Oxytocin blunts social vigilance in the rhesus macaque

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Exogenous application of the neuromodulatory hormone oxytocin (OT) promotes prosocial behavior and can improve social function. It is unclear, however, whether OT promotes prosocial behavior per se, or whether it facilitates social interaction by reducing a state of vigilance toward potential social threats. To disambiguate these two possibilities, we exogenously delivered OT to male rhesus macaques, which have a characteristic pattern of species-typical social vigilance, and examined their performance in three social attention tasks. We first determined that, in the absence of competing task demands or goals, OT increased attention to faces and eyes, as in humans. By contrast, OT reduced species typical social vigilance for unfamiliar, dominant, and emotional faces in two additional tasks. OT eliminated the emergence of a typical state of vigilance when dominant face images were available during a social image choice task. Moreover, OT improved performance on a reward-guided saccade task, despite salient social distractors: OT reduced the interference of unfamiliar faces, particularly emotional ones, when these faces were task irrelevant. Together, these results demonstrate that OT suppresses vigilance toward potential social threats in the rhesus macaque. We hypothesize that a basic role for OT in regulating social vigilance may have facilitated the evolution of prosocial behaviors in humans.

attention | primates | face gaze | neuropeptide

Oxytocin (OT) is a mammalian neuromodulatory hormone that modulates social behavior in a variety of species. Experiments across taxa implicate OT in promoting social behavior. For example, OT induces maternal bonding with offspring and partner preference (1). In humans, these findings are paralleled by studies using economic games (2). Although this body of research has led to the common interpretation of oxytocin as a "prosocial" neuropeptide, other findings suggest OT has a more complex role in primate social behavior. In squirrel monkeys, for example, intracerebral OT administration increases male–male aggression in dominant individuals, but also social contact in subordinate males (3). In rhesus macaques, intranasal OT increases the number of rewards a monkey chooses to deliver to another monkey when there is no cost to himself, but also enhances a selfish bias when there is an option to reward himself (4). These complex effects of OT are also observed in humans (5). For example, in addition to enhancing trust, OT enhances negative social judgments (6) and heightens in/out group biases in social decisions (7).

One possible mechanistic explanation for these complex effects is that OT may alter social attention, which would necessarily adjust the information available for social perception and decision making (4, 5, 8–10). Inhaled OT increases gaze toward the eye region of faces in humans (8, 10, 11) and increases the frequency and duration that rhesus macaques look at other monkeys (4). However, OT may not generally enhance social attention, but instead may bias social attention. For example, OT reduces amygdala responses (12–14), self-reported affective responses (13), and self-reported arousal (15) following threat cues in humans. Thus, it is possible that OT reduces attention to some social information. Moreover, in shifting attention away from these typically salient social cues, OT may permit rather than promote prosocial behavior.

Here, we examined how OT affects species-typical social attention in the rhesus macaque (*Macaca mulatta*). Rhesus macaques live in strongly hierarchical social groups where social rank among males is achieved through selective aggression. Rhesus males must be adept at recognizing social threats and responding appropriately. Thus, rhesus macaques exhibit a state of heightened attention to threatening social signals and unfamiliar or dominant individuals (16). Although such social vigilance reduces vulnerability to aggression, it also imposes significant time and opportunity costs (16). Thus, for the greatest adaptive advantage, social vigilance must be deployed selectively as a function of social context. Critically, the neural mechanisms that determine social vigilance in this and other primate species are unclear.

We determined the effects of intranasally delivered OT on social vigilance in male rhesus macaques. We used a battery of three social attention tasks. We first looked at gaze patterns during unconstrained social image viewing. As reported previously in humans (8, 10, 11), we found that OT increased gaze to the eye regions of photos of other monkeys. However, in contrast to the hypothesis that OT generally heightens social attention (4, 5, 8–10), OT reduced species-typical vigilance for unfamiliar, emotional, and dominant faces in two additional experiments. In a social image choice task in which monkeys chose between symbolic targets to view or not view social images, OT prevented the emergence of a typical vigilance state for faces of dominant males. In a third experiment, we examined the effect of OT in a social interference task, in which potential social threats compete for attention during performance of a reward-guided saccade task (17). OT mitigated the attentional interference of unfamiliar faces in this task, particularly blunting the effects of fearful and threatening face images. Thus, whereas OT promotes social gaze in rhesus macaques, just as it does in humans (8, 10, 11), it blunts rather than enhances species-typical social vigilance. This basic role for OT in regulating social vigilance may have been coopted to permit prosocial behaviors in humans.

Results

To determine whether OT has similar effects on social gaze in humans and rhesus macaques, we first probed the effects of inhaling OT on unconstrained viewing of faces. In experiment 1, two images were displayed on either side of fixation until the monkey stopped looking at the images for at least 500 ms. OT increased the total time that the monkeys looked at the images [$F(1,1) = 6.78$, $P < 0.001$]. Moreover, OT significantly increased the duration of fixations within the eye region [$F(1,1) = 14.74$, $P < 0.0001$]. This effect was consistent across monkeys, as indicated by a nonsignificant main effect of subject identity ($P > 0.2$). OT thus promotes gaze to the eye region in rhesus macaques, replicating previous reports in humans (8, 10, 11).

We next determined how OT affected the decision to acquire social information about various classes of social images (Fig. 1*A*; experiment 2). In this task monkeys shifted gaze to one of two identical targets to receive a juice reward and to display (target 1) or not display (target 2) an image. Trials were blocked by image category and the monkeys learned quickly within blocks

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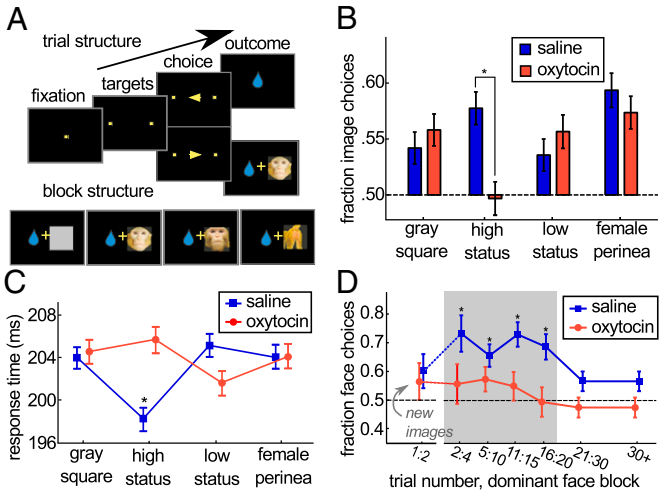

Fig. 1. OT reduces vigilance for dominant (high status) faces. (*A*) Social choice task. (*B*) OT reduced choices to view dominant face images (*$P < 0.05$; post hoc Tukey LSD; no other significant comparisons, $P > 0.1$). (*C*) OT obliterates the typical facilitation of decision making during dominant face blocks (*$P < 0.05$, post hoc LSD). No difference in response time was observed between any of the categories after OT treatment ($P > 0.2$). (*D*) OT suppresses emergence of social vigilance during dominant face blocks. After saline treatment, the frequency of image choices increases rapidly in dominant face blocks (blue trace; *$P > 0.05$, binomial test). After OT treatment, this preference never emerges (red trace; all points indistinguishable from chance, $P > 0.1$).

which image classes were available (Fig. 1*D*). Following saline inhalation, monkeys chose to display high status faces and female perinea more often than low status faces or gray square control stimuli (Fig. 1*B*, blue bars), as reported previously (18–20). Although monkeys spent more time viewing perinea than control stimuli ($P < 0.0001$), they spent less time viewing the faces of dominant monkeys ($P < 0.01$), as reported previously (19–21). Monkeys also responded about 8 ms faster in blocks with dominant faces compared with other blocks [Fig. 1*C*, blue trace; post hoc least significant difference test (LSD), $P < 0.05$]. This behavior is consistent with the hypothesis that monkeys monitor dominant individuals, but avoid directly gazing at them because this gesture is threatening (18).

OT significantly reduced the frequency of choosing to view dominant monkeys [saline: 57.8 ± 1.5% SEM, OT: 49.6 ± 1.6% SEM; $F(1,12) = 5.08$, $P < 0.005$; Fig. 1*B*]. This effect was selective for dominant faces. No significant difference was observed in the frequency of choosing to view gray squares (saline: 54.2 ± 1.4% SEM, OT: 55.8 ± 1.4% SEM), subordinate faces (saline: 53.6 ± 1.4% SEM, OT: 55.7 ± 1.5% SEM), or female perinea (saline: 59.3 ± 1.6% SEM, OT: 57.3 ± 1.5% SEM). Following saline, monkeys rapidly developed a preference to see images during dominant face blocks (Fig. 1*D*, blue trace), but OT completely blocked the development of this choice preference (Fig. 1*D*, red trace). OT also reduced the response time facilitation normally obtained during dominant face blocks [Fig. 1*C*; $F(1,12) = 6.88$, $P < 0.0001$]. Although OT had no global effects on image choice, OT treatment did increase the amount of time monkeys spent viewing all social and nonsocial images once they were chosen for display [$F(1,4) = 5.07$, $P < 0.005$]. OT also enhanced the time monkeys spent inspecting dominant faces but not other image types (paired post hoc *t* test, $P < 0.05$, T statistic = −2.84, df = 8, Bonferroni corrected). These findings indicate that OT simultaneously enhances social gaze and blunts the voluntary choice to acquire information about salient potential threats.

In contrast to experiment 2, in which monkeys had to intentionally decide to acquire social information, directing attention rapidly and adaptively to real social cues in the environment may involve different neural pathways and may therefore be affected differently by OT. Therefore, in experiment 3, we examined whether OT affects the attentional interference of unfamiliar and emotional face images and determined a partial dose–response curve for this effect. We used a social interference task (Fig. 2*A* and *Materials and Methods*) in which unfamiliar face and nonface distractor images (examples in Fig. 2*B*) were briefly flashed during performance of a visually guided saccade task. This task produces two separable but modestly correlated indices of distraction (Pearson correlation, $P < 0.0001$; $r = 0.12$): saccadic deflection and response time interference (*Materials and Methods*). Distractor images impaired task performance. After saline treatment, saccades were more strongly deflected by social distractors than by nonsocial distractors (Fig. 2*D*, saline data). Distractors also affected response times. Spatially incongruent distractors slowed saccade initiation, whereas spatially congruent ones speeded saccades relative to no-distractor trials (Fig. 3*A*). Social distractors magnified these effects by slowing response times on incongruent trials and speeding response times on congruent trials more than nonsocial distractors did (Fig. 2*A*). Incongruent emotionally expressive faces, particularly threat displays and fear grimaces, imposed the greatest response time costs (Fig. 3*C*, blue bars).

Both low and high doses of OT abolished the saccade deflection typically evoked by faces [Fig. 2*D*; significant treatment by distractor image type interaction, $P < 0.05$, $F(1,1) = 5.59$]. OT did

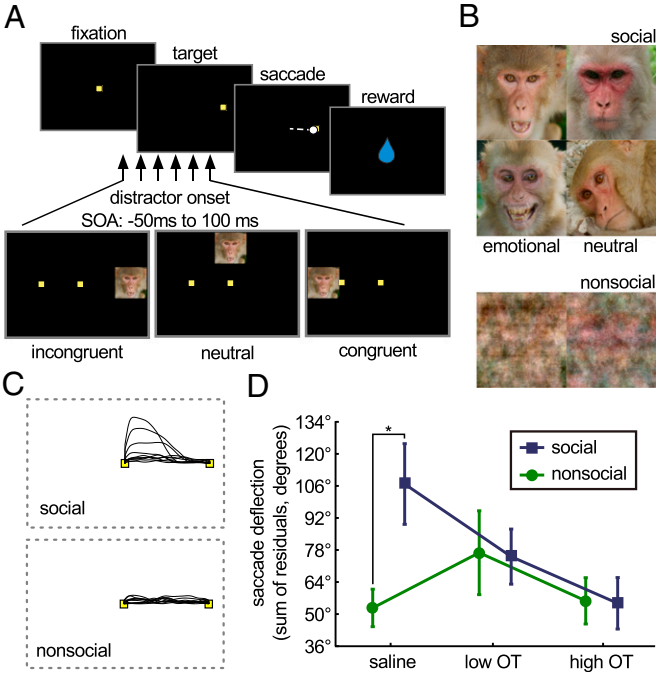

Fig. 2. OT blunts the impact of unfamiliar faces on saccades. (*A*) Social interference task and trial types. (*B*) Example distractors: social images (*Upper*) and their phase scrambled, nonsocial counterparts (*Lower*). An example threat face is depicted on the *Upper Left*, and a fearful face on the *Lower Left*. The *Upper* row contains example direct gaze faces; the *Lower* row contains averted gaze images. (*C*) Ten representative saccade residual traces from trials with social distractors (*Upper*) and nonsocial distractors (*Lower*) presented at the neutral location, smoothed for plot (Gaussian filter, SD = 2 ms). (*D*) Oxytocin reduces saccadic interference of distractors. Typically saccadic deflection is larger for social distractors than nonsocial distractors (*$P < 0.01$, Bonferroni-corrected post hoc Tukey LSD test). No difference was observed between deflection caused by social and nonsocial distractors after any OT dose ($P > 0.8$). Bars represent SEM.

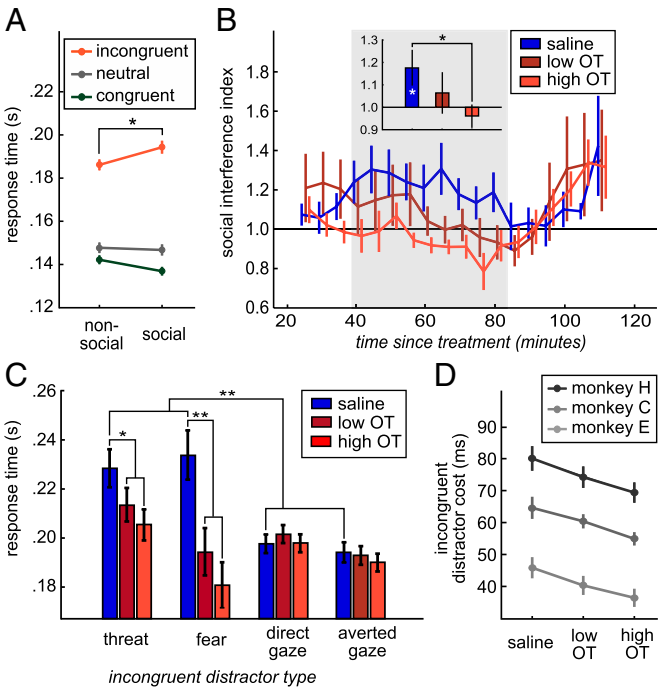

Fig. 3. Oxytocin reduces the response time interference of unfamiliar and emotional faces. (*A*) Response time is affected by distractor congruency and this effect is enhanced for social distractors [two-way ANOVA, significant interaction of social content and distractor congruency, $F(1,2) = 3.81$, $P < 0.05$]. Social distractors increase the response time slowing caused by spatially incongruent distractors (*$P < 0.05$; post hoc Tukey LSD test). (*B*) The social interference index reflects the enhanced response time interference of social images compared with nonsocial images (averaged over a moving 30-min window, 5-min steps). Shaded area reflects significant bins ($P < 0.05$). The *inset* illustrates relationship between OT doses and the social interference index during this time window (*$P < 0.02$, Wilcoxon rank sum). (*C*) After saline treatment emotionally expressive images are more distracting than nonexpressive images (**$P < 0.0001$). However, OT significantly reduced the typical response time interference caused by fearful (**$P < 0.0005$) and threatening (*$P < 0.05$) facial expressions compared with saline baseline (Bonferroni-corrected post hoc LSD). (*D*) OT speeds target response time in this task in the same dose-dependent magnitude and pattern across animals. Bars represent SEM.

not alter saccade deflections by nonsocial distractors or saccade trajectories in the absence of distractors. OT also reduced response time interference. Because response time interference was enhanced for social distractors over nonsocial distractors, we quantified the relative response time interference of social and nonsocial distractors with a social interference index (*Materials and Methods* and Fig. 3*B*, blue bar): the ratio of the variance in response times following social distractors to the variance in response times following nonsocial distractors.

In humans, plasma OT is elevated by 30 min following intranasal OT and then returns to baseline after ∼90 min (21). The effects of OT on the social interference index (Fig. 3*B*) showed a similar temporal profile. During the time window when high OT significantly reduced the social interference index, we observed a negative, dose-dependent relationship between OT and the social interference index [Fig. 3*B*, *Inset*; two-way ANOVA, significant main effect of treatment, $F(1,1) = 6.9$; $P < 0.02$; nonsignificant main effect of animal, $F(1,3) = 0.94$, $P > 0.4$]. Social images did not bias response times any more than nonsocial images after either dose of OT ($P > 0.47$). Moreover, OT significantly reduced response time interference for emotionally expressive faces [Fig. 3*C*; red bars interaction of treatment and face expression category, $P < 0.0001$, $F(1,3) = 7$; no other significant effects, $P > 0.24$].

OT speeded response times globally in experiment 3. Both low and high OT doses reduced the within-session response time costs of incongruent distractors [*Materials and Methods* and Fig. 3*D*; two-way ANOVA, significant main effect of treatment condition, $F(1,1) = 118.25$, $P < 0.01$]. Incongruent distractor costs differed slightly between monkeys [at trend: $F(1,2) = 3$, $P = 0.06$], but no interaction of monkey and treatment was observed ($P > 0.9$). No-distractor response times were also modestly sped following OT treatments [$F(1,1) = 4.59$, $P < 0.05$]. Thus, inhaled OT generally blunted reflexive attention, possibly by relaxing vigilance state.

Discussion

In direct contrast with hypotheses linking exogenously applied OT to increased social attention (4, 5, 8–10), we report multiple circumstances in which OT reduces attention to social stimuli. Specifically, our results are consistent with a model in which OT alleviates a species-typical state of vigilance toward social threats. For most primates, dominant individuals are potential sources of threat and are preferentially attended over other social cues (18, 22). Similarly, primates are more vigilant for unfamiliar animals relative to familiar individuals (23). We found that OT attenuated the emergence of social vigilance in response to images of dominant and unfamiliar individuals. Whereas OT generally promoted gaze toward social stimuli once displayed, OT did not increase the frequency of choosing to view any social stimuli or the attentional capture of any stimuli. These processes may then rely on distinct neural substrates, which in turn are differentially affected by the peptide.

Experiment 3 replicates observations in unrestrained rhesus macaques that intranasal OT blunts orienting toward unfamiliar, emotionally expressive faces displayed in the context of a dot-probe task (24). The present results extend the previous report in two significant ways. First, we also observed a general decrease in the attentional capture of faces, regardless of emotional expression. Second, whereas the previous study reported a trend toward increased attention to direct gaze faces displayed for 500 ms (24), we observed no such effect when face stimuli were presented for 67 ms. It is possible that the trend reported in the earlier study was due to a promotion of gaze to the eyes, as we found during unconstrained viewing, rather than to a promotion of attentional salience per se. However, the results from both studies support an emerging model in which OT has profound effects on the earliest stages of social information processing.

Reduced social vigilance may contribute to the increase in prosocial behavior previously observed following OT treatment (4, 5). By reducing the typical state of vigilance for social threats, OT may impede the acquisition of information about negative social cues, thereby permitting, rather than promoting prosocial behaviors that might otherwise be inhibited by those cues. For example, whereas men are typically averse to choosing high-dominance partners as allies in intergroup conflict, OT delivery reverses this preference (25), perhaps in part through affecting vigilance for threat cues in these faces. Reduced vigilance for negative social cues may also generally impede the acquisition of social information by reducing the attention allocated to social partners.

Social decisions are influenced by both accumulated social knowledge and by the immediate social context. OT may influence social decisions in part through shaping the attentional salience of information in the immediate social context (5). OT renders social decisions less responsive to the immediate social environment and more consistent with preexisting preferences (5, 26). OT magnifies preexisting biases in emotion classification (27) and in-group/out-group decision biases in economic games (7). In the macaque, OT also increases both prosocial and selfish choices in a reward allocation task, magnifying the preferences observed in the absence of OT (4). Moreover, OT slows response times for accurately

identifying facial expressions (13, 27) and for making social decisions in the presence of others (4). These results indicate that less information about the immediate social context may be available for decision processes following OT.

Paradoxically, we also found that OT increases gaze to faces and eyes, as reported previously in humans (8, 10, 11). Several plausible hypotheses can explain this finding. First, OT may make gaze more determined by perceptual features of the stimulus and less responsive to the goals of the animal. The eye region is a high contrast area (28) and contrast is an image feature which normally attracts gaze during image viewing (29). OT may increase the impact of this stimulus feature on gaze (30), perhaps through down-regulating goal-directed social attention and species-typical social vigilance. This is an intriguingly simple mechanism through which OT might promote eye contact. The use of nonsocial control stimuli with high contrast features will be essential in future studies of the social gaze effects of OT. Second, OT may disinhibit gaze toward the eyes of others. Eye gaze may be threatening or stressful, and thus tonically inhibited. OT may promote eye gaze by reducing the anxiety the behavior provokes (9). Lastly, OT may affect the efficiency of social information gathering. OT increases pupil dilation (31), which reduces visual acuity (32). High spatial frequencies in face images are important for determining characteristics like identity and age (33). Because increased pupil size necessarily reduces the perception of high spatial frequencies, it may impair the efficiency of social gaze and increased social gaze may be a compensatory behavior.

Reduced social vigilance is consistent with known neurological effects of OT. Inhaling OT reduces activity in structures that are important determinants of attention and arousal, including the amygdala (10, 12–14, 34) and the noradrenaline (NE) system (35). The amygdala regulates vigilance (36, 37), and neurons in this structure encode complex properties of faces, including emotional expression and identity (38). Although attending to faces enhances activity in the amygdala (39), OT attenuates amygdala activity (10, 12–14, 34), perhaps through increasing activity in inhibitory interneurons that regulate the activity in the central output nucleus of the amygdala (34), which in turn regulate brainstem autonomic centers. OT also down-regulates NE neurons in the locus coerruleus (35). The activity of these neurons is an important determinant of stimulus-driven attention (40). Social vigilance may be reduced through actions in either or both of these pathways.

Monitoring others consumes time and energy and is done at the expense of other goals. It is suboptimal to maintain a state of high social vigilance when the absence of threat has been clearly signaled. In humans, OT is released in response to affiliative signals and positive contact like social touch (41), affiliative vocalizations (42), and eye contact (43). Our findings suggest that positive social interactions can reduce social vigilance via OT release, thereby freeing attentional resources for other social and goal-directed behaviors. Thus, our findings resonate with the idea that OT biases global social processes away from negative information and toward positive information (24, 26). For example, OT promotes positive implicit associations with in-group members, but has mixed effects on associations with out-group members (7). Because the macaque equivalent of a happy facial expression is unclear, the present experiments could not determine whether OT promotes attention to positive facial expressions. However, OT did not increase the frequency of choices to view female perinea, although these stimuli are positive social signals for male rhesus macaques (18). OT may reinforce positive social information by enhancing memory for positively valenced social experiences (44, 45) or by inducing a perceptual bias in decision making (26).

It is unclear if OT will have similar effects on attention to others in humans. However, the gaze effects reported here and the decision making effects reported previously in this species (4) are strikingly similar to previously reported findings in humans. Like humans, the rhesus macaque is a group-living primate that uses visual displays to communicate and guide social behavior (28). Moreover, the neural circuits mediating visual social perception are largely homologous in humans and rhesus macaques (46). Our baseline behavioral data show that faces capture attention in the rhesus macaque in much the same way as they do in humans (47–49). Task irrelevant faces interfere with task performance and attentional capture is greater for emotional expressions such as fear and threat than for neutral faces. These findings indicate that the attentional prioritization of faces has either evolved in parallel across these species or has been evolutionarily conserved for at least 30 million years. In either case, the attentional prioritization of faces is clearly an important determinant of fitness in social primate species. Moreover, this result extends the utility of macaques as a model for exploring the mechanisms underlying the basic social attentive processes that contribute to the social dysfunction in autism (50, 51) and anxiety disorders (52).

Materials and Methods

Animals. All procedures were approved by the Institutional Animal Care and Use Committee at Duke University. Seven male rhesus macaques participated in these experiments, two in the preferential viewing task (experiment 1; monkeys E and O), four in the pay-per-view task (experiment 2; monkeys E, B, N, and D), and three in the social interference task (experiment 3; monkeys E, C, and H). These macaques were selected based on their availability at the time of each experiment. The macaques lived in a colony of 12 male rhesus macaques. The cages were arranged facing toward the center of the room, along two walls, permitting all animals to be in continuous visual contact. At the time of experiment 2, all macaques were pair housed. Dominance status was determined based on unidirectional submissive displays within cagemate pairs and was stable for at least a year in all cases (19). Of the monkeys who participated in experiment 2, two were subordinate (monkeys D and E) and two were dominant (monkeys N and B) relative to the monkeys used in the stimulus set. All animals were between the ages of 4 and 11 at the time of the experiments and had been in the colony for at least a year.

To allow eye position monitoring, the monkeys were surgically prepared with head restraint prostheses, as described previously (53). They were maintained on controlled access to fluids to motivate them to perform tasks. Monkeys sat in a primate chair in front of a computer monitor, although details of the experimental setup differed between experiments (see below).

Experimental Setup. In experiments 1 and 3, eye position was monitored at 1,000 Hz via an infrared eye tracking system (SR Research; EyeLink). Matlab (Psychtoolbox-3) was used to display stimuli and record eye position. Task stimuli were presented on a 51-cm wide liquid crystal display (LCD) monitor (60-Hz refresh rate, 1,920 × 1,080 resolution), located 60 cm in front of the monkey. In experiment 2, eye position was sampled at 60 Hz with an infrared camera (Arrington Research). Custom software (http://ryklinsoftware.com) controlled task presentation and recorded eye position. Task stimuli were presented on a 24-inch cathode ray tube (CRT) monitor (60-Hz refresh rate, 1,024 × 768 resolution), located 50 cm in front of the monkey. Chronologically, experiment 2 was conducted first, followed by experiment 1 and then experiment 3.

Pharmacological Manipulations. Details of OT delivery have previously been described (4). Briefly, monkeys were conditioned to accept a pediatric nebulizer mask (Pari Labs; Baby Nebulizer) over the nose and mouth through which OT (25 IU/mL; Agrilabs) or saline was delivered at a constant rate over a set period. In experiments 1 and 2, a single dose of OT (25 IU, 5 min) was used, an equivalent volume to that used previously in our laboratory (4) and typically used in humans (5, 21). We included a second, lower OT dose (10 IU) in experiment 3.

In experiments 1 and 2, behavioral testing began 30 min after treatment delivery and continued for 45 min to 1 h, depending on the speed at which the monkey completed the required trials. This timing protocol was similar to that typically used in humans (2, 8). In experiment 3, we began behavioral testing 10 min after treatment to map the time course of the behavioral effects. Behavioral testing in this task continued for 1.5–2 h, depending on the length of time the monkey was motivated to work. Treatments were delivered on alternating days, 3–5 d per week. Although the same treatment was never delivered on two consecutive days, the same treatment could be delivered in two consecutive experimental sessions. The order of treatments was counterbalanced across monkeys as well as within monkeys between weeks. Counterbalancing the order of treatments in this way allowed us to mitigate any possible order effects.

Data Analysis. Data were analyzed with Matlab. Unless otherwise noted, ANOVAs treated monkey identity as a random effect. OT treatment was included as a fixed effect nested within monkey, based on previously reported differences in cerebral spinal fluid concentrations of the peptide across animals after the same treatment dose, as well as differences in resting state concentrations of the peptide (4). All other independent variables were modeled as fixed effects. Where multiple doses of OT were delivered, treatment effects were modeled as an ordered variable. The same algorithm was used to separate saccades and fixations in all three tasks. Saccades were identified as high-velocity periods (continuously above 3° per s) that attained a minimum velocity of 15° per s. Saccade onset and offset were identified as the first and last gaze points, respectively, above the 3° per s threshold. Fixations were defined as the periods between saccades.

Experiment 1: Unconstrained Viewing Task. The unconstrained viewing task was used to look at natural viewing behavior in the absence of any task demands. Faces of two cage mates were simultaneously presented, one on the left and one on the right of a central fixation square. During the course of the experiment, the dominance relationships of several cage-mate dyads became unstable thus the impact of dominance status was not analyzed for this experiment. The monkeys fixated centrally (±3° of error) for 400–600 ms, at which point a juice reward (0.16 mL) was delivered, the fixation point extinguished, and the eccentric images illuminated 14° eccentric to fixation. The images stayed on the screen until the monkeys averted their gaze from both images (±3° of error) for at least 500 ms. Each monkey participated in four sessions of 300 trials in each of the two treatment conditions. The monkeys frequently avoided looking at the social images by saccading off screen, perhaps because looking at direct gaze faces is aversive for rhesus macaques, so this large number of trials was required to obtain a sufficient number of fixations within each image.

Task Stimuli. Images were of familiar monkeys from the colony. These images subtended ∼8° square, were selected to include only neutral expression, direct gaze faces, and were cropped to align the eye position across images. The stimulus set was composed of 20 images of each individual from each of four cage-mate dyads.

Data Analysis. Identically sized regions of interest (ROIs) were centered on the eye and mouth regions for all images. Fixation duration was determined by calculating the time that elapsed between the first and last gaze point within each identified fixation within the eye and mouth ROIs. Fixation duration within the eye region was normalized by dividing it by fixation duration within the mouth region for each presentation of each image to control for variation in the typical duration of fixations within features of the social images. The number of fixations within the eye region of the face was divided by total fixation count within the image to determined eye region fixation frequency.

Experiment 2: Image Choice Task. A previously described "pay-per-view" image choice task (18) was used to assess the voluntary choice to view images with and without OT treatment. Monkeys chose between two targets, one of which gave them a juice reward and one of which gave them a juice reward and an image. The task was blocked, so monkeys learned over the course of a block which target was associated with an image and which category of images was available. Monkeys had 300 ms to fixate (±5° of error) a central square to initiate the trial. After 300–500 ms of fixation, the yellow square extinguished and two identical 1° targets appeared (T1 and T2), displaced 15° along the horizontal axis. Fixation offset cued the monkey to choose a target by shifting gaze to it. After 500 ms of fixation (±5° of error), the chosen target was extinguished and reward was delivered. Reward varied in size between blocks, every 30–40 trials. Choosing T1 resulted in juice reward only. Choosing T2 resulted in simultaneous delivery of juice reward and display of an image that could be a gray square, a female perineum, or the face of a dominant or subordinant other. The image pool associated with T2 changed every 30–40 trials. The locations of T1 and T2 were fixed within a session, but varied across sessions. A solenoid valve controlled the delivery of juice rewards, which varied linearly and symmetrically around 0.16 mL. Single target (i.e., no choice) trials were included at a low frequency to encourage target sampling (10%). Each monkey performed four to six sessions composed of five to seven counterbalanced blocks of 30–40 trials in each treatment condition.

Task Stimuli. Social images were of familiar monkeys, all of which lived in the same colony room. These images subtended ∼5° square and their mean intensity was adjusted to match the gray square control. Each pool of social images contained 80 pictures, 20 each of four different monkeys. The faces were selected to contain only neutral expressions although a variety of gaze directions were depicted.

Experiment 3: Social Interference Task. The social interference task is a reflexive attention task, adapted from the Posner exogenous cueing paradigm (17). In this task, monkeys performed visually guided saccades while nonpredictive distractor images were flashed. Trials proceeded as follows: the monkey first fixated a central 1° target (±3° of error) for 450–650 ms and then shifted gaze to an eccentric target (1° square, 14° offset) appearing on either the left or right. Fixation on the eccentric target (±3° of error) for 150–450 ms resulted in a juice reward, which was constant within monkey across sessions and ranged from 0.15 mL to 0.35 mL per trial. In 75% of trials, a nonpredictive distractor was presented 15° from fixation at one of three locations: congruent (same hemifield), incongruent (opposite hemifield), or neutral (directly above fixation). These images were briefly flashed (for 67 ms) and presented with a variable stimulus onset asynchrony (SOA) ranging from 50 ms before target onset to 100 ms after. This SOA range minimized the predictability of the distractors and allowed quantification of both response time interference and saccadic accuracy. Intertrial intervals (ITIs) ranged from 1,750 to 2,500 ms. Each monkey participated in four sessions of 800–1,200 trials in each treatment condition.

Distractor Images. Distractors in this task were drawn from a database of pictures of rhesus macaques from Cayo Santiago Island, Puerto Rico. Faces maximized heterogeneity across sex, age, emotional expression, viewing angle, and gaze direction, although no images depicted a three-quarter or greater profile. All of the faces were unknown to the subject monkeys. The images were cropped to the face, resized to a standard size (∼7° width on screen), and intensity adjusted within each color channel to match across the stimulus set. Nonsocial control images were generated by phase scrambling the face images. The phase scrambling added identical randomly generated noise (between –pi and pi) within each Fourier-transformed color channel. To confirm that the attentional draw observed in the present experiment was not due to any luminance of social images, we compared the intensity of intact and phase scrambled images. Intact images were not brighter than phase scrambled images in terms of their mean intensity [one-sided t test, $P = 0.6$, $t(398) = 0.04$], or in terms of their median intensity [$P = 1$, $t(398) = 4.55$].

Data Analysis. In this task, spatially incongruent distractors slow response time, whereas congruent distractors speed response time relative to neutral and distractor-absent trials (17). Additionally, we examined saccade deflection, a measure of oculomotor capture (48). Saccadic deflection was defined individually for each trial by drawing a straight line from the mean location of central fixation points to the mean location of eccentric target fixation points, and taking the residuals of the actual saccade from that line at each observation (every 1 ms) along the actual saccade line. Saccadic deflection was calculated as the sum of absolute value of those residuals. Long-latency saccades (above 2 SDs from the within-session mean response time) and anticipatory saccades occurring within 30 ms of target onset were not included in these analyses. Approximately 5% of trials were discarded by these criteria.

Social Interference Index. We quantified the effect of social and nonsocial distractors on response time with a ratio of the coefficient of variation (CV) in response times following social and nonsocial distractors.

$$\frac{(\sigma_{social} \div \mu_{social})}{(\sigma_{nonsocial} \div \mu_{nonsocial})}.$$

CV is the SD of the response time distribution across congruent and incongruent trials divided by the mean. The ratio of CV for social and nonsocial distractor images reflects the amount that social interfere with response time beyond the capture caused by nonsocial images.

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