as similar to some great apes in their components of affective reaction as some species of non-human primates are similar to each other. And human infants share some components of taste-elicited affective reactions in common with all the other primate species examined in this study. This identification of relationships between human and non-human primate facial patterns helps place human affective reaction into a larger comparative context for considering its psychological and biological nature [10,24,29,74]. The intensity of positive affective reactions may be usefully assessed and compared to the intensity of negative affective reactions by quantitative analyses of behavioral affective taste reactivity patterns, even in creatures that cannot speak about their affective reaction, such as a human infant, great ape, or monkey.

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