Context modulates signal meaning in primate communication

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Context modulates signal meaning in primate communication

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A central issue in the evolution of social complexity and the evolution of communication concerns the capacity to communicate about increasingly abstract objects and concepts. Many animals can communicate about immediate behavior, but to date, none have been reported to communicate about behavior during future interactions. In this study, we show that a special, unidirectional, cost-free dominance-related signal used by monkeys (pigtailed macaques: *Macaca nemestrina*) means submission (immediate behavior) or subordination (pattern of behavior) depending on the context of usage. We hypothesize that to decrease receiver uncertainty that the signal object is subordination, senders shift contextual usage from the conflict context, where the signal evolved, to a peaceful one, in which submission is unwarranted. We predict and find that deceasing receiver uncertainty through peaceful signal exchange facilitates the development of higher quality social relationships: Individuals exchanging the peaceful variant groom and reconcile more frequently and fight less frequently than individuals exchanging signals only in the conflict context or no signals. We rule out alternative hypotheses, including an underlying reciprocity rule, temperament, and proximity effects. Our results suggest that primates can communicate about behavioral patterns when these concern relationship rules. The invention of signals decreasing uncertainty about relationship state is likely to have been critical for the evolution of social complexity and to the emergence of robust power structures that feed down to influence rapidly changing individual behavior.

cost-free signal | social complexity | subordination | uncertainty-reduction | innovation

Some primates use a fascinating but poorly studied signal to communicate about dominance. This signal is unidirectional: It is always emitted by the same individual in a pair (1–3). The sender emits the signal when a conflict arises once it has learned, based on its agonistic interaction history with its opponent, it is likely to lose contests with that opponent. The signal is a shortcut preventing the conflict from escalating. It is a cost-free signal (4, 5), in that both sender and receiver, in knowing the likely conflict winner, benefit from the signaling interaction. It has been argued that the invention of unidirectional dominance signals has enabled communication about subordination, a pattern of behavior, rather than just submission in the present interaction (1, 2, 6). The basis for this argument is that, unlike other dominance indicators (direction of aggression, withdrawal behavior, etc.), unidirectional signals are highly reliable and not subject to extradyadic influences, including leverage, presence of third parties, or availability of allies (1).

Bound up in this claim are two important issues: (*i*) the functional significance of subordination for social complexity (1, 7, 8) and (*ii*) whether unidirectionality is sufficient to reduce receiver uncertainty that the signal object is subordination (2, 9). In our study species, the pigtailed macaque, this unidirectional signal is the silent bared-teeth display (SBT). The signal occurs in two contexts. It is emitted in response to aggression or threat of it by the receiver. This "conflict context" is the context in which the signal is thought to have evolved (10). It is also the context in which it has been studied. The signal additionally occurs in apparently peaceful contexts, during pass-bys and approaches in the absence of any overt aggression or threatening behavior by the receiver. Unfortunately, in those studies in which data on peacefully emitted SBTs have been collected, the data have been lumped with agonistic context data in the analyses (3, 11).

We investigate whether individuals exchanging the peaceful variant have closer, less antagonistic relationships than those exchanging the signal only in the conflict context. The hypothesis is that shifting contextual usage to the peaceful context, where submission is unwarranted, reduces receiver uncertainty that the sender is communicating agreement to a pattern of subordinate behavior (Table 1). Reducing receiver uncertainty changes the nature of the relationship by decreasing the rate of aggression required to assay status. This, in turn, reduces constraints on positive social interactions between sender and receiver. Elsewhere (12) it has been shown that a temporally stable, highly predictive power structure arises from the network of peacefully exchanged signals. This power structure makes possible a particular type of conflict management that has systemic effects on organizational robustness by significantly changing the structure and complexity of social networks that constitute essential social resources in gregarious primate societies (8, 13, 14). The emergence of power structures that arise slowly from, and influence, rapidly changing individual-level interactions appears to depend on the capacity to communicate about a behavioral pattern, rather than just immediate behavior.

We are simultaneously addressing two questions: the role of context in modulating signal meaning (behavioral pattern vs. immediate behavior only) and whether the capacity to communicate about a behavioral pattern facilitated development of higher quality social relationships. If peacefully emitted SBTs reduce receiver uncertainty that signal meaning is subordination, individuals signaling in peaceful contexts should engage less frequently in contests, and more frequently in grooming and relationship repair, than individuals exchanging only conflict SBTs or no signals at all. To assess the likelihood that any observed relation between peaceful signal exchange and relationship quality is causal, we test alternative hypotheses, including reciprocity, temperament, and proximity effects, which potentially could produce a spurious relation between relationship quality and peaceful signal exchange. Details on pigtailed macaque social organization and dominance-related signals are reported in *Methods*.

Results

We observed 1,218 peacefully emitted SBTs and 403 SBTs emitted in response to threatening behavior or aggression by the

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Abbreviation: SBT, silent bared-teeth display.

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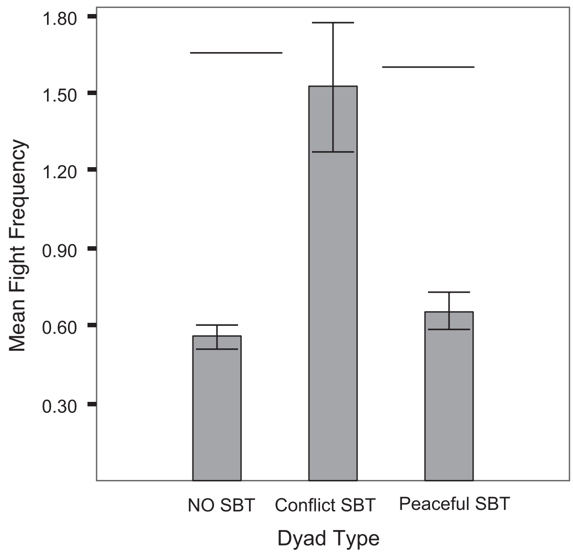

Fig. 1. Repeated measures results for fight frequency across SBT conditions. Bars represent mean fight frequency ± 1.0 SE. Nonsignaling dyads engage in fighting significantly less frequently than conflict signaling dyads (mean difference = 0.87, SE = 0.24; $P = 0.001$) but with similar frequency to nonsignaling dyads (mean difference = 0.098, SE = 0.08; $P = 0.20$). Nonsignaling dyads engage in significantly less fighting than conflict signaling dyads (mean difference = 0.97, SE = 0.25; $P < 0.001$).

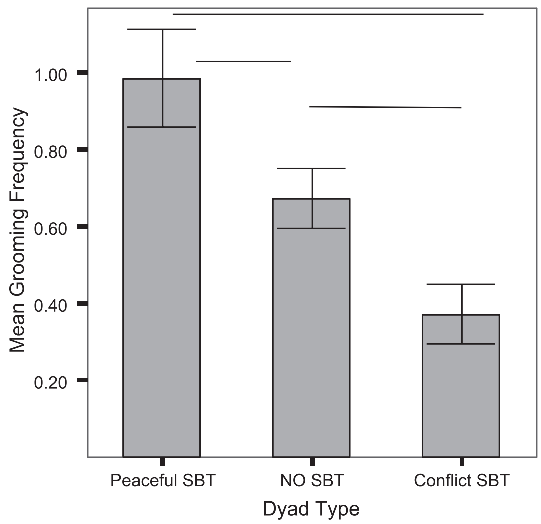

Fig. 2. Repeated measures results for grooming frequency across SBT conditions. Bars represent mean grooming frequency ± 1.0 SE. Peaceful signaling dyads engaged in grooming significantly more frequently than nonsignaling dyads (mean difference = 0.31; SE = 0.09; $P = 0.004$) and significantly more frequently than conflict signaling dyads (mean difference = 0.63, SE = .11; $P <$ 0.011). Nonsignaling dyads engaged in grooming significantly more frequently than conflict signaling dyads (mean difference = 0.32, SE = 0.07; $P <$ 0.001).

receiver, 2,404 total agonistic dyads, 575 reconciliations, 1,781 grooming bouts, and 3,983 proximity bouts. The rate of peaceful SBT displays emitted was 0.16 per individual per hour. The rate of conflict SBTs emitted was 0.05 per individual per hour.

We calculated mean fight, grooming, reconciliation and proximity frequencies for each individual for those nonkin partners with whom it exchanged (*i*) at least one peaceful SBT, (*ii*) only conflict SBTs, or (*iii*) no SBTs. If individuals exchanging peaceful SBTs have closer relationships, they should be distinguishable from individuals only signaling in the conflict context, and from individuals with neither overlapping nor conflictual interests or with unresolved dominance relationships (nonsignalers). We evaluated interaction patterns with only nonkin because kin are likely to have strong relationships independent of dominance. We used repeated measures to compare means across conditions, using a pure within subjects ($A \times B \times S$) design in each analysis and Sidak correction for multiple tests (15). Repeated measures design controls for individual variation in, for example, tendency to signal, ruling out (in this case) the possibility that frequent signalers, regardless of context, have higher quality social relationships with signal receivers. Individuals were included in each analysis if the following conditions were satisfied: (*i*) they had at least one partner in each partner condition (peaceful signalers, conflict signalers, and nonsignalers) and (*ii*) they engaged in the behavior under evaluation (e.g., if they performed no grooming at all, they were not included in the grooming analyses). This procedure determines the *n* for each analysis.

Fighting and Signal Exchange. Peaceful signalers fight (with one another) significantly less frequently than conflict signalers (Fig. 1). Nonsignalers engaged in fighting least often, but this difference was not significant (P, peaceful signal exchange; C, only conflict signal exchange; and NO: no signal exchange, repeated measures: $n = 43$, $m_P = 0.66$, SD = 0.47; $m_{NO} = 0.56$, SD = 0.32; $m_C = 1.52$, SD = 0.63, $SS = 24.28$; df = 2; $F = 13.88$; $P < 0.001$; partial eta^2 = 0.25; pairwise comparisons are reported in Fig. 1 legend).

Grooming and Signal Exchange. Peaceful signalers groom (with one another) significantly more frequently than conflict signalers and nonsignalers. Nonsignalers groom significantly more frequently than conflict signalers (repeated measures: $n = 43$, $m_P = 0.98$, SD = 0.70; $m_{NO} = 0.67$, SD = 0.45; $m_C = 0.35$, SD = 0.50, $SS = 8.55$; df = 2; $F = 23.38$; $P < 0.001$; partial eta^2 = 0.36).

In *Appendix*, we present additional analyses ruling out several alternative explanations for the above results. We find that the relationship between grooming and peaceful signal exchange is not a spurious one resulting from a "reciprocity agreement" in which (*i*) individuals groom powerful (frequently signaled to) group members in return for support during fights or (*ii*) low-ranking individuals give grooming to high-ranking ones in return for social tolerance. The data refute the hypothesis that status signals are power commodities traded for grooming (individuals "up for election" curry support among voters; ref. 12). The data also refute the hypothesis that temperament accounts for the observed relationship between grooming, reconciliation (see below), fighting (see above), and peaceful signal exchange (Fig. 2).

Reconciliation and Signal Exchange. Here we investigate how a third dimension of relationship quality, reconciliation (16), varies with condition. Because reconciliation is conditional on the occurrence of fighting, we controlled for individual variation in tendency to fight. We calculated the observed minus expected (*o*-e) frequency of reconciliation for each individual in each of its dyads given its total frequency of conflict, following a procedure from Flack *et al.* (13) controlling for underlying variance in fight frequency. There was no effect of condition on mean *o*-e frequency of reconciliation (repeated measures: $n = 36$, $m_P = 0.42$, SD = 3.08; $m_{NO} = -0.11$, SD = 1.38; $m_C = -0.57$, SD = 0.82, $SS = 6.19$; df = 2; $F = 0.80$; $P < 0.45$; partial eta^2 = 0.02). Although mean reconciliation was highest for peaceful signaling dyads and lowest for conflict signaling dyads, the means were not significantly different because of high variance in the peaceful signaling dyad condition. Inspection of the data revealed this was due to erratic behavior of individuals in the subadult male age-sex class. We reevaluated this relationship after removing all subadult males from the analysis. As shown in Fig. 3, peaceful signalers reconciled significantly more fre-

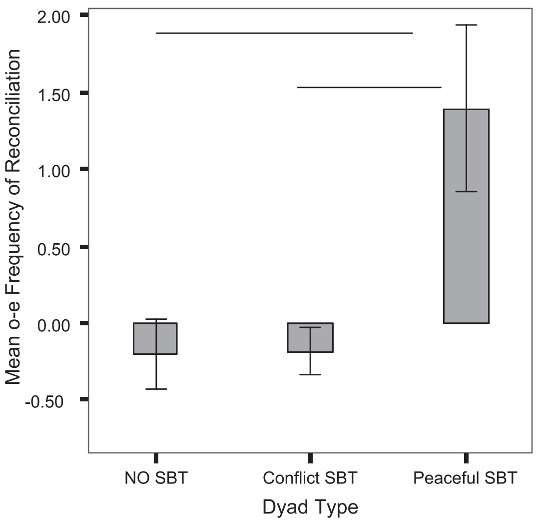

Fig. 3. Repeated measures results for reconciliation across SBT conditions. Bars represent mean observed minus expected (o-e) reconciliation frequency (see text for explanation) ± 1.0 SE. Peaceful signaling dyads engaged in reconciliation significantly more frequently than nonsignaling dyads (mean difference = 1.59; SE = 0.52; $P = 0.015$), and significantly more frequently than conflict signaling dyads (mean difference = 1.58, SE = 0.51; $P < 0.014$). There was no difference between conflict signaling dyads and nonsignaling dyads (mean difference = 0.01, SE = 0.30, $P = 1.0$).

quently than conflict signalers and nonsignalers, but there was no difference between nonsignalers and conflict signalers (repeated measures: $n = 27$, $m_P = 1.39$, SD = 2.80; $m_{NO} = -0.20$, SD = 1.18; $m_C = -0.18$, SD = 0.78, $SS = 45.10$; df = 2; $F = 8.11$; $P = 0.001$; partial eta^2 = 0.24).

Interaction Frequency and Signal Exchange. Here we explore the possibility that peaceful signalers have closer relationships simply because they interact more frequently. We use proximity frequency (assessed by using scan sampling, see *Methods*) to assay interaction frequency. We found that conflict signalers and peaceful signalers interact equally frequently, meaning that they have equal opportunity to signal and affiliate (repeated measures: $n = 43$, $m_P = 2.67$, SD = 1.33; $m_C = 2.76$, SD = 2.74; $m_{NO} = 1.94$, SD = 0.98; $SS = 17.39$, df = 2, $F = 3.58$; $P = 0.03$; partial eta^2 = 0.08; mean difference = 0.08, SE = 0.37, $P = 0.99$). Nonsignalers spent less time in proximity than peaceful signalers (mean difference = 0.73, SE = 0.19, $P = 0.001$), but there was no significant difference between nonsignalers and conflict signalers (mean difference = 0.82, SE = 0.41, $P = 0.15$).

Discussion

Identifying potential behavioral and signaling inventions and investigating their consequences for social relationships can provide important insight into the evolution of social complexity. In this regard, one of the most often discussed innovations is human language (17). One important feature of language is that signals (conceived of here as words and sentences) can represent ideas as well as objects and events that are temporally or spatially divorced from the signal itself (18–20). For example, "I saw a lion yesteday" or "John is in the tree at the end of the road," stand in contrast to "Lion!". This required a transition from a signaling system in which communication was possible only about the "here and now," as in the "Lion!" case, to more abstract concepts, such as where the lion was yesterday. A potential, albeit simpler, animal analog, which we study here, is the distinction between dominance-related signals that communicate willingness to withdraw in the present fight, and the same signals that, outside the fight context, communicate agreement to a subordinate behavioral pattern. An important question concerning both the evolution of communication and social complexity is how receivers decode signals representing objects that have no material correlates in the world, or that are spatially and/or temporally decoupled from the objects they stand for. In all three cases, forming an association between the signal and its object is nontrival. In the case of dominance-related signaling, our data suggest that context of signal emission plays a critical role in reducing receiver uncertainty that the signal stands for the more general, and less verifiable, concept of subordination, rather than simply willingness to yield in the present interaction. In the following paragraphs we discuss implications of signaling about future behavior/behavioral pattens for dyadic and organizational complexity, why context is important, and we suggest how a signaling system could be structured to facilitate receiver decoding of novel signals.

Signaling Behavioral Patterns and Social Complexity. It has been argued that unidirectional status signaling allows for the development of more cooperative, cohesive relationships by decreasing uncertainty about the state of the relationship (1, 21). We have explored the possibility that the actual innovation is twofold: Decreasing receiver uncertainty that the signal object is subordination requires both signal unidirectionality and a contextual shift in usage from the conflict context to the peaceful one where submission is unwarranted (Table 1). Our data are consistent with this hypothesis. In pigtailed macaques, a unidirectional dominance-related signal, the silent-bared teeth display, is used in two contexts: the conflict context, in which it evolved to signal submission (10), and a peaceful context. These signals are, in fact, three times more common in the absence of any overtly agonistic behavior than during conflicts, showing that they have achieved a high degree of divorce from their original context. Receivers and senders exchanging silent-bared teeth displays during peaceful interactions have higher quality, more cohesive relationships, marked by less conflict, more grooming, and more relationship repair, than those exchanging these signals only in response to aggression or the threat of it. The data refute alternative hypotheses, including reciprocity, temperament, and proximity effects, that could produce a spu-

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Table 1. Posited role of context in modulation of signal meaning

Social context	Example receiver behavior	Example sender response	Possible signal object	Uncertainty reduction about. . .	Social implications
Conflict	Threaten	Emit unidirectional dominance signal; withdrawal-related behavor	Submission or subordination	Immediate behavior in present interaction	Prevent escalation of present conflict
Peaceful	Pass-by	Emit unidirectional dominance signal	Subordination	Pattern of behavior	Reduce need to assay status using aggression; facilitate affiliative interactions; emergence of slow-time scale power structure

rious relation between relationship quality and signal exchange. The proximity result is particularly important because it addresses the possibility that individuals with higher quality relationships are more likely to signal in peaceful contexts because they have more opportunities to do so. Refuting it makes it unlikely that we have the causality backwards.

The implications of being able to communicate about a pattern of behavior, rather than only immediate behavior[¶], extend beyond the development of higher quality dyadic relationships. The invention of signals communicating agreement to behavioral patterns, which change slowly (during this study there was only one relationship reversal over the course of 5 months), also appears to have influenced organizational complexity by allowing the emergence of power structures that change over relatively slow time scales (12, 13). These temporally stable power structures support special forms of third-party conflict management that are advantageous at the group level (8, 13, 14).

The potential importance of this type of communication, which we term "relationship state signaling," for complexity at the dyadic and organizational levels begs for follow-up behavioral, cognitive, and neurological studies. Particularly useful would be experimentally investigating how context modulates receiver decoding of the signal object (including the extent to which submission and subordination as signal objects have different neural "representations" and how these representations are differentially triggered by contextual features), the role of memory decay, interference, or retrieval error in repeated signaling, as well as how the contingency between peaceful signal emission and dyad interaction style is established. Directly documenting contingency would require either a group formation study in which a time-series analysis is conducted of how relationships and signaling patterns are established and change, or a longitudinal study investigating how signaling patterns and relationship quality change over the course of social development. The hypothesis that unidirectional, peaceful signal exchange decreases receiver uncertainty about relationship state would be refuted if time series data reveal no correlation between onset of signal usage and improvement in relationship quality.

In addition to the above studies, a comprehensive cross-species analysis, with phylogenetic corrections, is needed to determine whether there is, as predicted for societies in which dominance is an important social variable, a correlation between social complexity and relationship state signaling. We expect that if relationship state signaling is an evolutionary innovation (22) in that it has increased potential for social complexity, interactions in species without these signals will be characterized by lower levels of cooperation, weaker affiliative relationships, infrequent triadic interactions, and the absence of power structures that influence rapidly changing individual level interactions.

[¶]Other signals used by monkeys also appear to have implications beyond the present interaction, but in a qualitatively different way than has been studied here. For example, Cheney and Seyfarth (48) have shown that baboons recognize one another's close associates. They showed this through an experiment in which they played two unrelated females in proximity to one another sequences of calls that mimicked a fight between their relatives. When call sequences involved relatives, subjects looked (in the 20 seconds after presentation of the stimulus) toward the playback speaker longer than when the call sequences involved nonkin. The dominant female "listener" also was (in the 15 minutes after the stimulus) more likely to supplant her subordinate proximity partner (and the subordinate was more likely to avoid the dominant) in the kin condition. Two critical differences between this study and ours are (*i*) that the females tested were listening to calls made by others and attending to information (e.g., call frequencies and other features identify the caller) in those calls that was specific to the callers regardless of context and, (*ii*) although the calls emitted by the combatants were shown to affect the behavior of other group members, the calls were not shown to have causal implications for future interactions, either between the combatants or other group members. Rather, what was shown is that the calls affect the behavior of other group members within 15 min, arguably within the same time step as the conflict in which the calls were produced.

How Novel Signals Arise. Finally, a deep theoretical and experimental question underlying our results is how receivers generalize from prior associations to decode novel signals (where novelty is defined by change to signal features, usage patterns, or context). This is essentially a problem of statistical inference. How do receivers infer properties of an unknown distribution from data generated by that distribution? A potential solution to this problem is pointing: cueing the receiver into the signal object by increasing its salience. Pointing can be built into signal usage through evolution or learning. Well-known forms include physical (23), temporal, indexical (4), and iconic (4). Decoding also can be facilitated by pairing two or more signals, each of which is associated with an object that overlaps on some dimensions with the target object (24–26). An advantage of this *compound-stimulus pointing* is that it can overcome the "learnability problem." By making use of prior associations and the capacity of the receiver to generalize, it can facilitate decoding of signal objects that are spatially or temporally divorced from the signal. One disadvantage is increased ambiguity resulting from the "degeneracy problem," which arises when a signal is associated with multiple objects. We suspect that in nonhumans, compound-stimulus pointing is critical to statistical inference when communicating about objects, like subordination, that exist in the mind of the sender in so far as they have no immediate behavioral or environmental correlates.

Methods

Data were collected from the socially mature individuals of a captive, breeding group of pigtailed macaques at the Yerkes National Primate Research Center near Lawrenceville, GA. The group contained 84 individuals, including 4 adult males (6 years of age by study start), 25 adult females (4 years of age by study start), and 19 subadults. Subadult males included males between ages 4 and 6, whereas subadult females included females between ages 3 and 4. We analyzed behavior of adults and subadults ($n = 48$) because the dominance relationships of juveniles are not yet established. The demographics of our captive population were similar to those reported for natural populations (27–29) in that males were removed at puberty, females remained in their natal groups, forming matrilines, and adult males were introduced and removed every four years.

The group was formed in 1985 and was housed in an indoor-outdoor facility, the outdoor compound of which was 125 feet by 65 feet. Observations were evenly distributed between 1100 and 2000 hours from June–October 1998. Provisioning occurred before observations and once per day during observations. Data were collected over 156 h. The first author was trained in observation by the second author to ensure agreement in coding of behavioral data. Statistical assessment of reliability was not performed because the signal under study occurs infrequently and video recording was infeasible (shadows, poor image resolution, etc).

Conflict, postconflict, and signaling data were collected by using all-occurrence sampling (also called event-recording), in which sequential data were collected from event onset (30, 31). All-occurrence sampling was chosen over focal sampling (*i*) to maximize samples collected, thereby improving statistical power, and (*ii*) because it allows for the entire interaction to be followed. Grooming and proximity data were collected by using scan sampling, in which all pairs (and, in the case of grooming, which is a directed behavior, the ID of the performer) engaged in either behavior were noted every 15 minutes. Data were collected by using a digital stopwatch and voice recorder. Operational definitions of behavior are available in *Appendix*.

Subordination Signals in Macaques. We study the bared-teeth display (BT). The BT has been reported in several macaque species, including rhesus macaques (*Macaca mulatta*), stump-tailed macaques (*Macaca arctoides*), long-tailed macaques (*Macaca fasicu-*

laris), pigtailed macaques (6), Japanese macaques (*Macaca fuscata* (32), Celebes macaque (*Macaca nigra*; ref. 33), Moor macaques (*Macaca maurus*; ref. 34), and Tonkean macaques (*Macaca tonkeana*; ref. 35). BT displays are marked by a retraction of the lips and mouth corners such that the teeth are partially bared (10). Two structural variants have been identified: one that is accompanied by screaming and one that is silent, the SBT. Although the facial morphology of the display is similar across the macaque species in which it occurs, the social function of the display varies. In rhesus, stumptailed, Japanese, and longtailed macaques, the BT/SBT is unidirectional and is thought to communicate subordination/submission (3, 6, 36). In Tonkean macaques, the SBT is not associated with dominance, it is bidirectional and is used by both individuals during greeting situations to signal peaceful intentions (37). In this study, we limit our investigation to the silent version of the SBT in pigtailed macaques. The peaceful SBT and the agonistic SBT are 99.7% and 96.5% unidirectional in our pigtailed macaque study group (assessed by using DCI; ref. 38).

Unidirectional subordination signals also have been reported in chimpanzees (39, 40) and, possibly, are used by wolves and dogs (41, 42), hyenas (43), and ring-tailed lemurs (44).

Analyses. Statistical tests were conducted by using SPSS (www.spss.com) and the statistical computing environment, R (www.r-project.org). Significance was set to 0.05. Details of analyses are provided as appropriate in *Results* and *Appendix*.

Appendix

Operational Definitions of Behavior. ***Aggression:*** Includes threat stares (head lowered and chin thrust forward), gruff vocalizations, lunging, slapping, chasing, wrestling, grappling, and biting.
Conflict context: Overt aggression or threatening behavior, including lowering shoulders and head, thrusting chin forward, and staring at second individual, lunging, slapping, chasing, running toward, pushing, poking, trampling, biting, and gruff vocalizations. Context also classified as conflict if at least one individual showed the following withdrawal-related behavior, including shrinking away, crouching, screaming, and fleeing, even if the other individual showed no apparent threatening behavior. These two types of "conflict context" were distinguished in the data: see *Appendix*.
Conflict SBT: (*i*) SBT display was emitted in conflict context, with or without withdrawal-related behavior including shrinking, crouching, moving away (but not screaming), and (*ii*) individual emitting the display was looking at the presumed receiver. The type of withdrawal behavior accompanying the SBT was noted in the data.
Contact-sitting: Individuals sit in contact.
Fight: Any interaction in which one individual aggresses a second individual. Fight was considered terminated if no aggression or withdrawal responses (fleeing, crouching, screaming, running away, and subordination signals) occurred for 2 minutes from the last such event.
Grooming: One individual moves hands through hair or over face (including eyes) of other individual.
Peaceful context: no overt aggression or threatening behavior; no withdrawal-related behavior other than SBT. Includes casual, directed and undirected approaches, and pass-bys.
Peaceful SBT: (*i*) SBT display was emitted during approaches or pass-bys, in apparently peaceful situations, (*ii*) individual emitting the display was looking at the presumed receiver and, (*iii*) individual emitting the display did not otherwise act submissively (crouch, withdraw, flee, or scream).
Proximity: Two individuals stand within arms reach of one another for at least 5 seconds or sit within arms reach.
Reconciliation: Genital inspection, muzzle–muzzle contact, directional and mutual grooming, embracing, mounting, and/or hip touching during the postconflict period (5 min after fight termination). Reconciliation has been documented in pigtailed macaques by using controlled methods to assess whether postconflict affiliation occurs at higher rates than baseline (45).

Alternative Hypotheses. ***Reciprocity hypotheses.*** We performed two analyses to evaluate whether the relation between grooming and peaceful signaling was a spurious one caused by a reciprocity agreement. In the first analysis, we tested two possibilities. The first is that higher-ranking individuals groom lower-ranking ones in return for SBTs, in which case there should be an asymmetry in the dyad in the distribution of grooming favoring the lower-ranking partner. The logic underlying this hypothesis is individuals receiving many SBTs from many group members are perceived more powerful than individuals receiving few SBTs (12, 13). Subordinate individuals differentially distribute SBTs over dominant partners, signaling repeatedly to some individuals and rarely to others. This suggests that subordinates might be using peaceful SBTs to confer power on dominants (12, 40). If so, dominant individuals might try to solicit "votes" through a variety of means, including grooming SBT senders. We evaluate this relation only to rule out the possibility that the observed correlation between grooming and status signal exchange is a spurious one resulting from the SBT having value as a power commodity. We are not testing whether the SBT is a power commodity. Results and statistical details are provided below.

The second possibility we test in this analysis is that lower-ranking individuals groom higher-ranking ones (with whom they also exchange peaceful SBTs) in return for social tolerance. In this case, we expect grooming to be asymmetrically distributed in the dyad, favoring the higher-ranking individual. Results and statistical details are provided below.

We used a Wilcoxon Signed-Ranks Test at the dyadic level to determine whether there is a grooming asymmetry in sender-receiver dyads. We compared the frequency of grooming given by each dyad partner for those nonkin dyads that satisfied the following two conditions: (*i*) at least one peaceful SBT was exchanged and (*ii*) at least one partner groomed the other. Dyads in which no grooming occurred were not included in this analysis. Of the 1,128 dyads possible, individuals in 702 dyads exchanged SBTs, and of these 702 dyads, individuals in 290 of them exchanged at least one bout of grooming. By comparing grooming frequency of each partner in these 290 dyads, we found no significant difference in the frequency of grooming given by either individual (Wilcoxon Signed-Ranks Test: positive ranks: 127, negative ranks: 141, ties: 22; $Z = 1.12$; $P = 0.27$).

To verify that these results are valid, we conducted a rowwise matrix correlation. Matrix correlation tests account for data interdependencies within matrices. The disadvantage of matrix-level analyses (and advantage of the dyad-level comparison) is that they do not control for pairs of individuals that do not engage in any grooming (see below).

A rowwise matrix correlation uses data within rows, rather than across rows and columns, to calculate a correlation statistic. It is appropriate to use a rowwise matrix correlation on the original matrix and its transposition when data in the matrix are directed. The analysis was conducted by using the software program MatMan developed by de Vries *et al.* (46). The matrices were permuted 10,000 times, meaning that the smallest probability of an observed correlation was 0.0001. We used the partial rowwise statistic, *Kr*, to correlate the groom-received matrix against its transposition, while controlling for dyads in which no SBTs were exchanged. In dyads in which individuals exchanged SBTs, we found a significant positive correlation between the frequency of grooming given by each partner (rowwise matrix correlation: $Kr\ \text{tau}_{\text{rw,x,y,z}} = 0.35$, $P < 0.001$). Taken together, the dyad-level and matrix-level analyses suggest that grooming is symmetrically distributed in dyads exchanging peaceful SBTs: Senders and receivers groom each other with similar frequency. These data refute the alternative hypotheses

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that individuals groom to receive SBTs, give SBTs to receive grooming, or groom to receive tolerance from powerful individuals during other activities, such as foraging.

In our second analysis, we evaluated whether senders give peaceful SBTs to higher-ranking individuals in return for support during fights. The same logic underlying the hypothesis in the above analysis applies here. We used a rowwise matrix correlation test to determine whether there is a correlation between peaceful SBTs received and support given (by directing aggression or threat at opponent). We found no relationship between receiving peaceful SBTs and giving support during conflicts (Kendall's *tau* = 0.001, $P = 0.47$), refuting the alternative hypothesis that SBTs are a power commodity traded for support.

Temperament hypotheses. We evaluated whether an individual-level characteristic, temperament, could account for the observed relationship between signal exchange and affiliation patterns.

Subservience hypothesis. Subordinate individuals signal in apparently peaceful situations because they are especially "subservient" in temperament and do not require overt threats by dominants to produce SBTs. Under this hypothesis, subservience, rather than peaceful signal usage, underlies relationship quality.

Tolerance hypothesis. Dominant individuals are especially tolerant by temperament and, consequently, only elicit very mild responses (SBTs) from subordinates. Under this hypothesis, it is tolerance, not context of signal usage, which accounts for relationship quality. The assumption here is that all interactions, even apparently peaceful ones, are inherently antagonistic.

To address the subservience hypothesis, we consider two alternative interpretations of subservience. One is that those subordinates who signal when dominants pass by in the absence of any overt threat do so because they have fearful temperament. If this were the case, we would not expect to observe, as we do, a difference in affiliation level as a function of signal usage.

The second interpretation of subservience is obsequiousness, such that the sender seeks the favor of the dominant individual through exaggerated and frequent use of deference. This is basically a conspicuous signaling hypothesis (although not Zahavian because the cost of production is low) (47). If this were the case, we would expect from both the production and decoding perspectives peacefully emitted SBTs to be highly conspicuous and co-occur with other submissive components (cringing, shrinking, crouching, etc.), as they do in the conflict context, rather than being simpler and less exaggerated (not accompanied by screams and other withdrawal-related behaviors).

Furthermore, if obsequious temperament is driving signal production, peaceful signals should be emitted at nearly the same rate as nonconflict interaction rate. Our data indicate that peacefully emitted SBTs occur infrequently, at a rate of 0.165 per individual per hour (all-occurrence sampling, see *Methods*). In contrast, a conservative estimate (conservative because these data are sampled only every 15 minutes, see *Methods*) of interaction rate calculated from the affiliation data (proximity, contact-sitting, and grooming) is 1.68. The opportunity to signal is therefore at least 10 times greater than signal emission.

The relative rarity with which the signal is emitted also makes unlikely an appeasement or preemptory hypothesis, that is, the possibility that the sender, having learned it is likely to lose, is simply using the signal to preempt even a threat from its dominant partner. If this were the case, and in contrast to what we find (see above), we would expect the signal to precede most, if not all, approaches to proximity and, frequently, to occur during pass-bys.

Futhermore, over the course of the study, there were only seven (0.001 per individual per hour) occurrences of withdrawal-related behavior (crouching, shrinking, fleeing, etc.) in the absence of any overt threat by a dominant individual, and in only two of those cases was the withdrawal-related behavior accompanied by an SBT. These data suggest that in the absence of an overt threat, subordinates perceive interactions as peaceful.

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1. de Waal FBM (1986) *Q Rev Biol* 61:459–479.
2. Preuschoft S (1999) *J Comp Psychol* 113:91–95.
3. de Waal FBM, Luttrell L (1985) *Am J Primatol* 9:73–85.
4. Maynard Smith J, Harper DGC (1995) *J Theor Biol* 177:305–311.
5. Lachmann M, Szamado S, Bergstrom CT (2001) *Proc Natl Acad Sci USA* 98:13189–13194.
6. Preuschoft S, van Schaik C (2000) in *Natural Conflict Resolution*, eds Aureli F, de Waal FBM (Univ California Press, Berkeley, CA), pp. 77–105.
7. Flack JC, de Waal FBM (2004) in *Macaque Societies: A Model for the Study of Social Organization*, eds Thierry B, Singh M, Kaumanns W (Cambridge Univ Press, Cambridge, UK), pp 157–181.
8. Flack JC, Girvan M, de Waal FBM, Krakauer DC (2006) *Nature* 439:426–429.
9. Maestripieri D (1996) *J Comp Psychol* 110:402.
10. van Hooff JARAM (1967) in *Primate Ethology*, ed Morris D (Aldine de Gruyter, Chicago), pp 7–68.
11. Preuschoft S, Gevers E, van Hooff JARAM (1995) in *'Laughter' and 'Smiling' in Macaques: An Evolutionary Perspective*, ed Preuschoft S (University of Utrecht, Utrecht, The Netherlands), pp 60–88.
12. Flack JC, Krakauer DC (2006) *Am Nat* 168:E87–E102.
13. Flack JC, de Waal FBM, Krakauer DC (2005) *Am Nat* 165:E126–E139.
14. Flack JC, Krakauer DC, de Waal FBM (2005) *Proc R Soc London B* 272:1091–1099.
15. Keppel G (1991) *Design and Analysis: A Researcher's Handbook* (Prentice–Hall, Englewood Cliffs, NJ).
16. Aureli F, de Waal FBM (2000) (Univ California Press, Berkeley, CA).
17. Maynard Smith J, Szathmary E (1997) *The Major Transitions in Evolution* (Oxford Univ Press, Oxford).
18. Jackendoff R (2002) *Foundations of Language: Brain, Meaning, Grammar, Evolution* (Oxford Univ Press, Oxford).
19. Krakauer DC (2001) *J Theor Biol* 213:145–157.
20. Foucault M (2001) *The Order of Things: An Archaeology of Human Sciences* (Routledge, Oxford).
21. de Waal FBM (1993) in *Life History, Development, and Behavior*, eds Pereira ME, Fairbanks LA (Oxford Univ Press, New York), pp 259–270.
22. Erwin DH, Krakauer DC (2004) *Science* 21:1117–1119.
23. Leavens DA, Hopkins WD, Bard KA (2005) *Curr Dir Psychol Sci* 14:185–189.
24. Partan SR, Marler P (2005) *Am Nat* 166:231–245.
25. Ay N, Flack JC, Krakauer DC (2007 *Proc R Soc London B*, in press.
26. Lakoff G (1990) *Women, Fire, and Dangerous Things* (Univ of Chicago Press, Chicago).
27. Fooden J (1980) in *The Macaques: Studies in Ecology, Behavior, and Evolution*, ed Lindburg DG (Van Nostrand Reinhold, New York).
28. Fleagle JG (1988) *Primate Adaptation and Evolution* (Academic, New York).
29. Oi T (1990) *Primates* 31:15–31.
30. Altmann J (1974) *Behaviour* 49:227–267.
31. Bakeman R, Gottman JM (1997) *Observing Interaction: An Introduction to Sequential Analysis* (Cambridge Univ Press, Cambridge, U.K.).
32. Chaffin CL, Friedlen K, de Waal FBM (1995) *Am J Primatol* 35:103–116.
33. Dixson AF (1977) *J Zool (Lond)* 182:63–84.
34. Petit O, Thierry B (1992) *Int J Primatol* 13:97–105.
35. Thierry B, Demaria C, Preuschoft S, Desportes C (1989) *Folia Primatologica* 52:178–184.
36. Angst W (1975) in *Primate Behavior*, ed Rosenblum R (Academic, New York), pp 325–388.
37. Thierry B (2000) in *Natural Conflict Resolution*, eds Aureli F, de Waal FBM (Univ California Press, Berkeley, CA), pp 106–128.
38. van Hooff JARAM, Wensing JAB (1987) in *Man and Wolf*, ed Frank HW (Junk Publishers, Dordrecht, The Netherlands), pp. 219–252.
39. Nishida T (1979) in *The Great Apes*, eds Hamburg DA, McCown ER (Benjamin Cummings, Menlo Park, CA), pp 73–121.
40. de Waal FBM (1982) *Chimpanzee Politics: Power and Sex Among the Apes* (Jonathon Cape, London).
41. Schenkel R (1947) *Behaviour* 1:81–129.
42. Schenkel R (1967) *Am J Zool* 7:319–329.
43. East ML, Hofer H, Wickler W (1993) *Behav Ecol Sociobiol* 33:355–370.
44. Pereira ME, Kappeler PM (1997) *Behaviour* 134:225–274.
45. Judge PG (1991) *Am J Primatol* 23:225–237.
46. De Vries GJ, Netto WJ, Hanegraaf PLH (1993) *Behaviour* 125: 157–175.
47. Grafen A (1990) *J Theor Biol* 144:517–546.
48. Cheney DL, Seyfarth RM (1999) *Anim Behav* 58:67–75.