Multi-dimensional social relationships shape social attention in monkeys

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Abstract

Social relationships guide individual behavior and ultimately shape the fabric of society. Primates exhibit particularly complex, differentiated, and multidimensional social relationships, which form interwoven social networks, reflecting both individual social tendencies and specific dyadic interactions. How the patterns of behavior that underlie these social relationships emerge from moment-to-moment patterns of social information processing remains unclear. Here, we assess social relationships among a group of four monkeys, focusing on aggression, grooming, and proximity. We show that individual differences in social attention vary with individual differences in patterns of general social tendencies and patterns of individual engagement with specific partners. Oxytocin administration altered social attention and its relationship to both social tendencies and dyadic relationships, particularly grooming and aggression. Our findings link the dynamics of visual information sampling to the dynamics of primate social networks.

Introduction

Social relationships bear profound significance for both the development and well-being of individuals within a community [1] and the cohesion and long-term success of their groups [2, 3]. Primates, including humans, engage in complex social relationships characterized by a wide range of interactions that are both diverse and multifaceted. Proximity serves as a cornerstone of social interaction, with individuals often seeking closeness to one another for communication, bonding, and safety [4, 5]. Grooming is another fundamental behavior for primates, facilitating hygiene maintenance, parasite removal, and the cultivation and maintenance of social bonds [6, 7]. By contrast with these affiliative interactions, aggression supports resource competition and the acquisition and maintenance of dominance rank [8, 9]. The interweaving of individual affiliative and agonistic interactions contributes to the formation of social networks [10, 11]. Social networks within primate groups can be characterized at multiple levels or scales [12-14], including broader patterns of social tendencies (e.g., whether a monkey is aloof or highly interactive), as well as individual engagement with specific individuals in that group (e.g., allies, friends, or enemies) [10, 13]. Together these affiliative and agonistic behaviors, both within specific dyads and in the aggregate, create the multi-level tapestry of social relationships in primate groups.

Primates, including humans, are highly visual animals [15], and actively sample their environments to acquire useful visual information to guide behavioral decisions [16-21]. From birth, both human and nonhuman primates prioritize acquisition of visual social information, orienting preferentially to faces [17, 22], and later during development using the gaze direction of others as a cue to important information in the environment [23, 24]. Primates, including humans, also selectively attend to visual cues associated with social dominance and mate quality [25-27], as well as emotional states [28]. Neural circuits supporting motivation and attention are intrinsically sensitive to visual social cues to dominance [29, 30], potential mate quality [31-35], and social dynamics [36]. These observations endorse the idea that the primate brain is "tuned" to support acquisition of visual information to guide adaptive social behavior.

Recent research highlights associations between social network dynamics and social attention. For example, patterns of grooming relationships predict patterns of mutual gaze in macaques [37]. Similarly, high-status monkeys selectively follow the gaze of other high-status monkeys whereas low-status monkeys follow the gaze of all monkeys [27]. These findings suggest more complex, nuanced, and dynamic relationships between social networks and social attention in primates. A complete understanding of the dynamics of social attention, and its underlying biology, in human or nonhuman primates, however, will require studying the visual orienting behavior of individuals living in groups whose social network dynamics have been quantitatively characterized.

In this study, we evaluated social network dynamics in a group of four laboratory macaques that were raised together for several years, based on their patterns of general social tendencies and specific dyadic relationships in proximity, grooming, and aggression. We then removed individuals from the colony to assess basic visual orienting behavior while distracted by images

of monkey faces of individuals both within and outside the social group, which were displayed on a computer monitor. Here we define "social engagement" as the broader patterns of interaction through which individuals express their social tendencies, observable in their interactions with all other members within the group [38]. By contrast, we define "individual engagement" as the interactions between specific pairs of individuals within the group [12, 39]. We examined correlations between patterns of social attention and patterns of overall social engagement with the group, as well as individual engagement with specific partners. This approach offers a quantitative assessment of how these social network dynamics shape patterns of social attention. Overall, we found that patterns of overall social engagement, based on aggression, grooming and proximity, strongly shaped social attention, especially towards unfamiliar individuals. Further, we found that exogenous administration of the social peptide hormone oxytocin (OT) blunted the impact of social engagement on social attention. By contrast, individual engagement in aggression within specific dyads shaped attention and OT administration increased the influence of aggressive relationships on social attention. Our findings reveal complex and nuanced interactions of multidimensional social relationships with social attention.

Results

An evaluation of multi-dimensional social relationships within a colony group

We assessed the social relationships of four rhesus macaques based on their spontaneous social interactions (Fig. 1a). These four monkeys have resided in the same colony room for a minimum of four years. In their daily interactions, they exhibited a rich array of social behaviors, including proximity, grooming, and aggression. These behaviors serve important functions in communication, bonding, conflict resolution, and social organization within monkey facilities and natural habitats alike. These behaviors were measured automatically from video using a multi-stage detection based on YOLOv5 (Supplementary Fig. 1, see Methods for more details), and then evaluated mathematically (as an example dyad depicted in Fig. 1b,c). We calculated interaction scores for pairs of monkeys using a dichotomous framework of 1 and -1 as in prior research [9]. Individual monkeys gained a social score of 1 for consistently displaying a tendency to approach others more frequently (proximity), receive more grooming from peers, and initiate aggression more frequently (shown by red arrows in Fig. 1d-f).

We quantified each monkey's social engagement index (SEI) and individual engagement index (IEI). These models combine the scores of three dimensions of social relationships with independent weights. SEI summarizes the general social tendencies of each monkey based on their overall interactions with the other three individuals in the group. IEI quantifies the interaction tendencies within specific dyadic relationships. For simplicity, we first set all weights to 1 for both SEI (Fig. 1h) and IEI (Fig. 1i). This can be done by summing all interaction scores, as shown in Fig. 1g with arrows indicating from individual with a higher score to one with a lower score. This approach yielded a quantitative account of social interactions, considering both the overall relationships and specific dyadic partnerships. For example, as depicted in Fig. 1f, Monkey A exhibited stronger social cohesion with Monkey K, as measured by higher frequency of proximity. Nevertheless, when aggregating the proximity scores from all partners (Monkey K, L and C), Monkey A had the weakest overall social cohesion, with a total proximity score of -1. Indeed, it was lower than Monkey K, who had a total score of 1 within the group. Three out of the four monkeys in the group (Monkey C, K and A), as shown in Fig. 1i, had individual engagement indices (colored symbols) that were not in line with their social engagement indices (gray open symbols). Hence, we use both SEI and IEI to understand the complexity of a social network. We next endeavored to probe how social attention varies with these two measures of multi-dimensional social relationships.

Social engagement shapes attention towards monkeys' faces

We first probed whether monkeys with different SEIs respond differently in a classic social interference task (Fig. 2a). In this task, a white square served as the visual target and the monkey had to maintain his gaze on it. A trial commenced with a fixation target appearing in the center of the screen for 800 to 1200 ms. In the social interference task (96% trials), an image (the distractor)

was randomly presented eccentric either on the right or left side for 100 ms. After the first 50 ms, a white gaze target was randomly illuminated either in the same hemifield as the distractor (congruent) or in the opposite hemifield (incongruent). Distractors were randomly selected from pictures of the faces of his three groupmates, pictures of the faces of three monkeys with whom he had no social interactions, or scrambled versions of these same face images. Each distractor had an equal chance of being presented (Fig. 2b).

Example trials from an experimental session illustrate gaze shifts to the same target when different distractors were displayed in two different locations (Fig. 2c,d). We calculated the response time to shift gaze to the target as our outcome measure of interest (see arrows in Fig. 2c,d). We then focused analyses on response times as a function of distractor type and location within single sessions, to account for differences in motivation or attentiveness across days. Response times were faster when monkey faces were illuminated on the same (congruent) side as the target, compared to the scrambled images (Fig. 2e, intact faces: 125.25±48.84 ms; scrambled images: 142.80±47.87 ms; Student's *t*-test, n_1 = 382 trials, n_2 = 372 trials, $p = 7.87\times10^{-7}$). Conversely, response times were slower when the target was incongruent with display of a monkey face versus a scrambled version (Fig. 2f, intact faces: 228.19±30.88 ms; scramble images: 213.97±29.96 ms; Student's *t*-test, n_1 = 373 trials, n_2 = 385 trials, $p = 2.17\times10^{-10}$). Distractor faces significantly impacted the behavioral performance of all four subjects, based on paired Student's *t*-tests across 72 conditions (6 intact faces × 12 experimental days) (Fig. 2g, Congruent: MA: $p = 1.90\times10^{-35}$, MK: $p = 3.81\times10^{-27}$, ML: p = 0.01, MC: $p = 4.37\times10^{-18}$; Incongruent: MA: $p = 8.91\times10^{-34}$, MK: $p = 5.77\times10^{-32}$, ML: $p = 8.66\times10^{-9}$, MC: $p = 3.86\times10^{-5}$).

We next calculated drifting time, which we defined as the difference between response times in the presence of intact faces and their scrambled versions (Fig. 2h). Then we defined distractor bias as the difference between the drifting time in the incongruent and congruent conditions to quantify the impact of monkey face pictures on visual orienting—our measure of social attention (Fig. 2i). Intriguingly, the distractor biases for individual subjects were negatively correlated with their social engagement indices ($SEI_{(1,1,1)}$) with an equal weight of one for all three social relationships (Fig. 2j, two-sided Pearson's correlation coefficient, r = -0.87, $p = 4.51\times10^{-88}$). These findings indicate that individual variation in general social tendencies—from aggressive to prosocial—shapes social attention. Specifically, individuals with higher SEIs—that is those monkeys who were overall more social—showed a reduced tendency to be distracted by social information when performing a simple visual orienting task.

General social tendencies differentially shape attention towards in-group and out-group monkey faces

In the wild, monkeys spontaneously differentiate between monkeys belonging to their own social group (in-group) and those belonging to other groups (out-group) [40, 41]. We next investigated the possibility that monkeys in our laboratory environment would exhibit similar behavior, and how this distinction would influence their social attention. We analyzed distractor bias according to

whether the depicted monkey was in-group or out-group (Fig. 3a). Before the study, subjects were familiarized with all distractor images on a daily basis for eight weeks, to rule out any novelty effects.

We compared response times to targets when either in-group or out-group monkey faces were displayed. On an example experimental day (Fig. 3b), the subject monkey displayed slower response times in the congruent condition (n_{in} = 195 trials, n_{out} = 193 trials, Student's *t*-test, p = 2.10×10^{-3}) and faster response times in the incongruent condition (n_{in} = 188 trials, n_{out} = 186 trials, Student's *t*-test, p = 0.03) when confronted with in-group monkey faces compared to out-group monkey faces. Next, we calculated distractor biases for the four subject monkeys when exposed to in-group and out-group monkey faces on individual experimental days. Distractor biases towards in-group monkey faces were significantly smaller than those towards out-group faces, across monkey subjects, on all experimental days (n = 4 monkey subjects × 12 experimental days, p = 1.45×10^{-7}). We examined data from individual monkey subjects (Fig. 3c, n=12 experimental days, paired Student's *t*-test, MA: p = 2.90×10^{-3}, MK: p = 1.49×10^{-2}, ML: p = 1.01×10^{-3}), with the exception of Monkey C, who gained the largest SEI with the highest social interaction frequency in the group (MC: p = 0.14).

We analyzed the probability of the first saccade being directed towards the distractor in the incongruent condition (Supplementary Fig. 2a,b). Monkeys showed a greater inclination to direct their initial saccades towards intact monkey faces (Supplementary Fig. 2c). Then, we calculated the difference in the probabilities of the first saccade that would be directed towards intact monkey faces and scrambled images. First saccades were more likely to be directed towards out-group than in-group monkeys relative to scrambled versions of the same images, for all monkey subjects on all experimental days (Supplementary Fig. 2d, n = 4 monkey subjects × 12 experimental days). Among them, Monkey A and L exhibited significantly higher first saccade probabilities towards out-group than in-group faces, relative to scrambled versions of the same images (Supplementary Fig. 2e, paired Student's t-test, n_{in} = n_{out} = 12, MA: p = 5.28×10^{-5}, ML: p = 2.41×10^{-3}; MK: p = 0.54, MC: p = 0.44).

Our analyses so far reveal that social interaction experience can blunt subjects' attentional capture by pictures of faces from monkeys within their group. Our experiments are limited by the fact that we only used 6 monkey faces as stimuli for both the in-group and out-group. Thus, the specific face pictures used might bias the observed differences between in-group and out-group faces (Fig. 3b,c). To address this potential confound, we randomly withdrew a single image from an in-group monkey and one from an out-group monkey from the dataset, and reanalyzed distractor biases from the left two pictures of faces (Supplementary Fig. 3a). For each individual subject, this resulted in 3 sets of two distractors from the in-group or out-group monkey faces. Then, we have gotten $81(3^4)$ combinations from 4 monkey subjects, and finally a total of $81(3^4) \times 81(3^4)$ combinations of subjects and distractors from both in-group and out-group. Within each combination, we statistically measured the difference of distractor biases towards the left two

pictures from in-group and out-group (Supplementary Fig. 3b). As depicted in Supplementary Fig. 3c, for 99.30% of the 6561 combinations distractor biases towards in-group monkey faces were significant less than those towards out-group faces (Two-sided Wilcoxon signed-rank test, $p < 0.05$). Thus, differences in social attention towards in-group and out-group monkeys are not likely driven by a specific picture in our stimulus set.

We next examined how general social tendencies of four monkey subjects varied with attentional capture by faces of in-group and out-group monkeys. We found that attention towards images of both in-group and out-group monkeys was highly correlated with the social engagement scores on three dimensions of social relationships: aggression, grooming and proximity (Supplementary Fig. 4a-f). The correlation coefficients varied across them, with aggression demonstrating the highest correlation with r values about -0.8. Grooming exhibited a lower correlation compared to aggression, while proximity was the least correlated of the three.

We computed SEIs using a linear model with an independent weight setting for each dimension (see Methods for details), which summarized these three dimensions within the network of social engagement. We computed the best-fit weights to quantify how social attention varied towards in-group and out-group monkey faces as a function of subjects' social relationships (Fig. 3d-g). The range of each ω was constrained to vary between 0 and 1, with a step size of 0.02. The correlations under different sets of ω_a, ω_g and ω_p were calculated based on social attention towards in-group (Fig. 3d) and out-group faces (Fig. 3e). The best-fit weights were chosen by searching for the values of ω_f, ω_g and ω_p, that maximized the correlations (with smallest negative r values) between distractor biases and SEIs. As depicted in Fig. 3f,g, the "best" weights for aggression, grooming, and proximity (ω_a, ω_g and ω_p) were 0.34, 0.54, and 0.58 respectively, when monkeys viewed distractors drawn from in-group monkeys. The set of "best" weights were 0.48, 0.62, and 0.92 when monkeys viewed distractors drawn from out-group monkeys. These weights of three dimensions for in-group data are smaller than those for out-group data. Comparing the weights for in-group and out-group distractors, the effect of proximity was larger than that of aggression and grooming. Then, the SEI was defined by these "best" weights on three dimensions of social relationships.

We next examined the correlation between distractor biases and the SEIs determined by the corresponding weights. In Fig. 3h, the yellow line indicates the correlation towards in-group with a slope of -26.22, whereas the green line indicates the correlation towards the out-group with a slope of -20.76. The difference of first saccade probability between intact and scrambled face pictures also showed a negative association with the SEIs (Supplementary Fig. 2f, two-sided Pearson's correlation coefficient, in-group: $r = -0.71$, $p = 1.21\times10^{-23}$; out-group: $r = -0.73$, $p = 1.12\times10^{-25}$). Differences in the SEIs between any two monkeys can serve as an indicator of the magnitude of general social tendencies within the group (Fig. 3i). The impact of social engagement was smaller when monkeys viewed distractors from in-group (orange lines) compared to those from out-group monkeys (green lines). The average difference of the SEIs dropped significantly

from 2.67±1.32 to 1.95±0.99 from out-group to in-group (paired Student's t-test, $p = 0.01$). However, there was no relationship between the SEIs and performance in visual motor trials without a monkey face distractor, effectively ruling out any impacts of social tendencies on general oculomotor functions (Supplementary Fig. 5d, two-sided Pearson's correlation coefficient, in-group: $p = 0.08$; out-group: $p = 0.18$). Together, these findings indicate that behavioral tendencies that in aggregate define social networks dynamically shape monkeys' attention to social cues.

Oxytocin blunts the impact of general social tendencies on social attention

Oxytocin (OT) is an endogenous peptide hormone that regulates crucial components of mammalian reproductive systems and influences social behavior more broadly [42-44]. Here we examined how oxytocin shapes the social attention of individuals as a function of general social tendencies. Monkeys were first acclimated to nebulized exposure to saline for around 2 weeks. During the experiment, monkeys were administered oxytocin (40 IU/mL, 2 mL; Beyotime) and saline by nebulization (Omron, infant nebulizer) for 2 minutes on alternating days. After a 15-minute period of relaxation in a dim room, the monkeys participated in the visual orienting task.

We first examined the overall impacts of oxytocin on social attention by averaging distractor biases for all individual monkeys across all experimental days. Figure 4a shows that oxytocin significantly increased distractor bias by enhancing social attention towards out-group monkey faces (green bars, paired Student's *t*-test, $n = 48$, $p = 0.01$). Although there was a minor increase in distractor biases towards in-group distractors, this was not statistically significant across all individuals and experimental days (orange bars, $p = 0.21$). We conducted additional analyses to investigate the impact of oxytocin on oculomotor function. We found no impacts on oculomotor behavior during visuo-motor trials without distractors (Supplementary Fig. 5e, $n = 48$, $p = 0.31$). There were also no significant effects on the probability of first orienting movement towards the distractor between saline and OT averaged across all monkeys (Supplementary Fig. 2g, $n = 48$, paired Student's *t*-test, in-group: orange bars, $p = 0.93$; out-group: green bars, $p = 0.41$).

We next examined the impact of oxytocin on social attention as a function of general social tendencies. To do so, we analyzed the correlation between distractor biases and SEIs after administration of saline or OT (Fig. 4), in a second set of experiments. The "best" weights for distractor bias towards in-group and out-group following OT or saline are shown in Fig. 4b-e. The impacts of OT were larger for in-group distractors compared with out-group distractors, with the weight of grooming showing the biggest effect (Fig. 4f). We uncovered consistent and significant impacts of all "best" weights on three dimensions of social behavior on social attention to both in-group faces (Fig. 4g) and out-group faces (Fig. 4h) (Two-sided Wilcoxon signed-rank test, $n_1 = n_2 = 6$, $p = 0.03$). Following administration of OT, we observed differences in the correlation between distractor bias and SEIs towards both in-group and out-group faces. The differences between saline and OT were greater for in-group faces compared to out-group faces (Fig. 4i,j, two-sided Pearson's correlation coefficient, in-group: saline: $p = 5.54\times10^{-45}$, $r = -0.87$, OT: $p = 1.20\times10^{-47}$, $r = -0.88$; out-group: saline: $p = 1.28\times10^{-40}$, $r = -0.85$, OT: $p = 1.35\times10^{-41}$, $r = -0.85$; the slopes of in-group:

saline: -26.07, OT: -60.47; the slopes of out-group: saline: -19.75, OT: -34.84). Subsequently, we compared the differences in the SEIs between any two subjects following administration of saline (empty circles in Fig. 4k), the magnitude of general social tendencies was reduced following administration of OT (filled circles in Fig. 4k). Thus, OT reduced the impacts of multi-dimensional social tendencies on social attention. Of the three measured dimensions, OT most strongly blunted the relationship between grooming—a prosocial, affiliative behavior—and attentional capture by both in-group and out-group faces.

Social attention varies as a function of individual social relationships

We examined how individual pairwise interactions, rather than general social tendencies towards the entire group, vary with social attention. To do so, we calculated individual engagement indices which evaluated interactions within specific dyads as a function of proximity, grooming, and aggression (Fig. 5a). Individual engagement scores varied with monkeys' social attention (Supplementary Fig. 4g-i), with aggression showing the highest correlation, followed by grooming, and then proximity.

We next estimated the best-fit weights for the correlations between distractor biases and IEIs, as detailed in the Methods and following the same procedure as for SEI analyses. Weights were chosen to maximize the correlations between distractor biases and IEIs (with largest positive r values, Fig. 5b). We found that distractor bias and the IEI showed a strong linear correlation (Fig. 5d, two-sided Pearson's correlation coefficient, $p = 2.59\times10^{-21}$, $r = 0.69$). Notably, there were large differences in the best-fit weights quantifying how SEIs and IEIs shape social attention towards in-group monkey faces. The "best" weights for aggression, grooming and proximity with SEIs were 0.34, 0.54 and 0.58 (Fig. 3g). The "best" weights of ω_a, ω_g and ω_p with IEIs were 0.54, 0 and 0.04 (Fig. 5c). Amongst all dimensions contributing to IEI, aggression was the most strongly associated with attentional capture by monkey face distractors.

We then assessed the impacts of oxytocin on social attention towards in-group members as a function of IEIs. To do so, we analyzed the correlations between IEIs and distractor biases towards in-group distractors following administration of OT or saline. Two sets of "best" weights were chosen by maximized the r values (saline: $r = 0.63$, Fig. 5e; OT: $r = 0.64$, Fig. 5f). Surprisingly, OT, compared to saline, doubled the weight for aggression (Fig. 5g). After OT administration, we observed a decline in the slope between IEIs and distractor biases (Fig. 5h, two-sided Pearson's correlation coefficient, saline: $p = 3.47\times10^{-17}$, $r = 0.63$; OT: $p = 3.65\times10^{-18}$, $r = 0.64$). Specifically, the slope for saline was 48.63, whereas the slope for OT was 23.21. These findings imply that OT amplifies the impact of dyadic aggressive interactions on social attention.

Discussion

Social relationships emerge from the way individuals perceive and interact with the world around them. In this study, our goal was to probe links between social relationships among four monkeys in a group and behavioral performance in a separate computerized attention task. We specifically investigated how potentially distracting pictures of in-group and out-group monkeys impacted performance of a simple visual orienting task. We focused on three dimensions of social interactions (aggression, grooming and proximity) at two distinct levels (general tendencies vs. dyadic relationships) and analyzed correlations with task performance. We mathematically assessed how social tendencies within the group, as well as specific dyadic relationships, varied with attentional capture by social stimuli. We also explored how the social peptide hormone oxytocin influenced the impact of multi-dimensional social relationships on social attention. Our findings offer insights into how social attention varies with both general social tendencies and specific dyadic relationships, thereby exposing links between visual social information processing and the dynamics of social networks in primate groups. Our study revealed that social attention is sensitive to group membership and reflects multi-dimensional social relationships (Fig. 3). Social attention reflected both general social tendencies (SEIs, see Fig. 3g) and individual dyadic relationships (IEIs, see Fig. 5c), even for the same social cues (e.g., in-group). Our work provides a nuanced perspective on the mechanisms mediating the acquisition and use of social information.

Neural processes that distinguish in-group and out-group conspecifics presumably evolved because cooperation within groups conferred survival advantages [45]. Individuals who formed strong bonds within their group were better equipped to secure resources, protect against predators, and navigate social hierarchies [46]. Consequently, abilities for recognizing and favoring in-group members, as well as kin, are thought to have evolved as adaptive strategies that maximize fitness and maintain social cohesion [47]. These adaptations can manifest as both in-group favoritism and out-group dislike [48]. Such biases foster solidarity and cooperation within a group, but can also fuel intergroup conflict, prejudice, and discrimination [49]. Here, we found that monkeys spontaneously differentiate members of their own social group (in-group) from those outside their group (out-group) when performing a simple visual orienting task. This distinction was evident in heightened vigilance towards the faces of out-group monkeys compared to those of in-group monkeys (Fig. 3c). Moreover, this tendency varied among individuals. Monkeys who were less social, as defined by lower SEIs, showed greater vigilance to out-group monkeys. On the other hand, the most social monkey, defined by the highest SEI within the group, was equally vigilant to in-group and out-group monkeys. These findings suggest that individual variation in sensitivity to group membership will be key for understanding the complexities of social networks in both humans and animals.

Oxytocin is fundamental to parturition in females and is released during lactation to promote bonding between mothers and infants. This peptide hormone also plays a crucial role in shaping social development and promoting prosocial behavior [50, 51]. Oxytocin also impacts social behavior in males by influencing intra-group affinity, coordination, trust, and empathy [52-54]. Both male and

female chimpanzees have shown increased levels of oxytocin before and after intergroup conflicts [55]. Recent evidence suggests that oxytocin influences in-group and out-group behavioral dynamics [56-58]. Specifically, oxytocin enhances empathy and cooperation towards in-group conspecifics but increases competitiveness and hostility towards individuals from other groups [57, 59, 60]. Our study demonstrates that oxytocin administration increases attention towards out-group individuals, while simultaneously blunting vigilance towards in-group individuals (Fig. 4), consistent with previous work [43]. These impacts were strongest for individual variation in prosocial tendencies indexed by grooming behavior (Fig. 4f). These findings resonate with prior work showing that individual variation in oxytocin concentration predicts social functioning in humans [61] and that exogenous administration of oxytocin only improves social function in children with low endogenous levels of the peptide hormone [62].

Primate brains evolved to navigate the demands of living in a complex social environment [63, 64]. A growing body of evidence indicates both brain structure and function reflect social behavioral complexity [65-67]. For example, the so-called "social brain network" varies in physical size as a function of both social network size and social status [66, 68, 69]. Such structural variation may both reflect and impact biological success. For example, rhesus monkeys who become more tolerant and friendly, thereby expanding their social networks, are more likely to survive natural disasters and subsequently degraded environments [3]. Our study unveiled subtle variation in social information processing as a function of both general social tendencies and specific dyadic social relationships, which we hypothesize arise from variation in the structure and function of components of the social brain network.

We further hypothesize that oxytocin serves as a gain control mechanism that regulates social information processing thereby shaping multi-dimensional social relationships via distinct but interacting neural pathways [70, 71]. OT modulation of meso-cortico-limbic circuitry facilitates approach-oriented behaviors related to affiliation, familiarity, and trust, particularly towards groupmates [56]. Oxytocin also modulates cortico-amygdala circuitry [72], resulting in anxiolysis and reductions in fear-motivated action towards groupmates [73], but heightened vigilance and defensive aggression towards out-group conspecifics [57, 73, 74]. Our findings are consistent with this body of evidence and help to elucidate how social perception and attention vary with and potentially support multi-dimensional social relationships (Fig. 4f-k, and Fig. 5e-h). The diverse impacts found here might be linked to many brain pathways, encompassing both the meso-cortico-limbic and cortico-amygdala circuitries. Our findings thus help to elucidate the links between the dynamics of multi-faceted social networks and the dynamics of visual attention through neuromodulatory gain control mechanisms. However, given the relatively small sample size and homogeneity of the stimulus set used in our study, we advocate future research focusing on larger, more diverse cohorts and incorporating a broader range of stimuli to enhance the generalizability and applicability of our findings.

Materials and Methods

Animal Preparation

Four adult male rhesus macaques (*Macaca mulatta*, 8–13 years old, 10–12 kg) served as subjects in this study. Animals were cared for in accordance with *Guide for the Care and Use of Laboratory Animals* established by the Society for Neuroscience. All experimental procedures were approved in advance by the *Institutional Animal Administration Committees* at the Institute of Biophysics, Chinese Academy of Sciences (IBP-NHP-002(22)). Prior to experiments, we implanted a head holder to keep head stable during experiments, and sutured an eye coil to the sclera to monitor eye position by using the magnetic search coil technique (Crist Instruments, Bethesda, USA), as described previously [75]. Monkeys were well trained to sit calmly in primate chairs (Crist Instruments, Bethesda, USA), and performed eye movement tasks in a quiet, dimly lit room. On the experimental day, all monkeys were simultaneously transported from the colony room into individual experimental rooms and participated in their tasks for about 2 hours in the morning. Then they were back to home cages and fed supplements regularly.

Social interaction dataset

All four monkeys who participated in the study were housed in the same colony room for more than 4 years. The monkeys lived in interconnected cages that permitted direct physical interaction but also allowed to isolated them by a sliding system of partitions for animal safety. Monkey interactive behaviors were recorded by six cameras (Xiaomi PTZ version SE+, China, sample rate: 20 frames per second) simultaneously in the afternoon to evaluate their social interactions. We have collected about 560 hours video data totally, with monitoring interactive behaviors in each dyad among four subjects through the whole study.

Automatic social interaction evaluation

YOLO or You Only Look Once is a one-stage target detection algorithm and can directly return the image pixel regression box coordinates and probability-like [76]. To quantify monkeys' interactive behaviors precisely and equitably, we first applied the architecture and loss function of YOLOv5 (https://github.com/ultralytics/yolov5). We used the LabelMe tool to translate the video data into image data. We randomly chose 396 images from 4 monkeys as the training dataset, and labeled them according to monkeys' different behaviors: postures (upright, sitting or lying), head orientation, and rump orientation. The YOLOv5 model was used to extract the monkeys' behavior by detecting frame by frame. After training, we checked the evaluation indicators of this model, including loss value of YOLOv5 in the training process, changes of mAP, confusion matrix and PR curve. And we found the YOLOv5 worked effectively on the dataset with mean average precision (IoU = 0.5) of 0.97 (Supplementary Fig. 1). The behavior performances of each subject in any given dyad were identified as three dimensions of social behaviors (Fig. 1d-f): proximity (approach more-approach less), grooming (groomee-groomer), aggression (aggressor-victim). To ensure accuracy, we also had two observers—one animal caretaker and one lab member, both blind

to the research purposes)—independently mark monkey social behaviors from representative videos for all possible monkey dyads. Their identifications of behavior aligned well with the automatic detections.

Then, we graded clearly delineated antagonistic engagements in a 1and -1 dichotomous fashion. In any dyad of interaction sessions, one monkey was deemed score 1 to the other if their actions occurred more times in one direction than in the other, such as showing more proximity, receiving more grooming and initiating a physical aggression more frequently, while the other one was scored -1. Aggressive behaviors unfold with remarkable swiftness, with reciprocal responses occurring on a timescale measured in seconds. Therefore, we initially employed YOLOv5 for temporal assessment, followed by manual determination of the initiation sequence of attacks. Subsequently, we meticulously recorded the durations during which each party actively initiated aggression, thereby discerning the victor and vanquished in instances of aggressive behavior. If there were no related social interactions happened, both of them gained zero as their interaction scores.

Visual orienting task

Visual stimuli were presented at a refresh rate of 100 Hz on a monitor (VG278Q ASUS, China) positioned 40 cm from the monkey. The screen was subtended a visual field of 73×45° with a 1920×1080 resolution. A computer running laboratory's Maestro software controlled experimental stimuli and task timing. In the daily experiments, a 0.5º white square was served as a target. A trial began with the target located in the center of the black screen (RGB: 0, 0, 0) for a variable period of 800-1200 ms to minimize anticipatory movements, and monkeys were required to fixate within an invisible 2º ×2º window. Every 50 trials were served as a session including forty-eight social interference trials (96%) and two visuo-motor trials (4%) for data evaluation (Fig. 2a). In the social interference task, a 7º circled picture was randomly presented 18º eccentric either on the right or left and briefly flashed as a distractor for 100 ms. After the first 50 ms, the white target relocated 14º from center point on one of two locations: congruent (same hemifield with distractor) or incongruent (opposite hemifield), to guide saccadic eye movements. In the visual-motor task, only the target was randomly presented on one of hemifield without a distractor interference in order to assess monkeys' behavioral performances. All social interference and visual-motor trials were introduced in a random order and one time in a session. All sessions were continuously run in an experimental day without pause. Thus, monkeys could be incapable to detect the testing session. Once monkeys made a correct saccade to the target within an interval of 300 ms from the target relocation, a few droplets of liquid were delivered as reward.

Distractors were composed of seven face pictures from different monkeys and their scrambled images and adjusted their luminance to 54.67±2.69 cd/m^2. Four of them were took from subjects participated in the study, who had social interactions in the same colony room. The other three monkey face pictures were sampled from outside the social group (Fig. 2b). For each trial, subject was introduced a distractor randomly chosen from face pictures of his three social interacted

groupmates, or the three out-group monkeys without social interactions, or the related 6 scrambled images (randomly shuffled the pixels), with equal chances. All face pictures were well controlled with a neutral expression and forward gaze, and subtended by a 7º circle. Prior to this study, all these distractors have been daily introduced to four subjects as a target to evoke visual guided saccadic eye movements for 8 weeks. Thus, subjects were well exposed to all monkey face pictures and the scrambled images, no matter having social interactions with the monkey back to home cages, or not.

Pharmacological manipulation

Prior to the pharmacological treatment, all monkeys had become habituated to the nebulizer-assisted aerosolized exposure procedure and had been receiving saline delivery for around two weeks. On the alternating experimental days, oxytocin (40 IU/mL, 2 mL; Beyotime) and saline (2 ml, served as control) were randomly delivered via nebulization (Omron, baby nebulizer) into monkey's nose and mouth continuously for 2 min [50]. After 15 min relax in the dim room, monkeys participated in the visual orienting task.

Data acquisition

We measured eye position signals using a magnetic search coil system (Crist Instruments, Bethesda, Maryland, United States) to estimate eye movements. After passing the signals through an analog differentiator, voltages proportional to horizontal and vertical eye velocity were generated. The differentiator contained a filter that rejected signals above 25 Hz (-20 dB per decade) and produced eye movement signals at lower frequencies. Eye signals were sampled at 1 kHz and stored for analysis off-line. Eye traces in each trial were inspected by a custom-built MATLAB program and then manually reviewed. The identification of saccadic eye movements was based on velocity and acceleration thresholds (velocity, 50º/s; acceleration, 500º/s^2). If saccade occurred during the 500 ms fixation interval preceding the onset of the distractor, the trial was discarded. Saccadic eye movements were quantified in terms of the response time (the latency of saccade to the target) and the initial eye movement direction profile.

Statistical Analysis

Drifting time and distractor bias. To evaluate the effects of the monkey face on saccadic eye movements, we calculated the drifting time (DT) between the saccadic latencies when the distractor was a monkey face picture (RT_f) or its scrambled image (RT_s) in a certain visual condition (congruent or incongruent) on each experimental session:

$$DT = RT_f - RT_s \ldots\ldots\ldots (1)$$

Furthermore, we found that our data were consistent with prior research: the congruent distractor accelerated the saccadic eye movement, whereas the incongruent distractor delayed saccade

initiation. To summary the face effects on monkeys' behavioral performances across two conditions, we defined the distractor bias to evaluate the influence:

$$Distractor\ Bias = DT_{Incon} - DT_{Con} \ldots\ldots\ldots (2)$$

where DT_{Incon} and DT_{Con} are the mean drifting times under incongruent and congruent conditions on each experimental day. This use of eye responses evoked by various monkey face pictures and their scrambled images under two conditions assigned the complete effect of the feature of face, with well control.

To assess the effect of distractors on the initial choice of gaze shifting, we calculated the probability of the first saccade being directed towards the distractor in the incongruent condition. We then computed the difference in the probabilities that would be directed towards intact monkey faces and scrambled images to evaluate the impact of face information on attention.

Social engagement index. We utilized linear models to combine the three dimensions of social relationships (aggression, grooming, and proximity). SEI summarizes the social interactions between a specific monkey and the other three monkeys in the group, which could provide an assessement on general social tendencies (Fig. 3a). We modeled the social engagement index as:

$$SEI = \omega_a \times \sum_{i=1}^{n} A_i + \omega_g \times \sum_{i=1}^{n} G_i + \omega_p \times \sum_{i=1}^{n} P_i \ldots\ldots\ldots (3)$$

where ω_a, ω_g and ω_p indicate the weights of three dimensions of social behaviors separately. The ω constrains between 0 and 1 with a step of 0.02. *i* presents the *n*th interact partner for each individual. In our dataset, *n* presents 3 socially interacting monkeys in the colony group. *A*, *G*, and *P* are interaction scores for aggression, grooming, and proximity.

Individual engagement index. IEI evaluates the social interactions between a given subject and his specific counterpart, which could offer a perspective at the specific individual dyadic level (Fig. 5a). The IEI was calculated as:

$$IEI_{A(B)} = \omega_a \times A_{A(B)} + \omega_g \times G_{A(B)} + \omega_p \times P_{A(B)} \ldots\ldots\ldots (4)$$

where ω_a, ω_g and ω_p again indicate the independent weights for three behavioral dimensions separately. We adopted identical ranges and step for ω, constraining it between 0 and 1, with a step of 0.02. $IEI_{A(B)}$ indicates the interactions within a dyadic interacted pair, actor Monkey A towards his partner Monkey B.

Statistical analyses were conducted to examine the significance of the results across four monkeys and experimental days, with the significance level at 0.05. Two-sided Pearson's correlation

coefficient was utilized to quantify the correlations. If not stated otherwise, data were analyzed using a two-tailed paired Student's t-test.

References

1. Taborsky, B. & Oliveira, R.F. Social competence: an evolutionary approach. *Trends Ecol. Evol.* **27**, 679-688 (2012).
2. Testard, C., *et al.* Rhesus macaques build new social connections after a natural disaster. *Curr. Biol.* **31**, 2299-2309.e2297 (2021).
3. Testard, C., *et al.* Ecological disturbance alters the adaptive benefits of social ties. *Science* **384**, 1330-1335 (2024).
4. Schutte, J.G. & Light, J.M. The Relative Importance of Proximity and Status for Friendship Choices in Social Hierarchies. *Soc. Psychol.* **41**, 260-264 (1978).
5. Stopczynski, A., Pentland, A.S. & Lehmann, S. How Physical Proximity Shapes Complex Social Networks. *Sci. Rep.* **8**, 17722 (2018).
6. Henazi, S.P. & Barrett, L. The value of grooming to female primates. *Primates* **40**, 47-59 (1999).
7. Spruijt, B.M., van Hooff, J.A. & Gispen, W.H. Ethology and neurobiology of grooming behavior. *Physiol. Rev.* **72**, 825-852 (1992).
8. Hobson, E.A. Differences in social information are critical to understanding aggressive behavior in animal dominance hierarchies. *Curr. Opin. Psychol.* **33**, 209-215 (2020).
9. Funkhouser, J.A., Mayhew, J.A., Sheeran, L.K., Mulcahy, J.B. & Li, J.-H. Comparative Investigations of Social Context-Dependent Dominance in Captive Chimpanzees (Pan troglodytes) and Wild Tibetan Macaques (Macaca thibetana). *Sci. Rep.* **8**, 13909 (2018).
10. Hobson, E.A., Ferdinand, V., Kolchinsky, A. & Garland, J. Rethinking animal social complexity measures with the help of complex systems concepts. *Anim. Behav.* **155**, 287-296 (2019).
11. Page, S.E. What Sociologists Should Know About Complexity. *Annu. Rev. Sociol.* **41**, 21-41 (2015).
12. Aureli, F. & Schino, G. Social complexity from within: how individuals experience the structure and organization of their groups. *Behav. Ecol. Sociobiol.* **73**, 6 (2019).
13. Hinde, R.A. Interactions, Relationships and Social Structure. *Man* **11**, 1-17 (1976).
14. Grueter, C.C., Matsuda, I., Zhang, P. & Zinner, D. Multilevel Societies in Primates and Other Mammals: Introduction to the Special Issue. *Int. J. Primatol.* **33**, 993-1001 (2012).
15. Tsao, D.Y., Freiwald, W.A., Knutsen, T.A., Mandeville, J.B. & Tootell, R.B. Faces and objects in macaque cerebral cortex. *Nat. Neurosci.* **6**, 989-995 (2003).
16. Krajbich, I. & Rangel, A. Multialternative drift-diffusion model predicts the relationship between visual fixations and choice in value-based decisions. *Proc. Natl. Acad. Sci.* **108**, 13852-13857 (2011).
17. Deaner, R.O., Khera, A.V. & Platt, M.L. Monkeys pay per view: adaptive valuation of social images by rhesus macaques. *Curr. Biol.* **15**, 543-548 (2005).
18. Chang, S.W.C., Gariépy, J.-F. & Platt, M.L. Neuronal reference frames for social decisions in primate frontal cortex. *Nat. Neurosci.* **16**, 243-250 (2013).
19. Chang, S.W., Barter, J.W., Ebitz, R.B., Watson, K.K. & Platt, M.L. Inhaled oxytocin amplifies both vicarious reinforcement and self reinforcement in rhesus macaques (Macaca mulatta). *Proc. Natl. Acad. Sci.* **109**, 959-964 (2012).
20. Chang, S.W.C., *et al.* Neural mechanisms of social decision-making in the primate amygdala. *Proc. Natl. Acad. Sci.* **112**, 16012-16017 (2015).
21. Platt, M.L. Neural correlates of decisions. *Curr. Opin. Neurobiol.* **12**, 141-148 (2002).

22. Heywood, C.A., *et al.* The role of the 'face-cell' area in the discrimination and recognition of faces by monkeys. *Philos. Trans. R. Soc. B-Biol. Sci.* **335**, 31-38 (1997).
23. Shepherd, S.V. & Platt, M.L. Spontaneous social orienting and gaze following in ringtailed lemurs (Lemur catta). *Anim. Cogn.* **11**, 13-20 (2008).
24. Rosati, A.G., Arre, A.M., Platt, M.L. & Santos, L.R. Rhesus monkeys show human-like changes in gaze following across the lifespan. *Proc. R. Soc. B-Biol. Sci.* **283**, 20160376 (2016).
25. Chance, M.R.A. Attention Structure as the Basis of Primate Rank Orders. *Man* **2**, 503-518 (1967).
26. Deaner, R.O., Shepherd, S.V. & Platt, M.L. Social context influences gaze-following and neuronal activity in macaque area LIP. *J. Vision* **5**, 394-394 (2005).
27. Shepherd, S.V., Deaner, R.O. & Platt, M.L. Social status gates social attention in monkeys. *Curr. Biol.* **16**, R119-R120 (2006).
28. Eastwood, J.D., Smilek, D. & Merikle, P.M. Differential attentional guidance by unattended faces expressing positive and negative emotion. *Percept. Psychophys.* **63**, 1004-1013 (2001).
29. Klein, J.T., Shepherd, S.V. & Platt, M.L. Social Attention and the Brain. *Curr. Biol.* **19**, R958-R962 (2009).
30. Watson, K.K. & Platt, M.L. Social signals in primate orbitofrontal cortex. *Curr. Biol.* **22**, 2268-2273 (2012).
31. Yorzinski, J.L. & Platt, M.L. Same-Sex Gaze Attraction Influences Mate-Choice Copying in Humans. *PLOS ONE* **5**, e9115 (2010).
32. Klein, J.T., Deaner, R.O. & Platt, M.L. Neural Correlates of Social Target Value in Macaque Parietal Cortex. *Curr. Biol.* **18**, 419-424 (2008).
33. Watson, K.K., Ghodasra, J.H., Furlong, M.A. & Platt, M.L. Visual preferences for sex and status in female rhesus macaques. *Anim. Cogn.* **15**, 401-407 (2012).
34. Adams, G.K., Watson, K.K., Pearson, J. & Platt, M.L. Neuroethology of decision-making. *Curr. Opin. Neurobiol.* **22**, 982-989 (2012).
35. Smith, D.V., *et al.* Distinct Value Signals in Anterior and Posterior Ventromedial Prefrontal Cortex. *J. Neurosci.* **30**, 2490 (2010).
36. Adams, G.K., Ong, W.S., Pearson, J.M., Watson, K.K. & Platt, M.L. Neurons in primate prefrontal cortex signal valuable social information during natural viewing. *Philos. Trans. R. Soc. B-Biol. Sci.* **376**, 20190666 (2021).
37. Ballesta, S. & Duhamel, J.R. Rudimentary empathy in macaques' social decision-making. *Proc. Natl. Acad. Sci.* **112**, 15516-15521 (2015).
38. Bentzur, A., *et al.* Early Life Experience Shapes Male Behavior and Social Networks in Drosophila. *Curr. Biol.* **31**, 486-501.e483 (2021).
39. Bowler, M., Knogge, C., Heymann, E.W. & Zinner, D. Multilevel Societies in New World Primates? Flexibility May Characterize the Organization of Peruvian Red Uakaris (Cacajao calvus ucayalii). *Int. J. Primatol.* **33**, 1110-1124 (2012).
40. Talbot, C.F., Leverett, K.L. & Brosnan, S.F. Capuchins recognize familiar faces. *Anim. Behav.* **122**, 37-45 (2016).
41. Pokorny, J.J. & de Waal, F.B.M. Monkeys recognize the faces of group mates in photographs. *Proc. Natl. Acad. Sci.* **106**, 21539-21543 (2009).
42. Olff, M., *et al.* The role of oxytocin in social bonding, stress regulation and mental health: an update on the moderating effects of context and interindividual differences. *Psychoneuroendocrinology* **38**, 1883-1894 (2013).

43. Jiang, Y. & Platt, M.L. Oxytocin and vasopressin flatten dominance hierarchy and enhance behavioral synchrony in part via anterior cingulate cortex. *Sci. Rep.* **8**, 8201 (2018).
44. Jiang, Y. & Platt, M.L. Oxytocin and vasopressin increase male-directed threats and vocalizations in female macaques. *Sci. Rep.* **8**, 18011 (2018).
45. Ten Velden, F.S., Daughters, K. & De Dreu, C.K.W. Oxytocin promotes intuitive rather than deliberated cooperation with the in-group. *Horm. Behav.* **92**, 164-171 (2017).
46. Jablonski, N.G. Social and affective touch in primates and its role in the evolution of social cohesion. *Neuroscience* **464**, 117-125 (2021).
47. Bergman, T., Beehner, J., Cheney, D. & Seyfarth, R. Hierarchical Classification by-Rank and Kinship in Baboons. *Science* **302**, 1234-1236 (2003).
48. Brewer, M.B. The Psychology of Prejudice: Ingroup Love and Outgroup Hate? *J. Soc. Issues* **55**, 429-444 (1999).
49. Halevy, N., Bornstein, G. & Sagiv, L. "In-Group Love" and "Out-Group Hate" as Motives for Individual Participation in Intergroup Conflict: A New Game Paradigm. *Psychol. Sci.* **19**, 405-411 (2008).
50. Bauman, M.D., Murai, T., Hogrefe, C.E. & Platt, M.L. Opportunities and challenges for intranasal oxytocin treatment studies in nonhuman primates. *Am. J. Primatol.* **80**, e22913 (2018).
51. Putnam, P.T., Roman, J.M., Zimmerman, P.E. & Gothard, K.M. Oxytocin enhances gaze-following responses to videos of natural social behavior in adult male rhesus monkeys. *Psychoneuroendocrinology* **72**, 47-53 (2016).
52. De Dreu, C.K., Greer, L.L., Van Kleef, G.A., Shalvi, S. & Handgraaf, M.J. Oxytocin promotes human ethnocentrism. *Proc. Natl. Acad. Sci.* **108**, 1262-1266 (2011).
53. Burkhart, J.C., Gupta, S., Borrego, N., Heilbronner, S.R. & Packer, C. Oxytocin promotes social proximity and decreases vigilance in groups of African lions. *iScience* **25** (2022).
54. Baumgartner, T., Heinrichs, M., Vonlanthen, A., Fischbacher, U. & Fehr, E. Oxytocin Shapes the Neural Circuitry of Trust and Trust Adaptation in Humans. *Neuron* **58**, 639-650 (2008).
55. Samuni, L., *et al.* Oxytocin reactivity during intergroup conflict in wild chimpanzees. *Proc. Natl. Acad. Sci.* **114**, 268-273 (2017).
56. De Dreu, C.K. Oxytocin modulates cooperation within and competition between groups: an integrative review and research agenda. *Horm. Behav.* **61**, 419-428 (2012).
57. De Dreu, C.K. & Kret, M.E. Oxytocin Conditions Intergroup Relations Through Upregulated In-Group Empathy, Cooperation, Conformity, and Defense. *Biol. Psychiatry* **79**, 165-173 (2016).
58. De Dreu, C.K.W., *et al.* The Neuropeptide Oxytocin Regulates Parochial Altruism in Intergroup Conflict Among Humans. *Science* **328**, 1408-1411 (2010).
59. Zhang, H., Gross, J., De Dreu, C. & Ma, Y. Oxytocin promotes coordinated out-group attack during intergroup conflict in humans. *Elife* **8** (2019).
60. Shamay-Tsoory, S.G. & Abu-Akel, A. The Social Salience Hypothesis of Oxytocin. *Biol. Psychiatry* **79**, 194-202 (2016).
61. Parker, K.J., *et al.* Plasma oxytocin concentrations and OXTR polymorphisms predict social impairments in children with and without autism spectrum disorder. *Proc. Natl. Acad. Sci.* **111**, 12258-12263 (2014).
62. Parker, K.J., *et al.* Intranasal oxytocin treatment for social deficits and biomarkers of response in children with autism. *Proc. Natl. Acad. Sci.* **114**, 8119-8124 (2017).
63. Dunbar, R.I.M. & Shultz, S. Evolution in the Social Brain. *Science* **317**, 1344-1347 (2007).

64. Cheney, D.L., Seyfarth, R.M. & Smuts, B.B. Social relationships and social cognition in nonhuman primates. *Science* **234 4782**, 1361-1366 (1986).
65. Sallet, J., *et al.* Social network size affects neural circuits in macaques. *Science* **334**, 697-700 (2011).
66. Testard, C., *et al.* Social connections predict brain structure in a multidimensional free-ranging primate society. *Sci. Adv.* **8**, eabl5794 (2022).
67. Sliwa, J. & Freiwald, W.A. A dedicated network for social interaction processing in the primate brain. *Science* **356**, 745-749 (2017).
68. Kanai, R., Bahrami, B., Roylance, R. & Rees, G. Online social network size is reflected in human brain structure. *Proc. Biol. Sci.* **279**, 1327-1334 (2012).
69. Noonan, M.P., *et al.* A neural circuit covarying with social hierarchy in macaques. *PLoS Biol.* **12**, e1001940 (2014).
70. Froemke, R.C. & Young, L.J. Oxytocin, Neural Plasticity, and Social Behavior. *Annu. Rev. Neurosci.* **44**, 359-381 (2021).
71. Arakawa, H. Dynamic regulation of oxytocin neuronal circuits in the sequential processes of prosocial behavior in rodent models. *Current Research in Neurobiology* **2**, 100011 (2021).
72. Striepens, N., *et al.* Oxytocin facilitates protective responses to aversive social stimuli in males. *Proc. Natl. Acad. Sci.* **109**, 18144-18149 (2012).
73. De Dreu, C.K., Scholte, H.S., van Winden, F.A. & Ridderinkhof, K.R. Oxytocin tempers calculated greed but not impulsive defense in predator-prey contests. *Soc. Cogn. Affect. Neurosci.* **10**, 721-728 (2015).
74. Harari-Dahan, O. & Bernstein, A. A general approach-avoidance hypothesis of Oxytocin: Accounting for social and non-social effects of oxytocin. *Neurosci. Biobehav. Rev.* **47**, 506-519 (2014).
75. Dou, H., *et al.* Form Properties of Moving Targets Bias Smooth Pursuit Target Selection in Monkeys. *Neurosci Bull* **39**, 1246–1262 (2023).
76. Redmon, J., Divvala, S., Girshick, R. & Farhadi, A. You Only Look Once: Unified, Real-Time Object Detection. in *2016 IEEE Conference on Computer Vision and Pattern Recognition (CVPR)* 779-788 (2016).

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Conceptualization: YY, SNL
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Investigation: SNL, JPH, SHC, MP, YY
Visualization: SNL, YY
Supervision: YY
Writing—original draft: YY
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Competing interests:
All other authors declare they have no competing financial interests.

Data and materials availability:
Datasets supporting the findings of this study are available from the corresponding author on reasonable request.

Figures

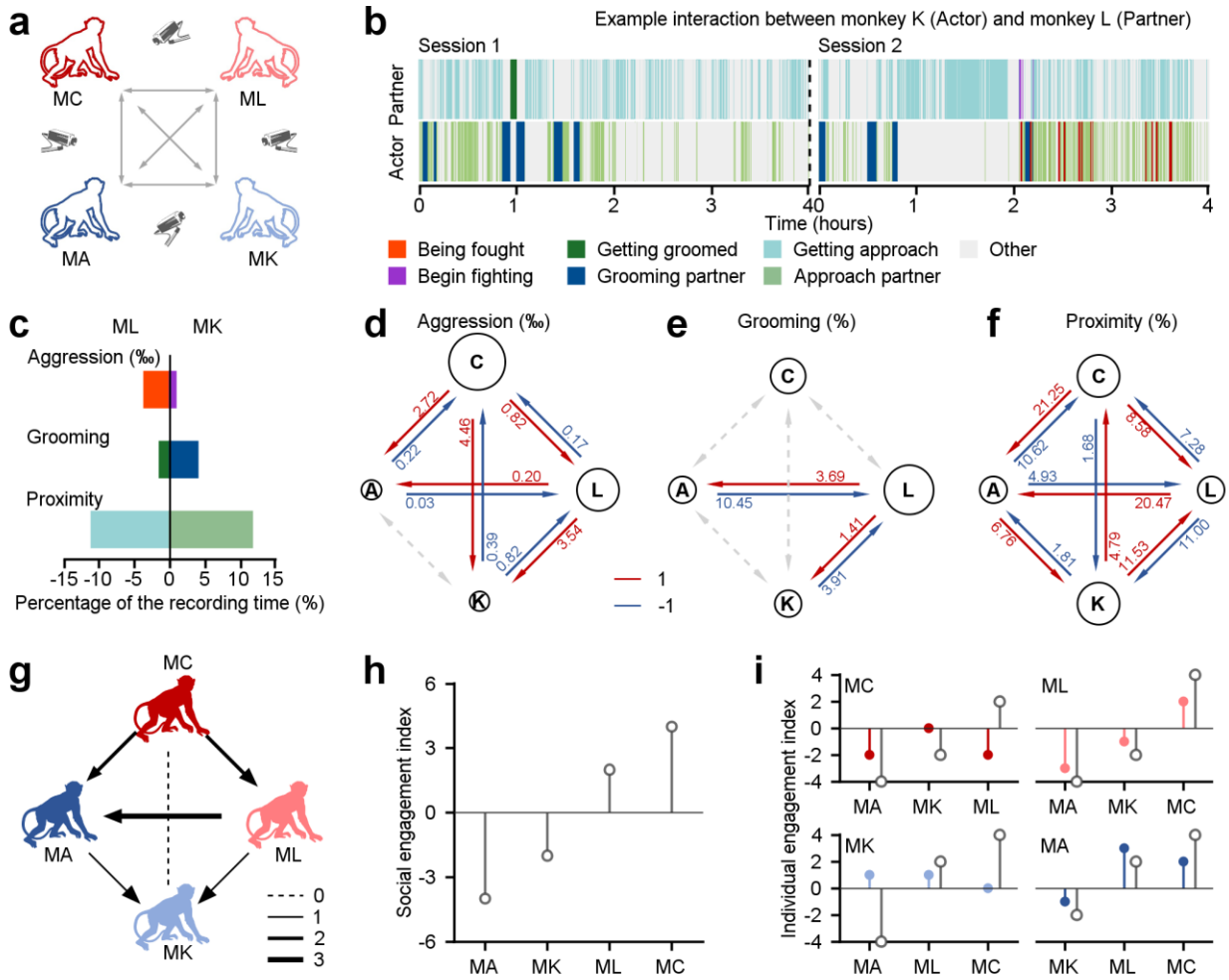


Fig. 1. Different behavioral dimensions of social relationships among a group of four monkeys within a colony room. a, The diagram depicts the procedure of acquiring social behaviors in various pairs of monkeys in the study. **b**, Different social interactions exhibited by an example pair throughout the course of two experimental days. **c**, The percentage of time engaged in three dimensions of behavior was quantified as a fraction of the total recording duration, in the given example pair. **d-f**, Three dimensions of interaction behaviors in all dyads were evaluated across the total recording duration using a dichotomous framework with values of 1 and -1. The diameter of a given circle presents the cumulative scores obtained by that monkey in aggression (**d**), grooming (**e**) and proximity (**f**). The number on each arrow indicates the proportion of individuals engaged in the corresponding social behavior. **g**, Social interactions among the group of four monkeys were quantitatively assessed based on three dimensions of social relationships, with an equal weight of 1 for each dimension. The thickness of lines corresponded to the interaction score in dyads. The monkey who receives an arrow is considered a negative score. Conversely, the monkey who sends an arrow earns a positive interaction score. **h**, Social engagement index (SEI), which quantifies general social tendencies within the group, was computed by aggregating the scores of three social interactions between a specific monkey and the other three groupmates. **i**, Individual engagement index (IEI; color-filled circles) evaluates the

social interactions between a given subject and his specific counterparts, compared to their related SEIs (gray-empty circles).

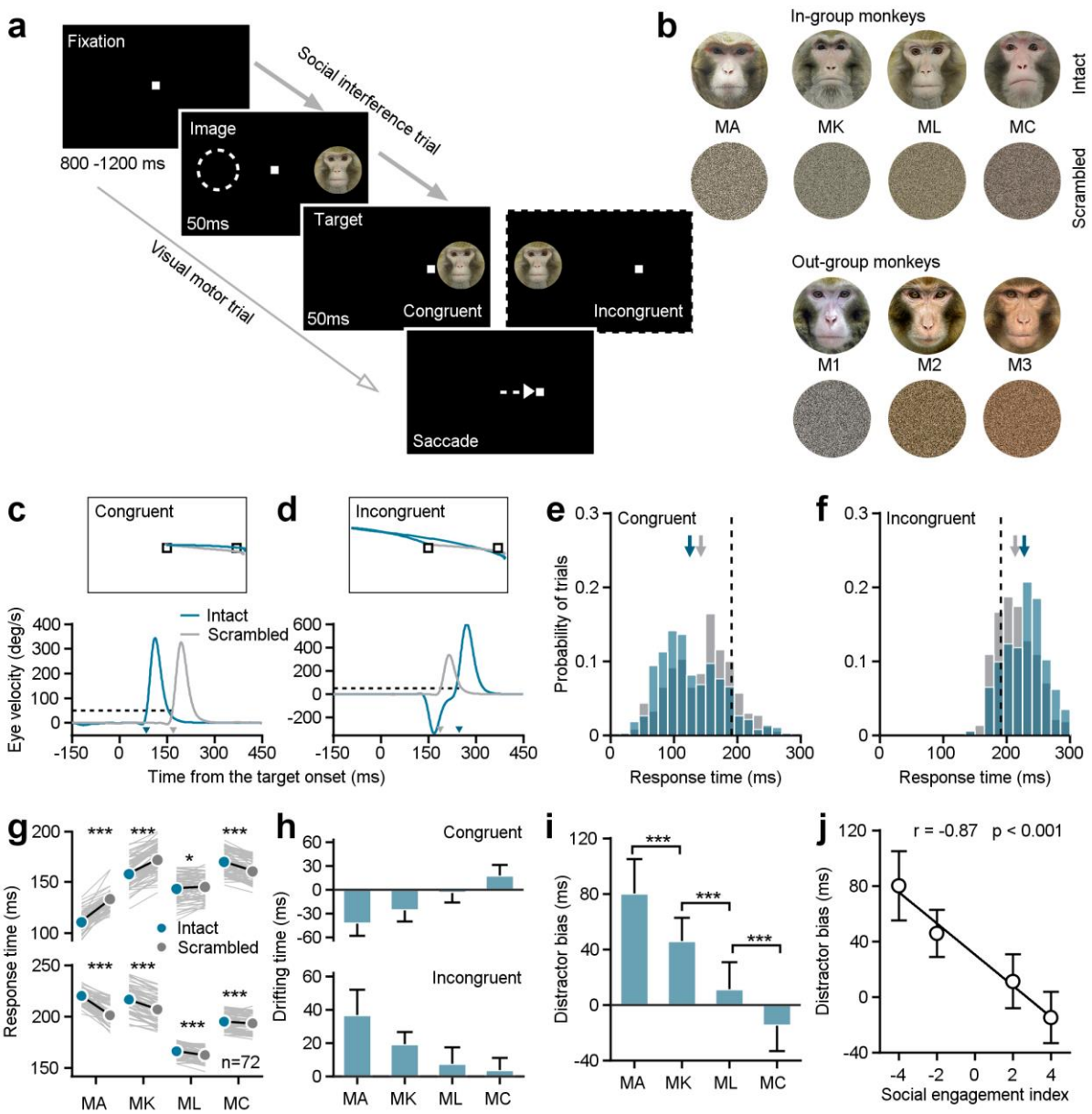


Fig. 2. Individuals' social attention in response to the social interference task. a, The experimental design encompasses both social interference trails and visual motor trials. **b**, The distractor stimuli consist of seven monkeys' neutral face photographs and the related scrambled images. Four monkeys among them were raised in a colony group (in-group) and served as subjects in the study. The left three ones were from outside the group (out-group). **c**,**d**, The eye position (top) and the horizontal eye velocity (bottom) on sample trials from Monkey A. The response times (arrows pointed) were determined utilizing a threshold of eye velocity at 50 deg/s and eye acceleration at 500º/s^2 (black dash lines). **e**,**f**, The response time distributions were shown based on social interference trials from subject Monkey A's example experimental day, including data to an intact face picture (blue bars) and its scrambled image (gray bars) under congruent (**e**) and incongruent (**f**) conditions. The arrows present the corresponding average values, and the black dash lines show the average response time in visual motor trials. **g**, The distractor of intact monkey

faces had a notable impact on the saccade latencies of all four subjects. Each gray line represents the behavioral responses to a certain monkey face picture and its scrambled image on a given day. **h**, The drifting time in the response time caused by the presence of both intact faces and their scrambled images. **i**, To synthesize the interference effects of social attention on monkey intact face pictures, the difference in the drifting times between the incongruent and congruent conditions was analyzed as the distractor bias. The distractor bias varies significantly among the four subjects. Student's t-test, ***, $p < 0.001$; *, $p < 0.05$. MA and MK: $p = 2.32\times10^{-17}$, MK and ML: $p = 6.77\times10^{-22}$, ML and MC: $p = 7.73\times10^{-14}$, Error bars: Mean ± SD. **j**, Distractor biases of four monkeys in the group are negatively correlated with their $SEIs_{(1,1,1)}$ ($r = -0.87$, $p < 0.001$), as determined by a two-sided Pearson's correlation coefficient. Error bars: Mean ± SD.

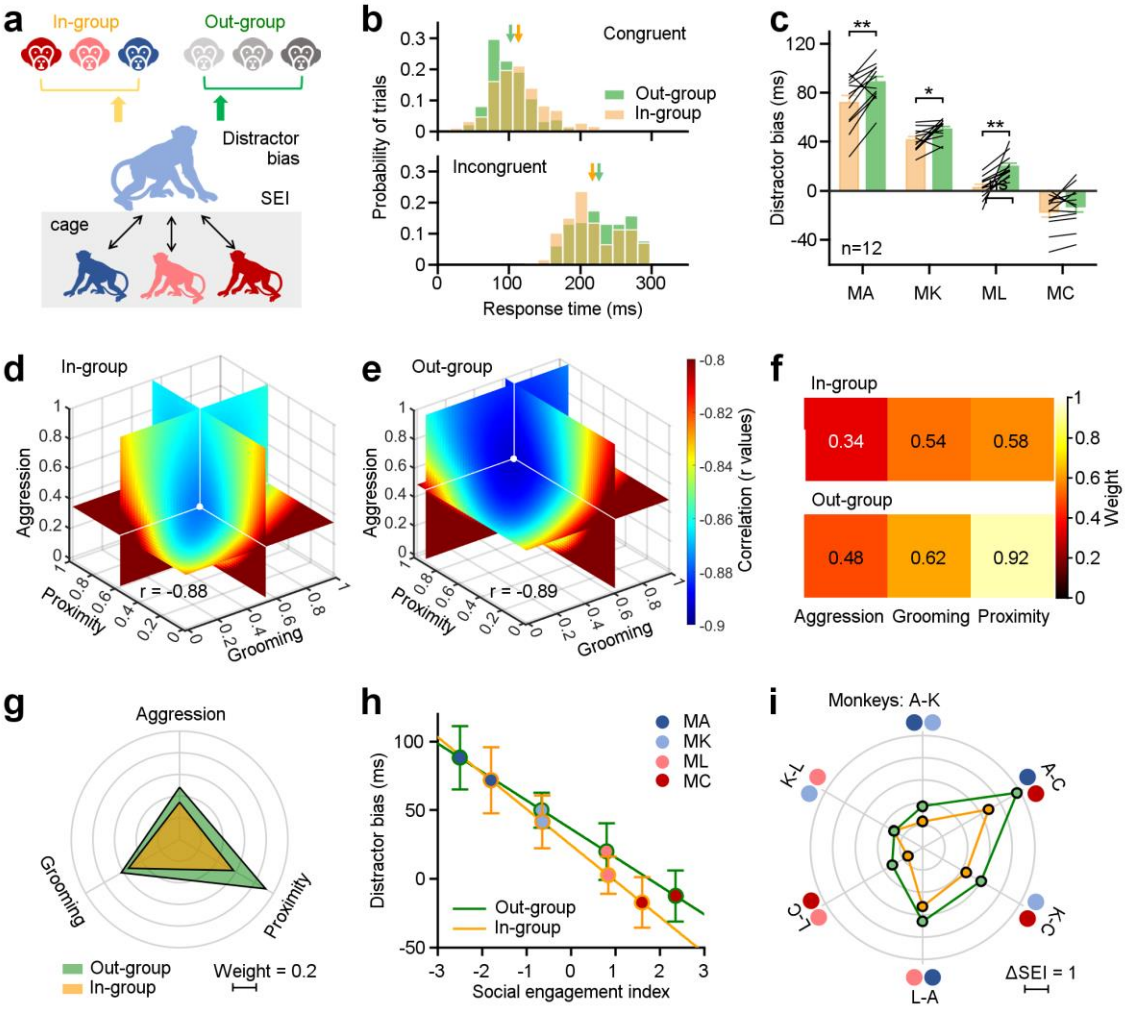


Fig. 3. Three dimensions of social relationships distinctly shape attention towards in-group and out-group members. a, Methodological schematic defining correlations between SEIs and distractor biases towards the in-group and out-group members. **b**, The distribution of distractor biases on an experimental day for the example Monkey A. Arrows indicate the related mean values (Congruent: In-group: 113.32 ± 37.05 ms, Out-group: 102.21 ± 33.34 ms; Incongruent: In-group: 216.94 ± 40.26 ms, Out-group: 226.08 ± 41.51 ms). **c**, Individuals in the same group exhibited more social attentions in monkey faces from the out-group, except MC (paired Student's t-test, MA: $p = 2.90\times10^{-3}$, MK: $p = 1.49\times10^{-2}$, ML: $p = 1.01\times10^{-3}$, MC: $p = 0.14$). Error bars: Mean ± SEM. **d**,**e**, Quantification of weights for three behavioral dimensions computed from the correlations between SEI and distractor bias for in-group (**d**) and out-group monkeys (**e**). X, Y and Z axes represent the weights of proximity, grooming, and aggression. The colormap illustrates the correlations between distractor bias and SEIs (r values), which were estimated by varying weights in the model from 0 to 1 with a step of 0.02. The white dot indicates the maximized correlation with the smallest negative r value. Each slice represents the r value surface along the X, Y, and Z axes, respectively. **f**,**g**, Pseudo-colored heatmaps (**f**) and polar graph (**g**) show the "best" weights for three social dimensions (in-group: $\omega_a = 0.34$, $\omega_g = 0.54$, $\omega_p = 0.58$; out-group: $\omega_a = 0.48$, $\omega_g = 0.62$, $\omega_p = 0.92$). **h**, The liner relationships between monkeys' distractor biases and their SEIs with the "best" weights. Error bars: Mean ± SD. **i**, The differences in the SEIs between any two monkeys

in H were scaled hexagonally in the circle, illustrating the magnitude of general social tendency in the colony. Compared to data towards out-group (green lines), the impact of social engagement was smaller when monkeys viewing in-group members (orange lines).

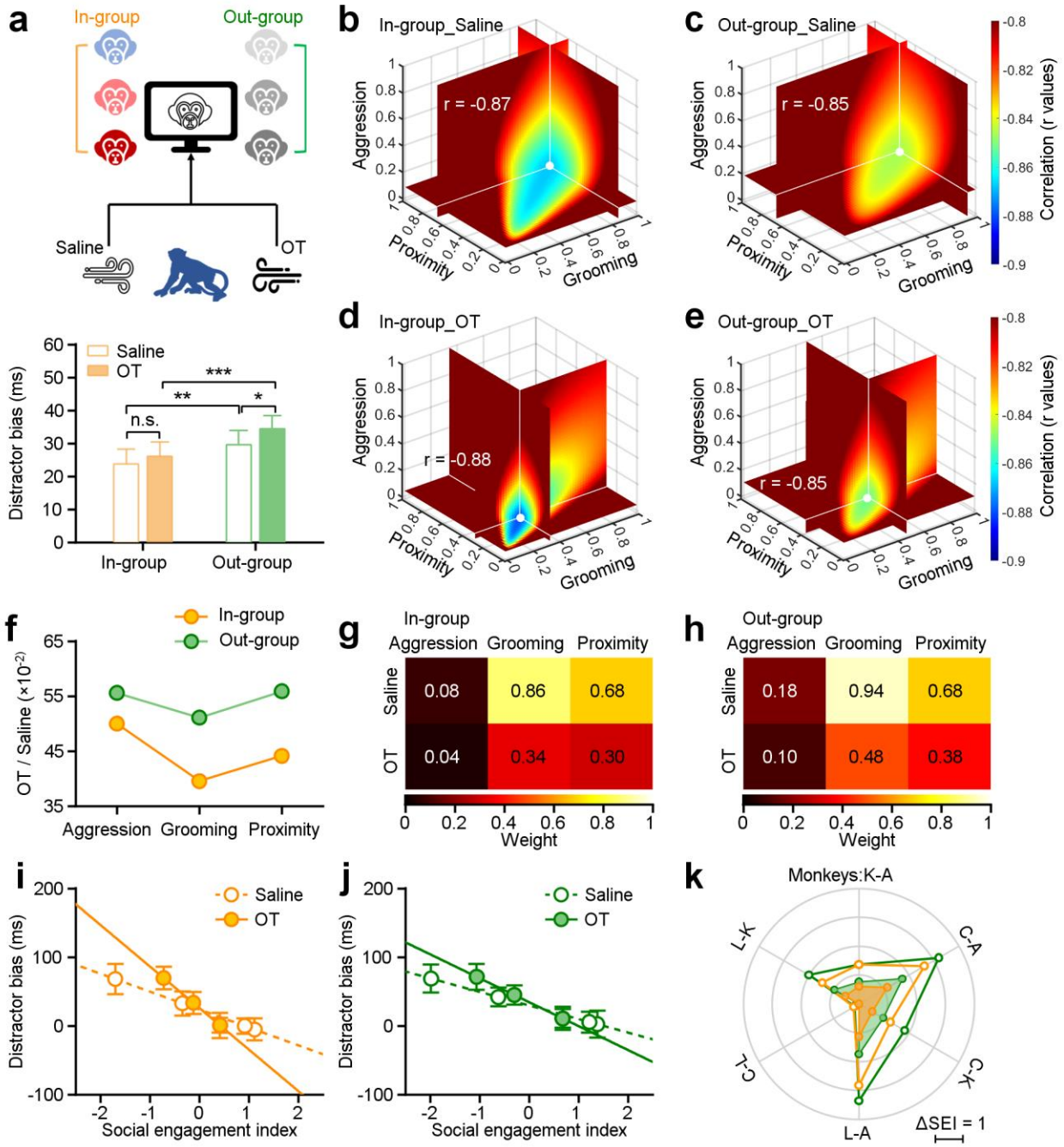


Fig. 4. Impact of oxytocin on social attention regulation by multi-dimensional social relationships. a, Experimental schematic (top) illustrating the administration of saline and oxytocin. Oxytocin greatly enhances the social attention towards distractors from outside the group (green bars, n = 48), while there was no significant change in the group's attention towards faces from the in-group (orange bars) (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$, paired Student's t-test. Error bars: Mean ± SEM). **b**-**e**, The "best" weights of three social dimensions by analyzing the correlations between SEIs and distractor bias towards in-group and out-group monkey distractors following administration of saline (**b**,**c**) and OT (**d**,**e**). **f,** Change ratios of weights after OT and saline administration for in-group and out-group distractors. **g**,**h**, Pseudo-colored heatmaps represent "best" weights relating three social dimensions to in-group and out-group distractor bias

under OT and saline. **i**,**j**, Relationship between monkeys' SEIs defined by "best" weights and their distractor biases towards in-group (**i**) and out-group (**j**) (the slopes of in-group: saline: -26.07, OT: -60.47; the slopes of out-group: saline: -19.75, OT: -34.84). Error bars: Mean ± SD. **k**, The differences in the SEIs between any two monkeys following administration of saline and OT (**i**,**j**) were scaled hexagonally in the circle. Compared to data under saline (empty circles), OT (filled circles) reduced the impact of social engagement on social attention under both conditions: viewing in-group and out-group monkey faces.

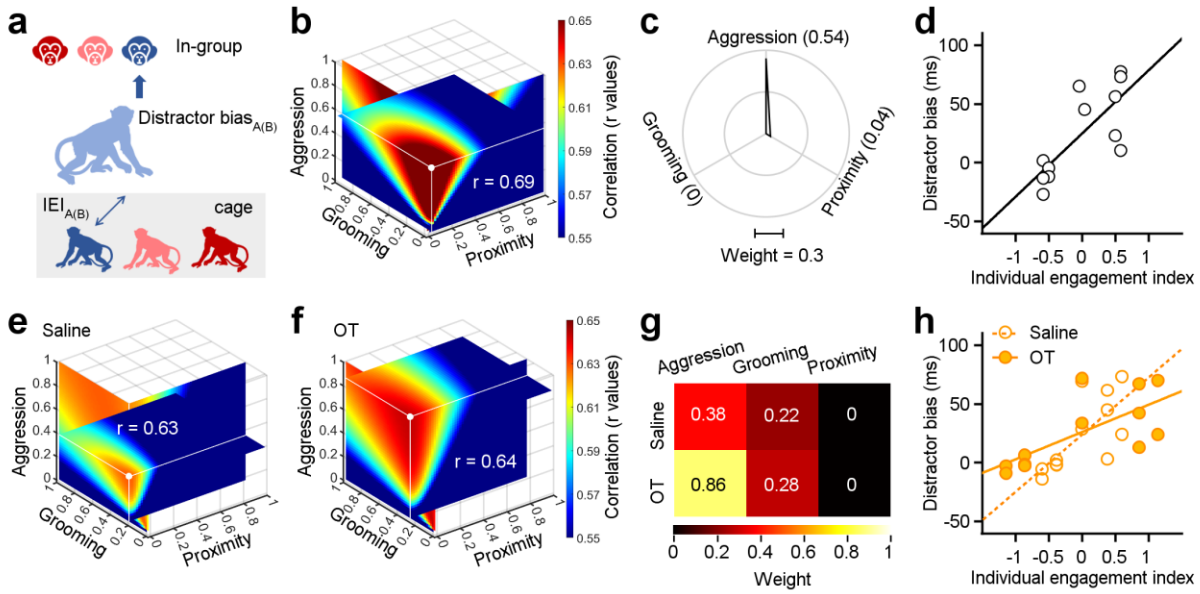
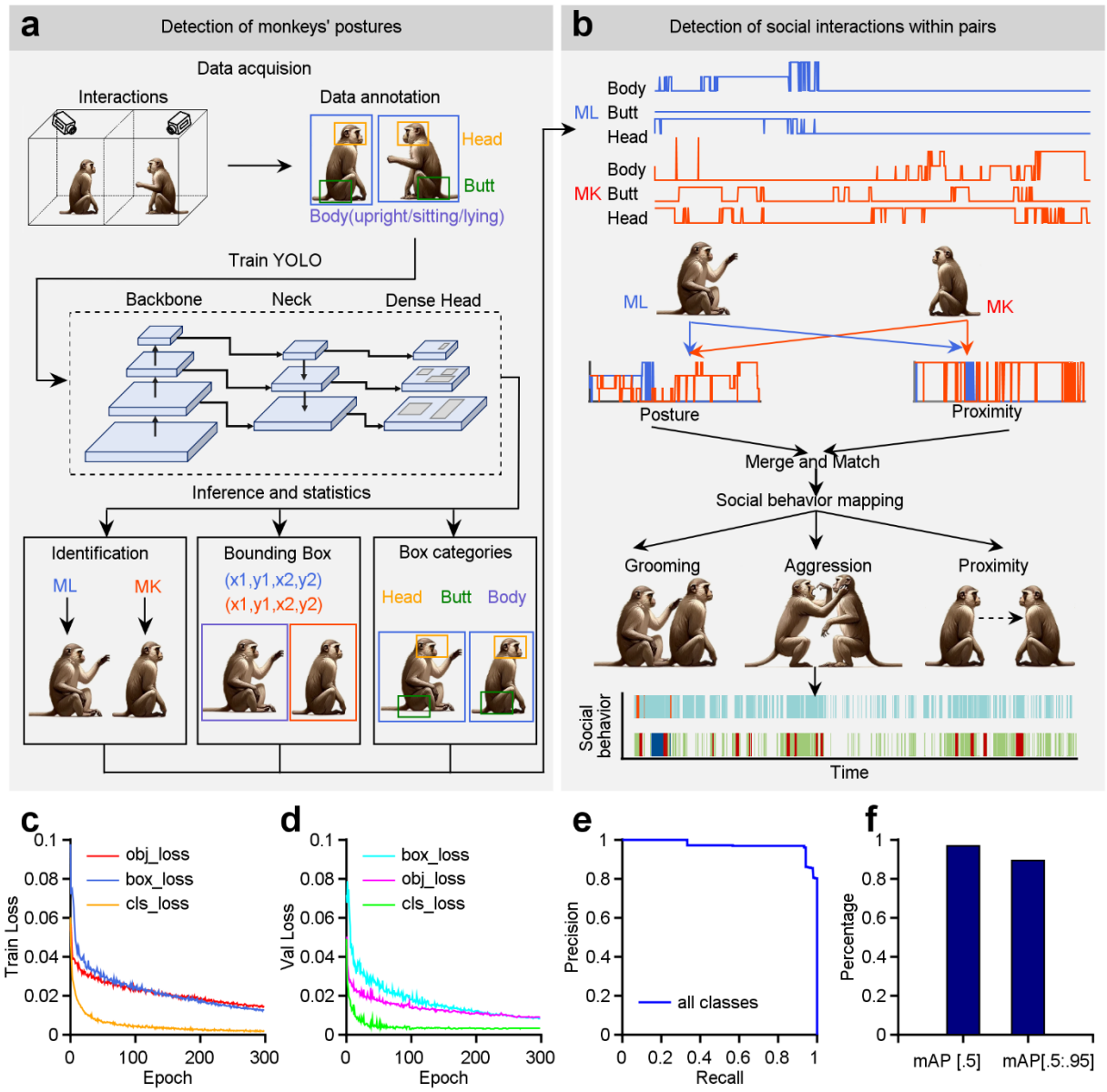


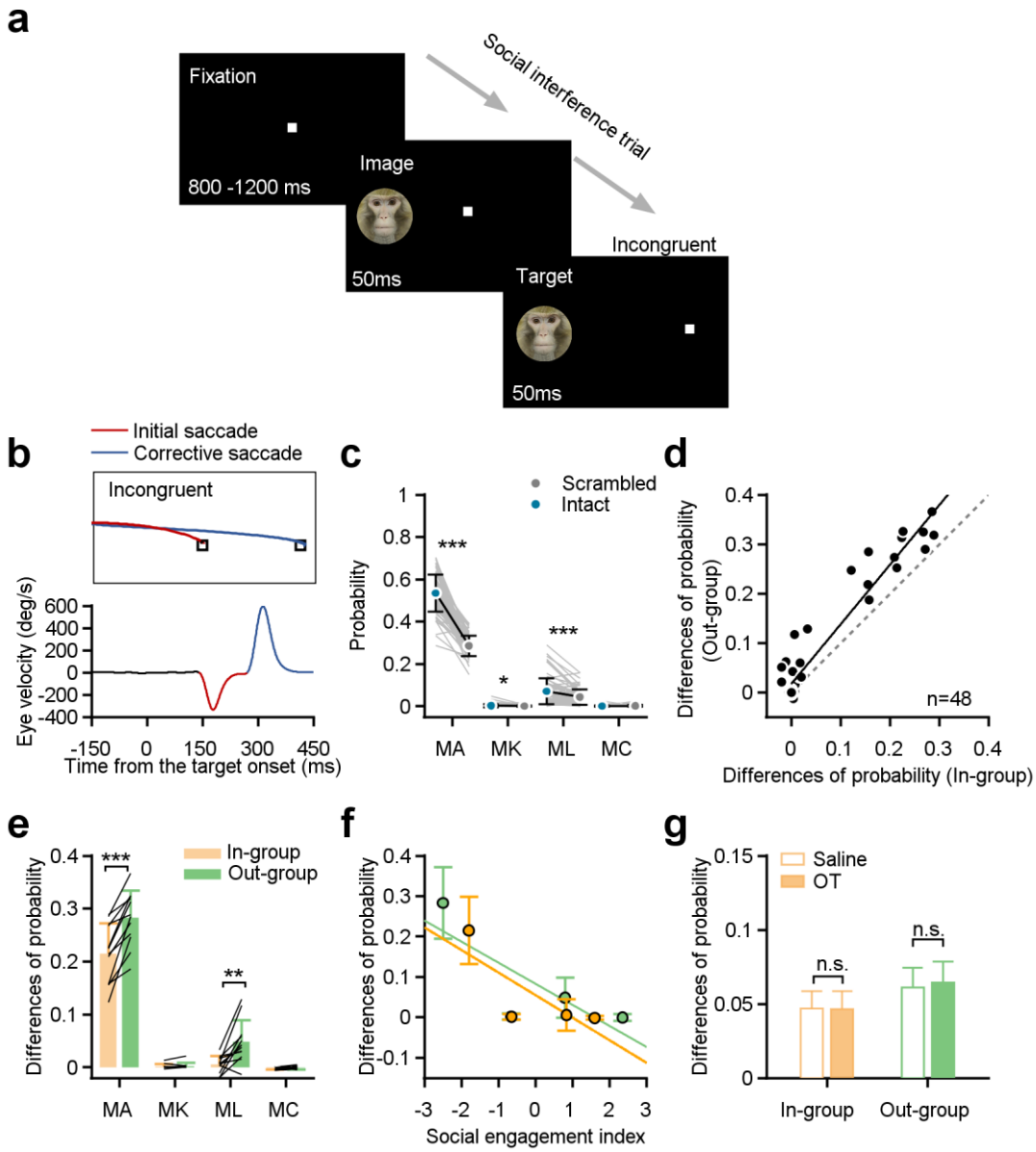
Fig. 5. Individual engagements on three dimensions of social behavior distinctly shape social attention towards in-group. a, Methodological schematic defining the correlations between the individual engagement index and the distractor bias towards in-group. **b**, Quantification of weights for three behavioral dimensions computed from correlations between IEIs and distractor biases. The intersection point of the three slices in the graph signifies the position of the maximal r value (white point), with each slice representing the r value surface along the X, Y, and Z axes, respectively. **c**, Polar graph shows the "best" weights for three social dimensions ($\omega_a = 0.54$, $\omega_g = 0.04$, $\omega_p = 0$). **d**, Relationship between IEIs with "best" weights and distractor biases (two-sided Pearson's correlation coefficient, $p < 0.001$, $r = 0.69$). **e**,**f**, The "best" weights of three social dimensions by analyzing the correlations between IEIs and distractor bias towards in-group following administration of saline (**e**) and OT (**f**). **g**, Pseudo-colored heatmaps represent the "best" weights of three dimensions of social interaction behavior in **e** and **f**. **h**, Relationship between IEIs and distractor biases (two-sided Pearson's correlation coefficient, saline: $p < 0.001$, $r = 0.63$; OT: $p < 0.001$, $r = 0.64$. The slope of saline: 48.63; the slope of OT: 23.21).

Supplementary Figures



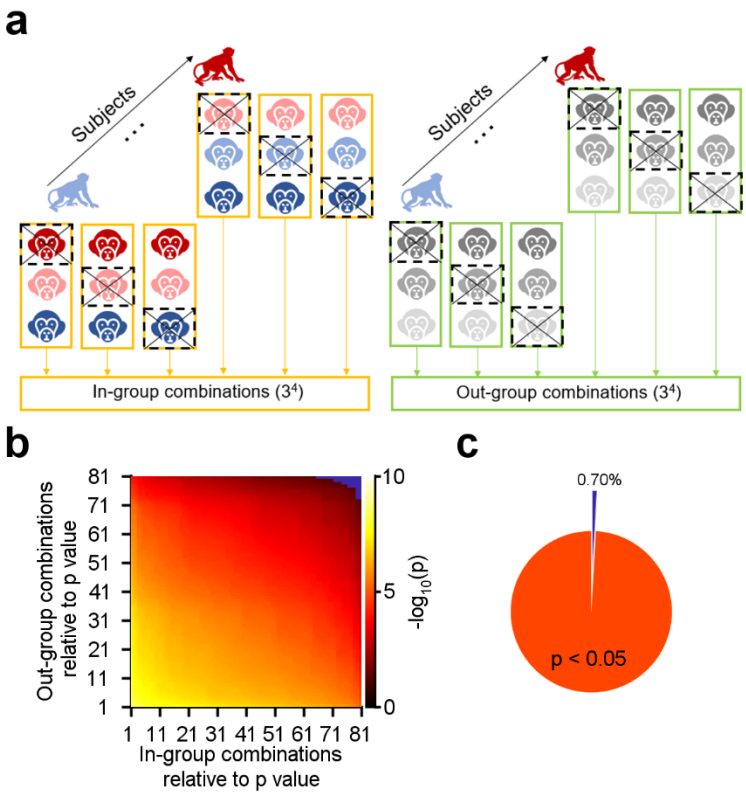
Supplementary Fig. 1. A multi-stage automatic detection system designed to recognize social interaction between monkeys. a, Detection of monkeys' postures using the YOLOv5 model: Two neighboring monkeys are recorded simultaneously by camera systems. Frames were randomly selected from the films and identified with individuals' postures, including information about their heads, bodies, and buttocks. These labeled images were applied for training the object detection framework YOLOv5s. Then the trained YOLO model was employed for inference, in conjunction with the records. This method can yield the identification of each individual monkey, the coordinates of the bounding box surrounding the object, and the category of the bounding box. Based on this information, an individual's postures can be assessed as a function of time. **b**, Detection of social interactions within pairs of monkeys by the analysis of time sequences. The posture sequences of dyadic monkeys were combined and compared frame by frame in order to

provide a mapping of social behavioral modes, such as grooming, aggression and proximity. **c**,**d** During the YOLO training process, the confidence loss of the object detection box (which measures the grid confidence), the localization loss (which quantifies the discrepancy between the predicted and annotated bounding box coordinates), and the classification loss (which measures the loss of category error between anchor boxes and their corresponding annotations) were tracked across epochs. **e**, The precision and recall curve represent the average curve for all categories. The area enclosed by the curve corresponds to the average precision (AP) value, when the IoU is 0.5. **f**, The mean average precision (mAP) value at IoU = 0.5 is 0.97, and the average of all mAP values, which are calculated by increasing the IoU threshold from 0.5 to 0.95 in steps of 0.05, is 0.89.

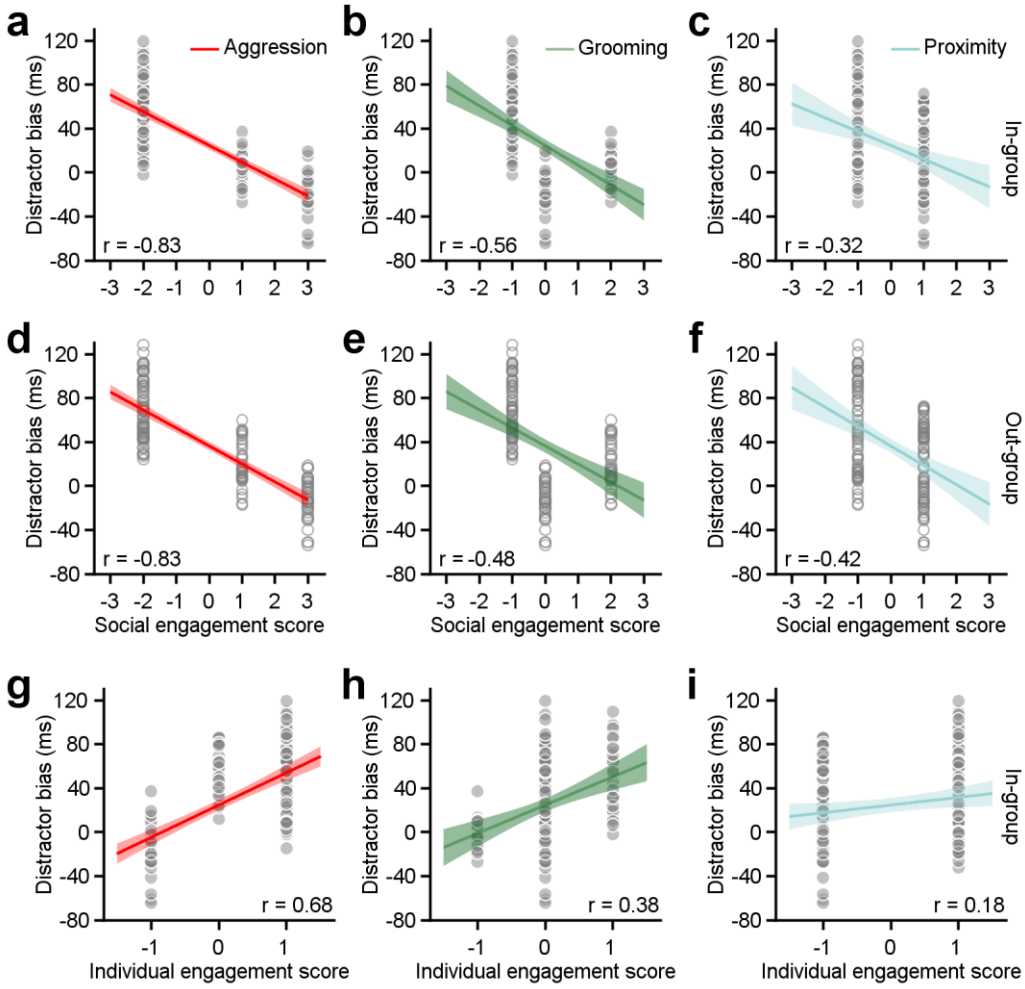


Supplementary Fig. 2. Statistical analysis on the initial saccade directing towards the distractor in the incongruent condition. a,**b**, In the incongruent condition, monkeys occasionally made their initial saccades to the distractor, and then quickly produced a corrective saccade towards the target. **c**, The choice probability of the initial saccade directing towards distractors in the incongruent condition. The monkeys exhibited a higher inclination to direct their initial saccades towards the distractor of intact monkey face (blue cycles), indicating a notable influence on attentional capture, except Monkey C who is scored by the highest SEIs (paired Student's t-test, MA: $p = 1.37 \times 10^{-34}$, MK: $p = 2.58\times10^{-2}$, ML: $p = 1.41\times10^{-5}$, MC: $p = 0.18$). Error bars: Mean ± SD. **d**, The differences of choice probability between intact monkey faces and scrambled images was calculated separately for the in-group and out-group. The change towards distractors from the in-group were significantly less than those towards distractors from the out-group across all four monkey subjects and all experimental days (paired Student's *t*-test, $p = 8.30\times10^{-6}$, $n_{in} = n_{out} = 48$).

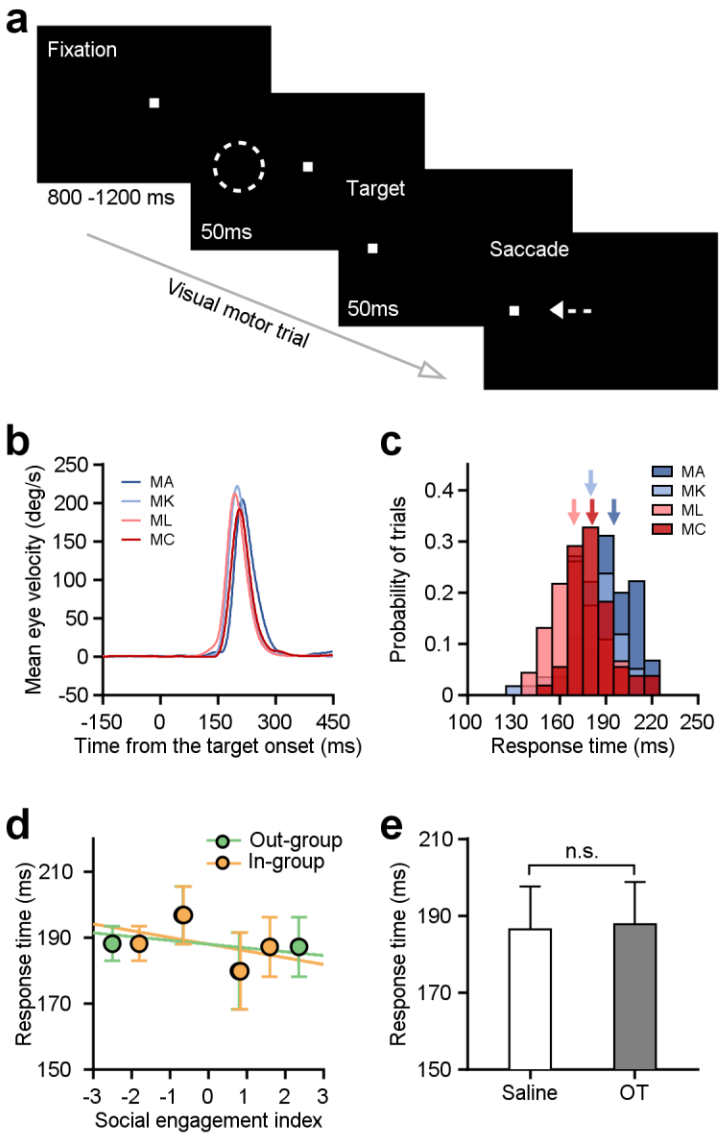
Data points lie well above the dashed unity line. **e**, The differences of choice probability in individual monkeys towards in-group and out-group distractors. Only Monkey A and L exhibited significantly higher changes towards out-group (paired Student's *t*-test, $n_{in} = n_{out} = 12$, MA: $p = 5.28\times10^{-5}$, ML: $p = 2.40\times10^{-3}$; MK: $p = 0.54$, MC: $p = 0.44$). Error bars: Mean ± SD. **f**, The differences of choice probability exhibited a negative correlation with individuals' SEIs calculated in Fig. 3**h** (two-sided Pearson's correlation coefficient, in-group: $r = -0.71$, $p = 1.21\times10^{-23}$; out-group: $r = -0.73$, $p = 1.12\times10^{-25}$). Error bars: Mean ± SD. **g**, The administration of oxytocin failed to significantly modulate the differences of choice probability in monkeys ($n = 48$, paired Student's t-test, in-group: orange bars, $p = 0.93$; out-group: green bars, $p = 0.41$). Error bars: Mean ± SEM.



Supplementary Fig. 3. The effect of a single facial stimulus on distractor biases. a, A monkey face distractor was randomly withdrawn from both the in-group and out-group stimuli for each monkey subject. This resulted in 3 combinations for each subject and a total of 81(3^4) combinations of subjects and distractors. **b**, The datasets were aligned using all p values calculated for each combination of in-group and out-group. The color map on the right side indicates the negative logarithm (base 10) of the p value. **c**, The pie plot summarized that 99.30% of 6561 combinations had significantly smaller distractor biases towards in-group monkey faces, compared to out-group faces, with p values of less than 0.05.



Supplementary Fig. 4. The correlation between distractor bias and three dimensions of social relationships in frameworks of social engagement and individual engagement. a-c, Correlations between distractor bias for in-group monkeys and social engagement scores for aggression, grooming, and proximity (two-sided Pearson's correlation coefficient, aggression: $p = 3.40\times10^{-37}$, r = -0.83; grooming: $p = 2.73\times10^{-13}$, r = -0.56; proximity: $p = 9.43\times10^{-5}$, r = -0.32). **d-f**, The correlations between distractor bias for out-group monkeys and social engagement scores for aggression, grooming, and proximity. (two-sided Pearson's correlation coefficient, aggression: $p = 5.10\times10^{-38}$, r = -0.83; grooming: $p = 8.86\times10^{-10}$, r = -0.48; proximity: $p = 1.29\times10^{-7}$, r = -0.42). **g-i**, Correlations between distractor bias towards in-group monkeys and individual engagement scores for aggression, grooming, and proximity (two-sided Pearson's correlation coefficient, aggression: $p = 3.83\times10^{-21}$, r = 0.68; grooming: $p = 3.01\times10^{-6}$, r = 0.38; proximity: $p = 3.31\times10^{-3}$, r = 0.18).



Supplementary Fig. 5. Saccadic eye movements observed during visual motor trials were unrelated to social relationships within the group. a, The design of visual stimuli in visual motor trials. When comparing social interference trials, there was an absence of distractor images given during these trials. **b**, Mean horizontal eye velocity traces of the four monkey subjects recorded on an example experimental day. **c**, The distribution of saccade latencies in individuals in B. The arrows symbolize the mean values of individual monkey subjects, presented separately. **d**, The saccade latency in visual motor trials failed to demonstrate linear associations with the SEIs calculated from the in-group and out-group settings in Fig. 3**h** (two-sided Pearson's correlation coefficient, in-group: $p = 0.08$; out-group: $p = 0.18$). Error bars: Mean ± SD. **e**, Oxytocin does not have a significant effect on the saccade latency in visual motor trials across all four monkeys, as compared to saline (paired Student's *t*-test, $n = 48$, $p = 0.31$).