Title: Social Structure Predicts Eye Contact Tolerance in Nonhuman Primates:

Evidence from a Crowd-Sourcing Approach

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Abstract: In most primates, eye contact is an implicit signal of threat, and often signals social status and imminent physical aggression. However, in humans and the more gregarious species of nonhuman primates, eye contact is more tolerated and used to communicate emotional and mental states. What accounts for the variation in this critical social behavior across primate species? We crowd-sourced primatologists and found a strong positive correlation between eye contact tolerance and primate social structure. In more egalitarian social structures, eye contact is more tolerated. In addition to constituting the first generalizable demonstration of this relationship, our findings can inform the related question of why eye contact is differentially avoided in some human cultures, while in others eye contact is both frequent and even encouraged.

Being looked at elicits a reflexive, involuntary response. Humans can detect that they are the target of another's gaze through subcortical neural pathways, even without conscious awareness (1). Detection of direct gaze in turn triggers a cascade of activation in social cognition centers of the brain that underlie the self-conscious state of arousal and endocrine responses we experience as the "feeling of being looked at" (2). Achieving eye contact with another has important significance both for the sender of this social signal and the recipient. Among most primates, direct gaze can serve as an explicit and implicit signal of threat or dominance, suggesting that overt physical aggression might soon follow (3-9). It is thus often associated with social status and may elicit an avoidance response in a subordinate individual or an antagonistic counter response by another higher in the social hierarchy (3, 5, 10). On the other hand, humans and members of some of the more gregarious primate species, while still recognizing the context in which direct gaze signals threat, are more tolerant of direct gaze and respond by making eye contact (7, 10-17). In these species, eye contact may be used to communicate complex emotional and mental states and to establish affiliative bonds (7, 14, 15, 17, 18). What accounts for the fact that in some nonhuman primates direct gaze typically signals threat and does not invite eye contact, while in other species eye contact is important for nuanced features of a social interaction?

We conducted an investigation into the relationship between tolerance of eye contact and the nature of the social structure in which different primate species live. In order to collect data that spanned numerous primate species, we used novel crowd-sourcing method. Specifically, primatologists were surveyed about the social behavior of the species that had been the subject of their scientific research for many years. In spite of some limitations (discussed below), the method offers the benefits of control over definitions and responses that represent numerous observations over a career rather than during a single experiment or time period. We hypothesized that eye contact is tolerated more in species that live in egalitarian groups with more social fluidity as compared to hierarchical groups with more rigid social stratification. Our *a priori* predictions were based on extant theory in social and cognitive psychology and derived from numerous previous ethological studies of nonhuman primates.

Eye Contact

Eye contact, defined as the prolonged looking of two animals directly into each other's eyes (13), is distinct from gaze following and joint attention, which has been defined as the ability to detect and interpret gaze and to mutually attend to an object or cooperate on a task (10, 19, 20, 21). While eye contact and gaze following are undoubtedly related, they serve different and distinct purposes among primates. Additionally, we recognize and expect that the use of gaze following and joint attention in one species may not directly align with the use of eye contact in that same species.

Eye Contact in Human Primates

Among humans, there are clear distinctions in how eye contact is used and tolerated, and these behaviors are socialized and entrained from early childhood. The initial basis for making eye contact starts soon after birth, with the ability to distinguish between direct and averted gaze arising in infants within 2-5 days after delivery. By 4 months of age, faces with a direct, as compared to averted, gaze elicit more attention and result in enhanced neural processing in infants (22). Across cultures, eye contact between mothers and infants is initially actively sought and sustained (23, 24) and plays an important role in bonding with parents. However, as infants

develop, the caregivers socialize their eye gaze patterns to encourage patterns of eye contact that are more congruent with culture-specific norms and expectations (23, 25-27).

The result of this shaping of looking behavior is that the meaning, use, and tolerance of eye contact in adults differs across cultures. For example, the frequency and duration of eye contact is lower in East Asian than in Western European and American cultures (13, 28, 29). Japanese adults engage in significantly less eye contact than do either Canadians or Trinidadians during face-to-face interactions (30, 31). There is also cultural variation in how eye contact is interpreted, with East Asians, as compared to Western Europeans, viewing eye contact as more aggressive and signifying that the person is less approachable (28-30). In addition, in many Asian as well as Middle Eastern cultures, the use of eye contact and staring is also a way to convey social status and rank, obliging subordinate individuals to avert or lower their gaze. Thus, there appear to be both universal and specific aspects to the meaning of direct gaze and eye contact which may correspond to how eye contact is used among nonhuman primates in more hierarchical versus egalitarian social systems.

Although the terms hierarchical and egalitarian as we understand them in the context of nonhuman primates are not commonly used to describe human social structures, we can still draw connections between nonhuman and human social structures by references to the strategies for accomplishing the social tasks common to group living within these structures. Such tasks include negotiating one's status in the social hierarchy, affiliative behaviors like consolation and trust building, and responding to unfamiliar and unrelated conspecifics. Human cultures and societies with tighter social norms and more rigid status social hierarchies employ strategies that are comparable to those used in hierarchical social structures seen in nonhuman primates. Conversely, cultures in which norms are looser and less based in explicit assertion and maintenance of social status, can be likened to the social structures of more egalitarian primates, such as the bonobo communities and muriqui troops.

Eye Contact in Nonhuman Primates

The idea that eye contact conveys primarily an agonistic message in nonhuman primates has been supported by many experimental studies in rhesus macaques using photographs of direct gazing monkeys or human faces with, wide-open eyed, intentional looking as threatening stimuli (20, 32, 33). However, the conclusions from this research generalize to other primates, including many prosimians, most monkeys, and the great apes, all of which use a directed stare as a threatening signal (10, 34, 35). Especially among the species that live in groups with clearer dominance hierarchies, the use of direct gaze is a means to convey higher social status and to exert control over the behavior and proximity of subordinates. In contrast, eye contact is used infrequently and typically not prolonged in joint action for many of these species (10, 15, 16, 19, 36). As an example, rhesus macaques typically make eye contact in order to impose their social standing or to challenge a conspecific, most often leading to avoidance and spatial displacement by the subordinate (6, 15, 18, 35). Even when engaging in prosocial behaviors such as reconciliation and consolation, rhesus macaques often avoid eye contact (17, 18). Similar findings have been obtained in the mostly solitary and territorial mouse lemurs, with prolonged eye contact initiating aggressive encounters, but avoided during affiliative behaviors or when first encountering an unfamiliar conspecific (34).

In contrast, the more gregarious bonobos rarely engage in affiliative behaviors without first establishing eye contact (16, 35, 37). In bonobos, marmosets that live in small family

groups, and other species of macaques, such as the stumptailed and tonkean macaques, eye contact is made more regularly in order to initiate non-agonistic social interactions, establish and maintain affiliative bonds, to initiate play, and serves to aid in cohesion when animals are searching for food and resources, even while a more prolonged direct stare is maintained in the behavioral repertoire as a threat signal (16, 17, 38, 39, 40).

Among nonhuman primates, the distinction between the use of eye contact as a threat or an affiliative signal appears to follow a logical pattern that is congruent with both their phylogenetic relationships and the nomenclature used to categorize different social group structures (10). Thus, rather than just focusing on gaze behavior in one type of primate and ascribing it to inherent dispositions of functions within that particular species (18), we sought a larger, overarching and parsimonious framework that could better inform research on this communicative behavior among humans.

Results

As hypothesized, there was a strong positive correlation between the rating of eye contact tolerance and the typical group social structure exhibited by the 19 species sampled, $r = .771$, $t(17) = 4.99$, $p < .001$ (Fig. 1). To further assess the relationship between eye contact tolerance and social structure, we estimated a linear mixed effect model in which eye contact tolerance was regressed on social structure (cluster means) as well as social structure (centered within clusters). A by-species random intercept and a by-species random slope for social structure (centered within clusters) was included in the model. As predicted, there was a significant relationship between social structure (cluster means) and eye contact tolerance, $b = .538$, $F(1, 13.8) = 14.6$, $p = .002$, such that eye contact is tolerated to a greater degree among primates whose sociality is more egalitarian as compared to hierarchical.

To ensure that this effect was not driven by differences in the environment in which primates were observed a linear mixed effects model was estimated in which eye contact tolerance was regressed on social structure (cluster means), social structure (centered within clusters), observation context (captive versus field), and the interaction between social structure (cluster means) and observation context. A by-species random intercept and a by-species random slope for both social structure (centered within clusters) and observation context were included in the model. Notably, there was no main effect of observation on eye contact tolerance, $p = .802$, and the effect of social structure (cluster means) on eye contact was not moderated by the context in which the species was observed, $p = .812$.

The potential relationship between social structure and the use of staring as a threat or dominance signal was also tested in two separate linear mixed effect models in which threat and dominance were regressed on social structure (cluster means) and social structure (centered within clusters). A by-species random intercept and a by-species random slope for social structure (centered within clusters) was included. Importantly, there was a significant relationship between social structure (cluster means) and the use of staring as a threat signal, $b = -.663$, $F(1, 14.8) = 15.4$, $p = .001$ (Fig. 2.), as well as the use of staring behavior as a dominance signal, $b = -.503$, $F(1, 15.3) = 7.99$, $p = .012$ (Fig. 3.). The frequency with which staring is used as a signal of threat or dominance is far lower among primates whose sociality is more egalitarian as compared to hierarchical.

Additionally, due to the novelty of the crowd-sourcing method used, the reliability of the surveyed expert ratings poses a potential limitation and concern for the validity and reliability of

the above findings. To bolster confidence in the reliability of the expert ratings and of the above findings, the inter-rater reliability of the expert responses was estimated with multiple intraclass correlations (ICC) for each species rated by more than one expert. ICC estimates and their 95% confidence intervals were calculated using the “icc” package in RStudio based on a mean-rating, absolute-agreement, 1-way random-effects model (Table 1.). An average ICC of .755, $t = 8.22$, $p < .001$, LoCI = .627, UpCI = .868, was calculating from the coefficients to provide an estimate of the average reliability of the expert responses. We also calculated an average ICC of .913, $t = 11$, $p < .001$, LoCI = .816, UpCI = .959, from only the species with significant ICCs. The t values and 95% confidence intervals for these coefficients were calculated through a Fisher Transformation. Based on these ICCs, we have evidence to support the claim that there was moderate to good (40) within-species reliability in the expert ratings of eye contact tolerance and social structure.

Discussion

The present findings document, for the first time, a positive linear relationship between the tolerance of eye contact and the extent to which the social relationships of primates are more egalitarian across a representative sampling of nonhuman primate species. A novel crowd-sourcing method of data collection was employed, which proved to be reliable and highly efficient in that each data point encompasses many years of observations for each species. In total, the survey method provided information about the social and communicative behavior of 19 different primate species.

Despite its novel methodology and clear findings, the study is not without limitations. First, while the data were acquired from a large number of experts ($n = 55$), the number of reports for each species were not evenly distributed (see Tables 2-3 for the exact number of reports per species). For six of the 19 species the ratings were obtained from only one expert, lessening the reliability of these singular responses. However, it should be reiterated that the conclusions drawn from our findings are based on cross-species comparisons, not individual scores. In addition, the intraclass correlations listed above revealed largely positive correlations indicative of the reliability of the survey methodology and expert ratings.

A second consideration is that while responses were solicited from professional scientists for individual primate species, this does not ensure that their expertise was focused on eye contact or social structure. Thus, some of the ratings could reflect commonly held notions, even stereotypes, about their species. However, for those species that had been rated by two or more scientists, there was reassuring concordance in responses. Future studies could use more precise terminology or provide an exemplar, such as the commonly studied rhesus macaque as a reference point. Such efforts would help to reduce the potential for bias in expert reports. Still, the good average inter-rater reliability shown in Table 3 should be highlighted, as well as the fact that our conclusions are congruent with more detailed studies on individual species in the published literature.

Finally, although our analysis focused on eye contact behavior in general, visual signaling among primates is most certainly influenced by context. An individual may be more tolerant of eye contact in one situation with a familiar and related conspecific but have little to no tolerance of looking behavior by an unfamiliar animal. This nuance was not captured by our survey. We recognize that the survey did not address the flexible use of eye contact, or even purposeful deviation from the norms in some circumstances. However, the present aim was to identify general principles that can lead others to interrogate these questions more specifically in

controlled studies, and to provide a larger comparative framework for understanding analogous behavior in humans.

The present findings provide the basis for hypothesis-generation about the reasons for variation in eye contact use among humans, including the negotiation and maintenance of social status in more hierarchical social systems. Primates, such as the muriqui and bonobo, who live in relatively fluid, egalitarian social groups are instead faced with how best to engender social cohesion and cooperation. (16, 41). Similar variation in the social norms and expectancies occur across human cultures. One solution to these social challenges would be to allow internal states and intentions to be known through eye contact and other non-verbal gestures, behavior that is used universally by all humans because of our common ancestry, but in culture specific ways (42). The current survey has advanced our understanding of the link between communicative behavior and sociality in nonhuman primates and provided foundational information on the ancestral antecedents of eye contact behavior among humans that can be used to examine its use in different cultures and societies.

Method

Fifty-five experts in primatology were recruited through the International Primatological Society (IPS), as well as email solicitation, on the basis of their reputation as experts for particular species, with the goal to represent all of the major taxa in the Primate Order. The survey included scientists who studied animals under natural conditions as well as in captive settings. They were queried with a standardized set of questions that asked about both typical eye contact behavior and the sociality of the species. Respondents were required to be researchers in the field of primatology and affiliated with an academic institution or accredited zoo. Responses from individuals that did not meet these requirements, or whose identity could not be verified, were not included in our analyses. Primate social structure was scored on a scale from 0 to 100, where 0 indicated a completely hierarchical social system and 100 indicated a completely fluid, egalitarian social system, such as the fission/fusion sociality of the spider monkey or muriqui. The central outcome variable, eye contact tolerance, was polled on two different scales, from 0 (no tolerance) to 100 (high tolerance). The first inquired about eye contact tolerance when approaching a conspecific, and the other inquired about eye contact tolerance when being approached by a familiar conspecific. We observed a strong positive correlation between the two ratings of eye contact tolerance, $r = .909$, $t(51) = 15.6$, $p < .001$. Based on the high similarity in the ratings, we averaged the two sets of scores into a composite variable labelled Eye Contact Tolerance. This composite variable served as the main outcome variable in our analyses. The degree to which staring is used a threatening signal and a signal of dominance was polled through two separate questions on a scale from 0 (never) to 100 (exclusively). Respondents also indicated whether their judgments were based on laboratory or field observations. In total, reports were received on the behavior of 19 different species.

The present study's methodology and experimental procedure were reviewed and approved by the University of Wisconsin Madison institutional review board (IRB), ID 2018-0736. This approval extends to the recruitment, email solicitation, and use of the surveyed information, all of which was performed in accordance with the guidelines and regulations set by the UW-Madison IRB. Participants were informed about the general goals of the study and provided their informed consent for use of the acquired data. The present study was given IRB exemption from the requirements to acquire signed consent and to provide debriefing on the full extent of the study goals.

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Christopher L. Coe: Supporting Conceptualization, Equal Investigation, Equal Supervision, Validation, Supporting Writing – Review and Editing

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Competing interests:

The Authors declare no competing interests.

Data and materials availability:

All data and code used in the analyses and figure creation has been made publicly available on the Open Science Framework (OSF) website. Data can be accessed with the following DOI: DOI 10.17605/OSF.IO/YBHAQ. Accessing this page will grant access to both the collapsed data set (scores averaged across species) and the full data set (containing individual scores). Both data sets were used in the analysis. Figure one was created with the collapsed data for viewing clarity. Statistical tests (as detailed in the results section) were completed using the full data set. Please contact us at eharrod@wisc.edu with any questions regarding the data or analysis code.

Figures and Tables

Table 1.

Species	<i>n</i>	Intraclass Correlations per Species			
		<i>ICC</i>	<i>p</i> =	<i>LoCI</i>	<i>UpCI</i>
<i>Howler</i>	2	.905	.023*	.047	.994 ⁵
<i>Capuchin</i>	6	.785	.056*	-.49	1
<i>Marmoset</i>	4	.594	.112	-.815	.972
<i>Vervet</i>	2	.863	.042*	-.363	.991
<i>Lemur</i>	2	.582	.632	-14.78	.895
<i>Gorilla</i>	2	.992	<.001***	.919	.999
<i>Gibbon</i>	3	.531	.200	-2.407	.988 ¹⁰
<i>Rhesus Macaque</i>	10	.937	<.001***	.78	.996
<i>Chimpanzee</i>	8	.688	.090	-.96	1
<i>Bonobo</i>	3	.93	.001**	.62	.995
<i>Orangutan</i>	3	.517	.183	-1.62	.967
<i>Tamarin</i>	2	.982	.001**	.818	.999
<i>Average ICC</i>	47	.775	<.001***	.627	.868 ¹⁵
<i>Average ICC of Sig. ICCs</i>	27	.913	<.001***	.816	.959

Table 1. Descriptive statistics for the intraclass correlations for each species rated by more than one expert. Confidence intervals for the average intraclass correlation coefficients were calculated through a Fisher Transformation.

Table. 2.

Species	<i>n</i>	Social Structure Rating		Eye Contact Tolerance	
		<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
<i>Howler</i>	2	20	14.14	80	0
<i>Muriqui</i>	1	100	NA	90	NA
<i>Titi</i>	1	100	NA	100	NA
<i>Capuchin</i>	6	33.33	22.29	61.25	22.52
<i>Marmoset</i>	4	69.25	40.57	77	13.26
<i>Diana</i>	1	87	NA	96	NA
<i>Vervet</i>	2	21	1.41	68.5	2.12
<i>Colobus</i>	2	40	14.14	40.25	14.5
<i>Lemur</i>	2	56	36.77	82.5	24.75
<i>Gorilla</i>	2	5	7.07	18	1.41
<i>Gibbon</i>	3	58.33	28.43	44.75	3.89
<i>Woolly</i>	1	90	NA	100	NA
<i>Rhesus Macaque</i>	10	16.8	14.79	49.95	30.31
<i>Chimpanzee</i>	8	28.88	36.71	59.19	29.71
<i>Bonobo</i>	3	60	17.32	83.83	13.29
<i>Orangutan</i>	3	57.67	6.81	71.83	20.25
<i>Tamarin</i>	2	86	5.66	82.75	10.25
<i>Siamang</i>	1	68	NA	71	NA
<i>Squirrel</i>	1	85	NA	90	NA

Table 2. Rating of the hierarchical nature of social interactions and the tolerance of eye contact for each primate species. Social structure is scored on a 0 (completely hierarchical) to 100 (completely egalitarian) point scale. Eye contact tolerance is scored on a 0 (no tolerance) to 100 (high tolerance) point scale

Table. 3.

Species	<i>n</i>	Use of Staring to Signal Threat		Use of Staring to Signal Dominance	
		<i>M</i>	<i>SD</i>	<i>M</i>	<i>SD</i>
<i>Howler</i>	2	25	21.21	15	7.07
<i>Muriqui</i>	1	10	NA	10	NA ⁵
<i>Titi</i>	1	10	NA	0	NA
<i>Capuchin</i>	6	38.6	39.11	38.39	39.62
<i>Marmoset</i>	4	38.5	38.73	49.5	43.87
<i>Diana</i>	1	60	NA	30	NA
<i>Vervet</i>	2	80	7.07	41	26.89
<i>Colobus</i>	2	50	28.28	45	7.07
<i>Lemur</i>	2	50	14.14	50.5	28.99
<i>Gorilla</i>	2	60.5	.71	59.5	.71
<i>Gibbon</i>	3	23.33	14.64	29	21.63
<i>Woolly</i>	1	0	NA	0	NA ¹⁵
<i>Rhesus Macaque</i>	10	75.8	16.82	75	16.59
<i>Chimpanzee</i>	8	54	35.69	51.14	30.89
<i>Bonobo</i>	3	17.5	3.54	25.33	18.58
<i>Orangutan</i>	3	28	23.52	42.67	32.62
<i>Tamarin</i>	2	8	2.83	11	11.39
<i>Siamang</i>	1	7	NA	41	NA
<i>Squirrel</i>	1	20	NA	20	NA

Table 3. Rating of the use staring as a signal of threat and dominance for each primate species. Use of staring is scored on a 0 (never used) to 100 (exclusively used) point scale.

Figures

Figure 1. Significant positive correlation between expert ratings of species-typical tolerance for eye contact and the more stratified or affiliative attributes of their social relationships (hierarchical versus more egalitarian). On the x-axis, a 0 (completely hierarchical) to 100 (completely egalitarian) scale of primate social structure. On the y-axis, a 0 (no tolerance) to 100 (high tolerance) scale of primate eye contact tolerance. Collapsed data are shown for 19 nonhuman primate species.

Figure 2. Significant positive correlation between expert ratings of species-typical use of staring as a threat signal and the more stratified or affiliative attributes of their social relationships (hierarchical versus more egalitarian). On the x-axis, a 0 (completely hierarchical) to 100 (completely egalitarian) scale of primate social structure. On the y-axis, a 0 (no use) to 100 (exclusive use) scale of primate use of staring as a threat signal. Collapsed data are shown for 19 nonhuman primate species.

Figure 3. Significant positive correlation between expert ratings of species-typical use of staring as a threat signal and the more stratified or affiliative attributes of their social relationships (hierarchical versus more egalitarian). On the x-axis, a 0 (completely hierarchical) to 100 (completely egalitarian) scale of primate social structure. On the y-axis, a 0 (no use) to 100 (exclusive use) scale of primate use of staring as a dominance signal. Collapsed data are shown for 19 nonhuman primate species.