Complex modulation of visual attention to 3rd person interactions in wild macaques

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Abstract

Social animals rely on socio-cognitive skills to monitor their social environment and make informed decisions. Visual attention to others' interactions in real-life scenes, however, remains understudied although dedicated neuronal networks have been identified for the processing of real-life social information and for social interactions in particular. Here we ask how subject characteristics, interaction valence, and social relationships between subject and stimuli interact to guide overt attention of 57 wild Assamese macaques to 962 3rd person social scenes that spontaneously unfolded in their vicinity. Social interactions drew more and longer attention than control scenes lacking the interaction, highlighting the relevance of interaction. The effects of both affiliative relationship strength and dominance rank difference between subject and stimulus on the probability to attend

were independently modulated by valence of the scene. Beyond reacting to the affordances of the social scene and independent of their social status, males differed in how long they attended to the interactions of others. Thus, visual attention is guided by the value an individual associates with different aspects of the social scene based on previous experience in both the agonistic and the affiliative realm and by current threat indicative of complex information integration in the brain.

Keywords: social cognition, information integration, valence, social status, social bonds

INTRODUCTION

Social neuroscience research employs a variety of social stimuli that vary in their naturalism[1]. On one end of the spectrum the subject is chair-seated and presented with static images of social agents and non-social controls, while their eye gaze and neuronal activity is tracked[2–4]. From there, naturalism is increased by using videos that are more salient, but also noisier, stimuli[5,6]. Virtual reality scenes can even more closely mimic real-life interactions, as avatars can display contingent behavior creating a live-stream of interactions[7,8]. However, real-life agents are the most naturalistic, yet also the most challenging to control[9,10] particularly in natural environments[1]. This study leverages the strengths of naturalistic animal observations, where large numbers of subjects can be studied allowing us to weigh individual differences in social attention against the affordances of the stimulus situation including subject's affiliative and dominance relations with the stimuli.

Social attention, i.e. monitoring conspecifics to extract information, is a crucial building block of advanced social cognition[11], involving specialized brain networks[12,13]. Social primates are willing to forgo an immediate food reward for the privilege to watch conspecifics in videos[14]. Yet, not all social information is equally relevant. For example, rhesus monkeys (*Macaca mulatta*) pay with forgone juice rewards for viewing a picture of the face of a dominant male, but have to be paid to look at a subordinate[15]. Visual attention for faces provides information about others' overt spatial attention, i.e. about gaze direction[16], and social signals encoded in ritualized facial expressions[2]. In fact, macaques pay more attention to facial expressions associated with threat than to those associated with benign intent and even less to neutral faces [17,18] and more readily follow the gaze of others, if they show an emotional as opposed to a neutral expression [19]. Single neurons in the amygdala show selective activity for threat, friendly and neutral facial expressions[2].

Thus, social attention targets faces, gazes, and facial expressions as well as relevancies unrelated to perceptual aspects of the stimulus, e.g. stimulus dominance status, all of which can be tested with static information. Testing with video recorded dynamic stimuli shows that sustained attention depends on additional ethogram elements contained in the video sequence[20]; rhesus macaques looked longer at areas of a frame with a grooming solicitation, aggression or submission[20]. During fMRI, macaques engage a prefrontal cortical area specifically when watching videos of two others interacting compared to two others acting each on their own or simply resting; there is a brain for interaction[6].

Presenting videos of longer natural scenes with multiple real-life agents hugely advances our understanding of selective social attention in complex environments and the associated neurophysiology[1,13]. However, dual eye-tracking and electro-physiology demonstrated that direct interaction with real-life agents draws even more attention and involves different networks across prefrontal cortical and amygdala areas than watching stills or even videos of the very same agents[10,21]. Neurons in the anterior cingulate cortex predict the behavior of others during social interaction in an iterated prisoner's dilemma task and disruption selectively hampers mutually beneficial interactions in rhesus macaques[9]. A network in the dorsomedial prefrontal cortex codes for social partner identity and tracks these partners' behavior as well as the distribution of food rewards in a real-life social task[22]. Thus, studies employing real-life interactions promise to shed new light on the processes involved in social information processing particularly if agents are freely moving[23].

Social attention is dictated by the affordances of the stimulus situation, but can also vary considerable between individuals. Social status within a group can be a strong predictor of how much attention an individual pays their group mates[24–26]. In a population with clearly defined and repeatable inter-individual differences in sociability, low-sociable rhesus macaques paid more attention to any social information in videos than high-sociable monkeys independent of social status[27]. Early life adversity, such as experimental maternal immune activation during gestation, can also affect social attention in juvenile offspring possibly via epigenetic effects[28]. Both, the genotype upstream of the serotonin transporter gene[29,30] and administered serotonin precursor[31] affect social attention suggesting the involvement of a serotonergic pathway in generating the observed inter-individual differences[32]. Additionally, an oxytocinergic pathway has been implicated in linking individual differences in affiliation and dominance with visual attention[33].

This study focusses on how individuals selectively attend to 3rd person situations, i.e. interactions among others[13], as they spontaneously unfold (or not) in the vicinity, excluding interactions involving themselves. We propose that the relevance of agonistic and affiliative 3rd person

interactions differs considerably, and that relational aspects add an additional layer of relevance[34] . For example, when conflicts arise, they can quickly escalate and involve the subject directly, either through redirected aggression[35] or by soliciting their help[36]. As a result, social attention for aggressive interactions may serve a risk avoidance function, and is likely modulated by the dominance relationship between the subject and the interacting parties. In contrast, the relevance of affiliation between others is often less immediate and typically indirect. Rates of grooming and agonistic support are often correlated[36] which means that the state of the grooming network provides indirect information about the alliance network in the group[37]. Information about grooming will affect the subject indirectly when it needs to decide whom to support or which affiliative relationships to invest in. Sometimes, primates also directly and immediately interfere in the grooming interactions of others to gain access to desirable partners or to manipulate others' relationships[38,39].

In a population of wild Assamese macaques in Thailand, we used behavioral event recording to quantify the overt attention of 57 adult males to 962 agonistic and affiliative 3rd person interaction unfolding in subject's proximity (≤5m) or controls where two other adult males came into close proximity of ≤1.5m without interacting by means of vocalization, facial expression, touch or pose gesture. With statistical models we show that valence of the social scene (agonism, affiliation, control) interacted with rank difference and affiliation strength between the subject and the stimulus monkeys to predict the occurrence of overt attention to the scene suggesting non-additive integration of different relevancies during processing of 3rd person real-life interactions. We further identify individual differences in social attention for agonistic interactions that are independent of subject social status.

METHODS

Study site and subjects

This study was conducted at the Phu Khieo Wildlife Sanctuary in North-Eastern Thailand (PKWS, 16° 05'-35' N, 101° 20'-55' E, 1573km^2) as part of a long-term research project on a wild population of Assamese macaques ongoing since 2005[40]. PKWS is part of the well-preserved Western Isaan Forest Complex covering an area of more than 6,500km^2 [41], which houses a diverse community of large mammals and predators, an indicator of low disturbance levels[41]. We collected data on 57 adult Assamese macaque males belonging to five different neighboring multimale-multi-female groups with 39 to 75 individuals each and a minimum of eight adult males and ten adult females.

Social attention data collection

Social attention data were collected from June 2022 until April 2023 through event sampling of behavior towards social scenes spontaneously unfolding in the group. A social scene was considered valid for recording each time a stationary adult male subject in the vicinity had an unobstructed view and the human observer clearly saw the onset of the social scene. We recorded head gaze (but also eye gaze if possible) towards three different social scene *conditions* that all started with two adult males (the stimulus individuals) arriving within 1.5 m of proximity of one another and continued either (1) as non-interacting *controls* if the males remained in close proximity without explicitly interacting via touch, vocalization or facial expression or (2) as *affiliation* if the two males only exchanged friendly behaviors, and (3) as *agonism* if the interaction included aggressive or submissive behaviors. Given the specificity of parameters and viewing conditions necessary to accurately record each attention event, these data were collected opportunistically outside the focal animal follows. Upon the unambiguous onset of a social attention event, we recorded the following variables: identities of the subject and two interacting stimulus individuals, behaviors displayed during the stimulus interactions, start and end times of stimulus interactions, timing and duration of each look. We additionally scored the interaction for conspicuousness (0/1) as a means to control statistically for loud or tumultuous interactions drawing attention[34]. We collected data from 962 social attention events, i.e. 17±9 events for each of the 57 subjects.

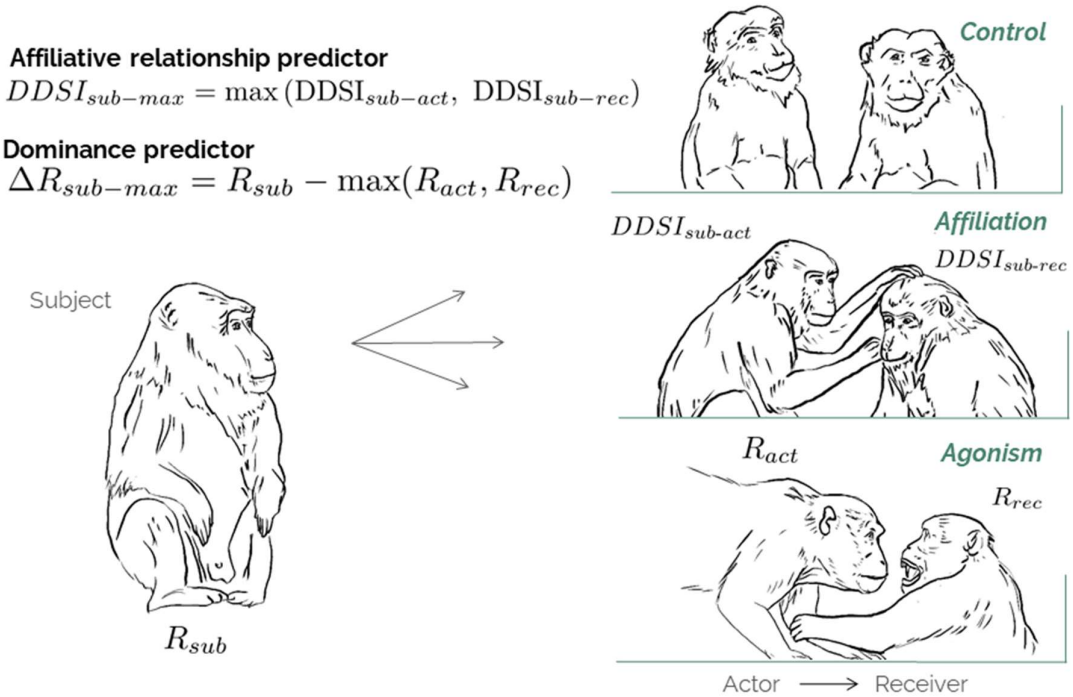

Figure 1: This field study integrates data on visual attention to social scenes spontaneously unfolding in the vicinity of a subject with information about the affiliative and dominance relationships among all males in five study groups. Social scenes with two adult males in close proximity were classified as non-interacting controls or interactions reflecting affiliation or agonism. The relationship of the subject to the males in the scene was quantified as the dominance difference to the higher-ranking of the other males (Rank difference sub-max) and the maximum affiliative relationship strength to either of the two ($DDSI_{sub\text{-}max}$).

Collection of social relationship data

Concomitant with the social attention data collection, all adult males were systematically observed as focal animals in 40 min protocols[42] from June 2022 through April 2023. We recorded continuously [43] all affiliative and agonistic (both aggressive and submissive) interactions including the identities of the actor and receiver as well as all approaches into and departures from a 1.5 m sphere around the focal animal. To inform our dominance and affiliation metrics (see below) about the state of relationships at the onset of the study in June 2022, we included data from January-May 2022. A total of 1,915.9h of continuous focal animal data were collected (mean ± standard deviation per male 33.6h ± 12.1).

Dynamic dominance score – Elo-rating

For the assessment of dominance, we scored submissive behaviors (i.e. bare teeth, make room, give ground) in decided dyadic conflicts (either unprovoked submission or submission following aggression) registered during our continuous focal animal observations and ad libitum recordings from January 2022 through April 2023. To avoid long burn-in periods when males immigrate or mature, we employed Bayesian Elo-rating[44] that estimates start values from the data and captures the state and dynamics of male dominance relationships, which can fluctuate remarkably in Assamese macaques[45]. We used the elo_seq_bayes and extract_elo_b functions of the EloRating.Bayes package[46] in R version 4.3.0[47]. A short burn-in period of one month was applied for each male immigrating into a study group or maturing into an adult male based on his morphological characteristics (fully developed testes and canines, full body length). For our statistical analysis, we extracted Elo-scores for the day that attention to a social scene was observed, modeled Elo-scores standardized per group[48] and include group ID as a random effect.

Dynamic affiliative relationship score - DDSI

As a measure of the strength of dyadic affiliative relationships, we calculated Dynamic Dyadic Sociality Indices (DDSI) and followed De Moor et al.[49] and Stranks et al.[45] in their application of this method originally developed by Kulik and Mundry[50]. We focused strictly on adult male dyads, including only interactions between adult males in our computations. We based our DDSI scores on the time each dyad spent in body contact and allo-grooming, with each of these behaviors being weighed by the inverse of their frequency. Scores for all dyads started at the standard value of 0.5 (DDSI scores range from 0 to 1), indicative of a neutral relationship. Since affiliative interactions were rare, DDSI values were not well differentiated during the first half of the study. Thus, in all models, the dyadic affiliative relationships strength was the DDSI value for that dyad at the end of the study period when calculations included a maximum of information.

Statistical analysis

Looking probability model

We first tested the probability of a subject to look versus to not look at a scene as the response variable. Looks were only considered when occurring in the first 5 seconds after the start of social scene or else we scored a zero. To estimate how the probability of looking at a particular social scene varies across different conditions, and combinations of dominance relationships and affiliative relationship, we fitted a Generalized Linear Mixed Model (GLMM)[51] with binomial error structure and logit link function[52]. We included a three-way interaction term between condition (agonism, affiliation, and non-interacting control), rank difference between the subject and the higher ranking of the two stimulus individuals ($\Delta R_{sub\text{-}max}$ = Elo subject minus Elo higher ranking stimulus), and maximum DDSI value between the observer and each one of the interacting partners ($DDSI_{sub\text{-}max}$). After we found that the three-way interaction term was not significant (see supplementary materials) we excluded it and ran a reduced model including the two-way interactions between the terms of the previous three-way interactions (see Table S2). In a last step, we excluded the non-significant interaction term rank difference x DDSI and report below the final model including only two of the three 2-way interaction terms. In all models, we included rank of the bystander (R_{sub}) as well as conspicuity of the interaction as further fixed effects.

To control for their effects and avoid pseudo-replication, we included random intercept effects for study group, identity of the subject, identity of the actor, and identity of the receiver in the social scene. To avoid an overconfident model and secure a type I error rate at the nominal level of 0.05 we included all theoretically identifiable random slopes[53], namely those of the three-way interaction term and all fixed effects within each random intercept. Though we initially aimed at

including also all correlations among random intercepts and slopes[54] , we were forced to exclude them to allow for successful model convergence.

Prior to fitting the model, we first re-leveled the different levels of our categorical predictor for condition, defining controls (non-interacting) as the reference level for more intuitive result interpretation. We then inspected the distributions of rank difference ($\Delta R_{sub\text{-}max}$), maximum DDSI ($DDSI_{sub\text{-}max}$), and rank of the subject (R_{sub}), which overall appeared roughly symmetrical and free of outliers. We z-transformed these predictors to a mean of zero and standard deviation of one to ease model convergence. We manually dummy coded and centered the control predictor (conspicuity of interaction) before including it as a random slope. The null model comprised only conspicuousness and the random effects.

The sample analyzed with the looking probability model comprised a total of 962 social attention situations, of which 337 were non-interacting controls, 354 affiliative interactions, and 271 agonistic events. These observations were linked to a total of 57 subjects and 57 stimulus individuals. Looks occurred in a total of 364 situations, out of the total 962.

Looking duration model

In order to quantify variation in the duration of sustained attention, we ran a looking duration model using a subset of our full dataset corresponding only to situations where looks occurred. Here, we used *looking time* as a response, which had been widely used in previous human and non-human primate studies as an indicator of preferences and discriminative abilities[55], potentially indicating a certain type of motivation to sustain observation.

To estimate the extent to which looking time varied across different conditions, and combinations of dominance and affiliative relationships, we fitted a Generalized Linear Mixed Model (GLMM)[51] with gamma error structure and log link function[56]. This model was strictly identical to our looking probability model in both fixed and random effects structure. Nonetheless, to control for the effect that longer social scenes may have on looking duration, we here included the duration of the stimulus interaction as a further fixed effect. We removed all correlations among random intercepts and slopes[54] in an attempt to achieve successful model convergence. Since we faced convergence issues from the start, we ultimately fitted a Bayesian model using the brms package in R. The model was run using 4 MCMC chains of 4,000 iterations per chain with adapt_delta set at 0.99 and a max_treedepth of 15, including 1,000 “warm up” iterations during which no divergent transitions were reported. This resulted in 12,000 posterior samples per model.

We assessed the distributions of rank difference ($\Delta R_{sub\text{-}max}$), maximum DDSI ($DDSI_{sub\text{-}max}$), and rank of the bystander (R_{sub}), which overall appeared roughly symmetrical and free of outliers. We z-transformed these predictors to a mean of zero and standard deviation of one to ease model convergence. We further inspected the distribution of the response (looking duration) and the added fixed effects of duration of the stimulus situation, both of which had heavily right-skewed distributions. To deal with this, we log transformed interaction duration. Given that we were fitting a model with a log link function, we kept the response as is. We manually dummy coded and centered the control predictor (conspicuity of interaction) before including it as a random slope. We defined weakly informative priors for all model parameters as to not strongly restrict posterior distributions. For all fixed effects we used a Normal (0, 1) prior, Exponential (1) priors for the standard deviations of random effects, and Exponential (1) for the shape parameter.

The sample analyzed with this model comprised a total of 441 social scenes, of which 99 were non-interacting controls, 160 affiliative interactions, and 182 agonistic events. These observations involved 48 different males as bystanders. Looking duration ranged from 1 to 49 seconds.

Statistical model implementation

The looking probability model was fitted in R (version 4.4.3)[47], using the function glmer of the package lme4 (version 1.1-35.1)[57]. We determined confidence limits of model estimates and fitted values by means of a parametric bootstrap (N=1,000 bootstraps; function bootMer of the package lme4). We determined model stability by dropping the levels of the grouping factors one by one, fitting the full model to each of the subsets, and finally comparing the range of estimates with those obtained for the full data set. This revealed moderate to good stability of the estimates (see Table 1 in the results section). We determined the significance of individual fixed effects by means of likelihood ratio tests[58] comparing the full model with models lacking them one at a time (R function drop1).

The looking duration model was fitted in R (version 4.4.3)[47], using the function brm of the package brms (version 2.22.0), which builds on the computational framework Stan [https://mc-stan.org] to fit Bayesian models[59]. The convergence and stability of the models were assessed with R-hat values, which were below 1.01[60] and a visual inspection of the plots of the chains[61]. In addition, all Bulk and Tail Effective Sample Sizes (ESS) for the estimated posteriors were >6000 [59,60].

RESULTS

Results are based on the behavior of 57 male subjects that had the opportunity to visually attend to 962 social scenes involving any combination of two males co-residing in their group. Social scenes included 271 agonistic events, 354 affiliative interactions, and 337 non-interacting control situations where two adult males were in close proximity of each other and did not interact via vocal exchange, facial expression, or tactile behavior.

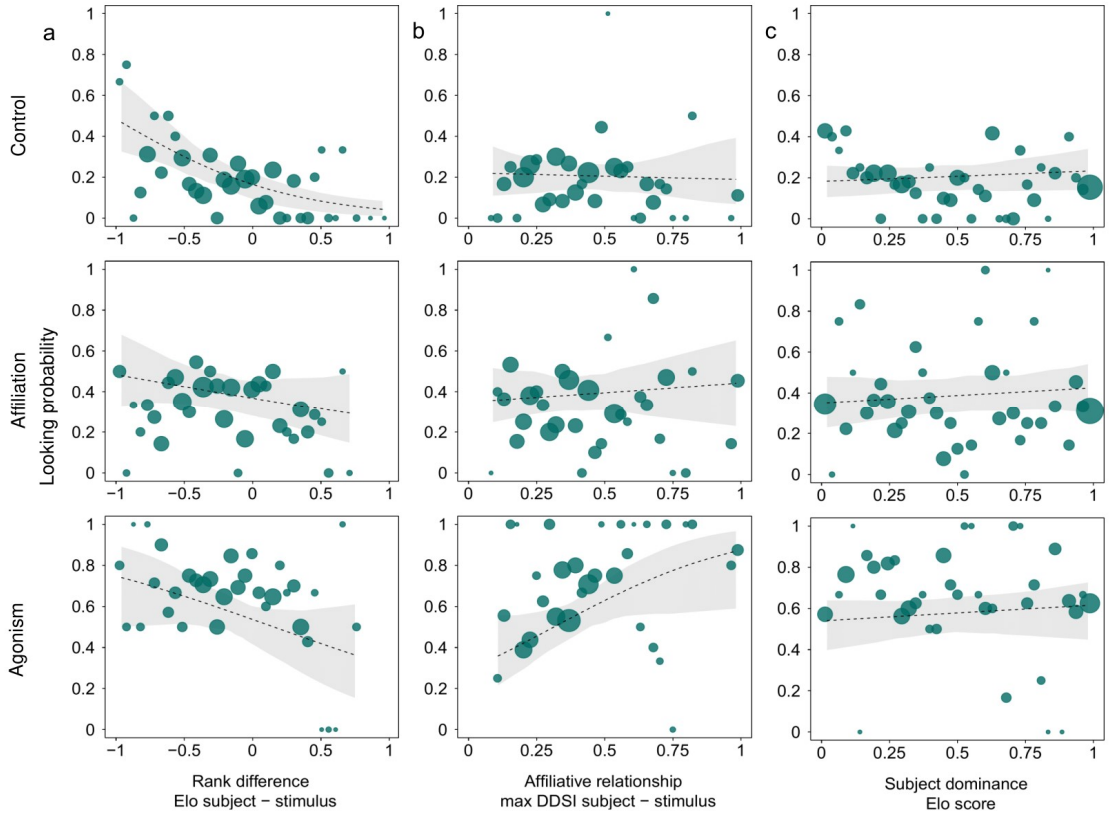

Figure 2: Variation in visual attention to 3rd person social scenes as predicted from the looking probability model. Subjects generally attended more often to interactions than control scenes and to agonistic than affiliative interactions. Both the 2a) negative effect of rank difference (subject minus dominant stimulus) and the 2b) positive effect of affiliative relationship strength (subject to stimuli) were modulated independently by condition and were stronger for agonistic than for affiliative interactions. Subject dominance score 2c) did not affect visual attention. Bubbles are average probabilities per observed value of the predictor with size representing the number of observations, lines are model fitted estimates and shades their confident intervals (Tab. 1). Data came from 57 subjects and 962 social scenes.

Selective attention (looking probability)

In the looking probability model, the three-way interaction term between condition, rank difference, and maximum DDSI was not significant and subsequently was excluded from our first reduced model

(Tab. S1). To arrive at our final model, we further excluded the non-significant two-way interaction maximum DDSI x rank difference (Tab. S2). The final full model differed significantly from the null model including only the control variable conspicuity of the interaction and the random effects of subject ID and group ($Chi^2 = 34.02$, df = 11, P<0.001).

Based on the parameter estimates and conditional on the interaction effects, subjects were more likely to attend to interactions than to non-interactive controls (Tab. 1, Fig. 2). The higher above the subject the higher-ranking of the stimulus individual was, i.e. the more negative the rank difference, the more likely was the subject to pay attention to an agonistic interaction and the lower below the subject the stimulus individuals were, the less likely the event was attended to. This effect of dominance rank difference on overt attention differed between conditions. Specifically, the effect of rank difference was stronger (more negative estimate) for non-interacting controls than for affiliative interaction stimuli, but not stronger than for agonistic scenes.

Furthermore, stimulus valence modulated the effect of DDSI on visual attention. The closer the subject was affiliated to the stimuli (the higher the maximum DDSI), the more likely they paid attention which was an effect exacerbated for agonistic interactions, still pronounced for affiliative 3rd person interactions and weakest for non-interacting control scenes.

Beyond the relational effects of rank difference, the individual dominance rank of the subject did not affect its probability to monitor stimuli across conditions (see Fig. 3). Situations that were more conspicuous were more likely to be looked at.

Table 1. *Model estimates for the reduced looking probability model, including as predictors only the interaction term between condition and rank difference between the subject and the dominant of the stimulus individuals. The full model was significantly different from the null model including only control factors (conspicuousness of the interaction), and random effects ($Chi^2 = 34.02$, df = 11, P<0.001). Significant effects of test predictors are highlighted in bold. Significance of the different levels of condition was assessed by releveling the intercept.*

	Estimate	Std. Error	z value	Pr(>|z|)
Intercept	-1.629	0.185	-8.817	
Affiliation vs. Control	**0.887**	**0.226**	**3.925**	**<0.001**
Agonism vs. Control	**1.658**	**0.264**	**6.267**	**<0.001**
Agonism vs. Affiliation	**0.770**	**0.241**	**3.198**	**0.001**
Rank difference	**-0.614**	**0.191**	**-3.208**	**0.001**
Max DDSI	-0.043	0.221	-0.192	0.847
Subject rank	0.099	0.137	0.726	0.468
Conspicuousness	1.777	0.411	4.321	<0.001
Affiliation vs. Control x Rank difference	**0.426**	**0.208**	**2.048**	**0.041**
Agonism vs. Control x Rank difference	0.243	0.253	0.96	0.337

Agonism vs. Affiliation x Rank difference	-0.175	0.230	-0.764	0.445
Affiliation vs. Control x Max DDSI	0.126	0.216	0.581	0.561
Agonism vs. Control x Max DDSI	**0.64**	**0.279**	**2.293**	**0.022**
Agonism vs. Affiliation x Max DDSI	**0.515**	**0.269**	**1.914**	**0.056**

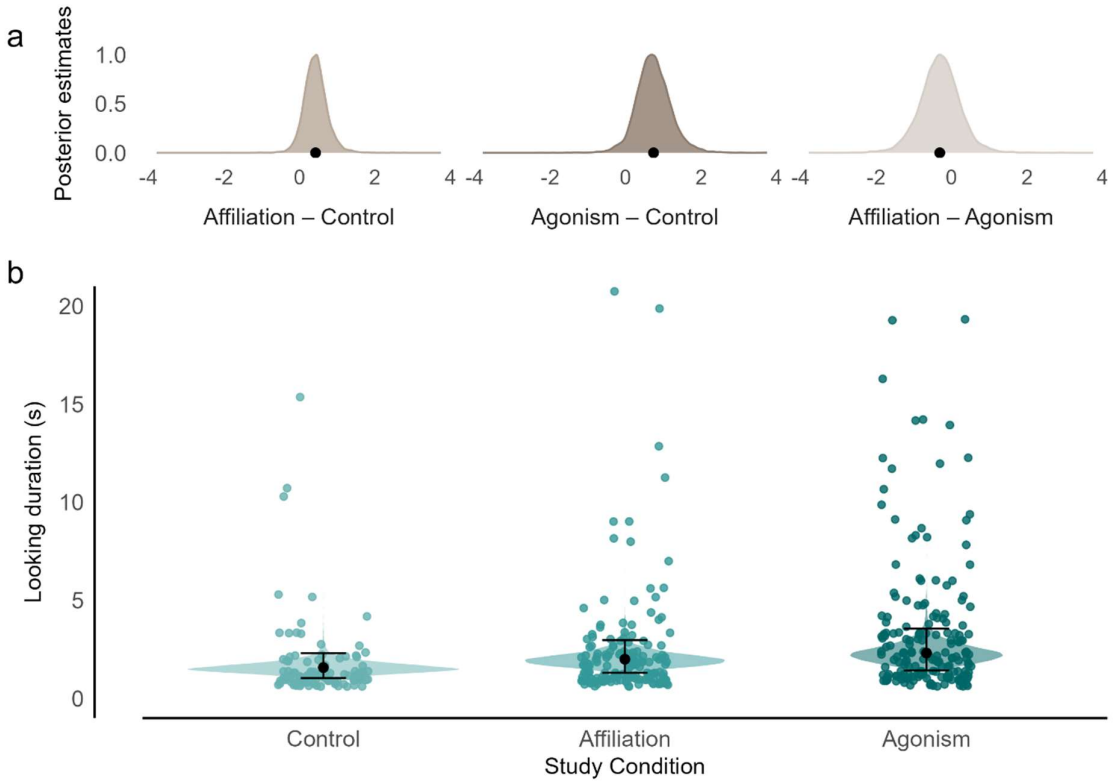

Figure 3: Sustained attention for 3rd person interactions was longer than for non-interaction social control scenes and longer for agonistic than for affiliative interactions (Tab. 2) with distributions of posterior estimates for the looking duration model shown in 3a). Violin plots are drawn for raw data 3b) and whisker plot shows model estimates with 95% credible interval.

Sustained attention (looking duration)

We used a Bayesian model to estimate the effects of the same predictor variables on the time spent looking at the social scene. The full model was a better fit for to the data than the null model (ELPD difference 16.5, SE 9.6). Comparison of expected log pointwise predictive density between the full looking duration and the associated null model with the conspicuousness control variable and the random effects of subject ID and group revealed a loo difference of 9.6 with a standard-deviation of 8.6. In the looking duration model, posterior probabilities for the three-way-interaction between rank difference, affiliative relationship strength and condition were centered around zero (Tab. S3). In a reduced model without the 3-way interaction term, we found no evidence supporting either of the

three 2-way interaction effects (all posterior probabilities centered around zero). The final model (Tab. 2) including only main effects provided clear evidence for sustained attention to vary with condition. Males demonstrated longer attention for agonistic interactions between other males than for scenes with two non-interacting stimulus males (posterior probabilities >0.95 for difference between control and each of agonistic and affiliative scenes). Furthermore, there was moderate evidence for longer looking time towards agonistic compared to affiliative interactions (posterior probability 0.84). Looking time during agonistic situations was on average 1.7s longer compared to non-interacting controls, and 0.9s longer than affiliation. Social relationships to the stimulus males and subject dominance did not affect sustained attention.

Table 2. *Model estimates for the reduced looking duration model including only main effects; posterior means are reported with their standard errors and 95% credible intervals for the fixed effects. Estimates are based on 4,000 posterior draws.*

	Estimate	Est.Error	Q2.5	Q97.5
Intercept	0.171	0.206	-0.234	0.573
Affiliation vs. Control	**0.239**	**0.164**	**-0.086**	**0.565**
Agonism vs. Control	**0.380**	**0.215**	**-0.082**	**0.774**
Agonism vs. Affiliation	0.141	0.244	-0.362	0.592
Rank difference subject – highest	0.014	0.105	-0.198	0.218
Max DDSI subject – stimulus	0.035	0.109	-0.184	0.251
Subject rank	-0.042	0.121	-0.263	0.194
Log interaction time	**0.095**	**0.058**	**-0.016**	**0.210**
Conspicuousness	**0.359**	**0.178**	**-0.020**	**0.684**

Inter-individual differences

Random effects from the both models suggest that individuals do not systematically differ in attention to just any type of social scene. Instead, significant individual differences were specific to and differed between sustained attention to agonistic scenes (mean individual random effect for agonistic scenes ± stddev. = 0.0012 ± 0.1921) and affiliative scenes (0.0013 ± 0. 1743). Random effects were extracted from a model with and are therefore controlled for subject dominance rank.

DISCUSSION

Our study makes a significant contribution to the development of real-life social neuroscience by elucidating the neural mechanisms underlying social information integration. Social interactions are inherently complex, requiring individuals to make predictions not only about their own actions but also about those of others, informed by observations of third-party interactions[13]. Our findings reveal that individuals allocate increased visual attention to third-party interactions, particularly those

involving agonistic versus affiliative behaviors, and that different dimensions of social relationships between the subject and third parties independently modulate this attentional bias. Furthermore, we observed significant individual differences in sustained attention to third-party interactions, underscoring the importance of considering personal factors in understanding social cognition. These results have important implications for our understanding of how the brain integrates social information and how emotion regulation and adaptive benefits influence sustained attention.

3rd person interactions draw more attention that non-interacting social controls

Using as a control a social scene with two individuals in close proximity without an interaction, we clearly demonstrated that both the probability of overt visual attention and the duration of sustained visual attention were increased for 3rd person interactions. The three social conditions were matched for salience by requiring the scene to have a clear starting point where two males arrived in close proximity, i.e. all scenes were initially dynamic. Exceedingly dynamic scenes that involved quick movements and/or vocalizations either in the agonistic or the affiliative context (e.g. ritualized male-infant-male interactions)[62] were scored to be conspicuous which was a control variable in all models. Thus, visual attention was not only guided by stimulus salience alone, but also by the mental representation of its social relevance[6,63,64] and was sustained into a range where MEG studies suggest different information integration events can be detected (1,100 and 2,000 ms)[65]. To our knowledge, the only other study to demonstrate that 3rd person interactions attract more visual attention is a three player experiment with rhesus macaques that identified neurons in the prefrontal cortex to be differentially activated when two others interacted[22].

Attention guided by valence of others' interactions

Visual attention was further guided by interaction valence, adding ecological validity to previous findings on selective attention for and differential processing of threat faces over photos of friendly teeth-chattering[2,66]. Here the naturalism scale seems particularly relevant, because the two facial expressions differ in important ways; teeth chattering is a repetitive and thus an inherently more dynamic and also a more auditory display than a threat face and therefore may be more difficult to identify from a still photograph. Yet even in our real-life scenes in proximity of the subject, monkeys were more likely to attend to agonistic than affiliative interactions of others. .

Agonistic interactions are more relevant, because the subject could be drawn into the conflict by redirected aggression[67] or be solicited to help one of the opponents[68,69]. The fact that watching

396 others fight increases rates of self-directed behaviors indicative of increased emotional arousal[70,71],
397 suggests that subjects do not only gather information about the state of the dominance relations of
398 others, but also about imminent threat to themselves. Others' affiliative interactions may also lead to
399 direct involvement of the subject, if they decide to interfere by joining or stopping the affiliation, but
400 this decision lies with the subject and not with a 3rd party and may therefore not require the same
401 level of attention as 3rd person agonism.

402 Despite the primacy of agonism, subjects still paid more often and more sustained attention
403 to 3rd person friendly interactions than non-interacting controls. Primates look towards the mother
404 (the main affiliate), if they hear an infant in distress from the other direction[72] and look longer at a
405 staged conflict, if it is between close affiliation partners compared to other dyads[73]. Selective attention
406 for 3rd person friendly interactions must underlie such findings, but had not been previously
407 demonstrated.

408

409 **Two dimension of social relationships independently guide visual attention**

410 Variation in imminent threat may also explain how the social relationships between the subject and
411 the stimulus individuals have moderated valence effects on selective attention. Since aggression flows
412 down the hierarchy in macaques[74], imminent threat increases the higher above the subject the
413 dominant stimulus male. This effect appears most pronounced in non-interactive control scenes,
414 because in controls, attention drops to zero for scenes that only have males subordinate to the
415 subject; at the largest rank differences (left of Fig. 2a) control scenes did not attract more attention
416 than agonistic or affiliative scenes. Attention to non-interacting control scenes with individuals out-
417 ranking the subject may serve in uncertainty-reduction[75]. Attention for conflicts was much higher than
418 for controls, even when both males were subordinate to the subject, so that the rank-difference had
419 a slightly weaker effect. Rank difference did not moderate visual attention to affiliative interaction
420 scenes which suggests that it is not the mere presence of a higher ranking individual that adds
421 relevancy, but the action of a dominant.

422 We expected that monitoring close affiliates may also contribute towards risk-avoidance,
423 given that the conflicts of closely bonded partners are the most likely to trigger risky interactions for
424 the observing party[76,77] which requires behavioral coordination between close affiliates[35,78]. Matching
425 these expectations, we found the attention-grabbing effect of affiliative relationships with stimuli to
426 vary with stimulus valence: the affiliative relations effect was most pronounced for conflicts and less
427 so for affiliation and control scenes. This highlights again the increased relevance of potentially risky

428 situations. In other real-life observational studies on captive populations, female rhesus macaques
429 and mandrills of both sexes also paid more attention to their closest partner and their kin,
430 respectively[34,79]. This is in contrast to a recent study on male rhesus macaques[33]; the grooming
431 relationship did not affect visual attention for pictures of a group mate, whereas the aggressive
432 relationship with a stimulus clearly correlated with attention for this male[33]. By moving from the
433 presentation of still photographs to real-life stimuli and from individual stimuli[79] to interactions, we
434 demonstrate that two dimensions of a subject's relationships to others have independent effects on
435 the allocation of visual attention which is more pronounced for agonism than affiliation of others.

436

437 **Individual differences in social attention**

438 The most controlled studies employing brain-imaging or electrophysiology often suffer from small
439 sample sizes prohibiting investigation of individual differences in social attention and underlying
440 processing[1]. Here, we find no evidence for individuals to generally differ in their social attention or for
441 social status. Instead, the 57 male Assamese macaques varied only in how they attended to agonistic
442 interactions and not to affiliation between others. These results match with a well-powered study on
443 rhesus macaques that found year-to-year repeatability in attention to threat over neutral faces but
444 not in attention to friendly teeth-chattering over neutral faces[80]. In contrast, differences between four
445 monkeys in the propensity to give aggression, grooming, and approaches over receiving these
446 behaviors were all associated to some degree with social attention in a distractor task[33]. Neither of
447 the rhesus macaque studies, however, controlled for dominance rank prior to extracting information
448 on individual differences. We can clearly show here that despite dominance changing throughout the
449 study period (Fig. 1), individuals maintain differences in how they attend to conflicts of others,
450 suggesting stable differences in underlying regulation via serotoninergic and oxytocinergic
451 pathways[32,33].

452

453 **Conclusion – information integration for visual attention**

454 Together, these results suggest that different relevancies of social information are integrated in
455 complex ways. Interaction versus non-interacting control, valence of the interaction, and two separate
456 relational aspects do not have simple additive effects on social attention. The social value of attention
457 is evident from increased attention to others' affiliation over non-interacting controls that is
458 unaffected by status differences or social bonds towards the stimuli. All other results can be explained
459 by risk-avoidance alone where information is not gathered for its own sake, but for immediate
460 preparation and activation in the face of danger. Thus, social attention serves at least two goals in

tandem which explains why it involves several brain areas in the dorsomedial prefrontal cortex, dorsal anterior cingulate cortex, the ventral striatum and the amygdala perhaps with pronounced mixed selectivity at the neuronal and network level[9,22,81,82].

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AUTHOR CONTRIBUTIONS

SP Investigation, Data curation, Formal analysis, Visualization, Writing - Original draft
SMa Resources, Project administration, Writing - Review & editing
SMe Resources, Project administration, Writing - Review & editing
JO Conceptualization, Funding acquisition, Data curation, Resources, Supervision, Writing - Review & editing
OS Conceptualization, Funding acquisition, Data curation, Resources, Supervision, Writing - Original draft

CONFLITCS OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY

Replication data are available at GRO.data https://doi.org/10.25625/XFN4B4

ETHICAL STATEMENT

The study was conducted with permission of relevant Thai authorities under a benefit sharing agreement and was purely observational, completely non-invasive and did not involve food provisioning or capture of the animals.

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