Emotion
2007, Vol. 7, No. 1, 172–181

1528-3542/07/$12.00 DOI: 10.1037/1528-3542.7.1.172

Classifying Chimpanzee Facial Expressions Using Muscle Action

Lisa A. Parr
Yerkes National Primate Research Center and
Emory University

Bridget M. Waller
University of Portsmouth

Sarah J. Vick
University of Stirling

Kim A. Bard
University of Portsmouth

The Chimpanzee Facial Action Coding System (ChimpFACS) is an objective, standardized observational tool for measuring facial movement in chimpanzees based on the well-known human Facial Action Coding System (FACS; P. Ekman & W. V. Friesen, 1978). This tool enables direct structural comparisons of facial expressions between humans and chimpanzees in terms of their common underlying musculature. Here the authors provide data on the first application of the ChimpFACS to validate existing categories of chimpanzee facial expressions using discriminant functions analyses. The ChimpFACS validated most existing expression categories (6 of 9) and, where the predicted group memberships were poor, the authors discuss potential problems with ChimpFACS and/or existing categorizations. The authors also report the prototypical movement configurations associated with these 6 expression categories. For all expressions, unique combinations of muscle movements were identified, and these are illustrated as peak intensity prototypical expression configurations. Finally, the authors suggest a potential homology between these prototypical chimpanzee expressions and human expressions based on structural similarities. These results contribute to our understanding of the evolution of emotional communication by suggesting several structural homologies between the facial expressions of chimpanzees and humans and facilitating future research.

Keywords: ChimpFACS, facial expressions, emotion, homology

Research over the past half century has considerably advanced our understanding of facial expressions and emotional communication in animals. This includes detailed descriptions of expression repertoires for a variety of primate and nonprimate species, including chimpanzees, bonobos, rhesus monkeys, capuchin monkeys, and canids (Andrew, 1963; Bolwig, 1964; de Waal, 1988; Fox, 1969; Goodall, 1986; Hinde & Rowell, 1962; Preuschoft & van Hooff, 1995, 1997; Redican, 1975; van Hooff, 1962, 1967, 1973; van Lawick-Goodall, 1968; Weigel, 1979). In the tradition of ethology, these facial expression ethograms include a name for the behavior, a description of its appearance, any accompanying vocalization, and perhaps some information about how it is used and/or its presumed social function. Parr and colleagues (2005), for example, published a comprehensive ethogram of chimpanzee facial displays that provides an objective description of the display, photograph, and spectrogram of any accompanying vocalization and describes their social context of use. Moreover, they cross-referenced the names for these displays with existing accounts from other investigators in an attempt to standardize descriptions and nomenclature. While there is little disagreement that the use of such ethograms has advanced our understanding of animal behavior (Tinbergen, 1963), there has been little formal attempt to standardize ethograms for the same species across research groups or any attempt to compare specific behavior across species. Therefore, the lack of a common metric for describing facial expressions has prevented a complete understanding of the evolution of communicative signals or their homology, both within and across species.

Facial expressions are difficult to describe accurately, even in humans (Ekman, Friesen, & Hager, 2002a), and this is especially challenging given their dynamic nature. Studies of human facial expressions, in contrast to those of animals, have been aided by the development of an objective and standardized observational tool for describing facial movement, the Facial Action Coding System (FACS; Ekman & Friesen, 1978; Ekman et al., 2002a). The FACS

Lisa A. Parr, Yerkes National Primate Research Center, and Department of Psychiatry and Behavioral Sciences, Emory University; Bridget M. Waller and Kim A. Bard, Centre for the Study of Emotion, Department of Psychology, University of Portsmouth, Portsmouth, Hampshire, United Kingdom; Sarah J. Vick, Department of Psychology, University of Stirling, Scotland, United Kingdom.

This study was supported by Grant RR-00165 from the National Institutes of Health/National Center for Research Resources to the Yerkes National Primate Research Center, Grant NIMH-R01-MH068791 from the National Institute of Mental Health to Lisa A. Parr, and Grant F/00678/E from the Leverhulme Trust to Kim A. Bard.

Portions of this article were presented on September 13, 2005, at the 11th European Conference on Facial Expression, Durham, United Kingdom. We thank Frans de Waal, Living Links Center, Emory University, and the Chester Zoo, Chester, United Kingdom, for the use of some photographic material. The Yerkes National Primate Research Center is fully accredited by the American Association for Accreditation of Laboratory Animal Care.

Correspondence concerning this article should be addressed to Lisa A. Parr, Yerkes National Primate Research Center, 954 Gatewood Road, Atlanta, GA 30329. E-mail: parr@rmy.emory.edu

is an anatomically based coding system, with each independent unit of observable movement on the face (referred to as action units, or AUs) described in terms of how the underlying muscle action alters the appearance of facial landmarks. Despite the fact that the FACS is now over 30 years old, its standardization across research groups has been enforced through a refereed certification process, maintaining it as the gold standard for describing facial action regardless of the specific research application (see Rosenberg & Ekman, 1997). Moreover, because of its anatomical basis and comprehensive approach to facial movements, the FACS is particularly well suited for modification for use with other populations, such as human infants (BabyFACS; Oster, 2001) and nonhuman primates (Vick et al., 2007).

To date, several nonhuman primate studies have attempted to incorporate various aspects of the FACS to better describe facial movement and to provide a more standardized method for identifying and comparing facial expressions across species. Steiner and colleagues, for example, examined facial responses to tastes in numerous species of nonhuman primates including prosimians, New World monkeys, Old World monkeys, and homonoids (Steiner & Glaser, 1984, 1995; Steiner, Glaser, Hawilo, & Berridge, 2001). Facial reactions were coded using detailed ethograms of facial movements, including components of the FACS and ethological descriptions of primate facial expressions in the published literature (Andrew, 1963). In this way, they were able to compare specific facial reactions to tastes across species using standardized terminology. In addition, Preuschoft and van Hooff (1995) used FACS to describe similarity in the appearance of the silent bared-teeth displays in related macaque species. Without detailed analysis of the muscular basis of these movements, however, these pioneering studies only provide a subjective impression of the facial behaviors, a criterion that is not sufficient to demonstrate structural homology.

Recently, we have developed a chimpanzee version of the FACS (Vick, Waller, Parr, Smith-Pasqualini, & Bard, in press). This was an extensive multidisciplinary project that began first with facial dissections of several chimpanzees in order to verify the presence and location of the mimetic facial muscles. These dissections confirmed the presence of all mimetic facial muscles in the chimpanzees that have been reported in humans (Burrows, Waller, Parr, & Bonar, 2006). Next, we conducted intramuscular stimulations of the mimetic facial muscles in both humans and chimpanzees to compare the muscular basis of chimpanzee and human facial movements (Waller, et al., 2006). The morphology of the chimpanzee face is quite different from the human face, making it necessary to confirm the presence of similar facial appearance changes when specific muscles were stimulated (see Figure 1). The final stage was to observe hundreds of photos and videos of chimpanzees performing naturally occurring facial movements and document the presence of similar facial appearance changes as have been reported in the human FACS. These facial movements were then labeled and described in a manner comparable with the human FACS, taking into consideration differences in the facial morphology (Vick et al., 2007). The culmination of this research has confirmed that the ChimpFACS describes facial movement on the basis of the underlying musculature and how it functions to change the appearance of the chimpanzee face.

The goals of this study are twofold. First, this article aims to determine whether ChimpFACS can validate the previous classification of chimpanzee facial displays, despite their often graded and blended appearance (see Parr et al., 2005). Second, one of the most important and exciting applications for the ChimpFACS is the potential for making comparisons of facial expressions between chimpanzees and humans, on the basis of their homologous musculature. This rigorous and objective tool will provide a necessary first step toward assessing the homology of emotional expressions in these two hominoid species, and will be critical in aiding future work to assess the emotional quality of these expressions and their potential social and emotional function.

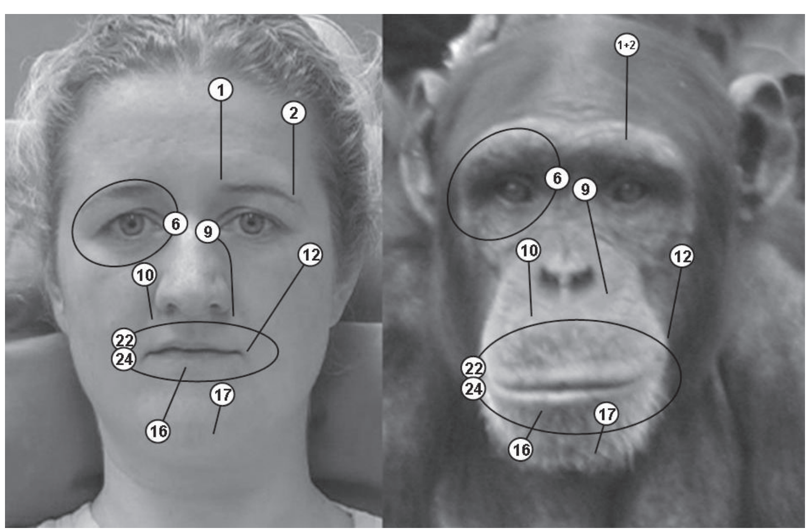


Figure 1. The action units (AUs) of the human and chimpanzee face. White circles correspond to approximate underlying muscle origins (excepting orbital muscles) and black lines show estimated length/orbit of the muscle. Muscles move toward the origin when contracted (orbital muscles reduce aperture of orbit). The chimpanzee photograph was taken by Lisa A. Parr at the Chester Zoo, Chester Zoo, United Kingdom.

Method

Stimuli and Classification

Facial displays came primarily from the large database of chimpanzee facial expressions maintained by Lisa A. Parr at the Yerkes National Primate Research Center. The majority of these photographs were taken using a digital camera (Canon EOS Rebel), but many were scanned from photographs or extracted from digital video using Adobe Premiere (single frames captured at 30 fps [frames per second]). These facial displays occurred naturally during social interactions and were never provoked by experimenters. All expressions in the database were used, unless it could be determined that the movement was nonexpressive, that is, the animal was in the process of feeding, yawning, and so forth, but some of these examples were included in an ambiguous category, described below. The only other exclusionary criterion was if the head angle prevented accurate ChimpFACS coding; however, this represented only a handful of examples, as these photographs would not typically be included in the database.

Once images had been selected, the analyses included over 250 facial displays (N = 259) from approximately 100 different individuals (87 individuals were identified by name and >10 others were not identified by name). These individuals lived in several colonies housed in the United States, several in the United Kingdom, and some from other colonies across Europe. The displays were categorized by expression type by Lisa A. Parr using published guidelines, resulting in nine major categories (Parr et al., 2005). The Parr et al. (2005) ethogram is unique in that it cross-references descriptions given to chimpanzee facial behaviors by other experts in the field and thus represents the most comprehensive published description of chimpanzee facial displays available to date. Some of these other sources included Goodall (1986), van Hooff (1967, 1973, Marler (1965, 1976, Marler and Tenaza (1976), Yerkes (1943), and Yerkes and Learned (1925). These categories include the bared-teeth display (n = 41), relaxed open-mouth face or play face (n = 31), pant-hoot (n = 56), ambiguous faces (n = 24), neutral faces (n = 15), scream (n = 34), alert face (n = 18), pout (n = 29), and whimper (n = 11). We also chose to include an ambiguous category, which contained faces that were difficult to isolate into any one discrete category as they were too graded in intensity, were produced during feeding, or were other nonexpressive movements, such as yawns. Also included in this category were funny faces—unusual facial movements, often asymmetrical, produced idiosyncratically by only a select number of individuals.

Procedure

All facial stimuli were delivered to Bridget M. Waller for ChimpFACS coding. Still images were compared with a neutral image whenever possible, and each image was screened at least twice (upper and lower face) to assign AUs. We did not include AU categories describing head or eye position or vocalizations. To assess interobserver reliability of the coding, Sarah J. Vick additionally coded 76 of the 259 displays (~30%). Waller and Vick are at present the only two certified ChimpFACS coders (Bakeman & Gottman, 1986). Reliability was determined for each facial expression using the following equation, as recommended in the human FACS manual (Ekman, Friesen, & Hager, 2002b):

$$\frac{2\ (\text{\#AUs agreed by both coders})}{(\text{\# AUs coded by BW}) + (\text{\# AUs coded by SJV})}$$

This calculation gives an agreement for each expression between 0 and 1 (0 = no agreement, and 1 = absolute agreement). The average agreement for the 76 displays was 0.78, which is above the criteria required to become a certified human FACS coder (0.70).

The expressions were coded using the entire ChimpFACS manual, not an a priori list of AUs. However, after the coding had been completed, there were 15 AUs that identified all the expression examples. Therefore, the following AUs were considered in subsequent analyses: AU1 + 2 = inner and outer brow raiser; AU6 = cheek raiser; AU9 = nose wrinkle; AU10 = upper lip raiser; AU12 = lip corner puller; AU16 = lower lip depressor; AU17 = chin raiser; AU19 = tongue protrusion; AU22 = lip funneler; AU24 = lip presser; AU25 = lips parted; AU26 = jaw drop; AU27 = mouth stretch; AU28 = lip suck; and AU160 = lower lip relax (an AU unique to the ChimpFACS). Most of these AUs are listed in Figure 1 according to their muscular origin and insertion on a chimpanzee face and its equivalent on a human face. It should be noted that some AUs cannot occur together; for example, the AU26 and AU27 are mutually exclusive. Given the variation in number of AUs present and possible combinations of movements, incompatible AUs notwithstanding, there are many possible combinations that can be formed from these 15 AUs.

Data Analysis

The data were entered into an Excel spreadsheet listing the stimulus name, expression category (as defined by Lisa A. Parr), and the presence or absence of any the 15 possible AUs included in the ChimpFACS that describe muscle movements. A discriminant functions analysis (DFA) was then performed to identify similarities and differences in action unit combinations across the nine expression categories. This analysis identifies a linear combination of quantitative predictor variables, represented as one or more discriminant functions ($N - 1$ canonical discriminant functions, one less than the number of independent variables entered into the analysis), that best characterize differences across groups of dependent variables, in this case, muscle action or AUs. In other words, the analysis provides a determination of whether our a priori category assignments for expressions would be predicted on the basis of the AU combinations. The present analysis also used a leave-one-out classification procedure, in which functions are generated from a sample of cases for which group membership is known (a priori coded expression categories) and then applied as a model to variables for which group membership is not known. This cross-validation of predicted groups is used to determine the overall success of the model. This approach was used to address the first aim of this article, whether ChimpFACS can validate the categories used by chimpanzee experts to classify facial expressions. The category assignment probabilities generated by the DFA were then used to identify the most prototypical combinations of AUs for each expression category. We defined these as the images that achieved over 90% correct assignment to a particular expression category. All statistics were performed using SPSS (Version 11.5.1, SPSS Inc., Chicago).

Our final aim was to present a potential framework for assessing the homology between chimpanzee and human facial expressions.

This was done by creating a table that illustrates representative examples of human facial expressions (taken from Martinez & Benavente, 1998) that were matched to chimpanzee facial expressions according to their similar FACS codes (using FACS and ChimpFACS). Therefore, the resulting table provides a suggestive framework for homology based on similar structural (muscular) morphology. Such a framework may then be used as a guide in future studies aimed at understanding the emotional similarity and social function of these expressions and, ultimately, to further understand the evolution of human emotion.

Results

Facial Expression Categories Using ChimpFACS

DFA, with expression category as the grouping factor, identified eight standardized canonical functions that accounted for 69.6%, 12.5%, 7.1%, 6.2%, 2.3%, 1.4%, 0.7%, and 0.1% of the variance, respectively. The eigenvalues ranged from 8.48 for Function 1 to 0.01 for Function 8. These first two functions accounted for over 82% of the cumulative variance. Wilks's lambda revealed significant differences across the means of each discriminant function, $\chi^2(112) = 1{,}198.403$, $p < .0001$.

The average correct assignment of expression categories was 71.0%, with a cross-validated assignment of 67.6%. This cross-validation procedure classifies each case in the analysis according to the functions derived from all other cases, as previously described, so it can be used to assess the success of the model. The percentage of expressions correctly assigned to each of the nine categories was as follows: bared-teeth display = 70.7%; relaxed open-mouth face = 87.1%; pant-hoot = 94.6%; ambiguous = 16.7%; neutral = 40.0%; scream = 97.1%; alert face = 50.0%; pout = 24.1%; and whimper = 63.6% (see Table 1 for the overall predicted classifications). Table 2 lists the number of AUs observed for each expression category, providing some detail on the range of possible AUs involved in each expression.

Determining Prototypical Facial Expressions From AUs

To identify which AU combinations best represented a particular chimpanzee expression category, we further analyzed expressions that showed over 90% probability of correct assignment to each of the nine groups, according to the DFA described above. These represented expressions with the most reliably coded AU configurations and can thus be considered the most prototypical configurations for each facial expression category. The following section also lists the number of expressions in each category originally included in the analysis and the number that agreed upon by both the DFA and the human rater (Lisa A. Parr). The readers are referred to Table 1 for information pertaining to what classifications resulted when the agreements were not high.

Bared-Teeth Displays

The DFA identified 34 bared-teeth displays from the original set of 41 expressions classified by Lisa A. Parr. Of these, 33 were classified as having greater than 90% probability of correct assignment to the bared-teeth category. Twenty-nine[1] of the 34 (88% agreement) were also identified by Parr as bared-teeth displays. Six AUs were included in these expressions with the following percentage of occurrence: AU6 = 18.18%; AU10 = 75.76%; AU12 = 100%; AU16 = 57.78%; AU25 = 100%; and AU26 = 18.18%. On the basis of this information, the bared-teeth display was best identified in two configurations: AU10 + 12 + 25 and AU10 + 12 + 16 + 25. In more descriptive terminology, the first configuration consists of an open mouth (AU26) with lips parted (AU25), a raised upper lip (AU10), and retracted lip corners (AU12) functioning to expose the teeth. The second configuration is the same, except the lower lip is also depressed (AU16), exposing more of the bottom teeth. Figure 2 shows an example of each of these bared-teeth configurations. Previous studies have found that the bared-teeth display is most typically used when contact is initiated, such as approaches, embraces, invitations, play, and in response to aggression (Parr et al., 2005). In line with these social contexts, Waller and Dunbar (2005) have recently suggested that the bared-teeth display is a signal of benign intent in that it functions to reduce uncertainty in a variety of both aggressive and affiliative situations and increase the likelihood of affiliative behavior.

Play Faces

The DFA identified 39 play faces from an original set of 31. Of these, 32 were identified as having greater than 90% correct assignment to the category of play face. Twenty-five of these (78%) were also identified by Lisa A. Parr as play faces. Six AUs were included in these expressions with the following percentages of occurrence: AU12 = 100%; AU16 = 9.38%; AU19 = 3.13%; AU25 = 100%; AU26 = 62.5%; and AU27 = 37.5%. On the basis of this information, the play face is best defined as two configurations, AU12 + 25 + 26 and AU12 + 25 + 27. These are mutually exclusive combinations as AU26 and AU27 are never coded together because they each describe actions of lowering the jaw, jaw drop, and jaw stretch, respectively. The descriptive interpretation is that the play face is lip corners stretched (AU12) with mouth open (AU26), or mouth stretched wide open (AU27), and lips parted (AU25) in both cases. Figure 2 shows an example of each play face configuration. Previous studies have shown that the play face (relaxed open-mouth face) is used almost exclusively in the social context of play, and more often by subadults than by adult individuals (Parr et al., 2005; van Hooff, 1973) and is associated with longer play bouts when used by both play interactants (Waller & Dunbar, 2005).

Pant-Hoots

The DFA identified 81 pant-hoots from an original sample of 56. Only 11 of these, however, identified as having greater than 90% correct assignment as pant-hoots. All of these 11 were also categorized by Lisa A. Parr as pant-hoots, and they consisted of AU22 + 25 + 26. The majority of the pant-hoots identified by the

[1] The data in Table 1 describes the agreement (N = 29) between the initial classifications provided by Lisa A. Parr and the classifications identified by the analysis based on action unit combinations. Thus, for the bared-teeth display, there were 29 expressions in agreement out of an original set of 41 (29/41 = 70.7%). The identification of prototypical action unit combinations was based on the top 90% of expressions identified by the analysis as belonging to that category; therefore, these numbers are not identical.

Table 1
Percentage of Agreement for Classifications of Chimpanzee Facial Expressions Using ChimpFACS

	Expression type								
Expression type	BT	PF	HO	AMB	N	SC	AL	PO	WH
Bared teeth (BT)	**70.7**	17.1	0.0	2.4	0.0	9.8	0.0	0.0	0.0
Play face (PF)	0.0	**87.1**	0.0	6.5	0.0	6.5	0.0	0.0	0.0
Pant-hoot (HO)	0.0	0.0	**94.6**	0.0	0.0	0.0	0.0	5.4	0.0
Ambiguous (AMB)	16.7	8.3	20.8	**16.7**	8.3	8.3	20.8	0.0	0.0
Neutral (N)	0.0	0.0	0.0	6.7	**40.0**	0.0	40.0	13.3	0.0
Scream (SC)	0.0	2.9	0.0	0.0	0.0	**97.1**	0.0	0.0	0.0
Alert face (AL)	5.6	16.7	22.2	0.0	5.6	0.0	**50.0**	0.0	0.0
Pout (PO)	0.0	0.0	72.4	0.0	0.0	0.0	0.0	**24.1**	3.4
Whimper (WH)	9.1	0.0	18.2	0.0	9.1	0.0	0.0	0.0	**63.6**

Note. A total of 67.6% of cross-validated grouped cases were correctly classified. Bold type indicates the percentage of agreement between expression groups identified by the discriminate functions analysis and the predicted group membership. ChimpFACS = Chimpanzee Facial Action Coding System.

DFA (n = 68) showed a slightly weaker probability of category assignment falling between 89% and 60%. These were all characterized by AU22 + 25. The further description of these movements is that the lips are funneled (AU22) and parted (AU25) either with an open mouth (AU26) or without. Figure 2 shows these two pant-hoot configurations. Previous studies have shown that pant-hoots are used in situations of general excitement, such as in response to noise at a distance, distress, bluff displays, play, and during piloerection (Parr et al., 2005; van Hooff, 1973). Moreover, data from field studies have suggested that the pant-hoot is a long-distance signal that may communicate excitement over food availability (Mitani, Gros-Louis, & Macedonia, 1996).

Ambiguous Facial Displays

We thought it would be interesting to see how ChimpFACS classified expressions that were very difficult for us to classify, including those that consisted of other types of facial movements like funny faces and yawns. The DFA identified 9 ambiguous faces, and all of these were identified as being correctly assigned to the ambiguous category above 90% probability. Lisa A. Parr agreed with the ambiguous label for 89% of these, from the original sample of 24. There were, however, no specific combinations of AUs identified for these faces by ChimpFACS, as was predicted. The AUs involved in these faces included 1 AU6 (cheek raiser), 3 AU9s (nose wrinkle), 2 AU10s (upper lip raiser), 4 AU12s (lip corner puller), 1 AU16 (lower lip depressor), 2 AU17s (chin raiser), 1 AU19 (tongue protrusion), 4 AU22s (lip funneler), 2 AU24s (lips pressed), 6 AU25s (lips parted), 1 AU26 (jaw drop), and 1 AU27 (mouth stretch).

Screams

The DFA identified 41 screams from an original sample of 34, and all of these were classified as having greater than 90% correct assignment to the scream category. Eighty percent of these were also categorized by Lisa A. Parr as screams. Six AUs were included in these expressions with the following percentage of occurrence: AU6 = 4.88%; AU10 = 100%; AU12 = 100%; AU16 = 75.61%; AU25 = 95.12%; and AU27 = 100%. On the basis of this information, the scream face was best defined as AU10 + 12 + 16 + 25 + 27. This is described as a raised upper lip (AU10) with lip corners pulled back (AU12) exposing the upper teeth, lower lip depressed (AU16) also exposing the lower teeth, and mouth stretched wide open (AU27) with lips parted (AU25). Figure 2 shows the scream configuration. Previous studies have demonstrated that chimpanzee screams are used in a variety of social contexts characterized by nervousness, fear and

Table 2
Action Units Associated With Expressions in Each Predicted Category, as Determined by the Discriminant Functions Analysis

		Action units													
Expression	*n*	1 + 2	6	9	10	12	16	17	19	22	24	25	26	27	28
Bared-teeth	34	0	7	0	25	34	19	0	0	0	0	34	6	0	0
Play face	39	0	0	0	0	39	8	0	1	0	0	39	25	12	0
Pant-hoot	81	1	0	0	0	0	2	0	0	81	0	81	11	4	0
Ambiguous	9	0	1	3	2	4	1	2	1	4	2	6	1	1	0
Neutral	9	0	0	0	0	0	0	2	0	0	1	0	1	0	0
Scream	41	0	2	0	41	41	31	0	0	0	0	39	0	41	0
Alert face	24	1	0	0	1	1	5	0	0	0	0	24	5	3	0
Pout	14	0	0	0	0	0	0	7	0	14	0	5	0	0	0
Whimper	8	0	6	0	1	8	2	0	0	8	0	8	0	0	0

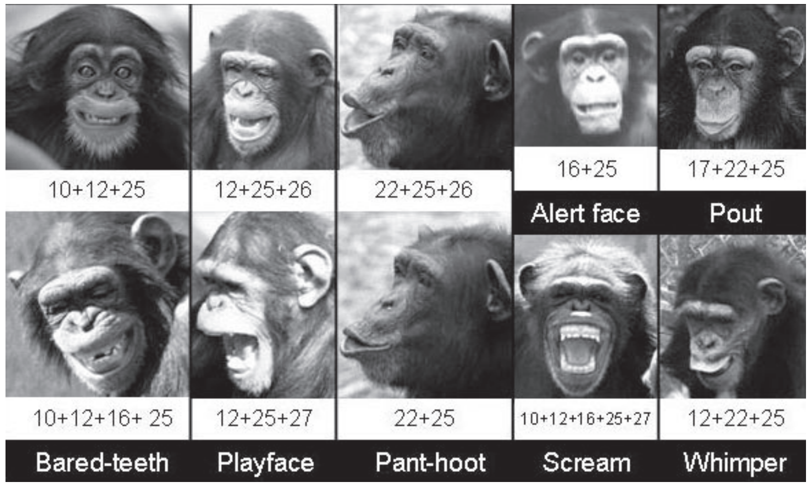


Figure 2. Examples of the prototypical configuration for chimpanzee facial expressions identified using the discriminant function analysis. Photographs are courtesy of the Living Links Center, Emory University (taken by F.B.M. de Waal or Lisa A. Parr).

distress, a prolonged response to aggression, during sex, fleeing an attacker, in some play contexts, and in contexts of general agonism. Recently, several authors have suggested that there may, in fact, be several distinct forms of screams that can be identified using acoustic analyses. There is a more submissive scream used by victims in a fight or by recipients of contact aggression, and there is a more aggressive scream that is used by the attacker or pursuer in a conflict (Siebert & Parr, 2003; Slocombe & Zuberbuhler, 2005). To date, it is unknown whether these acoustic categories may also be identified in the visual domain. For the purposes of this study, all screams were considered the same.

Alert Faces

The DFA identified 24 alert faces from an original sample of 18, and all of these were classified as having greater than 90% correct assignment to the alert face category. These were represented by AU25. Only 46% of these were categorized by Lisa A. Parr as alert faces. This proved to be a difficult category both for us and for the analysis. There were six additional AUs identified for this expression category with the following percentage of occurrence: AU10 = 4.17%; AU12 = 4.17%; AU16 = 20.83%; AU26 = 20.83%; AU27 = 12.5%; and AU160 = 20.83%. Thus, a strict interpretation would give a prototypical configuration for the alert face as only AU25, but the following combinations were also common, AU16 + 25 and AU25 + 26, or AU25 + 160 or AU16 + 25 + 26. This is described as lower-lip depressed (AU16) and lips parted (AU25), lips parted (AU25) with mouth open (AU26), or lips parted (AU25) with lower lip relaxed (AU160). Figure 2 shows the AU16 + 25 configuration. Previous studies have shown that the alert face is used most often during play, bluff displays, and in response to aggression, all situations in which there may be some element of anxiety or uncertainty (Parr et al., 2005).

Pouts

The DFA identified 14 pout faces from an original sample of 29, 9 of which were identified as having greater than 90% correct assignment to the pout category. All of these had AU22 and only 2 (11.11%) also had AU17. Seventy-eight percent of these were categorized by Lisa A. Parr as pouts. However, as for the pant-hoot, the majority of these expressions were classified by the DFA as having less than 90% predicted membership to the pout category. Five expressions were classified between 96% and 50%, and these all consisted of AU17 + 22 + 25. The remaining expressions had only weak probability of assignment to the pout category (<40%), and when these were examined individually, they were all found to be classified as pant-hoots by the analysis. Therefore, the most prototypical combination of AUs to identify the pout and, in particular dissociate it from the pant-hoot, was AU17 + 22 + 25 (see Figure 2). This is described as chin raised (AU17) with lips funneled (AU22) and lips parted (AU25). Previous studies have shown that pouts are used during the contexts of embraces, invitations, play, approaches, and in response to aggression (Parr et al., 2005; van Hooff, 1973). Therefore, pouts may represent a need for contact, or reassurance, and physical affinity.

Whimpers

The DFA identified 8 whimper faces from an original sample of 11, and all of these were identified as having greater than 90% correct assignment as whimpers. Lisa A. Parr agreed with 88% of these classifications. The expressions all contained AU12 + 22 + 25. Three whimpers each had an additional AU, AU6, AU10, and AU160, and two had AU16. Therefore, the prototypical configuration for the whimper was AU12 + 22 + 25. This is described as lip corners retracted (AU12) and lips funneled (AU22) with lips parted (AU25). Figure 2 shows the configuration of all AUs. Previous studies have shown the stretch pout whimper to be associated with response to aggression, signaling nervousness or fear in tense situations (Parr et al., 2005). van Hooff (1973) clusters the whimper with affinitive behaviors, including the silent bared-teeth face, so it might function to induce succor from others.

Post Hoc Validation of AU Configurations

As a final validation of the uniqueness of these configurations and their predictive value, we were able to acquire a second set of images (>70) subsequent to the original submission of this article. These were ChimpFACS coded by Bridget M. Waller, and an Excel sheet listing the image name and ChimpFACS codes was then given to Lisa A. Parr to interpret using the prototypical AU configurations described above. For example, an image with the codes AU10 + 12 + 25 would be given the code of bared-teeth display. The list was also given to a second individual who had no knowledge of ChimpFACS, human FACS, or the purpose of the exercise. After this, Lisa A. Parr visually categorized each image and calculated a percent correct based on the classifications objectively arrived at from the AU configurations alone. This agreement for Lisa A. Parr's categorizations was 83.6%, and for the second naïve rater, it was 80.8%. Thus, a human rater with no knowledge of how the coding system worked could identify them accurately >80% of the time solely by referencing these AU configurations.

Comparing Chimpanzee and Human Facial Expressions

One of the main applications of the ChimpFACS is to aid in understanding the evolution of emotional communication by facilitating comparisons between human and chimpanzee facial expressions. This has, to this point, only been done using subjective morphological descriptions (i.e., Chevalier-Skolnikoff, 1973; Ladygina-Kohts, 1935/2002). The final aim of this study was to compare expressions in these two species by grouping them according to shared AUs, thus presenting a suggested homology based on the structure, or muscular basis, of the expression. To meet this goal, we constructed Table 3. This shows several chimpanzee facial expressions listed with their AU codes derived from this study, and a comparable human facial expression with its AU codes (photos were taken from Martinez & Benavente, 1998). Codes shared by each expression type are in bold type. Thus, the two sets of facial expressions have been coded for homologous facial movement using the two comparable FACS systems. We have included the bulging lip face as a potential homologue of human anger (based on ChimpFACS codes), although this category was not included in the DFA analysis because of small sample sizes. This table is descriptive in that it presents the potential application of FACS and ChimpFACS in understanding homologous facial expressions of emotion in these two species.

Discussion

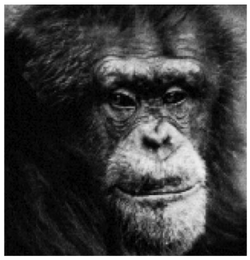
The continuity of facial behavior across primates has long been considered in terms of underlying musculature (Huber, 1931), expressiveness (Darwin, 1872; van Hooff, 1967), and emotional valence (Ladygina-Kohts, 1937/2002). The relative importance of these different aspects for the assessment of homology is still debated, but we propose that it is insufficient to look only at one level of analysis; for example, similarity of appearance (Preuschoft & van Hooff, 1995), muscular basis (Burrows et al., 2006), or signal function (e.g., Preuschoft, 1995; Waller & Dunbar, 2005). In terms of examining the homology of primate facial displays, we need to describe facial behavior in greater detail, with greater units of analysis and, ideally, make cross-species comparisons using equivalent methodologies. Here we have reported the first application of the ChimpFACS, an anatomically based system for classifying facial movements, to characterize the naturally occurring facial behavior of chimpanzees.

First and foremost, this study validates the ability of the ChimpFACS to classify chimpanzee facial expressions in a manner similar to those identified by human ethological observation. Second, and perhaps more important from an application approach, the analyses presented here made it possible to identify unique combinations of AUs that were most highly predictive of specific expression categories. This is an extremely useful application because chimpanzee facial expressions are both highly graded and blended signals, and capturing them at their peak intensity from photographs, or even from still frames of video recordings, is extremely difficult. These unique configurations may then be used to further identify the appropriate set of peak intensity stimuli for use in playback experiments or computerized tasks involving the discrimination of emotional stimuli by chimpanzees (see Parr, Hopkins, & de Waal, 1998). Moreover, these prototypical AU configurations are so robust that they could be used to identify expression categories with >80% accuracy by individuals totally naïve as to the appearance of the expressions or the purpose of the classifications.

For our second aim, we have proposed that the ChimpFACS will be extremely useful for understanding of the evolution of emotional expressions as it provides the necessary first step in establishing the structural homology between chimpanzee and human facial expressions, and that it provides a common language for describing their similarities and differences. We have presented several suggestive comparisons in Table 3, but we caution readers in their interpretation of this table for the following reasons. First, in several of the examples, some AUs are clearly present in one species but not in the other. This is particularly true for upper face AUs that are present in the human expressions but were never part of the prototypical configuration for the chimpanzee expressions. However, the codes listed for the human expressions represent the full FACS codes for those specific images and not the statistically derived prototypical configurations, as is true for the chimpanzee. Thus, it is unclear what the prototypical configurations would be for human facial expressions, although the FACS Investigator's Guide provides some likely combinations for each expression (Ekman et al., 2002a). Second, the human expressions were posed, so some nuances of emotion might be lacking. In future studies, researchers will need to develop stimulus sets for human expressions based on spontaneously occurring behavior in order to generate prototypical AU configurations and to provide more accurate comparisons. Finally, to date, only minimal information is available concerning the emotional function of chimpanzee expressions, so these comparisons should be interpreted only in terms of the structure of the expression, not their meaning or function. Future studies will examine these issues in more detail and with more precise methodologies, including data on the antecedent conditions that elicit these expressions in both chimpanzees and humans in order to more rigorously address the issue of homologous emotional expressions.

The results of this study demonstrate the utility of ChimpFACS in distinguishing between subtle expressions that have previously been difficult to characterize from the literature. The alert face is one such example. Parr and colleagues (2005) originally described this expression as a tense face in their observational study of facial expressions in captive chimpanzees. This label was derived largely

Table 3
Prototypical Facial Expressions Coded for Humans With and for Chimpanzees With ChimpFACS

Chimpanzee			Equivalent human facial expression?		
Facial expression		Prototype AUs	Facial expression		Prototype AUs
	Bulging-lip display	**AU17** **AU24**		Angry face	AU4 AU5 AU7 **AU17** **AU24**
	Silent bared-teeth display	AU10 **AU12** AU16 **AU25**		Smile	AU6 **AU12** **AU25**
	Scream	**AU10** **AU12** **AU16** **AU25** **AU27**		Scream	AU4 AU6 AU7 **AU10** **AU12** **AU16** **AU25** **AU27**
	Pant-hoot	AU22 AU25 AU26	?		
	Relaxed open mouth	**AU12** **AU25** **AU26**		Laughter	AU6 **AU12** **AU25** **AU26**

Note. From "The Evolution of Human Emotion," by L. A. Parr & B. M. Waller, *in Evolution of Nervous Systems, Vol. 5: Evolution of Primate Nervous Systems,* 2006. Copyright 2006 by Elsevier Press. Adapted with permission. Action units (AUs) in bold type are found in both the chimpanzee display and the proposed human equivalent. FACS = Facial Action Coding System.

from the morphological description of the tense face reported in Catterhine primates by van Hooff (1967), where the lips are stretched exposing the lower teeth. van Hooff (1973), however, further characterized the tense-mouth face in the chimpanzee as a component of the bulging-lip face (van Hooff, 1973). However, the morphology of these two expressions appears to be quite distinct: The lips are not open but pressed together in the bulging-lip face. Apart from these references, descriptions of the chimpanzee tense face have previously been neglected, and this is likely because it is quite subtle and may often be interpreted as a neutral face with open lips. Here we have identified a specific combination of AUs associated with what we now refer to as the alert face, AU16 + 25 + 26 (lower lip depressor, lips parted, lower jaw drop; see Figure 2), thus validating this as a specific facial expression. Parr and colleagues (2005) reported this expression as used most often in the context of vigilance and agonism and, thus, the alert face appears to be a more appropriate label.

There were some facial expressions that ChimpFACS had difficulty discriminating between, such as pant-hoots and pouts. Only 24% of pouts were correctly identified as belonging to that category. The majority of pouts (over 72%) were identified by the DFA as pant-hoots. This, however, should not be seen as a failure of the ChimpFACS. First, the current ChimpFACS does not include measures of intensity of displays. The visual distinction between pouts and pant-hoots in terms of AUs and perceived configuration is minimal, so adding intensity may provide a clearer delineating marker for ChimpFACS. Moreover, not only do pouts and pant-hoots look very similar on initial inspection, but they often co-occur in the same behavioral sequences. Parr and colleagues (2005) found that the social contexts that elicited pouts and pant-hoots in a large social colony of chimpanzees were highly correlated. They can be further differentiated using FACS terminology by adding the AU that codes for a vocalization, for example, AU50. Pouts can occur with vocalizations, but these are not hoots. They are typically described as pout-moans (van Hooff, 1973; Parr et al., 2005). Pant-hoots are often used during bluff displays that have a dynamic movement component and can be followed by a climax scream. Thus, the future inclusion of intensity ratings, plus adding an AU50 to an auditory pant-hoot, would distinguish it from the pout.

Another interesting finding was the apparent absence in the chimpanzee expressions of some highly salient and frequent AUs involved in human emotions. We only coded an AU1 + 2 combination, the combined inner and outer brow raiser, in two chimpanzee expressions (DFA identified as a pant-hoot and an alert face) and the AU9, nose wrinkler, in three expressions that the DFA all identified as ambiguous. The brow raising denoted by AU1 + 2 is commonly associated with human surprise, and the nose wrinkling of AU9 is a main component of disgust. Both of these movements have been reported in the published ChimpFACS (Vick et al., 2007), and the movements have been stimulated using intramuscular electrodes in a study designed to validate the appearance changes of these muscles on the chimpanzee face (Waller et al., 2006). Last, we never observed an AU4, or brow lowerer, and this movement is not included in the ChimpFACS manual despite being one of the most salient and relevant movements for human emotional expressions, such as anger, fear, and sadness (Kohler et al., 2004). Two possible explanations may be put forth to explain these absences. The first is that some of these movements are difficult to code in still photographs, such as the AU1 + 2. Moreover, most facial movements are generally more difficult to see on the chimpanzee face because of morphological differences in the shape of the head, size of features, and the availability of contrasts in color and textures. The chimpanzees do not have an elongated forehead and, in combination with their heavy brow ridge and lack of distinguishable hairy eyebrows, the brow-raising movement of AU1 + 2 is extremely difficult to see and most likely has little signal function for conspecifics. The nose wrinkle (AU9) has been observed, but more often in association with extraneous movements such as when chimpanzees squint during a camera flash or find some food distasteful (Steiner et al., 2001). This perhaps explains why these movements were more often associated with expressions in the ambiguous category. The lack of an AU4 in the chimpanzee is very puzzling. One very tentative explanation, as with AU1 + 2, might be that the heavy brow ridge precludes this movement from being very salient in the chimpanzee, and thus, it has not evolved a specific role in expressive communication. Moreover, although the muscles involved in this movement are present in the chimpanzee face, the corrugator, depressor supercilli, and the procerus (Burrows et al., 2006), they may not be strong enough to contract the skin across this brow ridge. Future studies will use histological techniques to gain insight into the microstructure of these facial muscles and may shed some light on these issues.

Finally, an unexpected finding was that neutral faces were not really neutral. The analyses presented here suggested that only 40% of the neutral faces were correctly assigned to the neutral category. The ChimpFACS provided a tool for coding subtle movements in those faces that were not identified on initial inspection and classification. Further analyses are needed to clarify whether faces that contain subtle, individual movements but appear neutral are able to communicate meaningful information to conspecifics. For example, in humans, an appraisal view of emotions has led to componential approaches to facial movement, ascribing specific meaning to the various components of facial expressions (Kaiser & Wehrle, 2004). Applications such as this are essential for the future development of ChimpFACS.

References

Andrew, R. J. (1963). The origin and evolution of the calls and facial expressions of the primates. *Behaviour, 20,* 1–109.

Bakeman, R., & Gottman, J. M. (1986). *Observing interaction: An introduction to sequential analysis* (2nd ed.). New York: Cambridge University Press.

Bolwig, N. (1964). Facial expression in primates with remarks on a parallel development in certain carnivores (a preliminary report on work in progress). *Behaviour, 22,* 167–193.

Burrows, A. M., Waller, B. M., Parr, L. A., & Bonar, C. J. (2006). Muscles of facial expression in the chimpanzee (*Pan troglodytes*): Descriptive, comparative and phylogenetic contexts. *Journal of Anatomy, 208,* 153–168.

Chevalier-Skolnikoff, S. (1973). Facial expression of emotion in nonhuman primates. In P. Ekman (Ed.), *Darwin and facial expressions,* (pp. 11–89). New York: Academic Press.

Darwin, C. (1998). *The expression of the emotions in man and animals* (3rd ed.). New York: Oxford University Press. (Original work published 1872)

de Waal, F. B. M. (1988). The communicative repertoire of captive bonobos (Pan paniscus), compared to that of chimpanzees. *Behaviour, 106,* 183–251.

Ekman, P., & Friesen, W. V. (1978). *Facial action coding system.* Palo Alto, CA: Consulting Psychology Press.

Ekman, P., Friesen, W. V., & Hager, J. C. (2002a). *Facial action coding system: The investigator's guide.* Salt Lake City, UT: Research Nexus.

Ekman, P., Friesen, W. V., & Hager, J. C. (2002b). *Facial action coding system: The manual.* Salt Lake City, UT: Research Nexus.

Fox, M. W. (1969). A comparative study of the development of facial expressions in canids; wolf, coyote, and foxes. *Behaviour, 36,* 4–73.

Goodall, J. (1986). *The chimpanzees of Gombe: Patterns of behaviour.* Cambridge, MA: Belknapp Press.

Hinde, R. A., & Rowell, T. E. (1962). Communication by postures and facial expressions in the rhesus monkey (*Macaca mulatta*). *Proceedings of the Royal Society of London B, 138,* 1–21.

Huber, E. (1931). *Evolution of facial musculature and facial expression.* Oxford, England: Oxford University Press.

Kaiser, S., & Wehrle, T. (2004). Facial expressions in social interactions: Beyond basic emotions. In D. Canamero & R. Aylett (Eds.), *Advances in consciousness research: Animating expressive characters for social interactions.* Amsterdam: John Benjamins.

Kohler, C. G., Turner T., Stolar, N. M., Bilker, W. B., Brensinger, C. M., Gur, R. E., et al. (2004). Differences in facial expressions of four universal emotions. *Psychiatry Research, 128,* 235–244.

Ladygina-Kohts, N. N. (2002). *Infant chimpanzee and human child: A classic 1935 comparative study of ape emotion and intelligence.* In F. B. M. de Waal (Ed.), New York: Oxford University Press. (Original work published 1935)

Marler, P. (1965). Communication in monkeys and apes. In I. DeVore (Ed.), *Primate behavior* (pp. 544–584). New York: Holt, Rinehart & Winston.

Marler, P. (1976). Social organization, communication, and graded signals: The chimpanzee and the gorilla. In P. P. G. Bateson & R. A. Hinde (Ed.), *Growing points in ethology* (pp. 239–279). London: Cambridge University Press.

Marler, P., & Tenaza, R. (1976). Signaling behavior of apes with special reference to vocalization. In T. Sebeok (Ed.), *How animals communicate* (pp. 965–1033). Bloomington: Indiana University Press.

Martinez, A. M., & Benavente, R. (1998). *The AR face database.* [CVC Tech. Rep. No. #24.] Barcelona, Spain: Computer Vision Center.

Mitani, J. C., Gros-Louis, J., & Macedonia, J. M. (1996). Selection for acoustic individuality within the vocal repertoire of wild chimpanzees. *International Journal of Primatology, 17,* 569–581.

Oster, H. (2001). *BabyFACS: Facial action coding system for infants and young children.* Unpublished manual, New York University.

Parr, L. A., Cohen, M., & de Waal, F. B. M. (2005). Influence of social context on the use of blended and graded facial displays in chimpanzees. *International Journal of Primatology. 26,* 73–103.

Parr, L. A., Hopkins, W. D., & de Waal, F. B. M. (1998). The perception of facial expressions in chimpanzees (Pan troglodytes). *Evolution of Communication, 2,* 1–23.

Parr, L. A. & Waller, B. M. (2006). The evolution of human emotion. In J. A. Kaas (Ed.) *Evolution of nervous systems, Vol. 5: Evolution of primate nervous systems* (pp. 447–472). Oxford: Elsevier.

Preuschoft, S. (1995). *"Laughter" and "smiling" in macaques—an evolutionary perspective.* Unpublished doctoral dissertation, University of Utrecht, Utrecht, the Netherlands.

Preuschoft, S., & van Hooff, J. A. R. A. M. (1995). Homologizing primate facial displays: A critical review of methods. *Folia Primatologica, 65,* 121–137.

Preuschoft, S., & van Hooff, J. A. R. A. M. (1997). The social function of "smile" and "laughter": Variations across primate species and societies. In U. Segerstrale & P. Mobias (Eds.), *Nonverbal communication: Where nature meets culture* (pp. 252–281). Mahwah, NJ: Erlbaum.

Redican, W. K. (1975). Facial expressions in nonhuman primates. In L. A. Rosenblum (Ed.), *Primate behaviour—Developments in field and laboratory research* (pp. 103–194). London: Academic Press.

Rosenberg, E., & Ekman, P. (1997). *What the face reveals.* New York: Cambridge University Press.

Siebert, E., & Parr, L. A. (2003). A structural and contextual analysis of chimpanzee screams. *Annals of the New York Academy of Sciences, 1000,* 104–109.

Slocombe, K., & Zuberbuhler, K. (2005). Agonistic screams in wild chimpanzees (Pan troglodytes schweinfurthii) vary as a function of social role. *Journal of Comparative Psychology, 119,* 67–77.

Steiner, J. E., & Glaser, D. (1984). Differential behavioural responses to taste stimuli in non-human primates. *Journal of Human Evolution, 13,* 709–723.

Steiner, J. E., & Glaser, D. (1995). Taste-induced facial expressions in apes and humans. *Human Evolution, 10,* 97–105.

Steiner, J. E., Glaser, D., Hawilo, M. E., & Berridge, K. C. (2001). Comparative expression of hedonic impact: Affective reactions to taste by human infants and other primates. *Neuroscience and Biobehavioural Reviews, 25,* 53–74.

Tinbergen, N. (1963). On aims and methods of ethology. *Zeitshrift für Tierpsychologie, 20,* 410–433.

van Hooff, J. A. R. A. M. (1962). Facial expressions in higher primates. *Symposia of the Zoological Society of London, 8,* 97–125.

van Hooff, J. A. R. A. M. (1967). The facial displays of the Catarrhine monkeys and apes. In D. Morris (Ed.), *Primate ethology* (pp. 7–68). Chicago: Aldine.

van Hooff, J. A. R. A. M. (1973). A structural analysis of the social behaviour of a semi-captive group of chimpanzees. In M. von Cranach & I. Vine (Eds.), *Expressive movement and non-verbal communication* (pp. 75–162). London: Academic Press.

van Lawick-Goodall, J. (1968). A preliminary report on expressive movements and communication in the Gombe Stream chimpanzees. In P. C. Jay (Ed.), *Primates: Studies in adaptation and variability* (pp. 313–519). New York: Holt, Rinehart, and Winston.

Vick, S. J., Waller, B. M., Parr, L. A., Smith Pasqualini, M. C., & Bard, K. A. (2007). A cross species comparison of facial morphology and movement in humans and chimpanzees using FACS. *Journal of Nonverbal Behaviour, 31*, 1–20.

Waller, B. M., & Dunbar, R. I. M. (2005). Differential behavioural effects of silent bared teeth display and relaxed open mouth display in chimpanzees (*Pan troglodytes*). *Ethology, 111,* 129–142.

Waller, B. M., Vick, S. J., Parr, L. A., Bard, K. A, Smith Pasqualini, M. C., Gothard, K. M., &. Fuglevand, A. J. (2006). Intramuscular electrical stimulation of facial muscles in humans and chimpanzees: Duchenne revisited and extended. *Emotion, 6,* 367–382.

Weigel, R. M. (1979). The facial expressions of the brown capuchin monkey (*Cebus apella*). *Behaviour, 68,* 250–276.

Yerkes, R. M. (1943). *The great apes.* Oxford, United Kingdom: Oxford Press.

Yerkes, R. M., & Learned, B. W. (1925). *Chimpanzee intelligence and its vocal expression.* Oxford, United Kingdom: Oxford Press.

Received March 29, 2006
Revision received August 8, 2006
Accepted August 28, 2006 ■