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Perceived Differences Between Chimpanzee (*Pan troglodytes*) and Human (*Homo sapiens*) Facial Expressions Are Related to Emotional Interpretation

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Human face perception is a finely tuned, specialized process. When comparing faces between species, therefore, it is essential to consider how people make these observational judgments. Comparing facial expressions may be particularly problematic, given that people tend to consider them categorically as emotional signals, which may affect how accurately specific details are processed. The bared-teeth display (BT), observed in most primates, has been proposed as a homologue of the human smile (J. A. R. A. M. van Hooff, 1972). In this study, judgments of similarity between BT displays of chimpanzees (*Pan troglodytes*) and human smiles varied in relation to perceived emotional valence. When a chimpanzee BT was interpreted as fearful, observers tended to underestimate the magnitude of the relationship between certain features (the extent of lip corner raise) and human smiles. These judgments may reflect the combined effects of categorical emotional perception, configural face processing, and perceptual organization in mental imagery and may demonstrate the advantages of using standardized observational methods in comparative facial expression research.

Keywords: facial expression, emotion, primates, perception, smiling

Observation is a key method in comparative psychology and animal behavior, and yet the tools we use to observe—namely, our senses and related perceptual processing systems—are rarely considered in relation to their application in scientific methods. Specifically, it is crucial that our skills in face perception are taken into account within the field of comparative facial expression research. In the present study, we investigated the processes at work when observers make comparisons between chimpanzee and human facial expressions.

The bared-teeth (BT) display (see Figure 1) is a facial expression common to most primates and has been proposed as a homologue to the human smile (Andrew, 1963; van Hooff, 1972). Assessments of homology have been based on appearance (Andrew, 1963; Preuschoft & van Hooff, 1995; van Hooff, 1972), similarity of social function (Preuschoft, 1995; van Hooff, 1972; Waller & Dunbar, 2005) and muscular basis (Waller et al., 2006). Some authors, however, feel that although morphologically similar, the emotional valence of the two expressions differs (e.g., Bard, 2000). Redican (1982) termed the BT display "fear grimace," which is now a commonly used term within the field, and also suggested that rather than featuring raised and upturned mouth corners (like the human smile), the BT has more down-turned and laterally pulled mouth corners. He suggested that this configuration is more similar to the human fear expression (or grimace) and is likely due to action of the risorius muscle as opposed to the zygomatic major muscle (which is the central movement underlying the human smile; Waller et al, 2006). This controversy highlights two important issues. First, without a system to standardize these scientific descriptions, we are unable to quantify the true degree of physical similarity between these proposed homologues. Second, it seems possible that there is a relationship between how scientists perceive the physical characteristics of other species' faces and how they interpret them emotionally.

Hebb (1946) argued that human observation can be used to infer emotion from animal behavior reliably, yet Foley (1935) found huge variation in nonexpert participants' emotional categorization of chimpanzee facial expressions. The reason this anthropomorphic approach may be particularly problematic when viewing faces could be due to the streamlined manner in which faces are processed. Face recognition has been a subject of inquiry within psychology for decades, and although initially this focused mainly on how faces are recognized in terms of identity (Bruce & Young,

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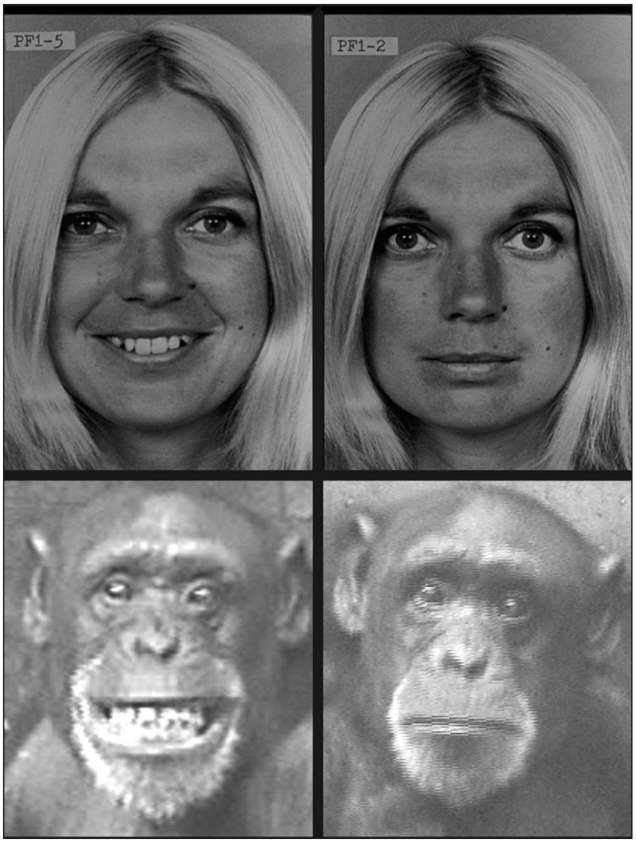


Figure 1. Example image of human smile (a) with chimpanzee bared teeth (BT) display and (b) with corresponding neutrals. Chimpanzee image was taken at Chester Zoo, North of England Zoological Society, Chester, United Kingdom. Human images are from www.paulekman.com. Copyright 1993 by P. Ekman. Reprinted with permission.

1986), recently more attention has been given to the specific processes involved in the perception of facial expressions. Calder, Young, Keane, and Dean (2000) suggested that expressions are processed in terms of configural content, so that features are understood with respect to the shape and position of other features. The authors presented composite facial expressions (e.g., sad upper face, disgust lower face) to participants and found that the emotional identity of each part (upper or lower face) is hard to place when seen in relation to a nonmatching expression part. The composite is processed as a perceptually "new" unit; a similar (although independent) effect to that found in facial identity processing (Young, Hellawell, & Hay, 1987) and eye gaze processing (Jenkins & Langton, 2003).

In practice, this means that the same feature can be perceived as different when embedded in a different configuration. For example, eyes are perceived as larger in happy faces than in surprised faces in composite photographs where eye size was held constant (Seyama & Nagayama, 2002). Leonard, Voeller, and Kuldau (1991) found a related effect when they asked participants to rate images of smiles for emotional valence. The eye region was kept constant between images, but many raters reported that they had used the eyes to infer emotional affect. These perceptual effects are particularly relevant to comparative face research in which the basic face shape of species is similar, but some elements of the configuration may differ. For example, the eyes of the chimpanzee are relatively close together (in comparison with humans), and the mouth appears wider from the frontal view and is curved around a more prognathic lower face (see Figure 1).

Many descriptions are made in direct comparison, but scientists may also rely on memory when considering comparisons between species. Given that caricatures of facial expressions are identified more quickly than standard expressions, it has been suggested that we might store in memory the way in which expressions deviate from a norm (the neutral face), rather than a specific structural description of features or feature configuration (Benson & Perrett, 1991). Halberstadt and Niedenthal (2001) demonstrated that when participants view an ambiguous facial expression accompanied by an emotional statement (i.e., this person is angry) the faces are remembered as more extreme than they really are. The ambiguous stimuli were intermediate frames taken from video clips of actors' faces digitally morphed from one expression to another (i.e., angry to sad). Later, participants viewed the whole video clip and were asked to stop the clip at the point that most closely resembled the image they had seen previously. Participants stopped the clip at a point closer to the parent expression associated with the label they had seen. Moreover, when participants were asked to explain the ambiguous face in more detail (why do you think this face looks angry?), bias was further increased. Halberstadt and Niedenthal suggested that language decomposes the configuration into its component parts and then reconstructs the images on the basis of the emotional categories available. Thus, whereas this coupling of emotional processing and memory aids identification of appropriate emotional content, the process impairs memory of the specific featural detail.

Further evidence of how categorization impacts on perception is found in studies involving mental rotation of ambiguous figures (e.g., duck/rabbit); Reisberg and Chambers (1991) argued that images are perceptually organized in terms of how the object is "understood" and that initial perceptual organization restrains how the shape can be interpreted and manipulated in imagery. Therefore, if a smile is retained in terms of the features that differ from a neutral face (i.e., upturned lip corners), then these features may be exaggerated in memory. Indeed, the curvature of a sketched "smiley" face rarely reflects the physical dimensions of a human smile but is readily identified as a smile. If the facial expression of another species is categorized by an emotional term, then this may also affect how the expression is retained in memory and compared with human expressions.

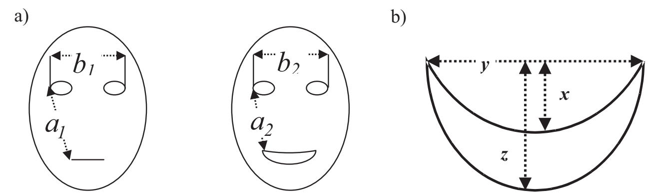
In light of these studies, it seems important to consider the accuracy of people's observation of other species' faces and to explore the relationship between emotional interpretation and comparison of facial features. If scientists differ in their emotional interpretation of the BT display and also differ in their descriptions of BT displays, then perhaps this can be understood as a function of how humans process faces. Two studies are reported here; the first evaluates the physical measurements of human smiles and chimpanzee BT displays, and the second considers how humans compare these characteristics when interpreting facial expressions of humans and chimpanzees in terms of emotion.

Study 1: Anthropometric Comparison of Human Smiles and Chimpanzee Bared-Teeth Displays

Method

Materials. Stimuli consisted of 13 photographs of posed human smiles (frontal view with lips parted, 6 male and 7 female, all adult) with their corresponding neutral expressions from Ekman and Friesen's (1976) *Pictures of Facial Affect* (see Figure 1). The presence of a neutral expression is essential for these analyses because of individual differences in facial morphology. Images were coded with the Facial Action Coding System (FACS; Ekman, Friesen, & Hager, 2002; see Discussion section for further information), and all expressions were characterized by Action Unit [AU] 6 (cheek raiser), which is indicative of Duchenne smiling (considered genuine smiles; Ekman, Davidson, & Friesen, 1990); AU12 (lip corner puller); and Action Unit 25 (lips parted). Some images included AU26 (jaw drop) but were excluded if the jaw was dropped at moderate intensity or above (AU26c), indicating the possible presence of laughter. Thirteen BT images of chimpanzees (*Pan troglodytes*) with corresponding neutral expression were selected from existing databases (51 BT displays in total: The Chester Zoo, United Kingdom; Yerkes National Primate Research Center, Emory University; The Madrid Zoo, Madrid, Spain). All chimpanzees were adult (8 females, 5 males). Images were selected if the following criteria were met: (a) the expression had been classified as BT display (by experts) when the database was collated, (b) the chimpanzee was facing the camera with minimal horizontal or vertical head tilt, and (c) a neutral image was available with minimal horizontal or vertical head tilt. Eighteen images met the screening criteria, but this was further reduced to 13 to ensure that they featured the same muscle movements (according to ChimpFACS; Vick, Waller, Parr, Smith Pasqualini & Bard, 2007). All selected expressions consisted of AU10 (upper lip raiser), AU12 (lip corner puller), AU16 (lower lip depress), and AU25 (lips parted). Images were excluded if the jaw was dropped at moderate intensity or above, which could indicate screaming, whereas the BT display is usually silent.

Procedure. First, we measured the extent to which lip corners were raised upwards (in relation to neutral), using a measure adapted from Pilowsky, Thornton, and Stokes (1985; formula given in Figure 2a.). Distance between outer eye corner and lip corner was measured (in millimeters) in both neutral (a_1) and expressive (a_2) images, normalized against a reference measurement (b; distance between outer eye corners), and the difference was calculated to give an index of movement (x). The difference (x) was calculated by subtracting the expression measurement from the corresponding neutral measurement. The greater the value of x, the greater the difference between lip corner position in the neutral compared with the peak expression: a high value of x indicates a large lip corner raise. Second, we measured curvature of the lips in the peak expressions using a simple method (formula given in Figure 2b). Curvature was measured as the vertical distance between lip margin and height of lip corner, divided by the mouth width, and should reflect the depth of the lip curve (assuming the line of the lip follows a smooth curve between lip corners and lowermost point of lip). The inner lip margins were used in preference to outer lip margins to achieve consistency between human and chimpanzee lips, where thickness of the lips differs. The degree of curvature of upper and lower lips was calculated in the peak expressions of chimpanzee BT displays and human smiles.



$$x = \left(\frac{a_1}{b_1}\right) - \left(\frac{a_2}{b_2}\right) \qquad ulc = \frac{x}{y} \qquad llc = \frac{z}{y}$$

Figure 2. (a) Procedure used to measure end lip raise in neutral and peak expression images and (b) procedure used to measure upper lip curvature (*ulc*) and lower lip curvature (*llc*) in peak expression. a = distance between outer eye corner and mouth corner; b = distance between eyes; x = vertical distance between upper lip and mouth corners; y = horizontal distance between mouth corners; z = vertical distance between lower lip and mouth corners.

Results

Non-parametric statistics (Mann–Whitney U) were used to test for a difference between lip corner raise in the human smiles and chimpanzee BT displays (because of the non-normal distribution of human data; kurtosis = 2.36). There was no significant difference in the degree of lip corner raise between human smiles and chimpanzee BT displays (Mann–Whitney $U = 62.0$, $N = 26$, $p = .25$), although the mean chimpanzee score was higher (chimpanzee = 0.27, confidence interval [CI] = 0.15 to 0.38; human = 0.15, CI = 0.13 to 0.18).[1] A significant difference was found in the index of upper lip curvature between human smiles and chimpanzee BT displays (t test, equal variances not assumed [Levene's test: $F(24) = 10.3$, $p < .005$]; $t(13.83) = -3.21$, $p < .005$, $d = 1.23$), with chimpanzee BTs exhibiting a greater curvature ($M = 0.14$, CI = .07 to 0.21) than human smiles ($M = 0.04$, CI = .02 to 0.06). There was also a significant difference in the index of lower lip curve between human smiles and chimpanzee BT displays, $t(24) = -5.25$, $p < .005$, $d = 2.15$, with chimpanzee BT displays exhibiting greater curvature ($M = 0.50$; CI = 0.43 to 0.56) than human smiles ($M = 0.32$; CI = 0.29 to 0.36).

Discussion

Chimpanzee BT displays showed equivalent degrees of lip corner raise in comparison with human smiles and a significantly greater degree of both upper and lower lip curvature. This study, therefore, establishes the physical parameters of these expressions across species. There was greater variation in the BT displays than in the smiles, and the distribution of the human lip raise data was leptokurtic (a peaked distribution indicating homogeneity). This may be because the human images were posed, whereas the chimpanzee images were taken from species-typical social interactions. If this is the case, these differences may reflect the extent

[1] Confidence intervals are 95% throughout.

Table 1
Responses to Questions Regarding Physical Comparisons Between the Human Smiles and Chimpanzee Bared-Teeth (BT) Displays

	No. participants			
In which set of faces is the mouth more	Human smiles	Chimpanzee BT displays	About the same	$\chi^2(2, N = 127)$
turned upwards?	51 (40%)	53 (42%)	23 (18%)	13.29*
drawn backwards?	104 (82%)	11 (8.5%)	12 (9.5%)	134.76**
"smiley"?	77 (61%)	34 (27%)	16 (12%)	46.41**
curved?	53 (42%)	55 (43%)	19 (15%)	19.34**

* $p < .05$. ** $p < .005$.

of variation found in spontaneous expressions versus posed expressions. The human smiles were Duchenne smiles, however, which, despite being posed, are morphologically similar to genuine, spontaneous smiles. In addition, given the differences in facial architecture between humans and chimpanzees (i.e., prognathism, flexibility of the lips: Vick et al., 2007), it is also possible that chimpanzees have a higher potential for variation in expressions that feature lip withdrawal.

Study 2: Emotional Judgments of Human Smiles and Chimpanzee Bared-Teeth Displays in Relation to Physical Observations

Our results from Study 1 showed that chimpanzee BT displays exhibit a similar degree of upturn at the mouth corner, and significantly more curvature of the lips, when compared with human smiles. The second study explored the hypothesis that human perception of these features is related to emotional interpretation. We expected participants' comparative judgments between human smiles and chimpanzee BTs to be related to how the faces were perceived emotionally. Specifically, we expected to find an interaction between participant's overall judgment of raised lip corners (which species has the greater degree of upturn) and the degree of positive and negative emotion perceived when viewing the faces. If participants judged lip corners to be more raised in human smiles, we expected chimpanzee BT displays to be rated highly for negative emotion (i.e., fear) and less so on positive emotion (i.e., happiness). If participants judged lip corners to be more raised in chimpanzee BT displays, we expected chimpanzee BT displays to be rated highly for positive emotion and less so for negative emotion.

Method

Participants. Participants were recruited for an online study via email (University of Portsmouth staff mailing lists, national and international colleagues, and personal contacts). A total of 127 people (77% of those who logged on to the site) completed the survey (97 female, 30 male; $M = 34.4$ years, range = 21–63 years). The majority of participants ($n = 109$; 86%) reported no experience with chimpanzees.

Materials. Five human smiles (2 male and 3 female) were selected from the Pictures of Facial Affect image set at random, and five chimpanzee BT displays were selected from the orginal image data set on the basis of quality (minimal shadow, blur, etc.; 3 male, 2 female) for presentation in the online survey.[2] Each image was presented on a separate page (human and chimpanzee alternated), with a list of six questions asking participants to make emotional judgments. This method of presenting multiple emotions and allowing participants to choose intensity has been used previously and resulted in high agreement (Ekman et al., 1987). The six questions (e.g. "How happy do you think this face looks?") were phrased similarly for each basic emotion (happy, angry, surprised, sad, disgusted, and fearful), and a 7-point Likert scale for each response was provided (1 = *not at all,* 7 = *extremely*). On the final page of the questionnaire, participants were asked to think about the mouth in all the previous images they had seen, and they were then asked the following questions:

> "Overall, do you think the. . ."
>
> "corners of the mouth are turned upwards to a greater extent in the human or chimpanzee faces?"
>
> "corners of the mouth are drawn backwards to a greater extent in the human or chimpanzee faces?"
>
> "human or chimpanzee faces look more 'smiley'?"
>
> "lips are more curved in the human or chimpanzee faces you have seen?"

Each question had three possible responses: "more in the human faces"; "more in the chimpanzee faces"; or "about the same."

Procedure. The questionnaire was placed on the Internet with Web-based forms (written in Activer Server Pages [ASP]) and a Microsoft Access backend database. Participants were sent a link to the study Website, and the study took approximately 10 minutes to complete. The order of the images was reversed for half of the participants.

Results

Featural comparisons. Table 1 shows the results of the comparative judgments. For all the questions, the majority of partici-

[2] The human subset did not differ from the remainder of the image set in upper lip curvature, $t(11) = -0.34$, $p = .74$ but had significantly less lower lip curvature, $t(11) = 5.55$, $p < .005$. The chimpanzee sample was not taken from the larger sample used in Study 1 but did not differ in terms of upper lip curvature, $t(16) = -0.10$, $p = .92$, or lower lip curvature, $t(16) = -1.11$, $p = .28$. Lip corner raise was not assessed, as neutrals were not presented.

pants judged there to be a difference between human smiles and chimpanzee BT displays, even given the option of similarity. No significant differences were found between participants who reported experience with primates and those who did not: upwards judgment, $\chi^2(2, N = 127) = 1.68$, $p = .43$, backwards judgment, $\chi^2(2, N = 127) = 0.25$, $p = .88$, smiliness judgment, $\chi^2(2, N = 127) = 1.20$, $p = .55$, or curved, $\chi^2(2, N = 127) = 1.94$, $p = .38$. Participants were divided almost equally in whether they chose humans or chimpanzees as having greater upturned mouth corners (with relatively few participants choosing "about the same"), and a similar pattern was seen for judgments of curvature. In contrast, the majority of participants chose chimpanzees to have mouth corners drawn further back, and the majority of participants chose human smiles as "smilier." In addition, there were some associations between judgments. Judgments of upturned mouth corners were associated with smiliness judgments, $\chi^2(4, N = 127) = 15.51$, $p < .005$, showing that if participants judged chimpanzee BT displays to have greater upturned mouth corners, they were also likely to judge them as smilier. There was also an association between upwards mouth corner judgments and curvature judgments, $\chi^2(4, N = 127) = 24.67$, $p < .005$; participants who judged BT displays as having greater upturned mouth corners were more likely to judge BT mouth corners as more curved.

Relationship between emotional ratings and featural comparisons. Overall emotional ratings for the BT displays and smiles were calculated for each participant (Table 2 shows a summary). Table 2 shows that human smiles were consistently rated as happy, and that the pattern of ratings for BT displays was less obvious, with the highest ratings being happiness, anger, and fear. Although the anger rating was rated as higher than fear, only happiness and fear were used in the following analyses, as these most closely reflect the theoretical positions from the literature. Participants with primate experience rated chimpanzee BT displays as less happy, $t(125) = -2.623$, $p < .05$, $d = -0.59$, and more fearful, $t(125) = 2.66$, $p < .05$, $d = 0.62$, compared with participants who did not report primate experience but because of small sample size, primate experience was not included in the multivariate analysis of variance (MANOVA). Participants were then grouped by their responses to the comparative judgments, and the overall emotional ratings of chimpanzee BT displays was compared between these groups. To include only those participants who had a clear impression of which set of images to choose for each question, participants who chose "about the same" were excluded from the following analyses (resulting in participant numbers between 101 and 115).

Table 2
Mean Emotional Ratings for the Chimpanzee Bared-Teeth (BT) Displays and Human Smiles

	Chimpanzee BT ratings			Human smile ratings		
Emotion	*M*	*SD*	Range	*M*	*SD*	Range
Happiness	3.80	1.40	6.0	5.20	0.70	3.8
Anger	3.04	1.22	5.0	1.39	0.54	2.6
Surprise	2.15	1.00	5.2	1.77	0.87	4.2
Sadness	1.76	0.91	3.6	1.57	0.71	3.4
Disgust	1.76	0.89	3.6	1.37	0.58	3.0
Fear	2.80	1.33	5.0	1.46	0.65	3.0

Note. Ratings are averaged across the individual images (5 BT displays and 5 human smiles) and across all participants ($N = 127$).

Emotional ratings of happiness and fear were entered into a mixed design MANOVA, where species of image was a within-subject variable and judgment group was a between-subjects variable. Participants were allocated to a judgment group depending on their overall judgment of upturn (mouth corners more upturned in chimpanzee BT displays vs. mouth corners more upturned in human smiles). There was a main effect of emotional rating, $F(2, 101) = 757.37$, $p < .001$, $\eta^2 = .94$, as overall participants differed in their fear and happiness ratings for the chimpanzee and human images (see Table 2), and there was a significant interaction between judgment and emotion, $F(2, 101) = 3.79$, $p < .05$, $\eta^2 = .07$. Univariate tests showed that this interaction was found only for chimpanzee emotional ratings (see Figure 3), $F(1, 102) = 5.24$, $p < .05$, $\eta^2 = .05$, and not for human emotional ratings, $F(1, 102) = .07$, $p = .392$, $\eta^2 = .01$. Specifically, participants who judged mouth corners as less upturned in chimpanzee BT displays in comparison with human smiles gave lower overall happiness rating for chimpanzee BT displays ($M = 3.44$, $CI = 3.05$ to 3.83) in comparison with those participants who judged mouth corners more upturned in chimpanzee BT displays ($M = 4.08$; $CI = 3.73$ to 4.43). Moreover, this finding contrasted with fear ratings: those judging chimpanzee BT displays as less upturned than human smiles had higher fear ratings for chimpanzee BT displays ($M = 3.00$; $CI = 2.61$ to 3.39) than those judging chimpanzee BT displays as more upturned ($M = 2.61$; $CI = 2.28$ to 2.94).

A similar analysis was conducted by splitting the participants into groups on the basis of their judgments of "smiliness." There was a significant interaction between emotional rating and smiliness judgment, $F(2, 108) = 9.88$, $p < .005$, $\eta^2 = 0.16$, but again this interaction was only found between emotional rating of chimpanzee BT displays and judgment group, $F(1, 109) = 14.65$, $p < .005$, $\eta^2 = 0.12$, and not human emotional ratings and judgment group, $F(1, 109) = 0.67$, $p = .42$, $\eta^2 = 0.01$. This interaction was due to a difference between the two judgment groups in their relative ratings of happiness and fear for the chimpanzee BT displays: Participants who judged the chimpanzee BT displays as more smiley also tended to interpret chimpanzee BTs as expressing greater happiness (human images smilier, $M = 3.38$; $CI = 3.09$ to 3.67; chimpanzee images smilier, $M = 4.57$, $CI = 4.08$ to 5.05); the opposite was true for fear ratings. Thus, participants who judged chimpanzee BT displays as less smiley were more likely to interpret chimpanzee BT displays as expressing greater fear (human judgment group, $M = 3.04$; $CI = 2.72$ to 3.35; chimpanzee judgment group, $M = 2.34$; 1.97 to 2.79; see Figure 4).

For the analysis on curvature, there was no significant interaction between emotion and curvature judgment, $F(2, 105) = 0.81$, $p = .45$, $\eta^2 = .02$. Given that the majority of participants ($n = 104$; 82%) judged mouth corners to be drawn backwards more in chimpanzee BT displays than in human smiles, we did not conduct similar analyses on those data.

Discussion

There was a significant association between participants' ratings of emotion for chimpanzee BT displays and subsequent comparative judgments of similar physical features between BT displays and smiles. Specifically, the participants who gave higher happi-

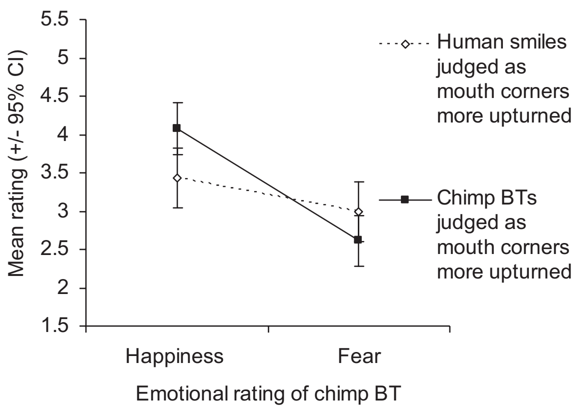


Figure 3. Mean emotional rating of bared teeth (BT) displays in relation to comparative judgment made between BT and smile (which set of images has the greatest upturned mouth corners). Emotional rating of chimpanzee BT displays (happiness and fear) is shown for participants who judged human smiles as having greater upturned mouth corners and for participants who judged chimpanzee BTs as having greater upturned mouth corners. CI = confidence interval.

ness ratings and lower fear ratings for the BT displays judged chimpanzees to have more upturned mouth corners (than human smiles). There was no influence of emotional rating for human smiles. First, given the measurements reported in Study 1 (illustrating that chimpanzee BT displays did not, in fact, have less upturning of the mouth corners), this demonstrates that comparative judgments were not always reflective of the precise physical dimensions. It is also possible that alternative physical measures were being used by participants in order to determine similarity. Second, however, the findings demonstrated that comparison of physical dimensions was connected to the perceived emotional valence of the chimpanzee expression. A similar pattern was seen for comparisons of smiliness, but not for curvature. This may be because smiliness and upturned lip corners are intuitively associated with smiling more so than is curvature of the lips and, therefore, are more likely to be associated with emotional perception. Moreover, participants may be considering the curvature of the mouth area as a whole, which is more prognathic in chimpanzees, and thus may appear curvier.

General Discussion

We have presented and tested an example of a perceptual bias that occurs when comparing a facial expression of another species to human facial expressions. Scientists have differed in their judgments of similarity between the chimpanzee BT display and the human smile (e.g., Redican, 1982; van Hooff, 1972) and (concurrently) have considered social function and/or emotional valence. In the present study, participants judged that there are differences in certain physical characteristics between these two expressions (even when no difference is found in geometrical measurement), and judgments were found to vary systematically on the basis of emotional interpretation. Specifically, when observers judged a chimpanzee BT to have high degree of positive valence (happiness), they also tended to judge features highly salient of a smile (upturned mouth corners) as more extreme (overall) than in human smiles. In contrast, when a chimpanzee BT was judged to have high negative valence (fear), these salient smile features were judged as less extreme than in human smiles.

There are two main implications of these findings. First, comparative observations did not always reflect the true dimensions of facial expressions. As facial expressions are typically processed as whole units (holistically and/or configurationally; Calder et al., 2000) it may be difficult to extract and compare features with accuracy. As the overall configuration differed between the two comparison groups (chimpanzee expressions and human expressions), the perception of specific features may have differed (Seyama & Nagayama, 2002), which in turn affected subsequent judgments. The extent to which the mouth corners seem to be raised is likely to be influenced by other elements of the face, which differ between the two species. Notably, the characteristics of the brows; the size of the mouth; and the relative spacing of eyes, nose, and mouth all differ between chimpanzee and human faces, which may affect judgments of comparison.

Second, comparative observations varied in relation to the type and strength of emotional category assigned to the chimpanzee facial expression. Halberstadt (2003) argued that emotional attributions conjoin language and face perception and can lead to inaccurate impressions of detail when the observer is trying to retrieve and identify the component parts of facial expressions. Also, mental rotation studies have shown that the initial perceptual organization places constraints on how a shape can be interpreted when encoded in mental imagery (Reisberg & Chambers, 1991). Thus, when observers initially interpret the human and chimpanzee faces in terms of emotion, the preserved mental image may be retained in terms of the features that best fit the emotional interpretation. When the chimpanzee BT is categorized as more fearful, the features salient of smiling (lip corner raise) are inhibited in memory, but when it is categorized as happy, these same features are amplified. Given the automatic nature of emotional perception (and the order of the questions in the questionnaire), we argue that the emotional categorization comes first and thus influences consequent featural decisions, yet we cannot rule out the possibility that this is not a causal process and that it is in fact the perceived dimensions of the features that are influencing the emotional decisions. More controlled experiments are needed to tease

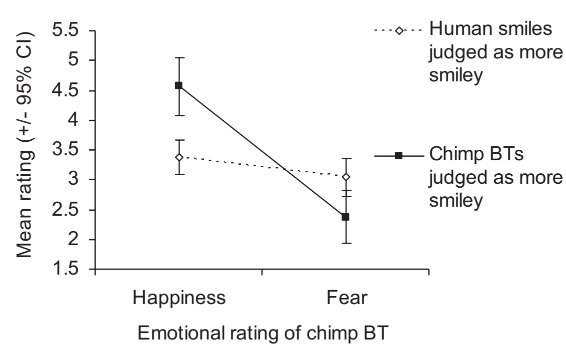


Figure 4. Mean emotional rating of bared teeth (BT) displays in relation to comparative judgment made between BT and smile (which set of images looks “smiliest”). Emotional rating of chimpanzee BT displays (happiness and fear) is shown for participants who judged human smiles as more smiley and for participants who judged chimpanzee BTs as more smiley. CI = confidence interval.

apart these alternative explanations; yet, the fact that these processes are intertwined seems clear.

An assumption underlying this research is that the processes used by the general population are the same as those used by primate experts, which may not be the case. Yet, no differences in the featural comparisons between chimpanzee and human expressions were found between participants with primate experience and those without. Chimpanzee expressions were interpreted differently in terms of emotion between primate experts and nonexperts; however, we could not ascertain whether this was related to specific judgments due to sample size. When human facial expression coders learn to use the FACS (Ekman & Friesen, 1978; Ekman et al., 2002), extensive training is required regardless of experience with human faces: throughout this process, previously unnoticed facial movements become increasingly apparent. A comparable system to the human FACS (Ekman & Friesen, 1978; Ekman et al., 2002) has recently been developed for chimpanzees (ChimpFACS: Vick et al., 2007). This system provides an objective language with which to describe the individual features of facial expressions and facilitate direct comparison with humans, and should therefore standardize observation between scientists.

Conclusions

Comparative psychology and animal behavior disciplines uphold a tradition of objective, systematic methods of description; anthropomorphism is acknowledged as an unwelcome influence on human observations and is carefully avoided. Yet, when people are observing faces, the manner in which bias is avoided may be less straightforward than when observing other aspects of behavior. Faces are an integral feature of human social interaction, and the human species has evolved efficient mechanisms to extract information from faces. These cognitive specializations function to greatly facilitate social interaction, and thus to force attention away from these shortcuts (the holistic configuration that indicates emotion) and adopt a bottom-up approach is a difficult task. As a result, in scientific inquiry about the physical dimensions of faces, the perceptual processes that are most intuitive may render some judgments unreliable. Indeed, the variation in participants' emotional interpretation of chimpanzee expressions found in previous studies (i.e., Foley, 1935) could be explained by this relationship between emotional and featural perception. It is crucial that researchers consider how these processes influence interpretations of what people see.

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