

Smiles when sharing[☆]

Marc Mehu^{a,*}, Karl Grammer^b, Robin I.M. Dunbar^a

^aBritish Academy Centenary Research Project, School of Biological Sciences, University of Liverpool, Liverpool, UK

^bLudwig Boltzmann Institute for Urban Ethology, c/o Department of Anthropology, University of Vienna, Vienna, Austria

Initial receipt 12 March 2007; final revision received 8 May 2007

Abstract

One of the proposed functions of human smiling is to advertise cooperative dispositions and thereby increase the likelihood that a social partner would invest resources in a relationship. In particular, smiles involving an emotional component would be honest signals of altruistic dispositions because they are not easy to produce voluntarily. In this study, 60 people were covertly filmed while interacting with a friend in two conditions: control and sharing. Smiles were classified into Duchenne (spontaneous) and non-Duchenne smiles. Participants also completed a series of questionnaires, including the Altruism Scale and a self-report questionnaire of emotional state. Interestingly, Duchenne smiles were displayed at higher rates in the sharing situation as opposed to the control situation, whereas non-Duchenne smiles were unaffected by the type of interaction. Furthermore, Duchenne smiles in the sharing interaction were positively affected by a measure of altruism. Self-reported emotional states did not vary between conditions and were poorly related to smiling. This study shows that the Duchenne smile is relevant to situations that involve the sharing of material resources because it would reliably advertise altruistic intentions. The Duchenne smile could therefore be an important signal in the formation and maintenance of cooperative relationships.

© 2007 Elsevier Inc. All rights reserved.

Keywords: Facial behavior; Evolution; Smiling; Duchenne smile; Altruism

1. Introduction

The functional use of facial displays in social interactions among primates is well documented (Andrew, 1963; van Hooff, 1972; Waller & Dunbar, 2005). Some authors have suggested that the variety and flexibility of primates' facial behavior result from evolutionary pressures imposed by the intertwinement between ecological factors and ever-increasing social complexities (Preuschoft & van Hooff, 1997). This implies that the main function of facial behavior is to negotiate particular aspects of social interactions in relation to specific ecological conditions (see also Hinde, 1985; Schmidt & Cohn, 2001). This study investigated whether this could also apply to human smiling, a facial expression that van Hooff suggested has deep roots in the primate

lineage. Indeed, comparative evidence suggest that the human smile is the homologue of the silent bared-teeth (SBT) display observed in nonhuman primates (Burrows, Waller, Parr, & Bonar, 2006; van Hooff, 1972).

The flexibility in the use of the SBT display across primate species seems to depend more on the type of social relationships brought about by particular ecological conditions rather than on phylogenetic aspects reflecting a common ancestry (Preuschoft & van Hooff, 1997). In some species such as the rhesus macaque (*Macaca mulatta*) and the hamadryas baboon (*Papio hamadryas*), the SBT display is shown exclusively by subordinates to appease dominants in aggressive contexts (de Waal & Luttrell, 1985; Kummer, 1957). In other species such as the Tonkean macaque (*M. tonkeana*) and the chimpanzee (*Pan troglodytes*), the SBT display is used not only bidirectionally but also in a wider variety of social situations, ranging from appeasement to reconciliation (Thierry, Demaria, Preuschoft, & Desportes, 1989; van Hooff, 1972). The SBT display can also be observed in clearly affiliative contexts, including greeting, grooming, embracing, and huddling [e.g., *M. nigra* (Dixon, 1977), *M. tonkeana* (Petit & Thierry, 1992; Thierry

[☆] This research was supported by an O. Aldis Award delivered to the first author by the International Society for Human Ethology (Charleston, SC).

* Corresponding author. 19 Avenue Reine Astrid, B-4500 Huy, Belgium.

E-mail address: marcmehu@yahoo.fr (M. Mehu).

et al., 1989), *P. troglodytes* (de Waal, 1988; van Hooff, 1972), and *Theropithecus gelada* (van Hooff, 1967)]. In addition, there is a body of evidence showing that the SBT display may promote social bonding as it has been found to increase the frequency of affiliative behaviors in captive chimpanzees (Waller & Dunbar, 2005) and in humans as observed in natural settings (Mehu, 2006). All in all, these findings suggest that the SBT display might not be limited to the inhibition of aggressive tendencies in dominants and that it could also extend to the development of prosocial relationships and, ultimately, social bonding.

The exact reasons why the SBT display would have emancipated into a behavior crucial to bonding are still unclear. Preuschoft and van Hooff (1997) suggested that the selection pressures responsible for its emancipation could lie in the interaction between social and ecological factors. In certain ecological conditions, when the management of vital resources requires joint action of several individuals, social strategies based on aggressive contests might not have paid off as much as cooperative exploitation of resources (Dunbar, 1988). In other words, the development of cooperative relationships could have been a successful alternative to intense competition over resources and could have led to the development of egalitarian relationships (at least within foraging groups). However, this could only be achieved if individuals restrain their competitive tendencies and if dominants allow their allies to obtain a fair share of the cooperative activity (Hand, 1986). Therefore, the need to effectively advertise one's willingness to engage in a relationship of this sort, as well as to identify individuals who are prepared to do so, became a major aspect of social behavior in cooperative species. Because the inhibition of aggressive tendencies is the first step toward social bonding (de Waal, 1986; Dunbar, 2004), the SBT display appeared like the ideal candidate display for emancipation into a signal of prosocial intentions.

This implies that when cooperative relationships replaced social conflicts as the primary mode of resource exploitation, the SBT display, which was first used to appease dominants through the advertisement of nonhostile intentions (Preuschoft, 1992), emancipated into a friendly gesture used bidirectionally to signify intentions to engage in a cooperative relationship. Consequently, the interdependence between social and ecological factors might have paved the way for the emancipation of the SBT display as a signal of cooperative dispositions and intentions. As a modern form of the SBT display, human smiling should therefore be prevalent in situations that involve the sharing of resources.

The postulated link between prosocial emotions and commitment (Frank, 1988; Hirshleifer, 1987; Trivers, 1971) further underlined the importance of smiling as a behavioral mechanism responsible for the maintenance of strategies based on reciprocal altruism (Brown, Palameta, & Moore, 2003). Recent research indeed suggest that smiling could be involved in cooperative interactions. For example, a study

that investigated the role of trustworthiness in bargaining games showed that smiling photographs can elicit cooperation from strangers in a trust game (Scharlemann, Eckel, Kacelnik, & Wilson, 2001). In addition, discrimination between different types of smiles should be important in the identification of cooperative partners because it would help people avoid exploitation by socially skilled individuals (Brown & Moore, 2002). Spontaneous smiles (also known as Duchenne smiles) could play a crucial role in that respect (Schmidt & Cohn, 2001) since the activation of muscles around the eyes (orbicularis oculi, one of the main markers of the Duchenne smile) is believed to be under emotional and involuntary control (Ekman & Friesen, 1982). Interestingly, research strongly suggest that the Duchenne smile could be a reliable indicator of altruistic dispositions because it involves facial movements that are not easy to produce on purpose (Brown et al., 2003). As indirect support for that proposal, judgments of sociability and generosity in faces were found to be significantly affected by the presence of subtle movements in the eye region (Mehu, 2006).

The possibility that people could smile more in situations that are relevant to the exploitation of resources has not been investigated thus far, however. In fact, the flexibility of human nonverbal behavior suggests that people signal selectively, according to the perceived benefits inherent to a particular interaction (Grammer, Fivola, & Fieder, 1997). Dawkins and Krebs (1978) emphasized that cooperative signals (those that are adaptive to senders and receivers) are likely to be inconspicuous and that receivers should not evolve particular resistance to them. These imply that smiles involving subtle facial movements such as the activation of orbicularis oculi (i.e., Duchenne smile) should reflect dispositions relevant to the development of cooperative relationships (i.e., altruism and positive emotion). In addition, people should display Duchenne smiles at higher frequencies when engaged in interactions that entail the sharing of material resources. Finally, it is expected that smiling will modify a receiver's internal state in a way that is positive to the development of a relationship.

2. Methods

2.1. Participants

The study took place at the Ludwig Boltzmann Institute for Urban Ethology, which is hosted by the University of Vienna Department of Anthropology. Sixty pairs of friends were requested to come to the university to participate in a study investigating social relationships. Participants were from a variety of backgrounds (students and nonstudents) and were between 18 and 30 years old. Pairs were composed of either same-sex or mixed-sex individuals, and it was specified that neither romantic couples nor pairs of relatives could take part in the study. Participants were given a show-up fee of €5 and a portion of the money to be shared (€40).

2.2. Materials

Emotional state was measured using seven scales on which participants had to report their feelings of anger, happiness, fear, sadness, surprise, disgust, and relaxedness. Participants were presented a 10-cm line for each emotion (with one end labeled *not at all* and the other labeled *very much*). They were asked to tick the line at the spot that corresponded best to their current feeling. The distance in centimeters between the origin of the line and the indicated spot constituted the self-reported measure of emotion.

Each participant's general disposition to altruism was assessed with a questionnaire developed by Johnson et al. (1989), a scale that contains 56 items measuring the number of instances in which an individual has given up time, effort, goods, status, and safety in order to help others. Participants are asked to report how often they performed each act described in the statement from 1 (*never*) to 5 (*very often*), how often they have been the recipient of such acts, and how important these acts are to them from 1 (*not important at all*) to 4 (*very important*). These measures showed high internal consistency, with the coefficient α ranging between 0.89 and 0.95 across seven cultures. In addition, the test–retest reliability over a 2-week period was 0.94 (Johnson et al., 1989). The Altruism Scale includes 20 items from the Self-Report Altruism Scale (Rushton, Chrisjohn, & Frekken, 1981)—items that were shown to be internally consistent across five samples. In addition, altruistic inclination toward a friend was measured by asking participants to indicate what proportion of their salary would they be ready to give up to help their friend should he or she experience financial problems (in percentage).

The experiment was conducted in two areas that will be named here as the *questionnaire area* and the *experimental room*. The questionnaire area consisted of a large corridor where two tables and chairs could be placed on each side of a large wall that was conveniently used to prevent communication between participants while they were completing the questionnaires. The experimental room was a small room where two comfortable seats were arranged at an angle of 90° in order to minimize discomfort while interacting (Argyle, 1988). The layout of the experimental room is illustrated in Fig. 1. Digital video cameras were concealed inside the room at three locations in order to allow the filming of each participant's face and the overall context of the interaction. For the sake of this study, the analysis only included footage obtained from one video camera, a Panasonic NV-GS280. Sound was recorded through the built-in microphone of that camera.

2.3. Procedure

Participants were welcomed by the experimenter, who led them to the experimental room where the procedure was explained. The experimenter then asked the participants to think of pseudonyms that they would use during the

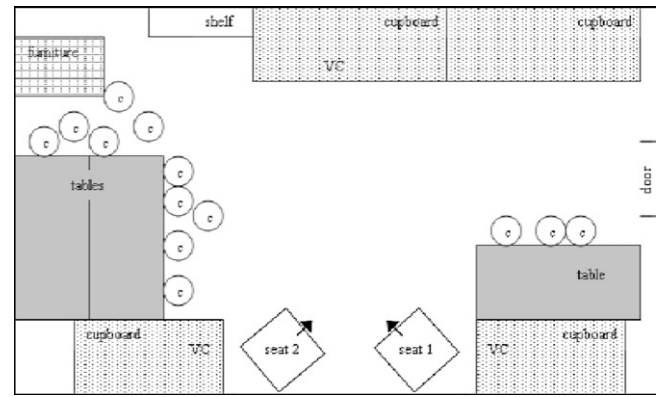


Fig. 1. Layout of the experimental room. VC=video camera; c=chair. The arrows indicate seating orientation.

experiment—names that should be chosen after famous pairs in history, legend, cinema, science, and so on (e.g., David and Goliath or Starsky and Hutch). The reason why we chose a selection of famous names was to make it clear to the participants that the experiment would be anonymous. It also made sure that the participants engaged in a conversation (which they did). The experimenter then left the room for 5 min to let them decide on their names. The participants were filmed during this period, which constituted the control interaction. The experimenter came back after 5 min and took the participants to the questionnaire area where they were first asked to complete an emotion sheet and then a questionnaire soliciting personal information.

After the completion of the first set of questionnaires, the participants were brought to the experimental room where they were instructed to share the experiment fee (€40). It was specified that after the decision has been made, the money should be placed in an envelope that had to be sealed and placed in a box located in the room. The sharing situation was filmed for a maximum period of 5 min, and this constituted the experimental condition. When the sharing was over, the participants were led to the questionnaire area to complete the second set of questionnaires, including an emotion sheet and the Altruism Scale. Once these questionnaires were completed, the participants were introduced to another person who paid them for and debriefed them about the experiment. Finally, the participants signed a consent form to authorize use of their personal data and video records for scientific and educational purposes.

2.4. Behavior analysis

Smiles were classified into four categories: Duchenne as well as non-Duchenne smiles (Ekman & Friesen, 1982) and open and closed smiles (Brannigan & Humphries, 1972). Smile categories were not exclusive of each other but represented two dimensions of smiling: cheek raise (also known as the Duchenne marker) and mouth opening. Because smiling does not always show a continuous offset (i.e., a smile can vary in intensity before it completely

disappears from the face), a new smile was recorded each time the lip corners were observed to be rising after a decrease in intensity. Therefore, gradual increases in smile intensity were not recorded as separate smiles. Smiles that co-occurred with laughter episodes were not included in the analysis. Smile frequencies were transformed into rates per minute. Because Duchenne smile rates did not follow a normal distribution, they were transformed using the square root function.

Smiles were coded by a certified Facial Action Coding System scorer (test reliability=0.76) during continuous focal sampling sessions (Altmann, 1974) performed on individuals sitting on Seat 1 (Fig. 1). The duration of the sampling sessions depended on the period needed to share the experiment fee. For the experimental interaction, sampling began as soon as the experimenter left the room and stopped when the envelopes were sealed and placed inside the box. For the control interaction, a sampling period was randomly selected within the 5-min waiting time, and it lasted as long as did the sharing. For example, if the participants needed 90 s to share the money, a 90-s control period was randomly selected within the 5-min waiting time. Of the 60 pairs invited to take part in the study, 12 had to be excluded from the sample because (1) some of the participants did not stay seated long enough to allow behavioral coding by the video and (2) technical problems made some videos unavailable for analysis. The remaining 48 pairs were included in the analysis. The total observation time for the control and experimental conditions was 130.93 min. The average duration for a sample was 81.83 s (S.D.=47.27).

3. Results

3.1. Smiles when sharing

A repeated-measures analysis of variance was carried out to test whether smiling rates differed between the control and experimental situations. The design was 2×2×2, with the sex of the focal subject as well as that of the friend as between-subject factors and the experimental condition as the within-subject factor. The dependent variables were the frequencies of non-Duchenne, Duchenne, and open smiles (rates per minute). Multivariate tests showed a strong effect of the

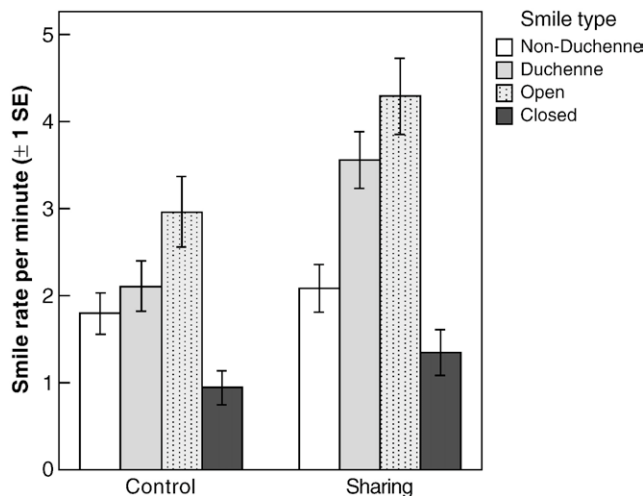


Fig. 2. Effect of interaction context on different types of smiles (mean rate per minute).

experimental condition ($F_{3,42}=5.71, p=.002$), indicating that smiling rates differed significantly between the control and sharing interactions. Neither sex of the focal subject ($F_{3,42}=0.29, p=.83$) nor that of the partner ($F_{3,42}=0.58, p=.63$) had an effect on smiling rates. There was no interaction effect between sex of the focal subject and that of the partner ($F_{3,42}=1.07, p=.37$). Interestingly, univariate tests revealed that the experimental condition had a significant impact on Duchenne and open smiles but not on non-Duchenne smiles (Table 1). These results are illustrated in Fig. 2. Note that the money was shared evenly in 93% of the cases, suggesting that high rates of Duchenne and open smiles occurred in parallel to a fair division of resources.

Because closed smiles were not normally distributed, the effect of the experimental condition was investigated using the nonparametric equivalent of the paired-samples *t* test, the Wilcoxon signed rank test. Results showed that closed smile rates were not influenced by the experimental condition ($z=-1.37, n=48, p=.17$), indicating that the rates of closed smiles in the control condition (median=0.39) were similar to those in the sharing interaction (median=0.81).

3.2. Smiles and altruism

The Altruism Scale (Johnson et al., 1989) generally gives three scores measuring people’s involvement in altruistic acts: a score for the number of altruistic acts performed in the past, a score for the number of altruistic acts received, and a score measuring the importance of these acts for the person. In addition to these measures, participants had to answer the following question: “What percentage of your salary would you give up to help your friend if he/she finds himself/herself in a difficult situation?” The number of altruistic acts received was not included in the analysis because the main interest of this study was to measure the influence of the sender’s altruistic dispositions and intentions on his or her own smiling.

Table 1
Effects of interaction context on smiling

Smile type	Control (n=48)	Sharing (n=48)	$F_{1,44}$	<i>d</i>
Non-Duchenne	1.80 (1.66)	2.08 (1.89)	0.70	0.16
Duchenne	2.11 (2.02)	3.65 (2.26)	17.18 **	0.67
Open	2.96 (2.82)	4.29 (3.03)	8.04 *	0.45
Closed	0.94 (1.34)	1.35 (1.83)	–	–

Note: Data are expressed as mean (S.D.) for smiling rates (per minute) in the control and sharing interactions.

* $p<.01$.

** $p<.001$.

Table 2
Relationship between smiling and altruism

	Acts given	Importance of acts	Financial offer to friend
Smile rate for the control interaction			
Non-Duchenne smile	0.12	-0.13	0.05
Duchenne smile	-0.15	-0.26	0.16
Open smile	-0.05	-0.27	0.15
Closed smile ^a	0.01	0.04	-0.12
Smile rate for the sharing interaction			
Non-Duchenne smile	-0.18	-0.22	-0.19
Duchenne smile	-0.01	-0.13	0.36*
Open smile	-0.08	-0.11	0.15
Closed smile ^a	-0.03	-0.07	-0.01

Note: Values are Pearson’s correlations between smiling and measures of altruism.

^a Spearman’s correlations.

* $p < .05$.

As presented in Table 2, smiles displayed in the control interaction were poorly related to measures of altruism. On the other hand, the Duchenne smile rate in the sharing interaction was positively associated with self-reported financial help that would be extended to a friend if in need. This indicates that people who would give a high proportion of their salary to their friend also showed elevated rates of Duchenne smiles while sharing (Fig. 3; Table 3). This relationship was not observed with the other types of smiles. There was a trend, although nonsignificant, suggesting a negative association between smiling and the reported importance of altruistic acts. The number of altruistic acts given in the past was unrelated to smiling (Tables 2 and 3).

3.3. Smiling and emotion

Note that the participants reported their emotional experience on two occasions during the study: once directly

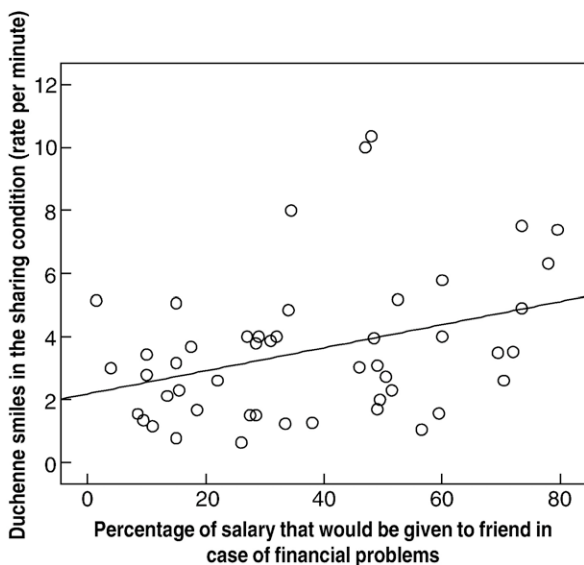


Fig. 3. Relationship between altruism and Duchenne smiles displayed while sharing.

Table 3
Impact of altruism on smiling

Duchenne smiles while sharing (rate per minute)						
$F_{3,44}$	R^2	Predictor	B	S.E.	β	t
3.44*	0.19	Constant	6.22	2.41	-	2.58*
		Financial help	0.90	0.30	0.44	3.05**
		Acts given	-0.31	0.96	-0.05	-0.32
		Importance of acts	-2.03	1.28	-0.24	-1.58

Summary of regression analysis. The dependent variable is the frequency of Duchenne smiles displayed in the sharing interaction (rate per minute).

* $p < .05$.

** $p < .01$.

after the control interaction and once directly after sharing the money. In order to check the effect of the experimental condition on emotional experience, we performed a paired-samples t test, with scores on self-reported emotions as the dependent variables. Results showed that emotional experience did not differ substantially between conditions (Table 4).

In addition, smiling was weakly associated with self-reported emotional states (Table 5). Unexpectedly, sadness was the only emotion that was significantly related to smiling, as non-Duchenne smiles shown in the sharing interaction were positively associated with self-reports of sadness (Table 5). This suggests that people who reported feeling sad after sharing the money had shown high rates of non-Duchenne smiles during that interaction.

Although the sender’s mood had no effect on his or her own smiling, it is possible that smiling had an impact on the receiver’s emotional state. Since the emotions were reported directly after the interactions took place, a possible effect of smiling on the receiver’s internal state could potentially be detected.

A linear regression analysis was performed with smiling rates per minute (non-Duchenne, Duchenne, and open smiles) as predictors and the friend’s self-reported emotions as criteria. Analysis showed that the friend’s self-reported happiness after sharing the money was positively affected by open smiles displayed by the focal subject during that interaction ($F_{1,46}=4.07$, $p=.049$, $R^2=0.08$, $\beta=0.28$),

Table 4
Effects of interaction context on self-reported emotion

Emotion	Control (n=48)	Sharing (n=48)	t	d
Happiness	6.23 (2.10)	6.50 (2.17)	-1.19	0.13
Surprise	3.76 (2.78)	3.28 (2.50)	1.25	0.18
Fear	1.18 (1.33)	0.96 (1.40)	1.57	0.16
Sadness	1.33 (1.74)	1.02 (1.46)	1.44	0.19
Relaxedness	6.06 (2.38)	6.16 (2.62)	-0.27	0.04

Emotion	Median		z	r
Anger	0.65	0.50	-0.48	-0.05
Disgust	0.25	0.22	-1.14	-0.12

Note: Data are expressed as mean (S.D.) scores of emotional experience reported after the control and sharing interactions. All t and z values are nonsignificant.

Table 5
Relationship between smiling and emotion

	Anger ^a	Fear	Sadness	Disgust ^a	Happiness	Surprise	Calmness
Smile rate for the control interaction							
Non-Duchenne smile	0.11	0.001	0.23	0.16	-0.14	-0.03	-0.06
Duchenne smile	0.01	0.20	0.26	-0.13	-0.26	-0.09	-0.13
Open smile	0.01	0.01	0.17	-0.06	-0.23	0.03	-0.05
Closed smile ^a	0.03	0.18	0.20	0.10	-0.13	-0.26	-0.19
Smile rate for the sharing interaction							
Non-Duchenne smile	0.09	0.23	0.30 *	0.04	0.01	0.07	0.10
Duchenne smile	0.08	-0.05	0.05	-0.07	-0.02	-0.03	0.15
Open smile	0.17	0.13	0.20	0.04	-0.05	-0.03	0.08
Closed smile ^a	-0.05	0.05	0.13	-0.02	0.09	0.002	0.09

Note: Values are Pearson's correlations between smile frequencies (rate per minute) and self-reported emotional experience.

^a Spearman's correlations.

* $p < .05$.

indicating that the participants reported greater feelings of happiness when their friend had shown a high rate of open smiles while sharing (Fig. 4).

4. Discussion

This study shows that smiling is relevant to situations that involve the sharing of material resources. Importantly, not all forms of smiling were affected by the experimental condition. Frequencies of Duchenne and open smiles were higher in the sharing situation as opposed to the control situation, whereas non-Duchenne and closed smiles were displayed at similar rates in the two conditions. These findings support the idea that Duchenne and open smiles play a particular role in social relationships and could be critical in situations that involve the sharing of material resources. In contrast, non-Duchenne and closed smiles would play a minor role in sharing between friends.

That Duchenne and open smiles appeared to be particularly relevant to the sharing situation supports the assumption that some aspects of smiling would function to regulate cooperative relationships. Although the experimental interaction itself was not a cooperative interaction per se, it did represent a situation in which the benefits from a cooperative activity (participation in the experiment) had to be shared. Pairs of friends were not taken randomly from the corridor; instead, people saw individual announcements on the Internet and had to recruit a friend who would be willing to participate with them. It can therefore be assumed that the relationships within the pairs were cooperative (if only because the partner had to agree to come along). In addition, friendship has often been considered as a particular type of relationship in which people value balanced exchanges, although friends tend to avoid keeping careful records of benefits that are given and received (Silk, 2003). Not surprisingly, most pairs divided the fee equally, implying that the context captured in the experimental interaction represented an opportunity for people to underline the prosocial and egalitarian aspects of their relationship. The findings suggest that Duchenne and open smiles could be used to emphasize these positive aspects and, in that sense, be socially adaptive.

Our data also provide evidence that smiling could regulate cooperative relationships through the advertisement of intentions relevant to the good functioning of such relationships. Research had shown that smiles involving an emotional component (e.g., the Duchenne marker) could be honest signals of altruistic dispositions and thereby help people negotiate interactions that entail cooperative aspects (Brown et al., 2003). This proposal was vindicated by two findings: (1) the frequency of Duchenne smiles increased in sharing contexts as opposed to control situations and (2) people who expressed high altruistic intentions toward their friend also showed higher rates of Duchenne smiles *only when they were engaged in active sharing*. These results show that people could use the Duchenne smile in a flexible and possibly adaptive way, as our participants displayed higher rates of that behavior in a social context that

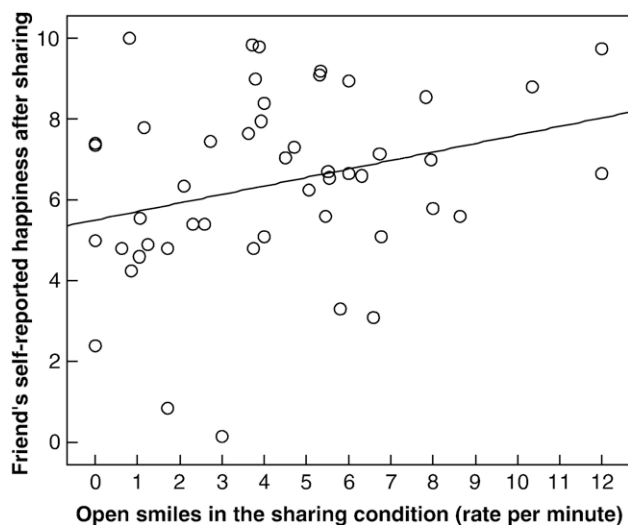


Fig. 4. Relationship between open smiles shown by the focal subject during the sharing interaction and the friend's self-reported happiness directly after that interaction.

involved the sharing of material benefits. Moreover, the positive connection between altruistic intentions and Duchenne smiles displayed while sharing suggests that this type of smile could reliably reflect people's motivations to be altruistic.

There was no relationship between scores on the Altruism Scale and the frequency of Duchenne smiles displayed in either the control or the sharing condition. Note that the study by Brown et al. (2003), who suggested a connection between altruism and Duchenne smiles, was based on a rigorous selection of altruists and nonaltruists, in which high scorers on the scale (top 10th percentile) were classified as altruists and low scorers (bottom 10th percentile) were categorized as nonaltruists. The absence of a relationship between scores on the Altruism Scale and Duchenne smiling in our study suggests that Duchenne smile frequency might not be an extremely sensitive indicator of a general propensity to help. Rather, the expression of this behavior could be more specific to self-reported altruistic intentions toward a particular person in a particular context (sharing). Given that the frequency of smiling was determined by the activation of lip corners and that this facial movement is under voluntary control, we should not exclude the possibility that people strategically adjusted their behavior to communicate their intentions in a situation in which it was important to do so.

The alternative explanation that people felt happier while sharing and showed more Duchenne smiles as a result was not supported. Indeed, self-reported happiness after sharing was the same as it was after the control interaction, a finding that excludes the possibility that increases in Duchenne smiles were due to an enhanced emotional experience. In addition, self-reported happiness was unrelated to the frequencies of smiling (of any type), regardless of the context in which people interacted. According to Ekman and Friesen (1982), the Duchenne smile is an indicator of positive emotions such as happiness and, eventually, relaxedness. If this were the case, Duchenne smiles should have been associated with self-reported emotions and not necessarily with the context of interaction (provided that the context had no effect on emotional experience). On the contrary, our data showed that social and contextual variables had a stronger impact on Duchenne smiles than did emotions in that the type of interaction and altruistic intentions were more important than self-reported emotions in explaining variations in Duchenne smiles. This supports the behavioral ecology approach to facial expression—an approach that emphasizes the role of facial behavior in the communication of social motives (Fridlund, 1994).

Although a sender's self-reported emotional state had no impact on his or her own smiling, emotions were not completely unrelated to smiling. Interestingly, the friend's feeling of happiness after sharing was positively affected by open smiles displayed by his or her partner during that interaction, indicating that the participants reported greater happiness when their friend had shown a high rate of open

smiles while sharing the money. Open smiles could therefore influence a receiver's positive feelings, a finding that supports the claim that social signals could work by modifying the receiver's internal state (Dawkins & Krebs, 1978; Owen & Bachorowski, 2003). Interestingly, the induction of a positive mood has already been observed to increase willingness to cooperate (Forgas, 1998). The link between emotion and social behavior might therefore be part of the mechanisms through which smiling has a positive impact on social relationships.

Overall, this study shows that open and Duchenne smiles could function to regulate social situations that involve the sharing of material resources. Our findings underline the importance of the Duchenne smile in the context of long-term cooperators (Schmidt & Cohn, 2001)—as this smile type was prevalent when the benefits of a common activity were actively shared. Moreover, specific dimensions of smiling could have different roles in such interactions: the Duchenne marker could advertise altruistic intentions toward the receiver, while mouth opening could positively affect the receiver's emotional state. Our data serve as further evidence that people adjust their facial expressions to particularities of social situations (DePaulo, 1992; Grammer et al., 1997) and that this adjustment not only reflects the sender's intentions toward the receiver but could also influence the receiver's internal state. In that sense, smiling could be a crucial element in the chain of consequences leading to the development of adaptive relationships.

Acknowledgments

We thank the Department of Anthropology of the University of Vienna for providing the infrastructure. We also thank Dr. A.-C. Wegria, Ines Blantar, Peter Abend, and Dr. E. Oberzaucher for their support during the study.

References

- Altmann, J. (1974). Observational study of behaviour: Sampling methods. *Behaviour*, *44*, 227–267.
- Andrew, R. J. (1963). Evolution of facial expression. *Science*, *141*, 1034–1041.
- Argyle, M. (1988). *Bodily communication* (2nd ed.). London: Routledge.
- Brannigan, C. R., & Humphries, D. A. (1972). Human non-verbal behavior, a means of communication. In N. G. Blurton-Jones (Ed.), *Ethological studies of child behavior* (pp. 37–64). Cambridge: Cambridge University Press.
- Brown, W. M., & Moore, C. (2002). Smile asymmetries and reputation as reliable indicators of likelihood to cooperate: An evolutionary analysis. In S. P. Shohov (Ed.), *Advances in Psychology Research*, Vol. 11 (pp. 59–78). Huntington, NY: Nova Science Publishers.
- Brown, W. M., Palameta, B., & Moore, C. (2003). Are there non-verbal cues to commitment? An exploratory study using the zero-acquaintance video presentation paradigm. *Evolutionary Psychology*, *1*, 42–69.
- Burrows, A. M., Waller, B. M., Parr, L. A., & Bonar, C. J. (2006). Muscles of facial expression in the chimpanzee (*Pan troglodytes*): Descriptive, comparative and phylogenetic contexts. *Journal of Anatomy*, *208*, 153–167.

- Dawkins, R., & Krebs, J. R. (1978). Animal signals: Information or manipulation? In J. R. Krebs & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (pp. 282–309). Oxford: Blackwell Scientific Publications.
- DePaulo, B. M. (1992). Nonverbal behavior and self-presentation. *Psychological Bulletin*, *111*(2), 203–243.
- de Waal, F. B. M. (1986). The integration of dominance and social bonding in primates. *Quarterly Review of Biology*, *61*(4), 459–479.
- de Waal, F. B. M. (1988). The communicative repertoire of captive bonobos (*Pan paniscus*) compared to that of chimpanzees. *Behaviour*, *105*, 183–251.
- de Waal, F. B. M., & Luttrell, L. (1985). The formal hierarchy of rhesus monkeys: An investigation of the bared-teeth display. *American Journal of Primatology*, *9*, 73–85.
- Dixson, A. F. (1977). Observation on the displays, menstrual cycles, and sexual behaviour of the “black ape” of Celebes (*Macaca nigra*). *Journal of Zoology London*, *182*, 63–84.
- Dunbar, R. I. M. (1988). *Primate social systems*. London: Chapman & Hall.
- Dunbar, R. I. M. (2004). *The human story*. London: Faber & Faber.
- Ekman, P., & Friesen, W. V. (1982). Felt, false and miserable smiles. *Journal of Nonverbal Behavior*, *6*(4), 238–252.
- Forgas, J. P. (1998). On feeling good and getting your way: Mood effects on negotiator cognition and bargaining strategies. *Journal of Personality and Social Psychology*, *74*(3), 565–577.
- Frank, R. H. (1988). *Passions within reason: The strategic role of the emotions*. New York: Norton.
- Fridlund, A. J. (1994). *Human facial expression: An evolutionary view*. San Diego, CA: Academic Press.
- Grammer, K., Fivola, V., & Fieder, M. (1997). The communication paradox and possible solutions: Towards a radical empiricism. In A. Schmitt, K. Atzwanger, K. Grammer, & K. Schäfer, (Eds.), *New aspects of human ethology* (pp. 91–120). New York and London: Plenum.
- Hand, J. L. (1986). Resolution of social conflicts: Dominance, egalitarianism, spheres of dominance, and game theory. *Quarterly Review of Biology*, *61*, 201–220.
- Hinde, R. A. (1985). Expression and negotiation. In G. Zivin (Ed.), *The development of expressive behavior* (pp. 103–116). Orlando, FL: Academic Press.
- Hirshleifer, J. (1987). On the emotions as guarantors of threats and promises. In J. Dupré (Ed.), *The latest on the best: Essays on evolution and optimality* (pp. 307–326). Cambridge, MA: MIT Press.
- Johnson, R. C., Danko, G. P., Darvill, T. J., Bochner, S., Bowers, J. K., Huang, Y.-H., Park, J. Y., Pecjak, V., Rahim, A. R. A., & Pennington, D. (1989). Cross-cultural assessment of altruism and its correlates. *Personality and Individual Differences*, *10*(8), 855–868.
- Kummer, H. (1957). *Soziales Verhalten einer Mantelpavian-Gruppe (Social behaviour of a group of Hamadryas baboons)*. Bern: Huber.
- Mehu, M. (2006). An evolutionary approach to human social behaviour: The case of smiling and laughing. PhD thesis, University of Liverpool.
- Owren, M. J., & Bachorowski, J. -A. (2003). Reconsidering the evolution of non-linguistic communication: The case of laughter. *Journal of Nonverbal Behavior*, *27*(3), 183–200.
- Petit, O., & Thierry, B. (1992). Affiliative function of the silent bared-teeth display in moor macaques (*Macaca maurus*): Further evidence for the particular status of the Sulawesi macaques. *International Journal of Primatology*, *13*, 97–105.
- Preuschoft, S. (1992). ‘Laughter’ and ‘smile’ in Barbary macaques (*Macaca sylvanus*). *Ethology*, *91*, 200–236.
- Preuschoft, S., & van Hooff, J. A. R. A. M. (1997). The social function of ‘smile’ and ‘laughter’: Variations across primate species and societies. In U. Segerstrale, & P. Molnár (Eds.), *Non-verbal communication: Where nature meets culture* (pp. 171–189). Mahwah, NJ: Erlbaum.
- Rushton, J. P., Chrisjohn, R. D., & Fekken, G. C. (1981). The altruistic personality and the Self-Report Altruism Scale. *Personality and Individual Differences*, *2*, 293–302.
- Scharlemann, J. P. W., Eckel, C. C., Kacelnik, A., & Wilson, R. K. (2001). The value of a smile: Game theory with a human face. *Journal of Economic Psychology*, *22*, 617–640.
- Schmidt, K. L., & Cohn, J. F. (2001). Human facial expressions as adaptations: Evolutionary questions in facial expression research. *Yearbook of Physical Anthropology*, *44*, 3–24.
- Silk, J. B. (2003). Cooperation without counting: The puzzle of friendship. In P. Hammerstein (Ed.), *Genetic and cultural evolution of cooperation* (pp. 37–54). Cambridge, MA: MIT Press.
- Thierry, B., Demaria, C., Preuschoft, S., & Desportes, C. (1989). Structural convergence between silent bared-teeth display and relaxed open-mouth display in the Tonkean macaque (*Macaca tonkeana*). *Folia Primatologica*, *52*, 178–184.
- Trivers, R. L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology*, *46*, 35–57.
- van Hooff, J. A. R. A. M. (1967). The facial displays of the catarrhine monkeys and apes. In D. Morris (Ed.), *Primate ethology* (pp. 7–68). London: Weidenfeld & Nicholson.
- van Hooff, J. A. R. A. M. (1972). A comparative approach to the phylogeny of laughter and smiling. In R. A. Hinde (Ed.), *Nonverbal communication* (pp. 209–241). Cambridge: Cambridge University Press.
- Waller, B. M., & Dunbar, R. I. M. (2005). Differential behavioural effects of silent bared-teeth display and relaxed open-mouth display in chimpanzees (*Pan troglodytes*). *Ethology*, *111*, 129–142.