Chapter 8
Chimpanzee Faces Under the Magnifying Glass: Emerging Methods Reveal Cross-Species Similarities and Individuality

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Abstract Independently, we created descriptive systems to characterize chimpanzee facial behavior, responding to a common need to have an objective, standardized coding system to ask questions about primate facial behaviors. Even with slightly different systems, we arrive at similar outcomes, with convergent conclusions about chimpanzee facial mobility. This convergence is a validation of the importance of the approach, and provides support for the future use of a facial action coding system for chimpanzees, *ChimpFACS*. Chimpanzees share many facial behaviors with those of humans. Therefore, processes and mechanisms that explain individual differences in facial activity can be compared with the use of a standardized systems such as *ChimpFACS* and *FACS*. In this chapter we describe our independent methodological approaches, comparing how we arrived at our facial coding categories. We present some Action Descriptors (ADs) from Gaspar's initial studies, especially focusing on an ethogram of chimpanzee and bonobo facial behavior, based on studies conducted between 1997 and 2004 at three chimpanzee colonies (The Detroit Zoo; Cleveland Metroparks Zoo; and Burger's Zoo) and two bonobo colonies (The Columbus Zoo and Aquarium; The Milwaukee County Zoo). We discuss the potential significance of arising issues, the minor qualitative species differences that were found and the larger quantitative differences in particular facial behaviors observed between species, e.g., bonobos expressed more movements containing particular action units (Brow Lowerer, Lip Raiser, Lip Corner Puller) compared with chimpanzees. The substantial interindividual variation in facial behavior within each species was most striking. Considering individual differences and the impact of development, we highlight the flexibility in facial activity of chimpanzees. We discuss the meaning of facial behaviors in nonhuman primates, addressing specifically

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30   individual attributes of Social Attraction, facial expressivity, and the connection of
31   facial behavior to emotion. We do not rule out the communicative function of facial
32   behavior, in which case an individual's properties of facial behavior are seen as
33   influencing his or her social life, but provide strong arguments in support of the role
34   of facial behavior in the expression of internal states.

8.1   Introduction: Chimpanzee and Bonobo Facial Behavior

36   We come to this chapter with different backgrounds: Bard applies principles of devel-
37   opmental psychology to the study of chimpanzees (Bard 2005, 2007; van IJzendoorn
38   et al. 2009; Bard et al. 2006); Gaspar applies principles of ethology to the study of
39   facial behavior across species, speaking to issues in evolution (Gaspar 2001, 2006);
40   and Vick applies principles of psychology to study primate communication (e.g.,
41   gaze and facial expression: Bethell et al. 2007; Vick and Anderson 2003; Vick et al.
42   2006). We collected evidence of individuality (Bard and Gardner 1996; Bard 1998;
43   Gaspar 1996; Gaspar et al. 2004), including group differences (Bard 2003; Bard
44   et al. 2005), and individual idiosyncrasies with facial behaviors (Gaspar 2006).
45   In this chapter, we ask questions about variation in facial expression from an
46   evolutionary perspective: Why should extensive individual variation occur within
47   the communication repertoire of a species? Should signals be unambiguous, stan-
48   dard, and species typical? We discuss this further, because there are indeed good
49   biologically, developmentally, and evolutionarily based reasons to explore interindi-
50   vidual differences in communication signals and sequences, although this type of
51   study continues to be rare in the literature.

8.1.1   From Universal Expressions to Individuality

53   The phylogenetic approach to understanding how facial expressions evolved is
54   based on the first scientific study of facial expressions by Darwin (1872/1965). The
55   earliest reports of nonhuman primate facial repertoires refer to facial communica-
56   tion in the chimpanzee (van Lawick-Goodall 1968; van Hooff 1967) and in the
57   gorilla (Schaller 1964; Fossey 1983), and describe prototypic facial expressions,
58   associated with emotion and/or communication: e.g., a "pout" face when individu-
59   als are feeling or communicating distress; a "play face" when individuals are happy
60   or signaling playful intent. Facial expressions were conceived as facial displays
61   (Andrew 1963), even in humans (Ekman and Friesen 1975), with universality in
62   both the sender and in the receiver (Ekman et al. 1969). One assumption underlying
63   this approach is that (at least some) facial expressions have an innate basis, with
64   stereotypical appearance across individuals. Therefore, comparative studies could
65   reconstruct the phylogenic history of facial displays (Pollick and de Waal 2007).
66   Yet, as we will demonstrate in this chapter, there are large individual differences
67   among facial displays in humans and chimpanzees. The magnitude of differences

among individuals has overwhelming implications for adhering exclusively to a phylogenetic approach based on universal facial displays. In this chapter, we discuss these issues and advocate for the importance of studying many noninnate variables to explain universal and idiosyncratic aspects of facial behaviors.

The search for species-typical inventories of facial displays has resulted in reports of repertoires varying in size, between 6 and 51 different facial expressions in chimpanzees (Berdecio and Nash 1981; Chevalier-Skolnikoff 1982; Gaspar 2001; van Lawick-Goodall 1986; Parr et al. 2005; Pollick and de Waal 2007; van Hooff 1962, 1967, 1972), and between 5 and 46 facial expressions in bonobos (de Waal 1988; Gaspar 2001; Pollick and de Waal 2007). Extensive idiosyncrasy occurs in communicative repertoires (Hopkins et al. 2007), with idiosyncratic gestures, individual differences in the frequency of gestures, group-specific gestures in gorillas and bonobos (Pika et al. 2003, 2005), and group differences between chimpanzee and bonobos in flexible use of gestures (Pollick and de Waal 2007). In human studies, a distinction is made between expressive and unexpressive individuals, particularly in children (Underwood 1997). Moreover, expressivity, transparency, and other properties of the facial communication of humans have important social interaction correlates (Boyatzis and Satyaprazad 1994; Underwood 1997; Murphy and Faulkner 2000).

Many studies providing an inventory for each species will discount interindividual differences and ignore the potential anthropocentric biases inherent in the human perception of faces (Waller et al. 2007). The reported number of distinct facial expressions (1) are categorized by human observers who have spent years viewing human faces with a speedy configural processing system that often ignores or misperceives incongruent features (for details see Waller et al. 2007); (2) falls below the high range of distinct *gestalten* that chimpanzees are capable of doing, as a result of their nearly identical-to-human facial musculature (Burrows et al. 2006; Waller et al. 2006); and (3) is highly influenced by the particular coding systems chosen by different observers. Coding systems vary based on the questions addressed (Bakeman and Gottman 1997). For example, if asking about the social value of a smile then a system that codes for happiness might be ideal, whereas if asking about the quality of emotion expressed in a smile, then coding for particular components of the smile is essential. These types of questions reflect the theoretical debate about whether facial behaviors are an index of emotion or of other internal states, such as moods or feelings, or are signals in social interactions (Fridlund 1994; Gaspar 2006; Hinde 1985; Parkinson 2005; Preuschoft and van Hooff 1997). Additionally, we urge caution in creating inventories of facial expression types, as these often rely exclusively on prototypic categories, ignoring the dynamic qualities of facial expressions.

8.1.2   FACS Approaches to Nonhuman Primate Facial Displays

At the basic level of description of facial expression, research has been limited by the lack of a standardized, objective descriptive system that can be applied equivalently to human and to chimpanzee faces. The Facial Action Coding System

109 (FACS: Ekman and Friesen 1978) is anatomically based and describes surface
110 appearance changes related to muscle action. The majority of Action Units (AUs)
111 describes the action of a single underlying muscle. The FACS approach allows us
112 to answer questions about the structure of primate facial displays. By identifying
113 component movements, the FACS codes from the bottom-up, rather than describ-
114 ing how appearance may fit onto gestalt expression templates thereby allowing
115 variation between similar facial configurations to be detected. Importantly, if the
116 specific muscle causing facial movement cannot be determined, these actions are still
117 described in detail but labeled as Action Descriptors (AD) (Ekman et al. 2002).

118 The top-down approach predominates in chimpanzee facial expression studies;
119 researchers start with the overall appearance of commonly observed expressions
120 and then dismantle these by describing the appearance of the component features,
121 some much more consistently (e.g., van Hooff 1967) than others. While providing
122 more detail on expressions and their variation than most approaches, coding is
123 nonetheless selective and focused upon specific combinations. Reliance on describ-
124 ing only particular landmark features (e.g., a distinctive mouth shape) means that
125 individual variation in facial morphology may result in the expression being diffi-
126 cult to recognize across individuals (Oster and Ekman 1978).

127 A few studies have used FACS to describe facial behavior in nonhuman pri-
128 mates. These initial attempts to employ a FACS approach to primate facial expres-
129 sions revealed that such detailed coding of facial expressions is possible in primates
130 (Preuschoft and van Hooff 1995; Steiner et al. 2001; Ueno et al. 2004). However,
131 these studies were selective in only using the most intuitive AUs. Moreover, the
132 manner of translating AUs across species is often understated: how one translates
133 the human FACS for use with other primates needs to be carefully specified
134 because primates differ in facial morphology, and the appearance of facial move-
135 ments differs, sometimes dramatically, with facial morphology. Most relevant
136 here, these initial FACS-based primate studies took a top-down approach: they
137 documented facial inventories for species, and then applied a FACS approach to
138 describe species-specific facial displays while individual differences in facial dis-
139 plays were not reported.

140 Past research has largely focused on peak expressions rather than movement of
141 the face per se. However, a bottom-up approach starting with how specific move-
142 ments may alter individual features is a more useful means for studying a species'
143 facial repertoire. Studying individual movements, rather than looking only for con-
144 figurations at their apex, broadens the field of communication studies allowing for
145 specification of smaller and more subtle facial movements (Dawkins 1986 cited in
146 Dawkins and Guilford 1991). Without a methodology to address subtle facial move-
147 ments, systematic exploration of their potential signal value is not feasible.

148 The need to specify how AUs are translated from adult humans for use in differ-
149 ent study populations is demonstrated by the FACS for human infants (BabyFACS)
150 created to take differences between infant and adult facial morphology into account
151 (Oster and Ekman 1978; Oster 2005). The FACS approach advocates using a par-
152 ticular methodological process in developing the coding system, specifically grounding
153 facial movements in the underlying muscle structure. While such a discussion may

seem pedantic, the standardization value of FACS is that it provides a common 154
language, based in musculature, for describing changes in facial appearance. To apply 155
FACS to distinct groups (whether babies or other species) means to fully consider 156
underlying muscular architecture in coding facial movements with established AUs, 157
or to identify that detailed facial ADs are being used that are not directly related to 158
muscle action (as for AUs). 159

Thus, in this chapter we depend on the independently created systems that code 160
facial movements (Gaspar 2001; Vick et al. 2007) to protect against the bias of top- 161
down classifications (Waller et al. 2007). Both systems allow delineation of features 162
that comprise particular facial expressions rather than assuming all facial expres- 163
sions of a category contain the same features for all individual cases (a bottom-up 164
approach). Both coding systems are atheoretical, protecting the descriptions of facial 165
behavior from conceptual bias. Component features (AUs or ADs, translated into 166
FACS equivalents when applicable) are used to describe facial expressions similar 167
to the processes used by Ekman and Friesen (1978) for human expressions and van 168
Hooff (1962, 1967) for nonhuman primate expressions. Facial expression, for us, 169
refers to a *gestalt* (or configuration) of AUs or ADs. 170

As this review indicates, there is little continuity among studies of chimpanzee 171
facial behavior; coding systems are usually designed to answer the specific research 172
question and therefore may have very limited applications or use in comparing indi- 173
viduals both between and within species. Thus, comparisons among studies are 174
hindered by differences in both methodology and definitions of facial behaviors. 175
It is possible that not only is there discordance in terms of the labels that these 176
expressions are given but that there may also be variation in terms of the facial 177
display classifications themselves, as reported for some manual gestures (e.g., 178
Whiten et al. 1999; Pollick and de Waal 2007). 179

8.1.3   Describing Chimpanzee and Bonobo Facial Events   180
"From Scratch": Creating Descriptor Systems   181

In 1997, Gaspar began a study of bonobo (*Pan paniscus*) and chimpanzee (*Pan* 182
troglodytes) facial behavior with three main goals: (1) to study the diversity of facial 183
expressions in each species; (2) to investigate whether expressions and their con- 184
texts differed across the two *Pan* species; and (3) to determine how similar in form 185
and function these were to human facial expressions as described by Ekman and 186
colleagues (Ekman and Friesen 1975; Ekman et al. 1987). In 2001, Bard and her 187
ChimpFACS team, Marcia Smith Pasqualini, Lisa Parr, Bridget Waller, and Sarah- 188
Jane Vick, with no knowledge of Gaspar's previous work, set out to develop and 189
subsequently disseminate a facial action coding system for chimpanzees that paral- 190
leled the FACS for humans. 191

Gaspar's project began with a decision to describe facial events "from scratch," 192
in other words to develop a coding system for chimpanzees and bonobos without 193
previous input of AUs from FACS. Three months during the summer of 1997 were 194

195   devoted to ad libitum description of unitary actions and other descriptors of bonobo
196   facial behavior, and another month was dedicated to ad libitum observation of chim-
197   panzee facial behaviors. Gaspar created a detailed coding system that would allow
198   for the composing of configurations in terms of facial actions and details of appear-
199   ance changes – thus forming *gestalten*, full face configurations of various descrip-
200   tive units.
201   Bard's ChimpFACS project began with 3 months of FACS training and certi-
202   fication. Subsequently, the team reviewed existing videotapes of chimpanzee
203   facial expressions concluding that they did not provide sufficiently detailed views
204   of the chimpanzee face movements to create and illustrate a detailed coding man-
205   ual to compare to FACS. Therefore, additional months were spent collecting new
206   videotaped records. The ChimpFACS team also consulted with Paul Ekman on
207   the process of developing ChimpFACS from naturalistic observations and with
208   Harriet Oster on the process of modifying and adapting FACS to develop
209   ChimpFACS. The team decision was to begin with a comparison of the facial
210   musculature of the chimpanzee (Burrows et al. 2006; see figure in Waller et al.
211   2006) in conjunction with a comparison of facial morphology (see Fig. 1, p. 7 in
212   Vick et al. 2007). ChimpFACS can now be learned by anyone. The manual with
213   video clips, practice coding, and certification test are available at the website
214   www.chimpfacs.com. Attaining reliability with experts allows for all users to
215   achieve standardization. Due to this process, observations of facial expressions
216   can be confidently coded using ChimpFACS (Parr et al. 2007; Vick and Paukner
217   2010).
218   Gaspar (2001) is the only study to date to use a detailed FACS-based approach to
219   study interindividual variation in facial repertoire. Gaspar used a random sampling
220   method to build a chimpanzee and bonobo *facial expression* repertoire from the
221   bottom up. In this method, she randomly selected the same amount of facial
222   configuration samples from all individuals. A minimum of 50 1-min video focal
223   samples of continuous facial behavior for each individual bonobo ($N = 15$) and each
224   chimpanzee ($N = 21$) were obtained from the video database. The video database
225   included proximate interactions so that the context of behavior was observable. In
226   addition, during the recording, verbal commentary clarified the context. The facial
227   behavior coding procedure from these videos comprised two stages: (1) extracting
228   two random still frames (hereafter snapshots) from each 1 min video focal; and (2)
229   analyzing each snapshot for the constituent facial descriptors (full list in Table 8.1).
230   Coding began with the still frame, but each AD was confirmed by analyzing the
231   original video motion transition to the extracted frame. With this sampling method,
232   2,100 chimpanzee snapshots were gathered (100 facial pictures each for 21 indi-
233   viduals) and 1,500 bonobo facial snapshots (15 bonobos). Context analysis was
234   conducted using a list of 32 possible contexts that had been elaborated from previ-
235   ous ad lib observations and video scans of the colonies. For these analyses, intra-
236   rater longitudinal reliability was calculated: 10% of snapshots were recoded after a
237   3-month interval and the index of concordance (Martin and Bateson 1994) was 0.86
238   for facial coding and 0.80 for context.

Table 8.1 List of action units (AUs), action descriptors (ADs), and musculature for different facial action coding systems (FACS)

Visual description (Gaspar)	FACS equivalence (Ekman et al. 2002)	Muscle (Burrows et al. 2006) or AD (Gaspar 2005)	Muscle action (Waller et al. 2006)	ChimpFACS (Vick et al. 2007)	Facial mobility (Dobson 2008)
1. Eyelids widely opened	AU 5 (D and E intensities)	Yes	–	No	–
2. Eyelids slightly opened	Pan descriptor	Yes	–	–	–
3. Eyelids moderately opened	Pan descriptor	Yes	–	–	–
4. Eyebrows raised	AU 1+2 brow raise	Yes	Yes	Yes	Yes
5. Eyebrows drawn together+inner corners raised	AU1+4 inner brow raised and drawn together	Yes	–	No	No
6. Eyebrows drawn together and downwards	AU4 brows lowered	Yes	No	No	No
7. Eyebrows relaxed	Baseline brows	–	–	–	–
8. Upper lip protruded	AU T18A (pucker upper lip)	Yes	No	No	Yes
9. Lower lip protruded	AU B18A (pucker lower lip)	–	No	No	Yes
10. Upper lip subducted	AU T28 (suck upper lip)	AD	–	Yes	–
11. Lower lip subducted	AU B28 (suck lower lip)	AD	–	Yes	–
12. Upper teeth exposed	Pan descriptor – not exclusive	AD	–	–	–
13. Lower teeth exposed	Pan descriptor – not exclusive	AD	–	–	–
14. Mouth slightly open (lips+teeth part)	AU 25+26	AD	–	Yes	Yes
15. Mouth moderately open (lips+teeth)	AU25+26 (lips part and jaw dropped)	AD		Yes	Yes
16. Mouth widely open	AU27 jaw stretch	AD	–	Yes	Yes
17. Upper lip lifted	AU10 upper lip raise	Yes	Yes	Yes	Yes
18. Upper lip folded up and outward	AU T22 (upper lip) lip funnel	Yes	Yes	Yes	Yes
19. Lower lip lifted	AU17 (chin raise)	Yes	Yes	Yes	Yes

(continued)

Table 8.1 (continued)

Visual description (Gaspar)	FACS equivalence (Ekman et al. 2002)	Muscle (Burrows et al. 2006) or AD (Gaspar 2005)	Muscle action (Waller et al. 2006)	ChimpFACS (Vick et al. 2007)	Facial mobility (Dobson 2008)
20. Lower lip dropped	Pan descriptor	AD	–	AD160	–
21. Upper gum exposed	Pan descriptor – not exclusive	AD	–	–	–
22. Lower gun exposed	Pan descriptor – not exclusive	AD	–	–	Yes
23. Lower lip folded down and outward	AU B22 (lower lip) lip funnel	Yes	Yes	Yes	Yes
24. Lip corners lifted	AU12 lip corner puller	Yes	Yes	Yes	Yes
25. Lip corners lowered	AU15 lip corner depressor	Yes	No	No	Yes
26. Lips stretched horizontally (withdrawn)	AU20 lip stretch	Yes	No	No	No
27. Lips pressed	AU24 lip press	AD	–	Yes	Yes
28. Lower lip overlapping (the upper lip)	Pan descriptor – not exclusive	AD	–	Yes	Yes
29. Upper lip overlapping (the lower lip)	Pan descriptor – not exclusive	AD	–	Yes	Yes
30. Lip area bulged	Pan descriptor	AD	–	–	–
31. Upper lip (area) bulged	Pan descriptor	AD	–	–	–
32. Mouth closed and relaxed	Baseline lips	AD	–	–	–
33. Cheeks lifted	AU6 cheek raise	Yes	Yes	Yes	No
34. Cheeks asymmetrically lifted (right bias)	Right AU6 (cheek raiser right)	–	–	–	–
35. Cheeks asymmetrically lifted (left bias)	Left AU6 (cheek raiser left)	–	–	–	–
36. Upper lip-below nose area wrinkled	Pan descriptor	AD	–	–	–
37. Nose wrinkled	AU9 (nose wrinkle)	Yes	Yes	Yes	Yes
38. Nostrils dilated	AU38 (nostril dilate)	Yes	Yes	Yes	–

39. Cheeks relaxed	Baseline cheeks	AD	–	–	–
40. Chin lifted (active)	AU17 chin raise	Yes	Yes	Yes	Yes
41. Chin lifted (skin laterally stretched-synergistically)	AU17 chin raise	AD	–	–	–
42. Chin lifted and wrinkled (active)	AU17 chin raise	AD	–	–	–
43. Chin relaxed	Baseline chin	AD	–	–	–
44. Jaw dropping (chin skin relaxed)	AU 26 (jaw lower)	AD	–	Yes	–
A. Not described	AU13 cheek puffer	Yes	No	No	Yes
B. Not described	AU 14 cheek dimpler	Yes	–	No	No
C. AD20 or AD22 or 13?	AU16 lower lip depressor	Yes	Yes	Yes	Yes
D. Not described	AU23 lip tightener	–	–	No	Yes

8.1.4   Problems with Inventories? Variation Within Categories

Most studies of chimpanzee facial expressions, both production and recognition, are based upon categorization of overall configuration; observers are concerned with the overall appearance or expression and may not focus upon individual components or level of intensity. Individual variation may occur in the context or frequency of expressions, i.e., the flexibility of usage. Information from other modalities, such as vocalizations and gestures, may encode individual identity. Pollick and de Waal (2007) compared chimpanzee and bonobo facial configurations using independence from a fixed context as a proxy measure of meaning and function. Some facial expression categories were used similarly across species and between groups while others were species typical. They recorded 18 facial/vocal signals and suggested these were used in similar contexts across species. Unfortunately, only 5 of 18 signals were recorded with sufficient frequency for the contextual analyses across species. Pollick and de Waal noted some cross-species differences including use of the silent pout face. However, without microanalyses of facial configurations, or more fine-grained analysis at the level of the individual, any variation would be masked by pooling of both expressions and individuals. The fact that concordance between facial/vocal expressions and context was less than 100% indicates flexibility in how or when individuals produce expressions in different contexts.

To examine variation in facial expressions, it is necessary to have a measurement tool that differentiates subtle differences in configuration. Gaspar (2001) generated facial expression categories (here *gestalten*), by grouping the facial behavior snapshots according to the quantitative similarity in facial descriptors: Those with identical descriptor composition received facial expression names, such as *semi-pouts*. Whenever *gestalten* matched literature descriptions the first published name was used (e.g., *relaxed face with drooped lip*, Goodall 1986). To incorporate *gestalten* that varied slightly from previous categorizations, two independent judges made classifications; agreement meant the photo was incorporated into one of the *gestalt* collections while disagreement led to adjacent groupings. In six chimpanzee photos and two bonobo photos, there were singular representatives of a gestalt *within* the species. For example, a category labeled *laughing face* had a single chimpanzee observation but was observed 10 times in the bonobos. This procedure resulted in inventories of facial *gestalten* (facial ethograms), with 57 facial *gestalten* for chimpanzees and 46 facial *gestalten* for bonobos.

Gaspar (2001) found considerable facial mobility in chimpanzees and bonobos. For example, *funny faces* – a facial behavior initially described by de Waal (1988) in bonobos was added to the list of *gestalten*, because chimpanzees and bonobos exhibited "face experimenting" sequences in which many expressions were performed with no apparent purpose other than experimenting with facial movement. In fact, one bonobo experimented with facial expressions while observing itself in a mirror. This is similar to testing of contingent movements as mentioned by Nielson et al. (2005), Bard et al. (2006), and Bard (2008). Because Gaspar's sampling method (described in the previous section) only captures a small proportion of ongoing facial behavior (a video frame is only 1/1,500 of 1 min of focal facial

movement) these ethograms may be considered preliminary. The full ethogram of 283
bonobo and chimpanzee facial gestalten, therefore, may be substantially higher 284
than, and considerably surpass the size of, existing inventories of facial displays 285
(Parr et al. 2005; Pollick and de Waal 2007). 286

Table 8.1 compares the findings about facial movement across studies showing 287
bottom-up facial movement repertoires in chimpanzees including anatomical 288
descriptions of underlying musculature (Burrows et al. 2006) and their movement 289
(Waller et al. 2006) as well as descriptions of observable chimpanzee facial move- 290
ments (Gaspar 2001; Vick et al. 2007; Dobson 2008). Note that this approach con- 291
trasts with studies that categorize expression types in the first instance and use a 292
top-down approach (Preuschoft and van Hooff 1995; Steiner et al. 2001; Ueno et al. 293
2004). The three observational studies of movement repertoire are not in full agree- 294
ment. Both Gaspar (2001) and Vick et al. (2007) agree on 12 out of 16 core facial 295
movements presented in Dobson (2008). Disagreement seems largely based on how 296
FACS labels are applied in relation to the precise anatomical basis of a movement 297
(e.g., specific muscle action) rather than whether a particular type of movement is 298
seen (Dobson 2008; Vick et al. 2007). 299

Even when using a top-down categorical approach, it is clear that there is some 300
configural variation within categories. For example, van Hooff (1967) distinguished 301
a horizontal grin from vertical bared teeth. Goodall (1986) distinguished full and 302
low grins, as well as closed and open grins. Parr et al. (2007) used ChimpFACS to 303
code static images of chimpanzee facial expressions, which were already catego- 304
rized into expression type. AUs combinations were sufficient for differentiating 305
expressions from one another, indicating its validity as a facial measurement tool. 306
The ChimpFACS approach was also able to identify within category variation for 307
already classified facial expressions by specifying the facial action components of 308
each case, and determining goodness of fit (Parr et al. 2007). For example, there 309
were 34 cases of Bared Teeth display, with analyses indicating two main variants: 310
one variant consisted of raised upper lip (AU10), lip corners pulled toward the ears 311
(AU12) and lips parted (AU25), and the second variant added a lower lip depressed 312
(AU16), resulting in the variant (AU10, AU12, AU16, AU25). In Gaspar's (2001) 313
ethograms, there are considerably more, namely, 12 types of facial *gestalten* with 314
bared teeth (7 types of closed grins and 5 types of open grins). One of the latter 315
gestalten "full open grin," for example, upper teeth exposed (AU10) and mouth 316
widely open (AU27) occurred in 100% of the cases, but additional AUs varied: 317
lower teeth exposed, lips horizontally stretched (AU20) occurred in 94% of the 318
cases, and eyebrow lowered (AU4) occurred in only 60% of the cases. At this stage 319
in our studies, the emotional and/or communicative meaning of these different types 320
of bared teeth facial expressions remains unclear. We therefore need to examine 321
more fully systematic differences in the production of expressions by individuals 322
and consider what impact this variation may have on perceivers, who may differen- 323
tiate, ignore, or not perceive subtle differences in expressions (Fridlund 1994). 324
Additionally, it is important to note that Gaspar (2001) found that although *gestalten* 325
were used in quite different proportions by chimpanzees and bonobos, by far the 326
most frequently sampled *gestalt* was the baseline relaxed face. 327

8.1.5   Comparing Action Descriptors: ChimpFACS and FACS

Gaspar produced a list of facial ADs shown with ChimpFACS AUs in Table 8.1. Overall there is significant comparability with human facial musculature, appearance changes, and FACS AUs. The majority of AUs were independently found in both of our projects. Similar conclusions followed from the use of these independently created systems. Chimpanzee facial AUs and descriptors (Gaspar 2001, 2006; Gaspar et al. 2004; Vick et al. 2007) overlap extensively with those seen in humans (Ekman and Friesen 1978; Ekman et al. 2002). The differences noted in Table 8.1, relate to the reliance on physical appearance changes by Gaspar (2001) and the reliance on anatomy by the ChimpFACS team (Waller et al. 2006). Two types of species differences were found: absence of some human actions in the chimpanzee face and absence of some chimpanzee actions in the human face.

Clear differences emerged in some appearance changes in the *Pan* species compared to humans, especially in AUs involving the orbital muscle of the lips, *Orbicularis oris* (i.e., AU18 Lip Pucker, AU22 Lip Funneler). Both teams also agreed that chimpanzees exhibit greater independence of movement in the upper and lower lips than is usually seen in humans. Human mouth movements are generally orbital in action, perhaps related to articulatory needs and precision of speech, but in chimpanzees and bonobos it is common to have movement occur in just one lip (Vick et al. 2007). Differences in facial morphology might also account for some differences in lip actions: for example, chimpanzees lack a chin boss so that their lower lip can droop down towards the jaw in a way not seen in humans. Therefore, both the ChimpFACS system and Gaspar distinguished between upper and lower lip for mouth actions (for AU22 Lip Funneler and for AU18 Lip Pucker) which are possible but rarely found in humans.
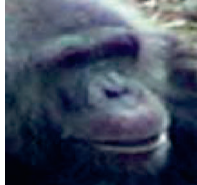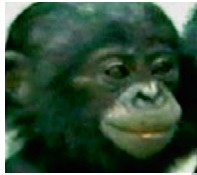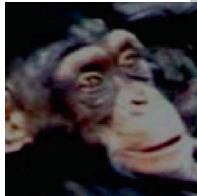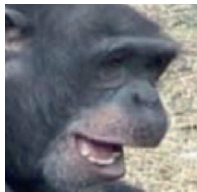
In the upper face, there are minor differences in the frequency of some actions and in the degree of flexibility of brow movement. For example, humans display more independence in Inner Brow Raise action (AU1), and more complexity in brow actions (e.g., combinations with AU4 Brow Lowerer) than found in chimpanzees. Overall, both groups concluded that the facial AUs of chimpanzees and humans extensively overlap (Gaspar 2001, 2004, 2006; Vick et al. 2007).

8.2   Chimpanzee and Bonobo Facial Behavior Compared

In the following section we compare the facial behavior of chimpanzees and bonobos, and consider the following ways in which individual differences might be apparent: (1) individuals could vary in the size or frequency of *gestalten*; (2) individuals could vary in how closely their facial behavior is tied with specific contexts; or (3) individuals could vary in how often certain gestalten occurred in particular contexts. The results are based on bonobo data from two colonies (Milwaukee County Zoo, Columbus Zoo and Aquarium) and chimpanzee data from three colonies (Cleveland Metroparks Zoo The Detroit Zoo; Burger's Zoo). We excluded AUs and ADs with low total frequencies (<5).
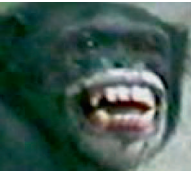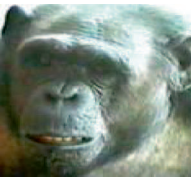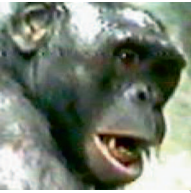
The facial expression repertoires of chimpanzees and bonobos are similar: 41 of the 60 gestalten were found in both species (Table 8.2; Gaspar 2001), but chimpanzees

Table 8.2 Joint chimpanzee and bonobo facial expression (*gestalten*) ethogram. Expression contexts are based on Chi-square associations with p values <0.01. This is a summarized version of Gaspar (2001) bonobo and chimpanzee facial expressions' ethograms (pages 69–88 and pages 152–184 respectively). The table omits brow only facial expressions, variations of baseline with tense mouth, variations of Low closed grin, of Full open grin, Full closed grin and of Subducted Lips face, Bulging lips face and Protruded lips face. Bonobo exclusive expressions were also excluded

		Joint chimpanzee and bonobo facial expression ethogram	
Photo	Name	Descripton:FACS Action Units equivalents & other descriptors	Signif. Contexts
	Bulging Lips Face	AU10+AU17+ AU23 + Upper lip are bulged + lower lip area bulged	Idle; attention shift (chimpanzee); ns associations (bonobo)
	Relaxed Open Mouth Face	AU25+26	Group excitment, Watch other's in affiliative interaction, Beg (chimpanzees); Affiliative contact other than grooming, Solitary play, Startle (bonobo)
	Closed Mouth Smile	AU12 + AU20	Affiliative contact other than grooming (chimpanzee); B27
	Open Mouth Smile	AU12+ AU25	Beg, Teasing & Quasi agonistic behavior (bonobo); give Invitation to Social play, Solitary play, Excitment (chimpanzee)
	Play-Face	AU12 + AU25+26	Invitation for Social play, Calm social play, rough social play (chimpanzee and bonobo); Solitary play, Effort/ physical challenge (chimpanzee)

(continued)

Table 8.2 (continued)

		Descripton:FACS Action Units equivalents &	
Photo	Name	other descriptors	Signif. Contexts
	Full Closed Grin	AU10+ AU20+ AU25+ Gums exposed	Fear related (chimpanzee); courtship (bonobo)
	Full Open Grin	AU10+ AU20+ AU25+AU27 +Gums exposed	Fear related, (chimpanzee); Rough social play, Anger & threat displays (chimpanzee and bonobo)
	Low Closed Grin	AU16+ AU20	Fear related (chimpanzee and bonobo), Frustration (chimpanzee)
	Low Open Grin	AU16+ AU20+ AU25+26	Anger & threat displays; ns associations in chimpanzee
	Subducted Lips Face	AU23 + AUT28 + D28	Effort/physical challenge (chimpanzee); ns associations in bonobo
	Open Mouth Subducted Lips Face	AU25+26 + AUT28+AUB28	Effort/Physical chalenge (bonobo); ns associations in chimpanzee

(continued)

Table 8.2 (continued)

Photo	Name	Descripton:FACS Action Units equivalents & other descriptors	Signif. Contexts
	Overlapping Lower Lip Face (Lip-Flip)	Lower lip overlapping upper lip (no corresponding AU)	Effort/Physical chalenge (bonobo); give Grooming, Mutual grooming (chimpanzee)
	Pout Face	AUT18+D18 AU24 AUT22+D22	Give grooming, Courtship, Mild-annoyance (bonobos); ns associations in chimpanzees
	Protruded Lips Face	AUT18 + D18	Non-agonistic display, give grooming (bonobos); mutual grooming (chimpanzees)
	Hoot-Face	AU(T18+D18)+ AU(T22+D22)+ AU25+AU26	Anger & threat displays, group excitment, fear related (chimpanzee and bonobo)
	Very Compressed Lips & Frown Face	AU4 + AU23	Attention shift (bonobo); ns associations in chimpanzee
	Stretched Lips Face	AU20 + AU23	Watch over infant (bonobo); ns associations in chimpanzee

Table 8.2 (continued)

		Descripton:FACS Action Units equivalents &	
Photo	Name	other descriptors	Signif. Contexts
	Tonge-Show Face	AU25+ tongue protruded	ns associations in chimpanzee or bonobo, but many different contexts in chimpanzee
FUNNY FACES		many faces, not a gestalt	self-entertainment

369 and bonobos differed significantly in the frequency of use for 3 of the 9 facial
370 descriptors. Bonobos, as a group, had significantly higher frequencies of AU4 (Brow
371 Lowerer – see Figure 8.1a–c), AU10 (Upper Lip Raiser), and AU12 (Lip Corner
372 Puller) than did chimpanzees, as a group (Gaspar and Bard, unpublished manu-
373 script). There is not a one-to-one correspondence between facial expression *gestalten*
374 (e.g., Bared Teeth facial display) and context (Gaspar 2001; Gaspar and Bard,
375 unpublished manuscript; Parr et al. 2005; Pollick and de Waal 2007). For example,
376 for the "full open grin" *gestalt*, 40% of occurrences were in the fear context, 40% in
377 rough and tumble play context, and 20% were in contexts of anger or aggressive
378 display. It is possible that across all contexts, there is a common highly excited emo-
379 tional state tied to the facial *gestalt* of full open grin (e.g., Goodall 1986), or this
380 *gestalt* might convey a precise "meaning" message not linked with contexts (perhaps
381 of the sort "Stop what you are doing," e.g., Bard et al., unpublished manuscript).

382 Individual differences are also apparent in the total diversity of *gestalten* within
383 each context. In this comparison, chimpanzees used a greater diversity of expres-
384 sions than did bonobos in the contexts of *groom*, and *close-up inspection*. Bonobos
385 used a greater diversity of expressions in *play*. The percentage overlap of expres-
386 sions between the two species varied across contexts: at least 50% *gestalten* overlap
387 in the contexts of *groom, concentration in activity,* and *anger and threat displays*,
388 and 30–40% of bonobo and chimpanzee *gestalten* overlap in *affiliative contact,*
389 *receive grooming*, and *fear* contexts. A curious observation is the fact that there are
390 no *gestalten* found in both species in the *startle* context. This evolutionarily based
391 basic reaction should register similarly in the face, so clearly this context needs
392 further exploration in the future (Gaspar 2001).

393 In conclusion, we find that individual chimpanzees and bonobos varied in their
394 use of different facial movements, in the frequency of different *gestalten*, and in the
395 diversity of *gestalten* across different contexts. The use of the bottom-up approach
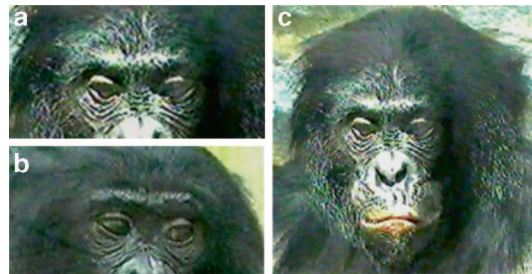396 is critical in this documentation of individual differences.

Fig. 8.1 Action Unit (AU) 4 in a bonobo (**a**, **c**). The same individual (Jimmy, at the Columbus Zoo and Aquarium. OH, USA) shown also with his typical relaxed brow shape in (**b**). ADs are detected during video playback and physiognomic differences between individuals require that we have a baseline referent of their facial features while relaxed (for instance, whereas Jimmy´s brows look arched in a baseline condition, but other individual's baseline looks horizontal or even slightly frowned)

8.3   Facial Behavior Is Important in the Study of Individual Differences: Relationships with Personality, Temperament, and Emotionality

In this section, we present our rationale for the study of individual differences in primate facial displays. We note that there is good reason to expect variation among primate individuals. Some primate facial movements are volitional, and therefore, we should not be surprised to find meaningfully large individual differences. We explore how individual differences in personality, temperament, and emotionality might be related to individual differences in facial behavior through higher order constructs such as "dominance," "attractiveness," "expressivity," and "extraversion."

8.3.1   Why Do We Think There Is Variation in Facial Behavior?

As evolutionary adaptations, we would expect phenotypic variation in the production and perception of expressions, with related fitness consequences (Schmidt and Cohn 2001). Given the challenges of studying facial expressions across species, and perhaps the pervasive influence of the universal emotions perspective, the focus has been on understanding the form and function of prototypical facial displays, with little consideration of idiosyncrasies in facial behavior. Important differences in facial behavior relating to sex, dominance, or age have not been fully addressed in nonhuman primates. Life experiences, in addition, may change communicative repertoires; studies of gestural communication reveal individual variation and idiosyncratic gestures (Liebal et al. 2004). Vocal research has identified individual markers within some types of call (e.g., Owren and Rendall 2003). Like humans, great apes also have

419   long periods of dependency during which time social skills are acquired, resulting in
420   great plasticity in their social behaviors as evidenced by cultures (Whiten et al. 1999;
421   van Schaik et al. 2003). Moreover, in humans, facial expression and individual iden-
422   tity are interlinked. Therefore, we should expect variation in signal production and
423   perception based on the individual characteristics of nonhuman primates.

424   At the individual level, several variables can shape variation in facial displays
425   (Schmidt and Cohn 2001). Anatomically, human facial musculature reveals some
426   interindividual variation in muscle presence and precise structure (Pessa et al. 1998;
427   Waller et al. 2008), but there has been little systematic investigation of variability for
428   nonhuman primates. There are some inconsistencies in the anatomical literature, but
429   it remains unclear whether these are due to differences or omissions in describing the
430   muscle plan, to individual variation, or small sample sizes (Burrows et al. 2006;
431   Waller et al. 2006). Interestingly, variation in muscle structure may lead to observ-
432   able differences in expression appearance. For example, in humans, a bifid form of
433   the zygomatic major muscle causes dimples when smiling (Pessa et al. 1998).

434   Neural control of facial movement may also affect expression production with
435   involuntary and voluntary control over facial actions well described in humans
436   (Rinn 1984) and rhesus macaques (Morecraft et al. 2001). Left–right asymmetry of
437   expressions (Fernandes-Carriba et al. 2002) may be caused by asymmetrical facial
438   structure or muscle innervation, with spontaneous production being more symmet-
439   rical than volitional movements. Cortical innervation may also underlie distinctions
440   between the upper and lower face (Ross et al. 2007).

441   There is clearly variation in expression production. Although traditional etho-
442   grams present stereotypical displays, some variations are based on the intensity of
443   expression and temporal patterns. In humans, the onset, offset, and peak of expres-
444   sion impacts expression perception and interpretation (Ekman and Rosenberg 2005).
445   It would be interesting to examine nonhuman primate sensitivities to such subtle
446   variations. Moreover, a combination of facial expressions, head position, and gaze
447   direction may interact with facial movement to allow even greater variation in
448   expression production (Redican 1975). Chimpanzees have distinct forms of gaze
449   (Bethell et al. 2007). Moreover, patterns of mutual gaze are modifiable in early
450   interaction with caregivers (Bard et al. 2005) suggesting that eye movement is
451   another source of variation in dynamic facial displays in nonhuman primates.

452   In cognitive and behavioral studies, there are variations at the level of individual
453   performance, but the basis for these individual differences is hard to determine.
454   Personality factors are likely to determine an individual's attention, behavioral flex-
455   ibility, accuracy, and response to reward schedules when performing tasks, and thus
456   personality measures should be able to predict some of this variation (Uher and
457   Asendorpf 2007). Similarly, chimpanzees may differ in overall expressivity which
458   may be correlated with their personality (King and Figueredo 1997). Temperament
459   may interact with previous experiences, so that the emotional valence of a given
460   context can vary across individuals (Bard and Gardner 1996; Bard et al., unpub-
461   lished manuscript). In addition, individuals may vary in volitional control of facial
462   behaviors, and vary in responsiveness to the expressions of others as a function of
463   attention, emotional sensitivity, or other individual factors.

Emotional contagion/induction or an individual's susceptibility to the emotional experiences of others is also likely to correlate with personality measures, such as extraversion. Even in early infancy, primates demonstrate variability in relation to their ability to imitate facial expressions (Bard 2007; Ferrari et al. 2006; Myowa-Yamakoshi et al. 2004) but we do not know whether this initial variation in tendency to imitate is correlated with personality attributes, or whether it has any impact upon future socioemotional experiences and learning. Contagious yawning is a robust phenomenon in humans and correlates positively with measures of empathy and theory of mind (Platek et al. 2003). Chimpanzees also demonstrate contagious yawning but there is individual variation; only 2 out of 6 female chimpanzees responded to video sequences of conspecific yawns with increased levels of yawning (Anderson et al. 2004). A more recent study in orangutans examined the rapid mimicry of play faces during dyadic play bouts; 16 out of 25 individuals showed rapid (<1 s) facial mimicry to the play face of their playmate but only 9 out of 25 did in a control condition (Davila-Ross et al. 2008). The quality of interactants' social relationships may affect both voluntary and involuntary mimicry of others as reported in humans (McIntosh 2006) but it would be valuable to examine these measures of emotional contagion across time and contexts in the same individuals in relation to personality traits.

The emotional state of receivers is likely to mediate the perception of emotion in nonhuman primates, as it does in humans, for example, by being more responsive to negative emotional expressions when already aroused by negative events. Finally, in humans, personality may bias perception of social signals. For example, trait anxiety leads to heightened perception of hostility when rating happy, neutral, and angry expressions (Knayazev et al. 2008). We do not yet know how chimpanzees' personalities affect their perceptual biases; it may be that individual variation in performance on perception tasks may reflect biases in expression processing that likely affects everyday social interactions with conspecifics. Attending to socially salient events is important for group living primates and is both cognitively costly and imperative for individual fitness (Barrett et al. 2002). We know that primate attention structures may reveal disproportionate interest in dominant individuals, mediated by an individual's rank (Shepherd et al. 2006), or the quality of dyadic relationships (Lane et al. unpublished manuscript). Attention to the expressive behaviors of dominant individuals is probably different than that directed towards other group mates. Some displays may automatically capture attention. For example, angry expressions may be processed rapidly and effectively (Gosselin et al. 1997). However, visual signals allow perceivers some degree of control, by disengaging gaze, to "cut-off" aversive stimuli, such as a facial threat (Kummer 1967; Altmann 1967).

8.3.2 Volition in Facial Expression Production

"A survey of the literature reveals that many who have commented on the signaling of animals ascribe to a view that all of their communicative signals are manifestations of emotion or affect" (Marler and Evans 1997, p. 133). That is, in this view,

facial behaviors are spontaneous and uncontrollable displays of internal affective states. New research indicates that some behaviors, such as the raspberry or the extended grunt vocalization found in captive chimpanzees but long dismissed as "merely" emotional displays, are individually invented (Hopkins et al. 2007). The issue of whether nonhuman primates have voluntary control over expressions is a difficult topic to study; if chimpanzees can control their facial displays how could we tell? Awareness or control of facial behavior could result in the (a) deliberate production of a display or (b) intentional showing or (c) concealment of a spontaneous display. Here we briefly consider the evidence in support of each of these possibilities.

8.3.2.1 Deliberate Production of Displays

Chevalier-Skolnikoff (1982) considered apes to be capable of deceptive use of facial signals since they can "manifest facial expressions that are inconsistent with emotional state" (p. 360). Of course, it is difficult to exclude the possibility that the inferred emotional state is erroneous rather than the expression being incongruent. In humans, there is some evidence that spontaneous and voluntary expressions can be identified when analyzed in sufficient detail; timing and symmetry may differentiate between them (Ekman and Rosenberg 2005). The deliberate production of a display would be difficult to ascertain in chimpanzees because even similarly detailed studies of expression production would be limited by the need to make an inference regarding whether the expression was voluntarily produced (the problem of circularity).

The "funny faces" as described by de Waal (1988) in bonobos, and both in chimpanzees and bonobos by Gaspar (2001) and more recently in gorillas (Gaspar et al., unpublished manuscript), also indicate volition over facial movement, although the degree of control over specific facial actions has yet to be described in detail. In addition, some voluntary control over some facial movements can be inferred from imitation studies which show that chimpanzees can copy arbitrary actions (Custance et al. 1995). Two chimpanzees, trained to copy 15 arbitrary actions using a "do this" command, were then presented with 48 novel actions including 6 facial actions. Overall the chimpanzees showed clear evidence of imitation, but performance on the facial actions was weaker with only "lip smacking" being reliably identified by both observers. However, humans also have considerable difficulty copying facial movements. FACS training requires coders to perform each AU and success requires considerable hours of practice (Ekman et al. 2002). Some facial movements are more readily performed than others and questions about voluntary control may need to take the specific action into account. Those expressions that are regularly used with particular combinations of AUs may be more readily imitated than isolated facial movements, or vice versa if selection pressure on detecting cheats means that honest signals (genuine expressions) are costly to produce.

8.3.2.2 Intentional Showing of Displays   546

Intentional showing of displays could be explored in terms of social context (pres- 547
ence of an audience) or the target of displays, that is, whether signals are intention- 548
ally directed towards specific target receivers. Volition can be addressed by examining 549
audience effects because if calls are automatic, the presence of conspecifics should 550
not influence call production (e.g., Marler and Evans 1997). In birds, call production 551
is influenced by audience effects (that are functionally relevant to each call). In 552
chimpanzees, audience effects occur in gesture production (e.g., Leavens et al. 2004) 553
and in vocal production (e.g., Hopkins et al. 2007). However, variation in call patterns 554
may be influenced by arousal levels of an individual which are related to character- 555
istics of the audience. Marler and Evans suggest that the former is unlikely for birds 556
as only calls, and not other concomitant behaviors or physiological responses, differ 557
according to social context.   558

Audience effects on facial behavior have rarely been directly examined in nonhuman 559
primates, perhaps because of the difficulty in distinguishing among conspecifics as 560
intended recipients of displays. Most primate communication is related to social 561
interaction; emotions are essentially an integral component of any social context so 562
that the social vs. emotional debate is based on an erroneous dichotomy (Parkinson 563
2005). However, van Hooff and Preuschoft (2003, p. 284) suggest that "the element 564
of emotional expression comes to the fore when the display is performed in the 565
absence of an audience." They suggest that solitary play accompanied by play faces 566
in young chimpanzees is indicative of joyfulness. However, the play face can also 567
be a socially mediated behavior as juvenile chimpanzees modify their signaling in 568
the presence of young playmates' mothers (Jeanotte and de Waal 1996, cited in van 569
Hooff and Peuschoft 2003).   570

The interaction between social context and facial behaviors and their function is 571
obviously an important direction for future study. We return to this topic later (in 572
Sect. 8.3.2), when discussing possible paths to study facial behavior predictors of per- 573
sonality. In addition to audience effects, facial behavior, unlike vocalizations, can also 574
be directed towards particular recipients (Altmann 1967), who could differ in respon- 575
sive characteristics. For example, expressions of vulnerability such as pain should be 576
differentially directed at those who might provide support (Krebs and Dawkins 1984). 577
There may also be subtle within-expression variations according to familiarity or relat- 578
edness of receivers. Animal signals may have low input specificity (Marler and Evans 579
1997) with a wide range of stimuli converging into one expressive display, which cor- 580
responds to both the emotion and communication view. Each signal can operate in 581
concert with a range of others (Forrester 2008) and these combinations can lead to high 582
specificity. For example, gaze and posture may indicate direction of an expression, age 583
and sex class of sender (or receiver) may alter the meaning of a display, and even indi- 584
vidual idiosyncrasies among familiar conspecifics may make the signal more precise. 585
Similarly, Fridlund (1994) suggests that displays would be likely to vary according to 586
other contextual features such as identity of interactants, their previous history, and the 587
situation in which display is given (e.g., competition over food, defense of young). 588

8.3.2.3 Concealment and Suppression of Displays

Apes are aware of the communicative function of their expressions and may, on occasion, try to conceal the signal (de Waal 1992; Goodall 1986; Mitchell 1999). For example, Tanner and Byrne (1993) reported that a gorilla covered its play face on multiple occasions. Moreover, examples of concealment suggest that the production of the expression itself may not be suppressed. Involuntary facial movements may be more clearly concealed during interactions by simply orienting or moving away from potential recipients, or engaging in displacement activities. However, facial expressions can interfere with other behaviors. For example, at the Chester Zoo we observed a female chimpanzee's unsuccessful attempts to take a drink because her mouth was fixed in an intense Bared Teeth display (Waller and Vick, personal observation). This suggests that, in at least some circumstances, chimpanzees are unable to control their facial behavior. In contrast, humans may use voluntary facial movements to conceal or suppress spontaneous expressions (Ekman et al. 1988); for example, suppressing a smile (AU12 Lip Corner Puller) by the antagonistic action of pulling the mouth corners downwards (AU15 Lip Corner Depressor). As yet, the FACS approach to chimpanzee facial behavior has not revealed any evidence of such masking behaviors. Moreover, the incomplete suppression of an expression may be better conceptualized as conflicting intentions rather than leakage (Fridlund 1994) so that making inferences about the meaning of "deceptive" facial displays would be challenging.

The issue of variation has been related to whether nonhuman primates are capable of voluntary control over their expressions. Steklis and Raleigh (1979, p. 257) dispute the view "that the fundamental contrast between human and nonhuman primates is that the latter's lack significant voluntary control over their vocalizations and facial expressions." According to their view, if responses are involuntary they should be invariable and thus individual variation indicates some degree of volition over expressions. As noted previously, individual variations may be predominantly caused by differences in underlying anatomical structure (Schmidt and Cohn 2001). However, within the variation there may be stereotypical components. Schmidt et al. (2003) found that in human smiling the onset (lip corner movement) did not differ in terms of timing or duration, while peak and offset showed variation. This suggests that within a variable display there may be conspicuous and stereotyped signals. Identifying consistent features would clarify the communicative function of chimpanzee expressions.

8.3.3 Interindividual Differences in Facial Behavior

It has long been proposed that humans and other animals are genetically programmed to decode and respond adequately to the facial behavior of conspecifics (Buck 1984; Dimberg 1988). Ekman (1984) pointed out that humans pay more attention to the face than to other parts of the body when processing other people's

nonverbal behavior, suggesting that this is why we are susceptible to being deceived   629
more easily by the face than the body, and why we train face control more than body   630
control. Our perceptions and attributions of personality may rely largely on facial   631
behavior. Examples from studies using prototypical static facial expressions of   632
emotion include perceived "friendly" social dominance and friendliness based on   633
"happy" facial expressions, "unfriendly" dominance based on the display of anger   634
facial expressions, and submissiveness based on the display of fear and surprise   635
expressions (Hess et al. 2000; Knutson 1996; Zebrowitz et al. 2007). In addition,   636
expressive people are seen as more attractive and likable than unexpressive people   637
(Friedman et al. 1988; Halberstadt 1984; Larrance and Zuckerman 1981).   638

Although relevant information about oneself is often multichannel and what the   639
face conveys is coordinated with what the body conveys (Grammer et al. 1997),   640
relying on the face is fruitful both for sender and receiver, inasmuch as it is a source   641
of accurate predictions of social outcomes. Rejected children display angry facial   642
expressions more often than other children (Hubbard 2001). Popular children display   643
an eyebrow frown less often than their less popular peers (Murphy and Faulkner   644
2000). A reliable cue to an altruistic nature and a willingness to share seems to be a   645
Duchenne Smile (Mehu et al. 2007), a smile *gestalt* comprised of FACS's action   646
units AU6 (Cheeks Raiser) and tightening of lids (with wrinkles and bulges below   647
the lower eyelid) in addition to the AU12 (Lip Corner Puller) that distinguish "felt"   648
spontaneous smiles from other types of smiles, e.g., posed smiles with only AU12   649
(Ekman and Friesen 1982).   650

It is plausible that in other primates, regulation of interactions based on expecta-   651
tions follows a similar pattern. This expectation is highest in the case of chimpan-   652
zees and bonobos, whom we now know have a very diverse facial behavior (Gaspar   653
2001; Gaspar and Bard, unpublished manuscript) and a facial musculature nearly   654
identical to that of humans (Burrows et al. 2006). This ought to make possible a   655
range of expressions in chimpanzees that is comparable to the diversity that humans   656
exhibit. Combinations of AUs generated by naturally occurring human facial move-   657
ments are countless and, most of the time, do not fall neatly into prototypical emo-   658
tion expressions (Fernández-Dols and Ruiz-Belda 1997; Grammer et al. 1997,   659
2004). Moreover, within each of the six "basic" emotions (anger, happiness, fear,   660
sadness, surprise, and disgust), there are a large number of different facial configu-   661
rations interpreted to portray the emotion (Grammer et al. 1997). Finally, within a   662
dynamic exchange, there are striking temporal variations in facial expressions.   663

A high degree of individuality in behavior has been documented in many nonhu-   664
man animals (Bard 1994; Bard et al. 2005; Maestripieri 1993; Hammershmidt and   665
Todt 1995; Baker and Aureli 1997; Clarke and Snipes 1998), including personality   666
dimensions similar to those of humans (Bard and Gardner 1996; Gosling and John   667
1999). It is clear that nonhuman primate personality at least partly overlaps with the   668
Five-Factor Model of human personality (King and Figueredo 1997; McCrae and   669
John 1992: Weiss et al. 2006). However, individuality in the facial behavior of non-   670
human primates has rarely been quantified (with notable exceptions of Gaspar 2001;   671
Gaspar et al. 2004; Jesus 2007; Jesus and Gaspar 2008). This lack of focus on indi-   672
viduality is not related to either the frequency or putative importance of facial   673

674 individuality in social interaction. Rather, most studies of human facial behavior do
675 not address spontaneous real-life events of facial behavior (more often focusing
676 instead on the categorization of posed facial configurations using a limited list of
677 expression terms). Exceptions, however, show that there is interindividual variation
678 in frequency and specific configuration of emotional facial expressions in human
679 children and adults (Buck 1975; Cohn et al. 2002; Fernández-Dols and Ruiz-Belda
680 1997; Grammer 1988 cited in Grammer et al. 1997) with notable stability of indi-
681 vidual differences in adult facial behavior over time (Cohn et al. 2002).

682 As with other behaviors that vary individually, a facial action may play a role in
683 the communication of individual qualities to interactors, including aspects of per-
684 sonality, if (a) it has a predictive value in "real world outcomes" or other behaviors;
685 (b) it is consistent over time; and (c) it is consistent in an individual over time
686 (Gaspar and Bard, unpublished manuscript; Gosling et al. 2003; Pervin and John
687 1997). Individuality in the communication repertoire of chimpanzees and bonobos
688 was expected based on evidence of voluntary control and flexibility in the gestural,
689 and on occasion vocal and facial behavior of gorillas, chimpanzees, bonobos, and
690 orangutans (Bard 1992; Hopkins and Savage-Rumbaugh 1991; Pika et al. 2003,
691 2005; Liebal et al. 2006; Tanner and Byrne 1993).

692 An ideal starting point in the research of socially relevant predictions from indi-
693 vidualized facial behavior is the assessment of its stability over time. A subsample
694 of several ADs of bonobos was analyzed for consistency. Of the facial descriptors,
695 8 of the 9 did not differ in frequency of use across the 5 years (Gaspar and Bard,
696 unpublished manuscript). The single exception was cheek raising (AU6), which
697 supports a link of this action with intensity of expressions, rather than with indi-
698 vidual expressivity (Messinger 2002). Therefore, we conclude that the frequency of
699 many facial behaviors of individual bonobos remains consistent over time.

700 Bonobo facial behavior is also intraindividually consistent. There are systematic
701 differences in certain facial action configurations across individuals, with some indi-
702 viduals significantly above the expected frequency for a given movement (Gaspar
703 2001; Gaspar and Bard, unpublished manuscript). Although male and female chim-
704 panzees appear to use ADs with equivalent frequencies, male and female bonobos
705 differ in some movements; females use Lip Stretch (AU20) more than males, and
706 male bonobos use Upper Lip Raise (AU10) more than females. Female bonobos
707 display more grin faces than males (Kano 1992), but there may be differences in the
708 frequency of the "grin" contexts between males and females. Females display more
709 grin faces in temper tantrums or frustrating contexts, which is fully compatible with
710 Gaspar's (2001) Milwaukee and Columbus bonobo observations. There were no sex
711 differences in the use of common facial *gestalten* in chimpanzees and bonobos.
712 Frequencies of some facial descriptors differ across age categories in both *Pan* spe-
713 cies (Gaspar 2001; Gaspar and Bard, unpublished manuscript; Goodall 1986; Kano
714 1992). For example, brow furrowing (AU4) in bonobos occurs most frequently in
715 adults (54%) and least frequently in infants (10%). This is an interesting result since
716 infant brow movements are easier to perceive. Infant bonobos performed more (67%)
717 lip corner movements (AU12) compared to adolescents (18%) and adults (15%).
718 Perhaps this is not surprising, as AU12 is a component of *play face* and *laughing face*,

and social play is much more frequent in infants. Chimpanzees displayed large age   719
differences in (1) brow raising (AU1+2): adults account for most of the observations   720
(70%), compared to adolescents and infants (both at 15%) and (2) lip corner raising   721
and stretching movements (AU12 and AU20) with infants accounting for most of the   722
occurrences, but adult chimpanzees showing more than adolescents. We do not know   723
whether these age-dependent facial movement differences relate to emotional, con-   724
textual, or other individual characteristics that may be age dependent as well.   725

8.3.4 *Predicting Individual Traits from Facial Behavior*   726

A major question that follows from finding that individuals are not only different from   727
their age-class peers in facial behavior but also are consistent across long time-spans   728
is whether individual differences in facial behavior are related to personality traits,   729
other individual attributes, or specific behaviors.   730

Top-down approaches to chimpanzee personality based on human questionnaires   731
and bottom-up approaches based on ethological methods differ (see Uher 2011) but,   732
in our view, are complementary rather than mutually exclusive approaches. Those   733
interested in using personality measures to predict specific behaviors in chimpan-   734
zees might be best off using a combined approach. To our knowledge, Carvalho   735
(2008), a graduate student at Coimbra University, Portugal, is the first to investigate   736
the relation between personality traits and three well-known chimpanzee facial   737
expressions: play face, hoot face (Goodall 1986), and silent bared-teeth (van Hooff   738
1972). Carvalho adopted a quasi bottom-up approach. She selected personality trait   739
descriptors from King and Figueredo's (1997) questionnaire and modified the   740
descriptors so that they referred to directly observable behavior units. She and   741
another researcher investigated the relation between traits and these expressions in   742
15 rehabilitant chimpanzees at the Jane Goodall Institute's Chimpanzee Eden   743
Sanctuary in South Africa. As she predicted, there was large interindividual varia-   744
tion in personality traits and in the use of the facial expressions, and some signifi-   745
cant relations. For example, the trait *active* was positively correlated with play face,   746
the trait *dominant* was positively correlated with Hoot-face (Carvalho 2008).   747

The key point in the application of an ethological approach to assessing personality   748
is that it circumvents a limitation of the questionnaire approach viz. the rater needs to   749
be well acquainted with each subject. When personality traits are linked with specific   750
behavioral measures, the behavioral measures can be used by any researcher, includ-   751
ing those having no acquaintance with the target individuals (Carvalho et al. 2008).   752
In addition, facial expressions can be useful in providing external validation for   753
personality questionnaire items. Ideally personality traits could be assessed with both   754
approaches (ethological behavior and personality questionnaires) for a large sample   755
of chimpanzees. The larger the overlap of results, the more opportunities there will   756
be for studying personality in great apes in different kinds of settings. Given valida-   757
tion, the behavior measures may be especially useful for longitudinal and ontogenetic   758
studies that require the participation of different observers over time.   759

Research on the prediction of other individual attributes by facial behavior is still in its early days. In several nonhuman primate species, several associations were found between facial behavior and formal dominance status, with certain facial expressions being more frequent in dominant individuals (Chevalier-Skolnikoff 1973; van Hooff 1973; Jacobus and Loy 1981; Preuschoft 1992; Reichler et al. 1998) or differing according to context in those individuals (Gaspar 2001).

Human children vary in social attractiveness which ranges from peer rejection to being the most popular. Albeit there is controversy surrounding the factor(s) that contribute towards lowering or enhancing a child or teenager's social attraction (Babad 2001), peer relational status and interactive style are highly stable across many years and contexts (Cillessen et al. 2000; Englund et al. 2000; Dodge et al. 2003). These findings suggest that social attraction must be strongly dependent on individual personality traits.

For these reasons, Gaspar and colleagues investigated Social Attraction in chimpanzees and bonobos. Social Attraction is an individual attribute defined as "the proportion of affinitive interactions in which the target individual was engaged, at the time of sampling, that were *not* initiated by the target individual," i.e., receptivity to the affinitive invitations of others (Gaspar et al. 2004). The question was whether Social Attraction could be predicted from facial behavior traits, such as *expressivity* (a measure of facial behavior diversity) or the frequencies of play faces (the combination of mouth opening movements such as AUs 25 + 26 present in relaxed open-mouth face, play face, and open mouth smile connected to positive affect) and AU12 (Lip Corner Puller), present in open mouth smile and play face. In bonobos, Social Attraction correlated significantly with expressivity, and frequency of AU 25 + 26 and AU12. For chimpanzees, Social Attraction was negatively correlated with frowning (AU4 Brow Lowerer). Social attraction in bonobos and chimpanzees is influenced by individual qualities of facial movements. One can argue that individuals use more play faces because they play more, regardless of whom starts the interaction, but the regression analysis on the bonobo data showed two interesting effects: The presence of AU25 + AU26 increases an individual's Social Attraction, but also when an individual is engaged in affinitive interactions (i.e., deemed by others to be socially attractive) there is an increased occurrence of AU25 + AU26 (Gaspar et al. 2004). Those results do not rule out the communicative function of facial behavior, specifically that an individual's facial behavior causes changes in social activities and/or relationships. However, it also shows that there is a two-way influence between individual quality and facial behavior. It provides support for the role of facial behavior in the expression of internal states, specifically that individual differences are more likely to result from variation in the intensity or frequency of emotions. Of course individuals will feel different emotions as a consequence of their different social interactions and different social roles (e.g., Parkinson 2005). Regardless of the directionality of the causal link, it is clear that the facial behaviors of chimpanzees and bonobos express their individuality.

With the facial behavior traits we used (Gaspar et al. 2004), it is clear that chimpanzees are less transparent in facial behavior than bonobos, and chimpanzee's

Social Attraction does not seem to be strongly affected by expressivity or specific   805
facial actions (with the exception of brow furrowing). In bonobos there is a two-way   806
connection between expressivity and certain facial actions on one hand, and Social   807
Attraction on the other. This difference may reflect differences between the two   808
species in social pressures. Bonobos are typically allowed a considerable amount of   809
behavioral freedom. Chimpanzees, on the other hand, are tightly bound to a formal-   810
ized social hierarchy that may not usually permit them to express their individuality. 811
This contrast has been anticipated by the *Power Asymmetry Hypothesis* (Preuschoft   812
and van Hooff 1995, 1997), which predicts that there should be greater plasticity in   813
the use of signals in species with an egalitarian society or at least a nonrigid formal 814
hierarchy than in species with an accentuated formal hierarchy. This is due to dif-   815
ferential costs in being misunderstood by interactors, i.e., low in bonobos and high   816
in chimpanzees.   817

The relation between these facial behavior traits and Social Attraction in apes   818
was similar to that seen in human preschool children (Gaspar et al. 2004). There is   819
no reason why these analogs should not be homologies in great apes and humans.   820
Predictions from facial behavior to personality in chimpanzees, bonobos, and human   821
children should be expected since chimpanzees and bonobos are humans' closest   822
phylogenetic relatives (sharing 96–99% of DNA and a common ancestor that lived   823
about 5 million years ago: Sarich and Wilson 1967; Sibley and Ahlquist 1984;   824
Gagneux et al. 1999; Kumar et al. 2005). Once we adapt our studies to human adults,   825
we should understand these factors more fully.   826

At a more basic level of analysis, predicting specific social behaviors from facial 827
actions, we have still to address the following general questions: (1) Are certain   828
types of interaction more common in individuals that display a particular expression   829
more often than expected? and (2) Are there predictable causal relations between   830
the intensity of facial movements and the intensity of emotion? Does the degree of   831
mouth opening, for example, relate to emotional intensity? We are beginning to see   832
other more specific questions addressed in a few promising studies: For example,   833
does a high frequency of brow lowering (AU4) predict increased aggression or dom-   834
inance or gender (Campbell et al. 1999)? Or can the dropped jaw/open mouth con-   835
figuration (AU25+26) of the play face predict that the actor will be subsequently   836
involved in a play bout? This seems a plausible prediction, since the invitation for   837
social play stands out among other social invitations received by those bonobos and   838
children who display it (Gaspar et al. 2004, Gaspar 2005; and see ongoing studies   839
of chimpanzees, Davila-Ross et al. 2011; Thorsteinsson and Bard 2009).   840

Gaspar (2006) made a case for the advantages of reliable personality cueing in   841
facial behavior based on game theory and on evidence that people make inferences   842
about other people's personality traits promptly at zero acquaintance or after brief   843
viewings of photos or videos of facial behavior (Borkenau and Liebler 1995;   844
Ekman and Friesen 1978; Gaspar 1994; Grammer 2004; Krull and Dill 1998; Laser   845
1982; Mueller and Mazur 1997; Uleman et al. 1996; Yamagishi et al. 2003;   846
Zebrowitz 1997). People spontaneously attribute personality or other traits to indi-   847
viduals even if specifically instructed to provide only emotional terms in an open   848
questionnaire (Gaspar 1994) attributing for example "mean" to "anger" faces and   849

850 "nice" to "happy" (Ekman and Friesen 1975) and make accurate predictions for the
851 other's future behavior (Grammer 2004). In the case of smiles (AU12) people at
852 zero acquaintance also make good matches with target self-reports of extraversion
853 (Borkenau and Liebler 1993). Bearing in mind that there are positive and negative
854 social outcomes associated with the use of some facial actions and that the "best
855 facial action readers" are also more popular children (Boyatzis and Satyaprazad
856 1994; Underwood 1997), we may be looking at a co-adaptation between expressivity
857 (sensu transparency) and decoding capacity.

858   This co-adaptation of expressivity and decoding of emotion may enhance both
859 actor's and receiver's fitness in a cooperative setting. The cost in vulnerability of
860 honest signaling can be overcome by the returns in the form of trustworthy reputa-
861 tion and preference as social partner in cooperative tasks that clearly benefit the
862 actor and his/her family. Forging good alliances for protection and food gathering is
863 a great asset in a resource-limited changing environment. However, honest signaling
864 is constrained by group size, as individual recognition is required (Dunbar 1988,
865 1993). Communication of intentions may be crucial in large complex societies, but
866 studies of honest signaling in *Pongo*, *Gorilla,* and *Hylobatidae* facial behavior high-
867 light a role for idiosyncratic variation in emotional responses in terms of generating
868 individualized facial behavior. A study by Mehu et al. (2007) indicated that honest
869 signaling is an asset for those collecting the benefits of cooperative relationships.
870 Mehu et al. found that the Duchenne Smile (AU6 Cheek Raise+AU12 Lip Corner
871 Puller) vary interindividually and was affected by situational factors, such as an
872 hypothetical altruistic act, rather than positive emotion.

873   Emotion-related factors, interindividual differences in temperament, and
874 appraisal-related personality traits may have a higher impact in the diversity of
875 facial behavior than has been acknowledged. For example, we recently found
876 (Gaspar and Esteves, in press) that "joy/playful" (Panksepp 2005), a prosocial ori-
877 ented emotion, is the most convergent in terms of the facial actions that are used by
878 toddlers. This prosocial emotional condition was the one where spontaneous emo-
879 tion-related behavior best matches the universal facial configuration of "happy"
880 (AU6+AU12+AU25 and eventually+AU26) as proposed by Ekman and Friesen
881 (1975). Although "happy face" received only 27% of hits, far fewer hits occurred
882 for the "fear face" (11%) or "surprise face" (5%). This leads us to hypothesize that
883 only emotions that are directed at immediately changing an interactor's behavior
884 will be highly stereotyped, indicating such action tendencies as readiness to interact
885 socially or to play, etc.

886   Some emotions can be more susceptible to facial behavior modulation than others,
887 as illustrated in Peleg and colleagues' (2006) elegant study of the heritability of
888 emotional facial behavior. The authors compared the facial movements in born-
889 blind individuals with those of their sighted relatives and nonrelatives and found that,
890 for at least three emotions (anger, sadness, and "think-concentrate"), facial behavior
891 is highly heritable.

892   Although some interindividual differences in emotional facial behavior can be
893 attributed to facial anatomy (differences in muscles, fat tissue, etc.), personality
894 traits related to temperament and situation appraisal are at the motivational basis of

individual differences in the facial display of emotions. Therefore, the application   895
of personality to the study of emotional facial behavior could be an important new   896
development. It would release facial behavior research from its current stalemate   897
between two underlying views: one view that discrete emotions have corresponding   898
universal facial expressions that are consensually and "correctly" appraised, and   899
another view that emotions have a componential nature (e.g., activation and valence)   900
that results in a large diversity of facial behavior and appraisals.   901

Extraversion appears to translate well into predictable facial behavior. Compared   902
with introverts, extraverts are more active and excitable (Eysenck 1975), and there-   903
fore they are expected to be more emotionally expressive. However, extraversion   904
per se is uninformative about whether individuals are honest signalers. Future stud-   905
ies should focus on behavioral phenotypes that can be characterized differentially   906
by quantitative aspects of the facial AUs and configurations they use, especially by   907
the interaction of facial actions by context by appraisal. Whether individuals have   908
higher or lower rates of spontaneous emotional configurations compared to a refer-   909
ence population should be useful in characterizing phenotypes at the high and low   910
poles of neuroticism and extraversion. This reasoning is based on the assumption   911
that not all that emotions include a "package" of typical facial actions and emotion,   912
and that some emotions may not even involve facial actions. Furthermore, this could   913
vary from individual to individual, since it would not be tied to an unequivocal mes-   914
sage destined to elicit a typical reaction from the observer. For example, the relative   915
inexpressiveness of introverts (Riggio and Riggio 2002) highlights the need to relate   916
"invisible" facial actions to personality and emotion, which may be achievable using   917
electromyography. Emotions that are not directed at modifying the behavior of the   918
interactor (e.g., fear) could vary much more interindividually and contextually than   919
those that evolved to modify the behavior of the interactant in specific ways (e.g.,   920
anger). Individuals with high neuroticism could use prototypical emotional expres-   921
sions as an efficient means to recruit more attention and assistance. Individuals high   922
in agreeableness may not have more frequent facial actions, but if agreeableness is   923
linked with altruism and sympathy, these individuals may display more facial mim-   924
icry (Davila-Ross et al. 2008; Mehu et al. 2007).   925

8.4 Future Directions   926

While variation in presence and differentiation of underlying facial musculature   927
occurs in humans (Schmidt and Cohn 2001), the paucity of data on nonhuman pri-   928
mates precludes any comparison in terms of phenotypes for facial displays at this   929
level. However, a detailed anatomically based approach to recording facial behavior   930
means that variance at the level of the display itself is detectable. For example, we   931
do not yet know whether all individual chimpanzees show the same basic set of   932
prototypical expressions, or whether there are consistent subtypes that could result   933
from either variance in underlying musculature or behavioral idiosyncrasies. It would   934
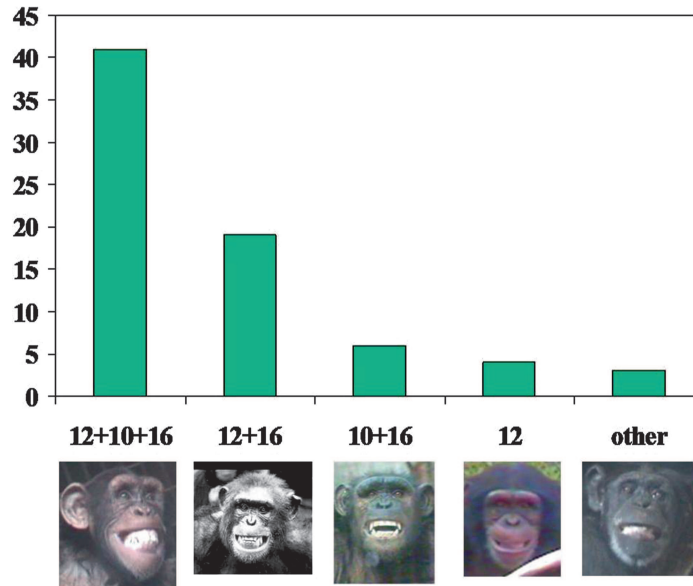be interesting to note whether humans and chimpanzees share common variance in   935

Fig. 8.2 A preliminary screening of approximately 70 photographs of chimpanzee Bared Teeth displays revealed a variety of combinations of AUs

facial myology or whether human variation is the result of more recent adaptations. For example, a relatively common variation in the zygomatic major muscle of humans is a bifid zygomatic major which causes dimpling during smiling (Pessa et al. 1998). This may serve to enhance the signal value of a smile (Schmidt and Cohn 2001). Given the universal emotions view, how can we reconcile variation with common displays? In fact, a recent anatomical study suggests that the muscles involved in the production of the "basic emotion" expressions are those that have the least individual variation (Waller et al. 2008). Facial displays may be fairly robust signals and perceivers may either not detect variation, or not attribute meaningfulness to variation (Fridlund 1994). Alternatively, since intensity, frequency, diversity, and efficacy of facial displays can be predicted by personality (e.g., extraversion or neuroticism: Riggio and Riggio 2002), we expect that quantitative variation will be found in "universal" displays of primate emotion expressions.

The most widely studied set of primate facial actions are those that fall under the nomenclature "grin" or *silent-bared teeth* display. Progress has been slowed because of the lack of comparability in definitions across studies. Here we present distinct types of bared teeth faces, based on a common coding system of facial actions that establishes quantitatively distinct variants (Figure 8.2). Future research can more appropriately consider whether "grins" systematically differ across contexts (Gaspar 2006).

In humans, the onset, offset, and peak of expression influences expression perception and interpretation (Ekman and Rosenberg 2005). It would be interesting to examine nonhuman primate sensitivities to such subtle variations. The perception

of variation in facial displays by conspecifics could also be tested empirically to determine whether variations in configuration that can now be identified by micro-analysis of facial appearance can also be reliably categorized by conspecifics. Understanding the causal relation between emotional intensity and variation in displays is also a necessary next step in conceptualizing variation in facial expression in nonhuman primates.

The future holds great promise for the extension of facial coding systems to additional species. Dobson (2008) has suggested that the degree of facial mobility is related to body size, so that the large bodied apes have the largest facial movement repertoires. Orangutans may be particularly expressive in terms of facial mobility (Maple 1980; Call personal communication). Preliminary studies of gorilla facial behavior indicate that gorilla faces are capable of virtually the same facial actions used by chimpanzees and bonobos and that their facial behavior varies interindividually (Jesus and Gaspar 2008; Gaspar et al. unpublished manuscript).

Multiple evolutionary questions remain to be addressed in future research. Why should faces be "transparent" to individual qualities, and why might this vary between Hominoidea and other primate families? What are the biological advantages of honest signaling in the face and do they differ based on whether emotion or intention is being signaled? What inferences can be made about the social scenarios in the evolutionary history of *Homo* and *Pan* and how can we understand the social pressures that may have contributed to shape facial behavioral evolution?

8.5 Conclusion

Excellent ethograms of peak or prototypic facial expressions exist for chimpanzees. However, until recently no common language existed for exact identification of appearance changes. This has made it difficult to compare expressions across groups or individuals. If facial displays are to be considered as adaptations, then such phenotypic variation needs to be understood and its potential fitness consequences assessed (Schmidt and Cohn 2001). This cross-over in methodology, with ethological human studies and new coding techniques in chimpanzee research, should facilitate more meaningful comparisons between species and generate testable hypotheses for future study.

Schmidt and Cohn (2001) place human facial expressions within an evolutionary framework. They view "coordinated facial displays" as behavioral phenotypes but also recognize individual variation at three levels: facial structure, including age and sex differences, movement, and perception. Thus, the study of nonhuman primate facial expressions needs to allow for individual variation in production and also discriminate any factors influencing perception.

The success of the FACS itself means that there are many studies with humans that can be readily adapted for chimpanzee facial expressions. That is, the development of these coding systems allows for directly comparable methods to be employed in cross-species research and contribute to the questions surrounding both chimpanzee

communication and the evolution of human facial expressions (Fridlund 1994; Oster and Ekman 1978). To date, questions of homology have primarily been answered on the basis of similarity in appearance of expressions (Preuschoft and van Hooff 1995; Steiner et al. 2001). More detailed, standardized, and anatomically based means of comparison is overdue. It is only by such cross-species comparisons that we can gain a better understanding of what is and is not unique to humans.

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