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Influence of Social Context on the Use of Blended and Graded Facial Displays in Chimpanzees

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Our understanding of social communication and emotional behavior in nonhuman primates has advanced considerably through research over the past half century. Chimpanzee facial displays have typically been described as highly graded communicative signals, but we propose an additional distinction: blended displays. They appear to be morphologically and acoustically similar to the expressions in ≥2 prototypical/parent categories. We describe the facial and vocal communicative repertoire of chimpanzees and examine how they use graded and blended signals in different social contexts. Data from behavioral observations revealed that they used facial displays differently depending on the social context. Specifically, the variability can be explained by 7 factors representing nervousness and distress, agonism, contact reassurance, excitement, greetings, play, and vigilance. Additionally, the use of blended displays was not simply divided between the contexts that elicited the parent types, nor were they used in totally unique contexts. Instead, the data showed that the contextual use of blended displays is primarily correlated with the social contexts that elicited only one of the parent expressions. Thus, the blended displays appeared to reflect conflicting internal motivational states in the sender, instead of expressing features of the external environment. We proffer several possible explanations for how the blended

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signals may be interpreted by receivers and why they would be contextually associated with only one parent group.

KEY WORDS: facial expression; communication; vocalization; behavior; graded displays.

Research over the past half century has considerably advanced our understanding of social communication and emotional behavior in nonhuman primates, including detailed descriptive reports of facial expressions in a variety of primate species, including chimpanzees, bonobos, macaques, and capuchins (Bolwig, 1962; Hinde and Rowell, 1962; van Hooff, 1962, 1967, 1973; Andrew, 1963a,b; Goodall, 1968, 1986; Fox, 1969; Redican, 1975; Weigel, 1979; de Waal, 1988; Preuschoft and van Hooff, 1995, 1997). Our 2 main goals have been to document the type of communication systems in our closest ancestral lineage and to examine whether the facial expressions and vocalizations are similar, both morphologically and functionally, to our own. Studying the communication system of other species is important not only to provide an understanding of how social systems are organized and maintained but also create a framework for interpreting the evolutionary function of social signals (Marler, 1976).

The raw material from which many social signals evolved include the elements or by-products of behavioral acts such as intention movements that precede an action (Lorenz, 1941), protective and autonomic responses (Andrew, 1963a,b; Rinn, 1984), and displacement activities that occur when an animal experiences conflicting motivations (Tinbergen, 1952). Many of the signals are ritualized, a process by which a formerly adaptive, unspecialized behavior becomes divorced from its originally adaptive context to take on a different, and typically more communicative, meaning (Huxley, 1966, cited from Redican 1982). The result of the ritualization is that signals become easily recognizable, highly conspicuous, and often stereotypical in their movement, helping to ensure that they are easily understood by conspecifics (Tinbergen, 1952).

The most comprehensive descriptions of chimpanzee facial and vocal behavior have been provided by van Hooff (1962, 1967, 1971), Goodall (1968, 1986), Marler (1965, 1976, Marler and Hobbett, 1975; Marler and Tenaza, 1976), and Mitani (Mitani and Gros-Louis, 1995; Mitani, 1996; Mitani *et al.*, 1996). Parr *et al.* (2002) reviewed their work. There are 20–30 different chimpanzee facial expressions and vocalizations in several main categories based on morphological similarity. The general expression categories—barks, screams, grunts, pants, hoots and pouts—occur in a variety of socio-emotional contexts, including aggression, dominance and submission, play, long-range communication, food announcements, and expressions of affection and consolation (Goodall, 1968; van Hooff, 1967;

Fig. 1. A blended facial display: the stretch pout whimper. The 2 parent types are at the far left (pout) and far right (bared teeth display). The stretch pout whimper is the 4th from the left. The second and third images reflect grading between the pout and the stretch pout whimper.

Marler, 1969). Similarity exists among all great apes in the production of the visual display types, though considerable acoustic differences have been reported (Chevalier-Skolnikov, 1973; de Waal, 1988; Marler, 1976; Mitani and Gros-Louis, 1995; Mitani, 1996).

Despite evidence that numerous species of nonhuman primates emphasize graded signals in their communications (Marler, 1976), most written descriptions of facial expressions and vocalizations—facial displays—in nonhuman primates describe only their peak intensity or prototypical form and pay little attention to the how displays can change or grade into one another as the animal transitions from one prototypical form to another. For example chimpanzees, have both ritualized and highly graded facial displays (Marler, 1976; Goodall, 1968), which we term blended displays. Figure 1 examplifies how the stretch pout whimper differs from traditional descriptions of signal grading. It is a blend between the peak intensity forms of the pout (far left) and bared-teeth display (far right). We follow Marler's (1976) definition of grading as variations in the intensity, completeness, and frequency of an expressive display, i.e., the displays are highly variable intra-categorically, and define blending as a small number of peak intensity displays that appear to share features in common with the expression of $\geq$2 prototypical categories. Chimpanzees are one of the only species apart from humans in which facial displays are so variable and in which individual differences, both within and between expressions types, are so prominent Marler (1976). Accordingly, the study of chimpanzee facial displays is particularly fascinating and complex. Thus, contrary to grading—expressions that vary along the dimension of one major category—blended displays appear as prototypical peak intensity displays that share features in common with $\geq$2 other prototypical categories. The blended displays that we discuss are yelps, squeaks, shrill barks, pant-grunts, pant-hoots, pout moans and the stretch pout whimper.

Van Hooff's (1970, 1973) is the most systematic attempt to provide an empirical, quantitative foundation to classify the motivational and functional aspects of chimpanzee behavior. He assessed which sequences of behavioral elements occurred together by entering their observed frequencies

into a matrix and standardizing them based on their expected outcomes given random variation. Via factor analyses, van Hooff (1970) assessed which behavioral frequencies occurred together in sequences, presumably because they shared a similar motivational basis. Motivational components were identified that explained over 80% of the variance in the use of these behavioral elements. Van Hooff (1970) described these systems as affinitive, play, aggression, submission, excitement, show, and groom. A slightly different methodology was adopted by de Waal (1988) in his ethogram of bonobo behavior which assessed behavioral elements across different social contexts. Thus, as opposed to comparing similarities in the motivation for behavioral sequences, de Waal (1988) assessed which behaviors were associated with a variety of well-defined social contexts. The discrepancy between the observed and expected frequencies of behavioral events and context type was assessed using a contingency matrix. The current study uses a similar analytical approach to both de Waal (1988) and van Hooff (1970), but compares similarities and differences in the use of specific display types in various behavioral contexts.

This paper has two main goals. The first is to identify a basic ethogram of facial displays in chimpanzees that cross-references previous published descriptions. The second goal is to examine the contexts in which these facial displays are used in a social group of chimpanzees, paying close attention to similarities and differences in the use of blended displays compared to the use of the prototypical expressions. For the purpose of this study, we chose not to isolate the visual and auditory elements of each facial display but examine the entire behavior. Thus, we do not aim to identify how expressions are blended, i.e. whether the blending is more in the vocal or visual aspect of the display. Future studies may attempt to do this, for example, using experimental playback techniques where expression categories may be artificially blended or visually morphed and then presented to subjects for categorization. Our approach here is simply to examine how blended displays are used in different social contexts.

We hypothesize that facial displays will be used differently depending on the social and/or behavioral context. We present 3 possible scenarios for the use of blended displays. The *first* hypothesis predicts no difference in the contextual use of blendedx facial displays and their parent groups. Thus, if the parent expression a is primarily associated with context A, and the parent expression b is primarily associated with context B, the blended expression ab may be produced equally as often in contexts A and B. Accordingly, blended displays will represent true motivational and functional blends between each parent group.

The *second* hypothesis predicts that the blended displays will be used in behavioral contexts that are distinct from each parent group. According to this scenario, the blended display ab is associated primarily with context

C, i.e., the blended display will be associated with a totally new context and perhaps a unique motivational state.

The *third* hypothesis predicts that the blended displays will be more similar to one or the other of the parent groups, but not both, despite visual and acoustic similarity to both. For example, the blended display ab would be produced more often in context A or B, but not both, and not in a totally new context C. In this scenario, the contribution of one parent group to the function and/or motivation of the blended display maintains dominance resulting in the blended display being associated with contexts similar to only one parent group. Context A typically elicits expression a but in situations where in the individual experiences conflicting motivation, the blended display ab may result, instead of simply a. We speculate that the data will support the third prediction more often than the first 2 based primarily on the fact that chimpanzees society is highly variable in terms of social composition and behavioral flexibility and blended displays would reflect a primary function similar to the dominant parent display, but conflicting motivation which leaks through as the other expression form. Thus, use of the displays may indicate behavioral uncertainty.

METHODS

Subjects

We collected data from 19 captive chimpanzees (*Pan troglodytes*) in a large indoor/outdoor compound at the Yerkes Primate Center field station, Lawrenceville, GA (Table I). The outer portion of the facility consists of an open enclosure *ca.* 550 m^2. The walls, 5.4 m high, are made of 5×5-cm^2 mesh on the lower portion and angled metal sheeting above. Within the outdoor enclosure is a large central wooden climbing structure that contains telephone poles as high as the enclosure walls so that the chimpanzees have a limited view of the activities outside of their home area. There are also numerous enrichment items in the outer portion, including plastic barrels, rubber tires, plastic balls, and large tree branches. Attached to the outer area are several indoor sleeping quarters. During test sessions, entry to the quarters was restricted and we observed the subjects in the outdoor enclosure only.

Procedure

Data were collected by one of 2 experimenters from an observation tower, 5.78 m high, at one end of the outer portion of the enclosure. It contains a platform approximately 3×3 m^2 and situated at a height above

Table I. The demographics of a social group of chimpanzees at the Yerkes Center field station

Name	Sex	Code	Date-of-birth
Amos	male	11	11/19/1981
Phineas	male	10	01/01/1966
Magnum	male	08	07/08/1989
Chip	male	09	03/30/1989
Ericka	female	20	10/20/1983
Virginia	female	21	04/18/1991
Jamie	female	22	05/17/1995
Tai	female	30	01/01/1967
Daisey	female	31	10/01/1989
Julianne	female	32	05/15/1998
Barbi	female	40	06/14/1976
Sean	male	41	03/16/1992
Waga	female	50	03/19/1982
Karri	female	51	01/02/1995
Cynthia	female	60	06/07/1980
Reid	male	61	07/05/1993
Vivienne	female	70	07/27/1974
Steward	male	71	09/08/1993
Pollyanna	female	80	02/17/1989

the enclosure walls. The chimpanzees were in view at all times while outside except when directly under the tower. The experimenter could lean over the tower to maintain visual contact with them. We collected data via a combination of focal sampling and ad libitum procedures (Altmann, 1974). Focal observations lasted 10 min per subject, while we collected ad libitum data throughout each daily session. We spoke data into a tape recorder and were later transcribed it into an Excel spreadsheet for analysis.

After a 1-mo familiarization period, we identified 25 facial displays and 30 different behavioral contexts. We used behavioral descriptions from established ethograms at the Yerkes field station and added others because of their apparent relevance for social and emotional communication. Behavioral contexts include social contexts, such as play, and individual communicative social gestures, such as the bent-wrist display. We identified facial displays primarily from previously published ethograms, and also after consulting with several resident chimpanzee behavior experts who watched video of specific expressive displays and discussed them with us (pers. comm., Aureli *et al.*, 1999).

We initiated a pilot data collection procedure, which consisted of watching until the focal subject engaged in one of the behavioral contexts and recording the facial display made by the focal subject. An observation ad libitum could be recorded during another focal record if any other group member engaged in any of the behavioral contexts. It did not take

precedence over the focal subject's behavior. If the facial displays changed within the same behavioral context, we recorded a new display so that the range of facial expressions possible in a particular context was maintained in the data. We maintained no datum on temporal occurrence. If no facial display was apparent, we recorded a neutral face. The list of facial expressions, vocalizations and behavioral contexts in Table II. Constitute our ethogram, provides a written description of each facial display and a picture (where appropriate) of its peak intensity, and cross-references these display types to previous descriptions in the literature. Specific spectrograms of the vocal components of these displays (where present) can be seen in Fig. 2.

Blended Display Types

After each individual facial display was identified, we grouped them according to several major categories described previously in the literature; barks, screams, grunts, pants, hoots and pouts. It became clear, however, that some expressions were much more difficult than others to place into a single category because their features, both acoustic and morphological appearance, crossed category boundaries. Figure 1, for example, shows a clear grading between a bared-teeth (far right) and pout (far left) as these two facial displays transition within a single expressive bout. However, the figure additionally shows a distinctive peak-intensity display, the stretch pout whimper, in frames 3–4. This is a unique, prototypical display type that shares features in common with both the bared-teeth display and the pout. Thus, unlike graded expressions that can vary in intensity, frequency or completeness within a category, blended displays cross category boundaries.

The eight blended displays that emerged from our classifications were *yelps* and *squeaks*, blends between screams and barks; *shrill-bark*, blended between barks, screams and grunts; *pant-grunts*, blended between pants and grunts; *rising* and *climax pant-hoots*, blended between hoots and pants; *pout moan*, blended between hoots and pouts; and *stretch pout whimper*, blended between screams and pouts. As can be seen from the descriptions in Table II, these blended displays are unique in that they shared both visual and auditory features with expressions in other groups. Yelps, for example, have the tonal vocal quality of barks, but lip-retraction exposing the teeth, similar to screams.

Data Analysis

Data were transcribed from audio tape into an Excel database. This included five major data fields representing either solitary or dyadic entries;

Table II. A list of behavioral categories and facial displays recorded during our study

Code	Behavioral categories
	Behavioral description
AP	Approach neutral: One individual approaches another within 2 m with no contact. This is only coded when the approach is observed.
NO	Neutral behavior: Sitting, ignore others without contact or response. This is coded if a facial expression is made with no obvious accompanying behavior, or within a dyadic interaction as a neutral response category.
NC	Netural contact: Ambiguous contact by one individual towards another. The contact is not easily defined as play or aggression, i.e. touching.
P1	Play: Two individuals wrestling, tickling, or chasing one another in nonagonistic ways. Code in each direction if the play is mutual. Only the initiator receives the code if the play attempts is unsuccessful. If the play is solitary, the recipient is n/a.
P2	Rough play: Play that includes restraining, or biting, or otherwise behavior that would be considered agonistic. This is also coded if the response of the partner is agonistic.
GM	Grooming: Note whether there is tooth-klacking/lip smacking (gv1), or spluttering (gv2).
FGM	Face to face grooming
KI	Kiss: Mouth contact on the mouth, or body of another individual. If mutual, note for both individuals.
EM	Embrace: Gentle contact to another individual using the arms or another body part. Note in addition to kissing if these occur together.
OV	Avoid/displaced: When the approach of another individual leads the focal subject to move immediately away >1 m.
FL	Fleeing: When the approach of another individual leads to rapid avoiding by running, or climbing a structure. Pursuit may be the cause. If this leads to a chase of >2 m, this behavioral category (a0) takes precedence.
GP	Greeting: A face-to-face interaction, head-bobbing, arm waving or other friendly contact of one individual to another that is not formal bowing. This can include pant-grunting (hg) and wrist presents (wp).
WP	Bent-wrist present: One individuals holds out their hand to another with wrist positioned first and bent. This is often forced into the face of the recipient.
BW	Formal bowing: Bending or crouching in front of a more dominant individual accompanied by pant-grunts.
WO	Walk-over: Dominant individual positioning their body so that the recipient passes underneath their arm or body. Code for dominant individual only, the one positioned over.
SO	Solicitation or recruitment: Eye monitoring by one individual engaged in a conflict to another individual not engaged in the original conflict using rapid gaze alternation. Arm may be extended by the solicitor, but don't note in addition to solicitation.
IV	Invitation: Offering an open hand to another individual, slapping the ground or other gesturing without sexual signals.
SU	Support: This can be either victim support or aggressor support. One individual comes to the aid of another who is engaged in a dyadic conflict. The supporter does not have to be recruited.
BF	Bluff display: Piloerection, swaggering, waving objects, stamp-trot, throwing objects, banging or other intimidation behaviors, performed either alone or directed at another individual.
SX	Sex: Sexual interest, i.e. genital inspection, mounting, or intromission.
SSX	Sociosexual behavior, i.e. sexual behavior used in a nonreproductive context.

Table II. Continued

Code	Behavioral categories
SD	Self-directed behaviors: Yawning, rough-scratching, self-grooming
PP	Rapid urination/defecation: After agonistic context, or in response to an identifiable event.
PL	Piloerection during a behavior
A0	Quasi-aggression: Threatening behavior including arm waving, lunging, chasing >2 m, or charging. Response of the recipient is the best defining feature.
A1	Aggression: Hitting, biting, trampling or otherwise attacking another individual.
A2	Recipient of agonistic response: Being the target of quasi- or serious aggression.
DT	Distress: A prolonged response by the recipient of aggression where victim persists in their negative response over 10 s. after initial incident.
EX	Response to outside: Behavior directed at external stimuli, or in response to conspecifics, or other individuals, in other compounds.
	Facial expressions and vocalizations (blended displays are in italics)
rl	*Relaxed-lip face.* In this and the neutral face, the eyes and mouth (including mouth corners) are relaxed, but in rl the lower-lip hangs low and the mouth appears slightly open although it is closed. The individual stares ahead with open eyes. The upper-lip covers the teeth and gums, while the bottom lip exposes the gums and some teeth. Vocalizations are absent. Goodall, 1968: none van Hooff, 1973: none
bg	*Bulging-lips face.* Individual stares ahead, eyes open, mouth closed with the lips bulging out as though individual is blowing air. Ears should be flat against scalp. Lips are together and mouth corners neutral. No vocalizations occur. Goodall, 1968: Glare, prior to attack or copulation, staring at another individual. van Hooff, 1973: Bulging lips, lips pressed tightly together with arching upper-lip, jaws firmly clenched (see also attack-face, van Hooff, 1962; tense mouth face, van Hooff, 1967). Redican, 1982: Tense mouth face.
pf	*Relaxed open-mouth face.* The eyes and face are relaxed, but may become tense if play becomes rough. The mouth corners are in their usual position, or slightly withdrawn, but the lower lip hangs open to expose the bottom teeth. The top teeth can be slightly visible, otherwise the top lip folds over them. Vocalizations may include a fast, rhythmic staccato breathing (see Fig. 2a). Goodall, 1968: Play face, accompanied by laughter. van Hooff, 1973: Relaxed open-mouth display, mouth is moderately open with mouth corners withdrawn slightly with lips in relaxed position. The upper teeth remain totally or partially covered by upper lip, while the lower teeth are slightly bared. Vocalizations are staccato, rhythmic breathing which may develop into grunting (see also laughing or play face, Andrew, 1963a,b; Bolwig, 1964). Redican, 1982: Play face, antithetical to the threat display.

Table II. Continued

Code	Behavioral categories
Barks	
bk	*Bark.* Open mouth with lips parted but slightly pursed and mouth corners are slightly retracted. There are repeated vocalizations that can be high or low pitched (see Fig. 2b). Eyes are open and gaze may alternate.
	Goodall, 1968: Barking, similar description given when individuals approach food. She also has an expression that looks like a tense face that is accompanied by soft-barks or coughs, given when threatening a subordinate or another species with confidence.
	van Hooff, 1973: Bared-teeth bark, mouth is only slightly open at the beginning but becomes wider during the middle of the call. At this time the mouth corners are pulled back and the lips withdrawn from teeth.
	Marler and Tenaza, 1976: Bark, loud and sharp but varies in pitch. The main energy of the call is at the onset, which helps distinguish it from a squeak.
th	*Waa-bark*. The lips slightly parted laterally, and the mouth and eyes are open. The top lip may curl up similar to a pout, and the top teeth may show. The mouth corners are slightly pursed, or relaxed. The expression is combined with "waa" bark vocalizations. During these vocalizations all the air is exhaled and vocalizations tend to be more low pitched than barks (see Fig. 2c).
	Goodall, 1968: Waa-bark, when threatening a superior from a distance, or when another chimp is being attacked. No separate bark.
	van Hooff, 1973: Waow-bark, similar to bared-teeth bark only at the beginning and the end the mouth is slightly open and lips cover the teeth. The mouth is opened widely at the middle of the call. The vocalization trails off at the end sometimes into a pout moan.
	Marler and Tenaza, 1976: Waa-bark. More drawn out than just a bark. Mouth is open wider, and the pitch can rise and fall audibly. Given when dominance is not established and individuals are at a distance.
sk	*Shrill Bark*. A vocalization blend between the categories of screams and grunts. It is higher pitched than the pant-grunt or grunts, but not as tonal as the yelp/squeal, or squeak (see Fig. 2d). The upper-teeth may be exposed as the barks become higher pitched and take on a more rasping quality than grunts
	Goodall, 1968: none
	Reynolds and Reynolds, 1965: harsh, shrill barks
Bared-teeth and Scream Expressions	
yp	*Yelp/Squeal.* This represents a blended expression between the categories of barks and screams. The teeth are typically exposed during these vocalizations but the pitch is more pure and tonal than the distinctive rasping of the bared-teeth screams. The calls are usually not prolonged, but are given in more distinct forms (see Fig. 2e).
	Goodall, 1968: This may be squeak calls, short, high-pitched squeaky screams made while grinning, given after attack or threat or during submissive gestures. Also incorporates very low intensity screams that are highly graded between bared-teeth screeches and squeaks.
	van Hooff, 1973: Bared-teeth yelp, high-pitched, moderately loud vocalization accompanied by bared-teeth, eyes open, partially open mouth and partially covered upper-lip (see also squeal, Reynolds and Reynolds, 1965, and scream without vibrato, Marler, 1969).

Table II. Continued

Code	Behavioral categories
sq	*Squeak.* Mild form of the yelp category, where the vocalizations are more quite high pitched and of less intensity than yelping (see Fig. 2f). They are also of a purer tonal quality than the bared-teeth screams, but are more mild than the yelps and occur much quicker, but the face still takes the form of bared-teeth expression. Marler and Tenaza, 1976: A high shrill call that occurs very quickly, tenths of a second, sometimes given in a series. It can be a sign of distress, given after an attack.
bt0	*Excited bared-teeth expression.* The mouth opens and closes, eyes open, teeth-bared w/varying degrees of lateral lip retraction. Mouth corners are retracted. Teeth are exposed. When very intense, wrinkles around the cheeks appear as mouth corners are obliquely retracted. Vocalizations include very high-piched and tonal "aich-aich" panting or "eech eech" squeaks as mouth opens and closes, but can be sustained in high intensity situations (see Fig. 2g). Goodall, 1968: no name but described similarly when individuals commence feeding. van Hooff, 1973: none (but perhaps tonal grunt, van Hooff, 1971) Marler and Tenaza, 1976: Rough grunt incorporates a wide array of sounds from squeaks to grunts. Given during excited social periods and during feeding on preferred foods. Figures suggest it has the bt component.
sc0	*Silent scream face.* The mouth is wide open, eyes open. Top and bottom teeth are exposed. Mouth corners are withdrawn to expose teeth and lips are fully withdrawn. Either none or very quiet raspy hisses are issued. Goodall, 1968: none van Hooff, 1973: none
bt1	*Silent bared-teeth display*. The mouth may be slightly open or closed, lips withdrawn and mouth corners retracted laterally, and the teeth fully exposed. Eyes may be open or squinted. The lack of vocalizations help define this from the other bared-teeth expressions. Goodall, 1968: Silent grin. van Hooff, 1973: Silent bared-teeth display. Horizontal bared-teeth display has mouth corners withdrawn and lips retracted from teeth and gums, but mouth is kept partially closed, and animal is usually still or moving slowly (see also silent grin, Goodall, 1968; grin, van Hooff, 1962). Open mouth bared teeth face, same as above but lips are maximally withdrawn and mouth is open, and contact with another animal usually occurs. Vertical bared-teeth display, mainly upper-lip is retracted, but mouth corners are in normal position and teeth are kept closed. This causes the upper lip in particular to protrude slightly, and animal posture is typically relaxed.  Redican, 1982: Grimace, and the open-mouth grimace which is a combination of all other bt expressions described by van Hooff.
sc1	*Low-intensity scream*. This is a category of display that includes all forms of scream that are of a lower intensity than the bared-teeth scream faces, but not clearly definable as any in the yelping/squealing, squeaking categories. The calls are highly variable, take many different facial forms where the teeth may or may not be exposed, and the mouth may or may not be open. The calls are not of a high intensity or of a prolonged duration (see Fig. 2h).

Table II. Continued

Code	Behavioral categories
bt2	*Screeching bared-teeth face.* The eyes are squinted or closed, ears flat, eyebrows lowered, body posture is typically crouched. Mouth is partially open, lips withdrawn as in screaming or staring bared-teeth face, but teeth are fully exposed. Vocalizations are loud and high-pitched rasping screams that are often very hoarse, and can be voiced on the inhalation. These are usually sustained for several seconds, but can also quickly spasmodic, turning into a sustained tantrum/distress episode (see Fig. 2i).
	
	Goodall, 1968: Pant-shrieks while grinning, made when submitting to a superior, or greeting a superior.
	van Hooff, 1973: Pant scream, breathy, emitted with sharp timbre, often given while crouching or fleeing. Inspirations can be noisy or tonal.
bt3	*Staring bared-teeth scream face.* The eyebrows are lifted wrinkling the forehead, eyes open, mouth is wide open with lips withdrawn exposing teeth completely. Individuals may have piloerection, and exhibit forward movements. Vocalizations include loud harsh screaming like "aach - aach" (see Fig. 2j).
	Goodall, 1968: Scream calls, threatening a superior or another species while afraid, may look for support. Does not mention of forward motivation, or counter-attack.
	van Hooff, 1973: Bared-teeth scream, most intense vocal display. Mouth is widely open and lips fully retracted. Vocalizations are high-pitched, intermittent screams with sharp timbre. Van Hooff divides screaming into several categories based on sonographic analysis; pulsed scream-rasping scream (see also rough scream, Marler, 1969; roars, growls and screams, Reynolds and Reynolds, 1965), double-tone scream-higher frquency, rasping disappears (see also Yerkes and Learned, 1925) and pant scream (see screeching b–t face).
	Marler and Tenaza, 1976: Scream, can intermix with other calls with a lot of variability, i.e. squeaks.
Pouts	
wh	*Stretch pout-whimper.* The lips are slightly puckered/pursed while being slightly withdrawn to expose the teeth, and mouth corners are pushed forward. Eyes are partially closed and mouth is partially open. Vocalizations are of the long low wailing type (see Fig. 2k).
	Goodall, 1968: Whimpering with whimper face, more intense form of hoo-whimper or if infant is ignored.
	van Hooff, 1973: Intermediate between bared-teeth yelp and pout-moan. Vocalization is pure and noiseless, mouth is closed with retracted corners. Lips curl out-wards and protrude slightly, especially the upper-lip.
	
	Marler and Tenaza, 1976: Whimper, context of use may vary. Goodall lists three different expressions in three contexts, but there is no spectrographical difference between these. The circumstances are being frightened by strange things or sounds, begging for food, and when clinging to their mother or searching for the nipple.

Table II. Continued

Code	Behavioral categories
po	*Silent pout.* Eyes are open and mouth is rounded with corners pursed forward. Lips are pursed into a round shape. No teeth are visible. No vocalizations are present. Goodall, 1968: none van Hooff, 1973: Silent pout face, lips are strongly pursed and pushed forward but no vocalizations are made (also see pout moan, van Hooff, 1962, 1967).
ho1	*Pout moan.* Same as pout face, but typically accompanied by short, hooting vocalizations "oo .. oo" although pout can occur without vocalizations (see Fig. 2l). Goodall, 1968: Hoo-whimper with pout face, given by infant searching for nipple, or in older ape when begging or ignored after requesting something like grooming. van Hooff, 1973: Pout moan (van Hooff, 1962 and 1967 refer to this as pout face), has low tone calls with pouting lips similar to the rising hoot display. Lips remain in contact near mouth corners, but are parted in middle showing a round opening (see also moaning hoots or soft moans, Reynolds and Reynolds, 1965).
Grunts and Pants	
hg	*Grunts*. Mouth and mouth corners are relaxed, slightly open. Eyes are open and face forward. Lips are relaxed and may hang open. No teeth are visible. Vocalization includes a low-pitched tonal call (see Fig. 2m). Goodall, 1968: Huu-calls van Hooff, 1973: Grunts, or grunt-barks, low-pitched tonal calls with maintained periodicity. Face is relaxed with mouth slightly open (see also grunts, gruff barks or panting barks, Reynolds and Reynolds, 1965). Marler and Tenaza, 1976: Grunt, soft, low-frequency sounds that are difficult to hear. Can be given during feeding and in some situations of social excitement. May be an intermediate stage between barking, pant-grunting and other similar calls. Cough is similar but the vocal comes from a rush of exhaled air during mild threats.
pa	*Pant*. Fast, rhythmic breathing accompanied by relaxed mouth, with no teeth typically showing. This is typically used during play, and can be called laughter (see Fig. 2a). Goodall, 1968: Panting van Hooff, 1973: Pant, soft but fast rhythmic breathing with smooth onset. Mouth is typically relaxed, with lips only slightly parted. Rhythmic nature often leads to slight body shaking. Marler and Tenaza, 1976: Pant, one of three calls that have phonation on inhalation and exhalation. Given during greeting, face to face contacts, copulation and whenever there may be a low probability of aggression.
ho0	*Pant-grunt*. Soft rhythmic vocalizations produced in a rapid sequence "huu - huu" accompanied by bobbing and/or bowing (see Fig. 2n). Because of the rapid series of vocalizations, the inhalation of the grunt is voiced, and therefore this represents a blend between the categories of panting and grunting. Goodall, 1968: Panting, or bobbing pants, described during social grooming and when kissing or bowing to another individual. Mouth may be open, no teeth showing. Eyes are open and lips are relaxed, and mouth corners pursed forward slightly.

Table II. Continued

Code	Behavioral categories
	van Hooff, 1973: Rapid ohoh series, more breathy, rough grunts delivered in rhythmic succession. The mouth is open fairly wide, with lips covering teeth and mouth corners drawn slightly forward, creating a round aperture. This may develop into a scream, yelp or shrill bark.
	Marler and Tenaza, 1976: Also voiced on inhalation and exhalation. Given after adolescence to dominants during greetings. If proximity is reduced the grunts may turn into bobbing and bowing, if individual loses their nerve and flees, the vocalization may turn into pant-screaming.
Hooting	
ho2	*Rising pant-hoot.* Lips are pursed with rounded mouth and forward pursed lips. Mouth can be slightly open as louder, rhythmic breathing hoot vocalizations "hoo-hoo" occur. There is no climax as in ho3. Because of the rapid sequence of vocalizations and the voiced inhalation, this represents a blended expression/vocalization between the panting and hooting categories (see Fig. 2o through 4.5 seconds).
	Goodall, 1968: Pant-hoots/hoot face, as others approach or in response to distant calls.
	van Hooff, 1973: none
	Marler, 1975: whimper hoot, one of 3 calls voiced on inhalation and exhalation
	Marler and Tenaza, 1976: Pant-hoot, most common call voiced on inhalation and exhalation. Given in response to distant pant-hoots, to food, or after separation.
ho3	*Climax pant-hoot.* In this version of hooting there is a loud, screaming "waaa" climax vocalization at the end of the rising hoots.
	Goodall, 1968: Pant-hoots with shrieks or roars, during displays.
	van Hooff, 1973: Rising pant-hoot, initially lips may pursed into a pout face, and at the end the mouth may be open widely with teeth bared. Vocalizations begin with moderate, low-pitched calls that become gradually louder and end with a scream or a waow-bark (see Fig. 2o). The inspiration phase is strongly vocalized (see same display by Reynolds and Reynolds, 1965; Marler, 1969; Nissen, 1931; Yerkes, 1943).

the type of data, focal or ad libitum, the individual who initiated the social context, the social/behavioral context, the facial display made by the initiator, and the interaction partner if the data described a dyadic event. The partner's response was recorded as a separate dyadic entry. Triadic interactions, or those involving more than three individuals, were recorded as dyadic bouts consisting of the main participants so as to avoid duplication of data. Inter-observer reliability was assessed using Cohen's Kappa coefficient (Bakeman and Gottman, 1997).

At the end of the study period, the data were combined for all subjects and summarized into a 25×30 matrix listing facial displays and behavioral context, respectively. Adjusted residual scores were then obtained for each cell in the matrix according to the following formula: standardized

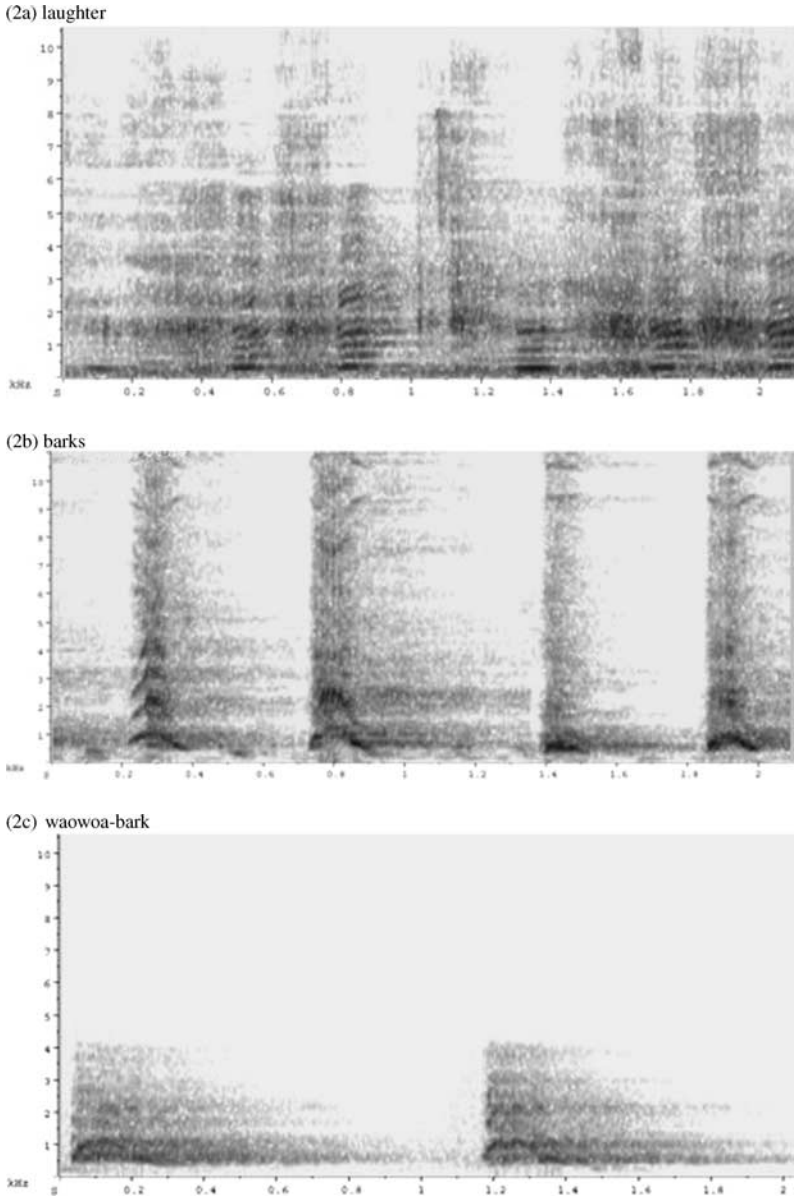


Fig. 2. Individual spectrograms of each vocalization type. They were generated from audio recordings digitized at 44.1 kHz at 16-bit resolution. The time frequency spectrograms were filtered via a Hanning fast fourier transform (FFT) windowing function, frequency grid spacing = 86.1 Hz (FFT size = 512 samples), frame overlap 50%, and 3 dB bandwidth = 124 Hz using Raven (version 1.0, Cornell Bioacoustics Lab, Ithaca, NY).

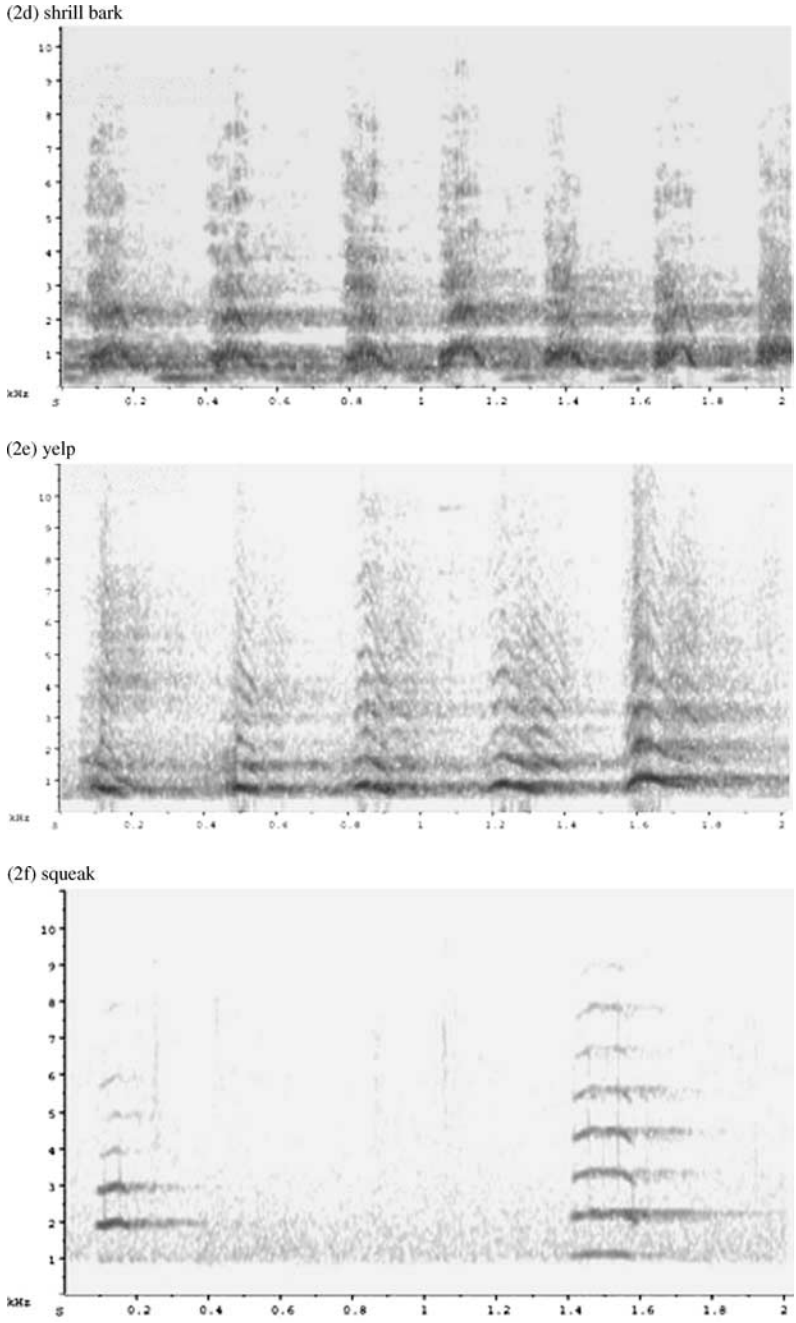
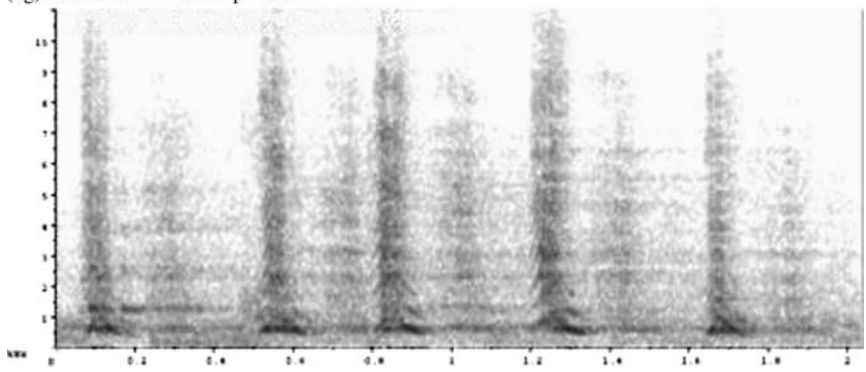
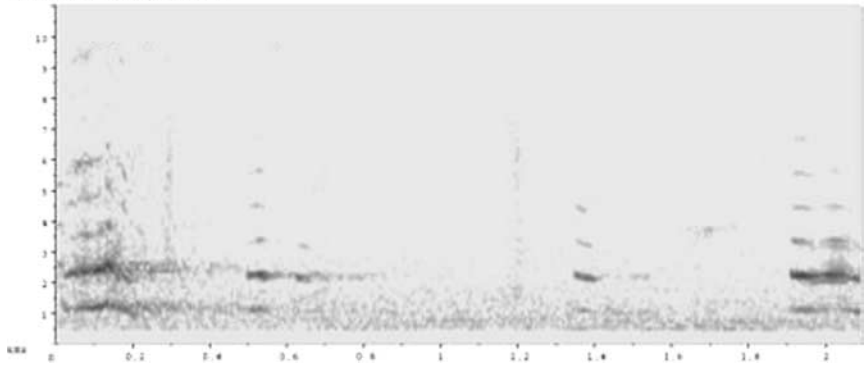


Fig. 2. Continued.

(2g) excited bared-teeth expression



(2h) low-intensity scream



(2i) screeching bared-teeth scream face

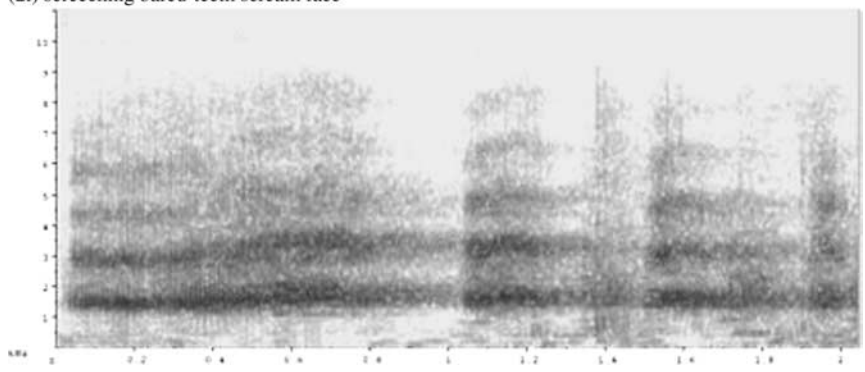
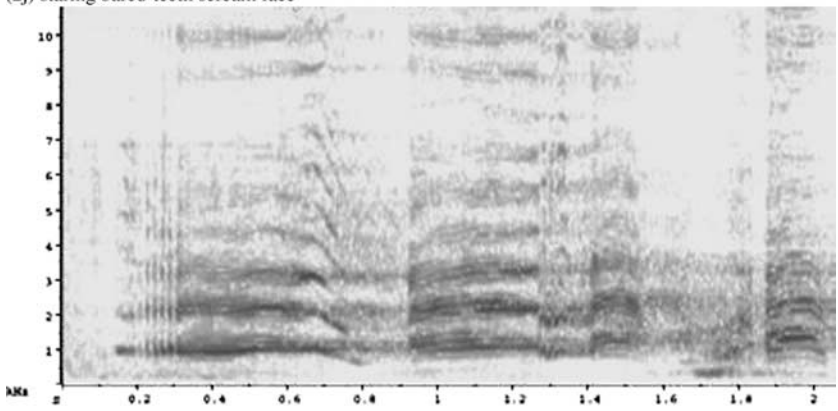
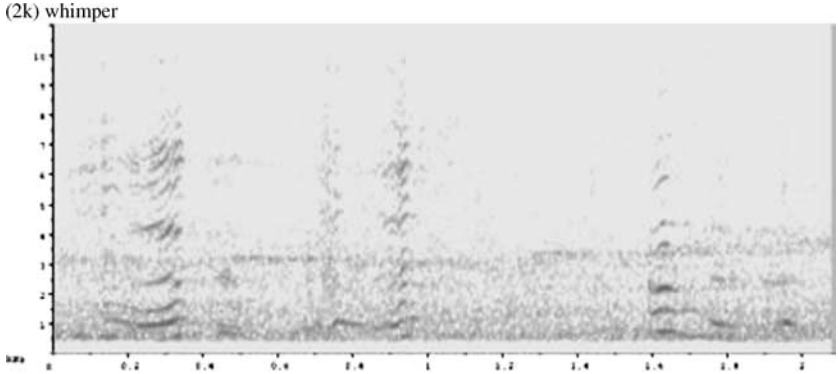


Fig. 2. Continued.

(2j) staring bared-teeth scream face



(2k) whimper



(2l) pout moan

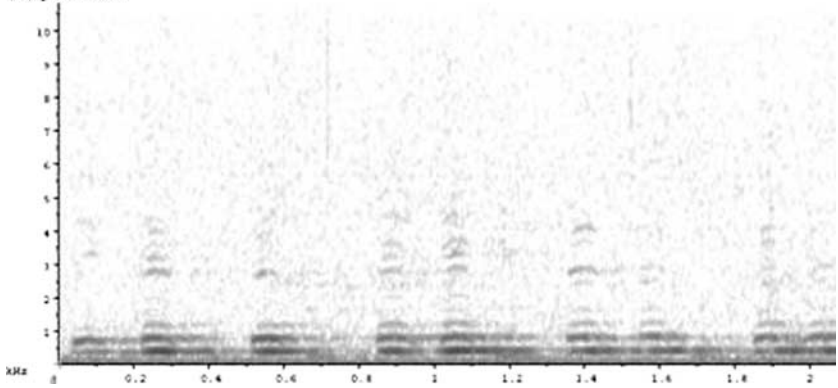
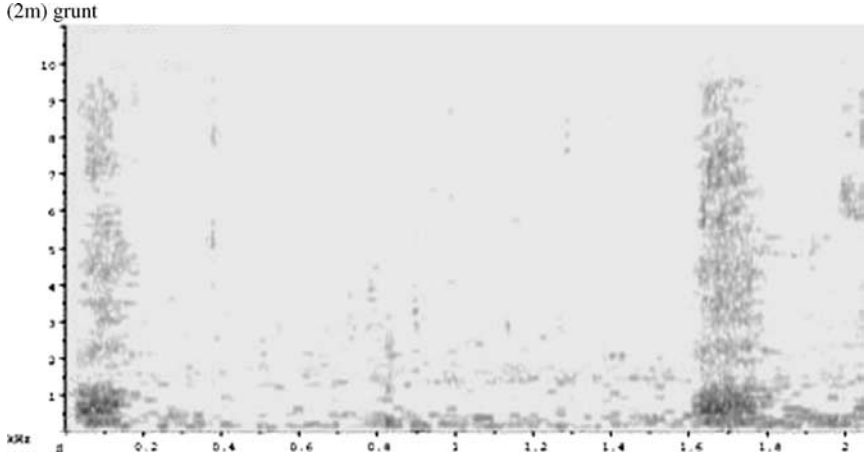
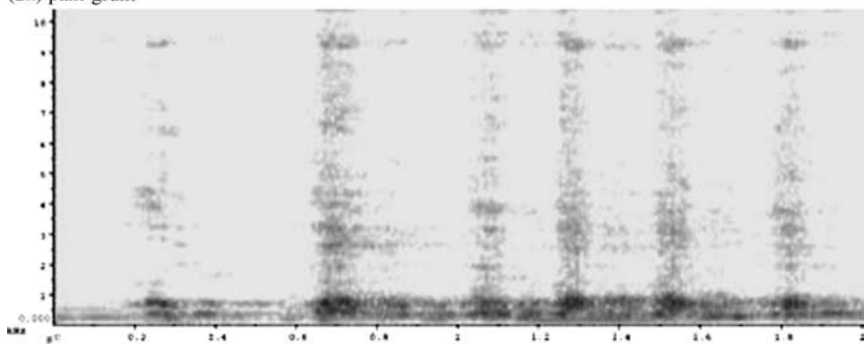


Fig. 2. Continued.

(2m) grunt



(2n) pant-grunt



(2o) pant-hoot

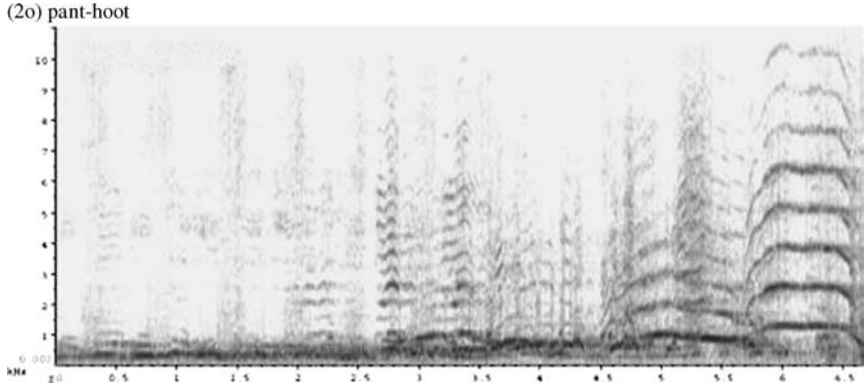


Fig. 2. Continued.

residual = (observed – expected)/$\sqrt{}$expected (Everitt, 1977). Expected values were computed by calculating the product of the marginal totals divided by the grand total, i.e. the product of each column (M_R) and row total (M_C) divided by the total number of observations (T_G). This provided a score for each behavioral category that was adjusted for the number of observations recorded for that category. Chi-square analyses were performed to provide an initial assessment of how the frequency of all facial displays was distributed across behavioral contexts. A factor analysis using principle components was then performed to help explain the variability in the use of facial displays across behavioral contexts. Finally, to specifically address the uniqueness of blended facial displays and test the three hypotheses outlined above, Pearson Product Moment correlations were used to compare the contextual use of blended facial displays with the parent categories that they were blended between.

RESULTS

Data Summary

Any facial display that was observed less than 15 times during the study period was either deleted from the data set or combined with another logical category. This data reduction procedure applied to only one facial display, the bulging-lips face, which was observed only twice. Because it could not easily be combined into any other facial display category, it was removed from the data set. All analyses were subsequently performed on a 24 × 30 matrix of facial displays and behavioral contexts, respectively.

We assessed inter observer reliability via Cohen's Kappa coefficient (Bakeman and Gottman, 1997). Two researchers observed the group simultaneously during a 1-h reliability session that included 5 individual focal observations, as well as observations ad libitum. They stood on opposite ends of the observation tower and whispered observations into a tape recorder. The following contexts and display types were seen and recorded by both researchers during the reliability session: aggression, embrace, external, groom, greeting/present, neutral contact, neutral behavior, avoid/displace, play, rough play, self-directed behaviors, and sex; silent bared teeth display, tooth clacking/spluttering, pant-hooting, neutral, play face, relaxed lip, and low-intensity scream. Interobserver reliability is excellent, ($\kappa > 0.75$ as qualified by Fleiss, 1981) for both facial displays ($\kappa = 0.80$) and behavioral contexts ($\kappa = 0.81$). We performed reliability analysis on behaviors seen by

both observers, since much of the data collected were ad libitum, and each observer was not always assured of seeing the same events at the same time. This was deemed appropriate because they recorded no datum on behavioral frequency.

Behavioral Contexts

Overall, 2,560 facial displays are in the analyses. Their frequency distribution across the 30 behavioral contexts are in Table III. The most frequent display is the play face (19% of the total observations), and the most infrequent is the shrill bark (0.6% of displays). The play face was highly context specific, i.e., >83% of play faces occurred during play. The least context specific expression is the tense face, which occurred 17% of the time during play, its most frequent context-of-use.

An initial chi-square analysis performed on the data in Table III ($\chi^2 = \Sigma(\text{observed} - \text{expected})^2/\text{expected}$) revealed that the subjects used facial displays differently depending on the behavioral context, thus rejecting the null hypothesis that facial displays would be equally distributed across all contexts ($\chi^2(667) = 8170.1$, $p < 0.0001$). In the event that this was due to only one display category being highly discrepant in terms of contextual use, i.e., like the play face, we summed chi-square values for each facial display, revealing similar results. The chi-square values ranged between 61.0 for the tense face and 1664.0 for the tooth-clack, where in the significant cutoff value is $\chi^2(29) > 49.59, p < 0.01$.

To explore the relationship between facial displays and their context-of-use, we performed a principle components factor analysis with varimax rotation on the adjusted residual scores. It revealed 7 factors using eigenvalues >1 that we visually identified via a scree plot. These accounted for >80% of the variance in the contextual use of facial displays. We assigned each facial display to only one factor according to its largest partial correlation coefficient. The loadings are in Table IV.

Facial displays in the first factor—screeching bared-teeth scream, low-intensity scream, squeak, stretch-pout whimper and yelp—are associated with the initial and prolonged response to aggression, fleeing, sexual interaction and some play. Thus, it is characterized by nervousness, fear, and distress. Factor 2 includes bark, staring bared-teeth scream, silent scream and tense face. The displays are associated with both initiation and response to aggression, thus factor 2 is characterized by general agonism and conflict. Factor 3 includes excited bared-teeth face, silent bared-teeth face, pout and relaxed-lip face. They are associated with the initiation of contact such as approach, embrace, invitations, play and response to aggression. Thus,

Table III. The observed frequency of each facial display in each behavioral context

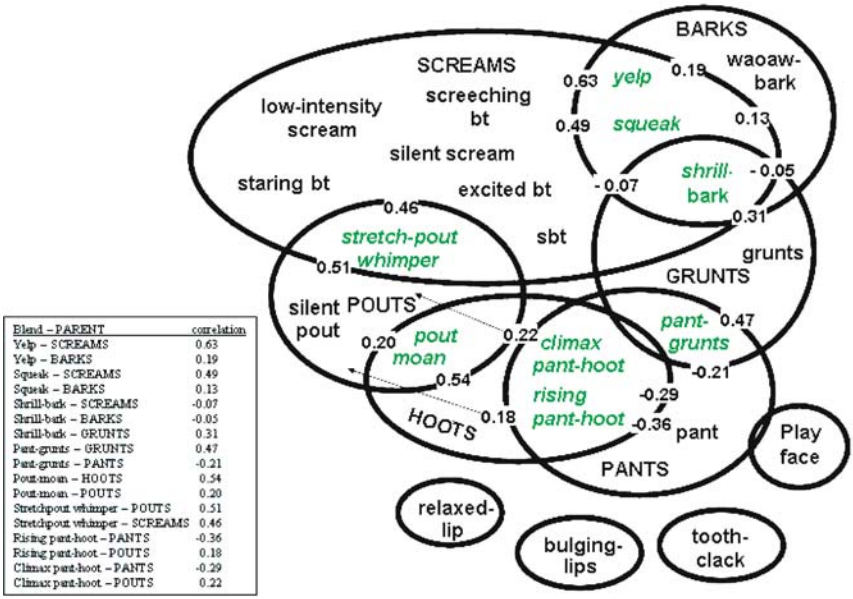
	bk	bt0	bt1	bt2	bt3	gvl	gv2	hg	hoO	ho1	ho2	ho3	pa	Pf	po	rl	scO	SC1	sk	sq	th	ts	wh	yp	total
A0	12	0	9	6	10	0	0	5	2	0	1	1	0	0	0	7	12	14	0	4	1	7	4	2	97
A1	3	0	6	7	10	0	0	2	0	0	7	1	0	0	0	1	22	8	0	0	0	2	0	1	70
A2	9	0	0	33	8	0	0	1	1	0	1	0	0	2	4	1	15	70	1	19	2	2	6	9	184
AP	1	5	10	4	2	0	8	2	10	1	4	0	3	9	6	38	0	3	0	2	2	0	2	1	113
BF	2	0	4	1	0	0	4	3	2	3	38	34	1	1	3	1	7	1	0	1	0	6	0	0	112
BW	0	0	0	2	0	0	1	0	14	0	0	0	0	0	0	0	0	0	3	1	0	0	0	0	21
DP	0	0	0	0	0	0	0	2	0	1	0	2	0	1	0	1	0	0	0	1	1	0	0	0	9
DT	0	0	3	18	1	0	0	0	0	7	0	0	0	0	1	0	0	17	0	7	1	0	4	5	64
EM	1	2	8	5	0	0	0	3	1	0	2	0	1	2	2	4	1	2	0	2	0	1	2	1	40
EX	8	6	16	0	0	1	0	5	8	3	70	11	1	4	3	10	0	2	1	3	14	3	1	1	171
FGM	0	0	0	0	0	44	12	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	58
FL	2	0	2	6	0	0	0	0	1	0	0	0	0	1	2	2	1	6	1	1	0	1	1	0	27
GM	0	0	0	0	0	120	33	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	2	0	158
GP	1	0	4	2	0	0	4	13	91	1	6	0	8	3	2	0	2	3	7	1	0	0	0	0	148
IV	0	0	0	0	0	1	4	0	1	1	0	0	0	6	3	7	0	1	0	0	0	2	3	1	30
Kl	0	0	2	2	0	0	1	0	4	1	0	0	1	1	0	0	0	0	0	2	0	0	0	0	14
NC	0	4	2	2	0	1	7	2	2	0	1	0	0	21	4	13	4	0	0	0	0	3	0	0	66
NO	5	6	25	4	0	1	19	18	13	27	68	36	5	12	12	15	6	16	1	7	1	4	8	4	313
OV	0	0	5	8	0	0	1	5	6	1	0	0	0	1	2	9	3	9	1	5	0	2	2	2	62
P1	0	0	1	0	0	0	2	0	0	0	0	0	113	401	0	17	0	1	0	2	0	8	0	0	545
P2	1	0	0	0	1	0	0	0	0	0	0	0	4	14	0	0	6	7	0	4	0	2	0	3	42
PL	1	0	2	0	0	0	5	0	0	10	23	6	1	0	0	2	0	0	0	0	0	1	0	0	51
PP	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	4
SD	0	0	0	0	0	0	16	0	1	2	1	0	0	1	0	7	0	0	0	0	0	0	0	0	28
SO	1	0	0	3	0	0	0	0	2	0	0	0	0	1	0	0	0	1	0	0	0	0	0	1	9
SSX	0	0	0	0	0	1	0	0	0	0	0	0	0	2	0	6	0	1	0	2	0	2	0	0	14
SU	1	0	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	5
SX	0	0	2	0	0	6	7	1	1	0	0	0	0	1	0	6	0	1	0	7	0	0	0	1	33
WO	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2
WP	0	1	6	8	0	0	3	2	34	0	2	0	0	0	2	0	4	5	0	3	0	0	0	0	70
total	49	24	108	113	32	175	128	64	194	58	226	91	138	484	46	151	84	170	15	74	22	46	36	32	2560

Table IV. Partial correlation factor loadings for each facial display across behavioral contexts. The 7 factors accounted for >80% of the variance in the adjusted frequency of display use

Facial Display	Factors						
	1	2	3	4	5	6	7
bark(bk)	.265	.703	−.025	.044	−.031	.068	.364
excited bared-teeth (bt0)	−.136	−.091	.769	.032	.002	.027	.477
silent bared-teeth (bt1)	.066	.285	.562	.288	.210	.058	.402
screeching bared-teeth (bt2)	.865	.159	−.024	−.119	.114	.065	.018
screaming bared-teeth (bt3)	.241	.873	−.078	−.170	−.048	−.005	.013
tooth-clack (gv1)	−.146	−.116	−.218	−.171	−.154	−.837	−.037
splutter (gv2)	−.196	−.214	.106	.013	−.110	−.830	−.192
grunt (hg)	−.034	.168	.316	.336	.637	.080	.069
pant-grunt (ho0)	−.086	−.119	−.027	−.112	.930	.024	−.034
pout-moan (ho1)	.167	−.248	.069	.788	−.043	−.051	−.036
pant-hoot (ho2)	−.227	.041	.055	.772	−.014	.041	.516
rising pant-hoot (ho3)	−.200	.100	.006	.882	−.036	.054	.022
pant (pa)	−.385	−.313	−.336	−.366	−.266	.586	−.226
play face (pf)	−.371	−.291	−.227	−.405	−.390	.571	−.245
pout (po)	.214	−.078	.825	.247	.119	.042	−.076
relaxed-lip face (rl)	−.097	−.059	.826	−.201	−.182	−.078	−.032
silent scream (sc0)	.162	.881	−.082	−.027	.041	.029	−.085
low-intensity scream (sc1)	.885	.285	−.117	−.075	−.022	.065	.011
shrill bark (sk)	.001	−.101	−.124	−.097	.834	.049	−.040
squeak (sq)	.774	.010	−.019	−.050	.014	.048	.042
woaow-bark (th)	.011	−.018	.108	.098	−.050	.069	.909
tense face (ts)	−.092	.610	.232	.195	−.265	.278	−.229
stretch pout whimper (wh)	.691	.089	.383	.142	−.109	−.119	−.135
yelp (yp)	.893	.105	−.020	.009	−.126	.073	−.002

Factor 3 appears to be characterized by contact seeking and reassurance. Factor 4 includes pout-moan, rising pant-hoot and climax pant-hoot. They are associated with distress, neutral behavior, bluffing, response to external events, play and piloerection. Factor 4 is best characterized by general excitement and intimidation. Factor 5 includes grunt, pant-grunt and shrill bark. They displays are almost exclusively associated with greetings and bowing, a behavior used almost exclusively for interactions with the dominant male. Thus, Factor 5 is charactrerized by status-related greetings. Factor 6 includes pants and play faces. They occur almost exclusively during play, characterizing Factor 6 as play. Factor 7 includes only the woaow-bark, which is a display associated primarily with responses to the external environment. Thus, Factor 7 is characterized by alarm and vigilance.

Our second aim was to examine similarities and differences in the contextual use of blended facial displays compared to the 6 basic expression categories. Figure 3 illustrates the major categories of facial displays in large circles, listed in capitals. We identified them based on descriptions in the literature and our own ethogram (Table II. Facial displays listed in italics in



Blend – PARENT	correlation
Yelp – SCREAMS	0.63
Yelp – BARKS	0.19
Squeak – SCREAMS	0.49
Squeak – BARKS	0.13
Shrill-bark – SCREAMS	-0.07
Shrill-bark – BARKS	-0.05
Shrill-bark – GRUNTS	0.31
Pant-grunts – GRUNTS	0.47
Pant-grunts – PANTS	-0.21
Pout-moan – HOOTS	0.54
Pout-moan – POUTS	0.20
Stretchpout whimper – POUTS	0.51
Stretchpout whimper – SCREAMS	0.46
Rising pant-hoot – PANTS	-0.36
Rising pant-hoot – POUTS	0.18
Climax pant-hoot – PANTS	-0.29
Climax pant-hoot – POUTS	0.22

Fig. 3. Six categories of chimpanzee facial displays. The circles illustrate the major facial display groups (in capitals) with the blended displays in spaces where the circles overlap (in italics). The numbers represent the correlations between the contexts-of-use for each blended display and their parent groups. The box insert summarizes the table and highlights the parent groups for each blended display type.

the areas where the circles overlap represent the blended displays. Overall, we identified 8 blended facial displays: yelp and squeak, blended between screams and barks; shrill bark, a blend between screams, barks and grunts; pant-grunt, a blend between pants and grunts; rising pant-hoot and climax pant-hoot, a blend between hoots and pants; pout moan, a blend between hoots and pouts; and the stretch pout whimper, a blend between pouts and screams. In their peak intensity, the displays overlapped ≥ 2 category boundaries based on their visual and acoustic similarities.

In order to test the various hypotheses outlined in the introduction, we correlated the contextual use of each blended expression with the expressions in each of the ≥ 2 major categories that they were blended between. The correlation values in Fig. 3 between the circles that denote the major expression categories, i.e., parent categories, and in the insert. Significant correlations occur at $r > \pm 0.36$, $p < 0.05$ and $r > \pm 0.48$, $p < 0.01$. The correlation indicates the contextual similarity between the blended displays and parent groups. Type II errors in the analyses sould be minimal because they compare hypothesis-driven indendent sets of

observations. Both yelp and squeak are significantly positively correlated with screams ($r = 0.63$, $p < 0.001$ and $r = 0.49$, $p < 0.007$, respectively) but not significantly correlated with barks ($r = 0.19$, $p = 0.33$ and $r = 0.13$, $p = 0.50$, respectively). Accordingly, while yelps and squeaks may represent morphological blends between the major categories of screams and barks, they are contextually similar only to screams. The shrill bark appears to be both visually and acoustically blended among 3 categories: screams, barks and grunts. Its context-of-use is positively correlated with grunts, $r = 0.31$, $p = 0.10$ though it did not reach significance, but weakly and negatively correlated with screams and barks ($r = -0.07$, $p = 0.73$ and $r = -0.05$, $p = 0.78$, respectively). Thus, the shrill bark is more grunt-like, than scream-like or bark-like. The pant-grunt is a blend between grunts and pants, but its context-of-use correlated significantly with grunts ($r = 0.47$, $p < 0.009$) than pants ($r = -0.21$, $p = 0.28$). The rising pant-hoot and climax pant-hoot are blended between pouts and pants. They were the only category of blended expression with no significant correlation. Rising pant-hoots and climax pant hoots are positively correlated with pouts ($r = 0.18$, $p = 0.35$ and $r = 0.22$, $p = 0.24$, respectively), but were negatively correlated with pants ($r = -0.36$, $p < 0.05$ and $r = -0.29$, $p = 0.12$, respectively). The pout-moan is a blend between hoots and pouts, but had only significant contextual correlations with hoots ($r = 0.54$, $p < 0.002$), not pouts ($r = 0.20$, $p = 0.30$). The stretch pout whimper, a blend between screams and pouts, was the only facial display that is morphologically and contextually blended across categories ($r = 0.46$, $p < 0.01$ with screams and $r = 0.51$, $p < 0.004$ with pouts).

The analyses indicate that among the blended displays performed by chimpanzees, most are clearly associated with the context-of-use of only one of the ≥ 2 parent categories between which they are blended. The exceptions being the stretch pout whimper, which is contextually similar to both parent groups—screams and pouts—and both the rising and climax pant-hoots which had no significant correlation to the context of use to either of their parent groups—pouts or pants—though they are positively correlated with the contextual use of pouts and negatively correlated with the contextual use of pants.

DISCUSSION

The study revealed several interesting findings with regard to the contextual use of facial displays in chimpanzees. First, several major groups of facial/vocal expressions can be identified in chimpanzees according to their morphological similarity. The 6 major categories include screams, barks, grunts, pants, hoots, and pouts. Parr *et al.* (1998) suggested that chim-

panzees are able to categorize their facial expressions into these major groups during a computerized task. There is major agreement among existing published classifications on the identity of the major categories (Table II). Production of the expressive behaviors differed depending on the type of social/behavioral context and the presumed motivational state of the sender, suggesting an association between the display type and its social/emotional function, though we include no detailed assessment of the functional outcome of the behaviors here.

Second, Marler (1976) reported the expressive behavior of chimpanzees to be among the most graded of nonhuman primate communicative systems. We additionally identified several facial displays that appeared to be blended between ≥ 2 parent groups, in that their peak intensities shared characteristics in common with the displays in the prototypical parent groups. This is a slightly different distinction from that described by previous researchers because the blended expressions were commonly observed display types in the behavioral repertoire of the chimpanzee, not simply intermediate display forms performed as the subjects transitioned between prototypical signals. This distinction is clear in Fig. 1, which shows signal grading between a pout and a bared-teeth display, but also the peak intensity blended display, the stretch pout whimper.

Our data strongly support the hypothesis that one parent type remains dominant and the blending reflects a conflicting internal motivational state on the part of the signaler. The expression of blended facial displays correlates significantly with contexts that elicited only one of the parent groups. Thus, although the expressions appeared to be blended physically, their context-of-use remained quite specific to only one major expressive group. This is true for all the blended displays we identified except the stretch pout whimper, which was produced in behavioral contexts that are significantly correlated with the displays in each of the parent groups: screams and pouts. Also, the rising and climax pant-hoots are not significantly correlated with either of their parent groups, though their expression is positively correlated with the use of pouts but are negatively correlated with the use of the pants. Thus, the trend to support the third hypothesis is present for these display types.

The association of blended facial displays with specific behavioral contexts is further supported in that both the parent expressions and blended displays loaded onto the same factor groupings. We identified 7 factors, 3 of which contain the 8 blended displays. Expressive behaviors that loaded positively onto Factor 1 includes screeching bared-teeth scream, low-intensity scream, squeak, stretch-pout whimper and yelp. The last 3 are blended displays whose contextual use correlates most with screams, not barks. Many examples of screams also load onto Factor 1. Factor 4 includes the pout-

moan, rising pant-hoot and climax pant-hoot. Each of them is a blend. Pant-hoots correlate positively with the contextual use of the parent group pouts, one example of which also loaded onto Factor 4. The pout-moan is significantly correlated with the contextual use of hoots, which were exclusively associated with Factor 4. Factor 5 included grunt, pant-grunt and shrill bark, the latter 2 of which are blended displays. Both the shrill bark and pant-grunt are significantly correlated with the contextual use of grunts, which is the only other display type to load onto Factor 5.

What might be the explanation for the existence of blended display types in chimpanzees? One approach to an answer is to examine the receiver's perspective or how group members interpret ambiguous facial displays. In humans, speech sounds are graded but are nonetheless perceived categorically, e.g., acoustic discriminations involving the basic phonemes ba and pa (Abramson and Lisker, 1970). In monkeys species-typical vocalizations are perceived categorically, which appears to be more prominent for intraspecific versus interspecific acoustic signals (Zoloth *et al.*, 1979). Chimpanzees also show that categorical perception might not be restricted to the auditory domain. We have demonstrated the ability of chimpanzees to discriminate photographs of facial expressions according to their prototypical categorical membership even when the expressions were produced by unfamiliar individuals, were shown a range of intensities, i.e., grading, or were presented as 2-dimensional photographs or short video clips (Parr, 2001; Parr *et al.*, 1998). Further, Brown and Boysen (2000) reported the ability of chimpanzees to discriminate categorically pairs of animal faces that were morphed to reflect different proportions of one versus the other category via a same-different paradigm. Therefore, categorical perception appears to be a likely explanation for how graded signals can be accurately discriminated despite their somewhat ambiguous morphological and acoustic structure.

Further, because the blended facial displays are primarily associated with specific behavioral contexts, and are not blended between contexts associated with each parent expression, additional cues such as the behavioral context itself might play a role in identifying the communicative intent of the signaler. In addition to behavioral context, cues available to amplify the correct identification of a signal might include ecological information, the identify of the signaler, or cues from other sensory modalities including a combination of visual and auditory elements (Marler, 1976; Partan and Marler, 1999). The recognition of emotions from human facial expression is easily accomplished despite a predominance of blended emotions by using distinctive features of the expressions or in combination with information about the environment, i.e., the same expression may be perceived differently, e.g., depending on whether the context is a surprise birthday party or

an encounter at night in an unfamiliar neighborhood (Calder *et al.*, 2001; Young *et al.*, 1997).

Another way to evaluate the use of blended facial displays in chimpanzees is to examine factors that might contribute to their production. Our data strongly supported our hypothesis that blended displays are more likely to reflect the presence of ≥2 conflicting motivations in the sender and thus be associated primarily with the motivation of the dominant expression type (Hinde, 1970; van Hooff, 1973). This explanation is rooted in earlier ethological studies on motivational systems (Hinde, 1970), a now all but forgotten field that nevertheless remains relevant to the study of emotion and animal communication. Indeed, previous studies of vocal behavior in free-ranging monkeys suggest that graded signals tend to be orderly in production in certain contexts and are not randomly produced (Green, 1975). Thus, the graded quality of expressive behavior does not appear to reflect aspects of a particular social or ecological context, but instead more likely reflects something inherent in the individual that produced the signal, such as their internal motivation. Similar explanations may hold for blended displays. In a highly complex social environment, such as that among nonhuman primates, in which individuals are often faced with situations for which there are multiple potential outcomes, motivational conflict is likely to be a common occurrence. Individuals must often weigh potential outcomes before selecting the most appropriate behavior in that specific situation. If these situations are ones in which 2 motivational tendencies come into conflict, e.g., approach or withdraw, attack or submit, a blended display type expressing components of both motivational tendencies is likely to occur. Our data suggest that one of the tendencies will remain dominant, which is supported by the fact that not all combinations of blended displays are possible. In fact, only a few display types were blended, most of which involved expressions associated with nervous and fear, excitement and intimidation, and greetings. This is not dissimilar to the way in which human facial expressions often reflect more than a single basic emotional state, but not all emotionaly blends are possible, e.g., anger and happiness, or joy and disgust (Ekman and Friesen, 1975).

Finally, why were the blended displays that we reported reliably associated with the context-of-use of only one parent expression over the other, instead of the contexts associated with both parent types, especially given the argument that they may reflect ≥2 conflicting motivations? An additional explanation for the contextual association might be reflected in the sequential use of the parent expressions. If, for example, expression b typically follows expression a in a behavioral sequence, one might predict that the primary context-of-use for the blended expression ab would be A, as a

is the expression that typically occurs first in a sequence with b. This may also be reflected in the temporal pattern of expression of a and b within the blended display. If expression a occurs first in context A, but quickly blends into expression ab, followed by b, the context in which the ab blend is first elicited is context A, given the fact that the display would change more quickly than the social context. Thus, the motivational state associated with context A remains dominant. A more detailed sequential analysis of expression grading would be needed to determine whether this may explain the contextual distinctness of morphologically blended displays.

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