**TITLE:**

Using Dynamic, Interactive Paradigms to Study Social Neuroscience in Rhesus Macaque Monkeys

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**SUMMARY:**

Here we present two protocols to examine the neuronal mechanisms underlying live interactions between pairs of rhesus macaque monkeys, in an effort to gain insight into the neurobiology of complex social behaviors in humans.

**ABSTRACT:**

Humans and nonhuman primates exhibit complex and dynamic behaviors during social interactions. Laboratory studies, however, typically probe social cognition using simplified, discretized tasks, and rarely examine the interactions between two live agents in real-time. To address this gap, we describe two experimental paradigms featuring pairs of rhesus macaque monkeys interacting in multidimensional decision spaces. First, we describe a task-free face-off paradigm used to study the effects of neuropeptides on dominance, an essential building block of macaque society that color all other aspects of social interactions. Then, a virtual soccer game is used to examine the neuronal mechanism of strategic competition, an important part of animals’ fight for survival when faced with limited resources. Utilizing these innovative paradigms, in combination with an array of behavioral and physiological measurements, we have uncovered how different key regions within the social brain network contribute to the complex behaviors observed in natural social interactions, and how neuropeptides modulate such behaviors.

**INTRODUCTION:**

Many animals, including humans, have evolved to live among large groups of conspecifics. Thus, various aspects of our everyday experience and consciousness are social in a most fundamental sense, as they are often determined by and directed against inputs from other people1-2. This social experience can be perceptual, such as recognizing a face or comprehending a speech, or more abstract and strategic, such as deciding whether to attend a party and, if at the party, whether to talk to someone or to avoid them. Social neuroscience examines the neuronal underpinning of these perceptual and decision-making processes. Many early studies in social neuroscience adopted a representationalism perspective3-4 and treated social cognition as an internalized process within an individual. As such, these studies predominantly featured individual subjects responding to “social” stimuli such as pictures or videos of other conspecifics. Even though such paradigms successfully identified a number of key brain areas contributing to social cognition5, it is unclear how these areas mediate everyday social interactions such as trusting, betraying, questioning, deceiving, competing, cooperating, bargaining, and offering, all of which require attending to the inputs from other people in real-time.

Some studies have aimed at filling this gap by using interactive behavioral paradigms inspired by or borrowed from game theory6, such as choosing between betraying or cooperating with someone7-8 or deciding whether to donate or invest in someone9-14. While preserving certain features of interpersonal interactions, these studies still feature discrete, static, often binary choices that do not necessarily reflect the complexity of real-life interactions15-16, as the latter often occur within an evolving decision space that is continuously reshaped by an individual’s own behavior and the behavior of other individuals.

To overcome these limitations, here we report two studies in which pairs of rhesus macaque monkeys interact in multidimensional decision spaces. Much like humans, macaques live in large, hierarchical, mixed-sex groups17 and use visual and vocal signals to communicate social information to each other18-20. These behaviors are mediated by a network of cortical and subcortical brain areas homologous with the human social brain network21-23. Together, these factors make macaque monkeys the ideal animal model for studying the neurobiology of social cognition and social deficits associated with psychiatric disorders24-26. In the first study, a task-free “face-off” paradigm is used to probe how neuropeptides oxytocin (OT) and arginine vasopressin (AVP) affect naturalistic, spontaneous behaviors in monkeys27. In the second study, the behavior and attendant physiology of monkeys playing a two-player competitive “soccer” game (aka “penalty kick”) is examined. We found that different key regions within the social brain network, namely the anterior cingulate gyrus (ACCg) and the mid-superior temporal sulcus (mSTS), significantly contribute to the naturally complex behaviors observed in social interactions, and neuropeptides OT and AVP can modulate such behaviors.

**PROTOCOL:**

All procedures reported in this study were approved by the Institutional Animal Care and Use Committee of the University of Pennsylvania and performed in accordance with their relevant guidelines and regulations.

**1. Experiment 1:** **Modulation of Spontaneous Social Interaction and Flattening of Dominance Hierarchy with Oxytocin and Vasopressin**

NOTE:The entirety of this experimental protocol has been described previously in detail27.

**1.1. Animals**

1.1.1. Use adult rhesus macaque monkeys (*Macaca mulatta*) for this experiment.

NOTE: For the experiment described here, the participants are seven monkeys from the same colony room.

1.1.2. Ensure that, for the duration of the experiment, all monkeys occupy the same colony room and are in continuous visual and auditory contact with each other within the colony.

1.1.3. Ensure that all animals have settled in the colony for at least half a year before starting the experiment; do not introduce new members into the colony for the duration of the experiment.

**1.2. Experimental set-up**

1.2.1. In each experiment session, place two monkeys in their respective primate chairs and position the two chairs close together (~30 cm apart from edge to edge) so that the monkeys can see each other face-on without touching.

1.2.2. Position a video camera (60 fps) on the right side of M1/the left side of M2 to simultaneously record both monkeys’ behaviors for 5 min.

NOTE: M1 is defined as the monkey that receives the pharmacological treatment each day; M2s are all the other monkeys who do not receive treatment for that day.

1.2.3. On each day, ensure one M1 faces all different M2s (six in total) sequentially, each for 5 min. In addition, ensure that the same M1 faces an empty chair for 5 min as a nonsocial control. Ensure that the order in which M1 faces the M2s and the empty chair is determined randomly each day.

**1.3. Pharmacological manipulation**

**1.3.1. Inhalation**

NOTE: The detailed procedure for the intranasal OT delivery in macaque monkeys has been described previously14.

1.3.1.1. Briefly, first train monkeys to accept a pediatric nebulizer mask over the nose and mouth through positive reinforcement.

1.3.1.2. On each day, deliver 1 mL of OT (25 IU/mL in saline), AVP (25 IU in 1 mL of saline), or saline through the nebulizer at a constant rate (0.2 mL/min) over a total of 5 min (only to M1, not M2s).

1.3.1.3. Ensure that the neuropeptide and saline treatments are delivered on alternating days, with each monkey receiving no more than five treatments per week.

1.3.1.4. Make sure that the video recording is done 30 - 120 min after the intranasal delivery.

1.3.1.5. Repeat each treatment 5x in each M1.

**1.3.2. Injection**

NOTE: The procedure for the OT injection has also been described previously28.

1.3.2.1. Briefly, first identify the location of ACCg through structural magnetic resonance images (MRI; 3Tesla (T), 1 mm slices) and then confirm it with electrophysiological recordings.

1.3.2.2. On each day, restrain the subject monkey *via* a head holder fixed on the primate chair, and inject 2 μL of OT (0.5 IU/μL of OT in saline), AVP (1 IU in 2 μL of saline), or saline into the ACCg *via* a microsyringe (only to M1, not to M2s). To minimize tissue damage, make sure all injections are delivered at a rate of 0.2 μL/min and restricted unilaterally in each animal.

1.3.2.3. Ensure that the neuropeptide and saline injections are delivered on alternating days, with each monkey receiving no more than one injection every other day.

NOTE: Do not inject OT and AVP in the same monkey within the same week.

1.3.2.4. Repeat each treatment 5x in each M1.

**2. Experiment 2: Examination of Strategic Competition with a Virtual Soccer Game**

**2.1. Animals**

2.1.1. For the competitive soccer game, train at least two adult macaque monkeys as kicker and two as goalie (see below for the initial training).

2.1.2. Ensure that, for the duration of the experiment, all monkeys occupy the same colony room and are in continuous visual and auditory contact with each other within the colony.

**2.2. Behavioral paradigm**

**2.2.1. General set-up**

2.2.1.1. Position a monkey player in a primate chair with its head restrained and facing a 120 Hz LCD monitor (27 inch) 60 cm away, with access to a joystick mounted in a clear box attached to the front of the chair.

2.2.1.2. Ensure that the monkeys can look around throughout the experiment without turning their heads. Record the eye movements and pupil size changes with an infrared eye-tracking system (1,000 Hz) mounted on the primate chair.

2.2.1.3. Use a computer running software (*e.g.*, MATLAB) and Psychtoolbox to control all aspects of the experiment, including displaying visual stimuli on the monitor, sampling continuous input from the joystick (at 120 Hz), and opening and closing solenoid valves to dispense juice rewards.

2.2.1.4. Use Psychtoolbox to render three stimuli on the screen—the ball (controlled by the kicker), the bar (controlled by the goalie), and the goal line—against a black background. Luminance-balance all stimuli on the screen by adjusting the corresponding RGB values.

2.2.1.5. At the beginning of each trial, render the ball and the bar in the middle of the screen. Ensure that the ball is on the left and the bar on the right in front of the finish line. Throughout the trial, render the ball across the screen (left to right) at a constant horizontal speed (~350 pixels/s).

2.2.1.6. Train the kicker to use the joystick to move the ball vertically to bypass the goalie. Train the goalie to use the joystick to move the bar vertically to block the ball (see section 2.2.2). Ensure the Y-axis speeds of the ball and the bar are constant, and that the joysticks only control the direction of the movement.

2.2.1.7. At the end of each trial, deliver a juice reward to the winner (~0.8 mL) but not to the loser. Ensure the juice tube is positioned with the mouthpiece attached to the primate chair and within the monkey’s reach.

**2.2.2. Initial behavioral training**

2.2.2.1. First, train the monkeys on the virtual soccer game by making them play with a computer opponent exclusively. Ensure that the computer kicker and goalie follow very simple movement algorithms and always move in straight lines (with no redirections).

NOTE: This stage of training is classic behavior shaping.

2.2.2.2. When training the goalie, first make the ball go in one direction every time (*e.g.*,45° up), and reward the monkey for any movement in the right direction, until it gradually approaches and finally catches the ball. Then, change the ball direction and repeat the process. When training the kicker, systematically make the goalie bar block off different portions of the screen and reward the monkey for any movement away from the goalie bar.

2.2.2.3. Train the monkeys with the same algorithms until their performance reaches at least an 80% win rate against a computer opponent in all movement directions.

**2.2.3. Live-play condition**

NOTE: All experiments should be carried out in a dimly lit room (20 - 35 cd/m2) to ensure the visibility of the opponent.

2.2.3.1. Refer to section 2.2.1 for the general experimental set-up, including monitors, programs, monkey restraint, and eye tracking.

2.2.3.2. During the live-play condition, position the two players at opposite corners of the room, allowing both visual access to their opponent. Place a monitor displaying the visual stimuli in front of each player (60 cm). In other words, ensure that each player faces a monitor directly ahead and an opponent at a 45° angle.

2.2.3.3. Throughout the experiment, use a video camera mounted on top of each monitor to record the facial and hand movements of the monkey facing that monitor.

2.2.3.4. Adjust the length of the goalie bar slightly (ranging 250 - 350 pixels) to ensure an average win rate of 35% - 65% for both players. Ensure that the colors, speeds, dimensions, and starting positions of the ball bar and the goalie bar are consistent across all sessions.

**2.3. Electrophysiological recording**

**2.3.1. Localization of the mid-superior temporal sulcus**

2.3.1.1. Use structural magnetic resonance images (MRI, 1 mm slices) to guide the placement of recording tracks (see Jiang and Platt27 and Chang *et al.*28 for more detailed descriptions of MRI methods).

NOTE: A mask consisting of a 3 mm sphere around a seed at the fundus of the STS was made (X = 18.75, Y = -10.00, Z = -2.25, according to the Montreal Neurological Institute [MNI] atlas), and this choice was based on previous research indicating that this region of mSTS exhibits a functional connectivity profile most similar to the human temporoparietal junction (TPJ)29.

2.3.1.2. Convert the mask to the individual monkey’s native-space structural scan to identify the target recording location.

**2.3.2. Single-unit recording**

NOTE: Single-unit recording should be performed while the monkeys are actively competing with each other in the virtual soccer game.

2.3.2.1. Make single-unit recordings with either single tungsten electrodes or multichannel linear arrays.

2.3.2.2. On each day, restrain the subject monkey *via* a head holder fixed on the primate chair. Secure a sterilized single electrode or electrode array onto the recording chamber *via* an X-Y stage and an adapter.

2.3.2.3. Penetrate the dura using a sterilized guide tube (22 G, stainless steel), and lower the electrode through the guide tube *via* a hydraulic microdrive.

2.3.2.4. Filter and record multiunit activity, as well as local field potentials (LFPs). Isolate the activity of single neurons offline using principal component analysis (PCA) and other sorting algorithms in three-dimensional feature space.

**REPRESENTATIVE RESULTS:**

**Experiment 1. Modulation of Spontaneous Social Interaction and Flattening of Dominance Hierarchy with Oxytocin and Vasopressin:**

Most prior studies have focused on examining how neuropeptides modulate performance in arbitrary laboratory tasks, thus limiting ecological validity and translational potential. As both OT and AVP are being extensively investigated for their therapeutic potentials in improving daily social interactions and communications, we decided to test their effects on spontaneous, naturally occurring social behaviors. We recorded a series of 5 min-long videos of pairs of adult male macaque monkeys interacting with each other in close proximity (see **Figure 1A**, as well as **Animated Figure 1**). Prior to each session, one monkey (hereafter M1) inhaled either saline or OT *via* a pediatric nebulizer, whereas the other monkey (hereafter M2) did not receive any treatment. Both monkeys’ behaviors were rated by independent observers and subsequently converted to a set of ethograms (see **Figure 1B,C** for example ethograms and a summary of quantifiable behaviors from one monkey pair in four consecutive saline sessions).

The results of this study have been published in their entirety27. Briefly, the overall effect of OT across the population was a small reduction in staring by the treated monkey (**Figure 2A**), as well as in his untreated partners (**Figure 2B**). As a direct stare is considered dominant behavior among male monkeys, a decrease in mutual staring indicates a relaxation of social interaction under OT treatment. Note that the monkeys’ staring behavior at an empty chair remained unchanged, indicating that the effect of OT was specifically social (**Figure 2B**, inset). Across all possible monkey pairs (*n* = 7 x 6 = 42), the difference between the staring durations of M1 and M2 varied greatly, reflecting the existing social hierarchy (**Figure 2C**). OT narrowed this gap and diminished the difference in staring durations, suggesting a flatter dominance hierarchy (**Figure 2D**).

Due to a strong similarity in molecular structure, OT can bind to AVP receptors with high affinity and *vice versa*30-32.Thus, delivering either OT and AVP at a high concentration may evoke behavioral changes by recruiting both neuropeptide systems. To address this, the effects of OT and AVP inhalation were systematically compared at the same concentration in the same subjects (25 IU delivered in a 1 mL saline vehicle). We found that, just as OT, AVP inhalation significantly reduced the staring by the treated monkeys, as well as by their untreated partners. Overall, AVP was more effective than OT in reducing staring by all monkeys. Notably, in neither condition did the treatment alter the monkeys’ staring behavior at an empty chair. Across all monkey pairs in this dataset (*n* = 3 x 6 = 18), OT and AVP similarly flattened the pre-existing social hierarchy (**Figure 2E**).

Finally, we investigated the neural circuitry mediating the behavioral effects of OT and AVP. To do so, OT or AVP (1 IU in a 2 µL saline vehicle) was injected focally into the ACCg, a subregion of ACC strongly implicated in social behavior33. We found that just as with the inhalation treatments, both OT and AVP injections significantly reduced the staring by the treated monkeys, as well as by their untreated partners, without altering their staring behavior at an empty chair. Across all monkey pairs (*n* = 2 x 6 = 12), both OT and AVP injections also effectively flattened the existing social hierarchy (**Figure 2F**).

**Experiment 2. Examination of Strategic Competition with a Virtual Soccer Game:**

In this experiment, the behaviors of monkey kickers playing virtual soccer against conspecific goalies were studied. Kickers used a joystick to move a ball across the screen (left to right) to reach the goal line; goalies used a joystick to move a goalie bar to try to block the ball. A trial ended when either the kicker maneuvered the ball to the goal line or the goalie intercepted the ball (see **Animated Figure 2** for recorded live trials). **Figure 3A** depicts representative trajectories of kicker and goalie movements in a 25-trial block, during which both players won with comparable probabilities. Although each trial began exactly the same way and ended with a simple, symmetric, zero-sum payoff, the task elicited complex, dynamic interactions between pairs of monkeys.

This complexity in competitive behavior was reflected in the variability of response times (RT, defined as the time of the first move made by the player) for both kickers and goalies across trials (**Figure 3B**). On most trials, however, goalies lagged kickers by a short delay (kicker = 0.60 ± 0.01 s, goalie = 1.00 ± 0.01 s, *r* = 0.17, *P* = 0.000). In addition, kickers often changed their trajectories online (hereafter ‘redirections’) to increase their chances of bypassing the goalie. A higher redirection rate was correlated with winning for the kicker but not for the goalie (the kicker redirection rate on losing trials = 0.79 ± 0.01, winning trials = 0.93 ± 0.01; the goalie redirection rate on losing trials = 0.80 ± 0.01, winning trials = 0.68 ± 0.01) (**Figure 3C**). Overall, goalies tended to redirect in response to kicker redirections, consistent with a reactive strategy (*r* = 0.46, *P* = 0.000). Furthermore, both kickers and goalies varied in their movement directions across trials (**Figure 3D**). Just like penalty kicks in real soccer34-38, goalies tended to do better when their movements perfectly mirrored those of the kicker (diagonal line, upper left to lower right corner, kicker win rate = 0.31). Nevertheless, not all movement combinations were equally effective. Generally, monkeys were able to align their plays with the probabilities of winning. For example, monkey kickers were less likely to win when their final shot was downwards (second and fourth columns, kicker win rate = 0.37) and, in fact, kickers were less likely to shoot downwards (48.2%) than upwards (51.8%). Additionally, as in real soccer, the kicker performance was positively correlated with the variability of ball end point (*r* = 0.32, *P* = 0.000).

In summary, the relatively unconstrained movements from pairs of players in the task presented here can be reduced to a set of quantifiable behavioral parameters that define each player’s strategies. Although the final outcome of the game is a result of the interaction between two players, the kicker and the goalie clearly benefit from very different strategies. In general, kickers win by being unpredictable, while goalies win by quickly and precisely responding to the kickers’ actions. It is worth noting that, as the same two players competed against each other over and over again, they relied more heavily on one strategy or the other at different time points. Most importantly, changes in the goalie’s strategy always closely followed changes in the kicker’s strategy (**Figure 3E-G**), illustrating the mutually evolving nature of this behavioral paradigm.

During gameplay, we also recorded neuronal activity in mSTS, an area of the macaque brain long associated with social perception39-43 and recently identified as the potential homolog of human TPJ29. We found that, in both kickers and goalies, mSTS neurons signaled the complexity of play, as well as trial outcomes (*n* = 133 mSTS neurons in kicker, 125 mSTS neurons in goalie) (**Figure 4A**). During the task performance, the kicker’s mSTS population showed increased activity, whereas the goalie’s mSTS population showed suppression (kicker: 41/133 = 30.8% neurons were significantly modulated, among which 80.5% were excitatory; goalie: 28/125 = 22.4% neurons were significantly modulated, among which 67.9% were suppressive). During and, especially, after reward delivery, in both kickers and goalies, the mSTS activity was significantly elevated above baseline (kicker: 55/133 = 41.4% neurons were significantly modulated, among which 72.7% were excitatory; goalie: 97/125 = 77.6% neurons were significantly modulated, among which 96.9% were excitatory). We also found that, during task performance, the neuronal activity in the kicker’s mSTS significantly distinguished whether any redirections were made (firing rate with no redirections = 18.42 ± 0.25 spikes/s, with redirections = 22.03 ± 0.29 spikes/s) (**Figure 4B**, upper panel). By contrast, the neuronal activity in the goalie’s mSTS was not correlated with the number of redirections made but, instead, was correlated with the response time of the goalie relative to the kicker (the firing rate when the goalie moved before the kicker = 31.77 ± 0.28 spk/s, when the goalie moved after the kicker = 28.54 ± 0.42 spk/s) (**Figure 4B**,lower panel). During the reward epoch, by contrast, both the kicker’s and the goalie’s mSTS activities were elevated for winning over losing (kicker: 54.1% neurons distinguished winning from losing, among which 93.1% preferred winning; goalie: 84.0% neurons distinguished winning from losing, among which 89.5% preferred winning) (**Figure 4C, D**).

Together, these findings demonstrate that mSTS activity correlates with various aspects of dynamic, strategic social interactions. During task performance, mSTS activity covaries with the level of effort exerted by the kicker, as well as the responsiveness of the goalie to the kicker. During and after reward delivery, mSTS neurons most reliably signal winning over losing. To our knowledge, these are the first abstract, strategic, nonperceptual social signals reported in the primate mSTS.

**FIGURE AND TABLE LEGENDS:**

**Figure 1:** **Ethograms and quantifiable behaviors.** (**A**) This panel shows the experimental design. The top shows the treatment administration: one monkey (M1) received saline, OT, or arginine-vasopressin (AVP) treatments *via* intranasal nebulization or intracortical injection. The bottom shows the experimental set-up (left: top-down view; right: side view). After receiving the treatment, the same M1 faces another monkey (M2) or an empty chair for 5 min in close proximity, with a camera on the side recording all behaviors to a video file. (**B**)This panel shows an example set of ethograms from one monkey pair facing each other in four saline sessions. M1 (Sh) inhaled saline; M2 (E) did not. (**C**) This panel shows a summary of behaviors demonstrated by the same M1 (Sh) facing different M2s under the influence of saline. X-axis: M2 identities, ordered by the time M1 spent staring at each. Y-axis (left): average M1 behavior (*i.e.*, staring, looking away, turning away) durations. Y-axis (right): average M1 behavior (*i.e.*, yawning) frequency. This figure has been modified from Fig. 1 of Jiang and Platt27.

**Figure 2:** **OT and AVP inhalation and injection modulate the pre-existing social hierarchy.** (**A**) Overall, OT treatment reduces staring by M1 (*n* = 7 male monkeys, 180 face-off sessions x 2 treatment conditions). The black line illustrates the gamma fit of the saline distribution, the magenta line the gamma fit of the OT distribution. The arrows indicate medians. (**B**) OT treatment also reduces the overall staring time by M2. The black line illustrates the gamma fit of the saline distribution, the magenta line the gamma fit of the OT distribution. The arrows indicate medians. The **insert** shows that,compared with saline (grey), OT (pink) does not change M1’s staring at an empty chair. The error bars = the mean ± the standard error of the mean (SEM). (**C**)As M1’s staring increases, M2’s staring decreases, and the difference between the two widens correspondingly. X-axis: monkey pairs ordered according to the difference between M1’s and M2’s staring times; left to right corresponds to an increasing dominance of M1 over M2. (**D**) OT inhalation narrows the gap between the staring durations of M1 and M2 and flattens the dominance hierarchy. X-axis: monkey pairs in the same order as in panel **C**. (**E**) In a different monkey colony (*n* = 3 male monkeys as M1s, 3 male and 4 female monkeys as M2s, 90 face-off sessions x 3 treatment conditions), both OT and AVP inhalations reduce the difference between M1’s and M2’s staring. X-axis: monkey pairs ordered by the difference in staring between M1 and M2 under saline; left to right corresponds to an increasing dominance of M1 over M2. (**F**) Both OT and AVP injections in the ACCg decrease the difference between M1’s and M2’s staring (*n* = 2 male monkeys as M1s, 3 male and 4 female monkeys as M2s, 60 face-off sessions x 3 treatment conditions). X-axis: monkey pairs ordered by the staring difference between M1 and M2 under saline; left to right corresponds to an increasing dominance of M1 over M2. This figure has been modified from Fig. 2, 4, and 5 of Jiang and Platt27.

**Figure 3: Monkeys display complex strategies in the virtual soccer game.** (**A**) This panel shows the movement trajectories of the kicker and the goalie in 25 consecutive trials. The ball (blue) moves across the screen from left to right with a fixed horizontal speed; the kicker only controls the ball’s movement vertically. The goalie only controls the goalie bar (red) vertically. X-axis: time. Y-axis: The Y-axis on the screen. For this display, the goalie’s trajectory is compressed along the X-axis. Crosses mark the response time (defined as the time of the first movement of the ball or bar); circles mark any redirections (defined as sudden (<0.1 s) changes in the ball or bar direction). The blue lines illustrate kicker trajectories in losing trials, the cyan lines kicker trajectories in winning trials, the red lines goalie trajectories in losing trials, and the pink lines goalie trajectories in winning trials. The white line illustrates the finish line. (**B**) This scatterplot shows the response times of the kickers and goalies in all live trials. (**C**)This panel shows the average number of redirections made per trial in winning and losing trials. The error bars = the mean ± the SEM. (**D**) This table shows the number of trials (black) and the associated win rate (kicker, blue) in each movement direction combination. Kicker left-to-right columns and goalie top-to-bottom rows: started upward and continued, started upward and finished down, started upward and ended down, started downward and continued. Blue cells show the kicker win rate >0.5 and pink cells the goalie win rate >0.5. (**E**) This graph shows the correlation between response time-related strategies and monkey performance (measured as the correlation between the kicker response time and the kicker win rate, and the goalie-kicker response time and the goalie win rate in every 100 trials). X-axis from left to right indicates the time. (**F**) This graph shows the correlation between redirection-related strategies and monkey performance (measured as the correlation between the kicker redirection rate and the kicker win rate, and the goalie-kicker redirection rate and the goalie win rate in every 100 trials). X-axis from left to right indicates the time. (**G**) This graph shows the kicker correlations from panels **E** and **F** plotted together to show the switches between strategies.

**Figure 4: mSTS neurons signal strategic information and trial outcomes during live competition.** (**A**) This graph shows the population peristimulus time histograms (PSTHs) for all mSTS neurons recorded during live trials, segregated by the trial outcome and aligned with trial onset (normalized to the pretrial baseline). The thin grey lines indicate the beginning and end of the gameplay. Reward delivery starts at the end of the gameplay and lasts 0.8 - 1 s, as indicated by the thick grey line. The thickness of each line indicates the mean ± the SEM.(**B**)The top panel shows the firing rate distribution (z-scored to the pretrial baseline) for the kicker’s neurons during the task epoch, segregated by whether any redirections were made by the kicker. The bottom panel shows thefiring rate distribution (z-scored to the pretrial baseline) for the goalie’s neurons during the task epoch, segregated by whether the goalie moved before or after the kicker. (**C**)This panel shows the firing rate distribution (z-scored to the pretrial baseline) for all kicker neurons during the reward epoch, segregated by the trial outcome. (**D**) This panel shows the firing rate distribution (z-scored to the pretrial baseline) for all goalie neurons during the reward epoch, segregated by the trial outcome.

**Animated Figure 1: Face-off.** A brief video clip (~1 min) taken from one experimental session. M1 (D, left) inhaled OT prior to the experiment, whereas M2 (S, right) did not receive any treatment. A variety of behaviors can be identified from the video clip, including (not necessarily in this order) staring, lip-smacking, looking away, turning away, and yawning.

**Animated Figure 2:** **Penalty kick.** Ten consecutively recorded trials of a monkey kicker playing against a monkey goalie. X-axis: The X-axis on and off screen (normalized). Y-axis: The Y-axis on screen (normalized). The white line is the finish line, the green circle the kicker eye position, and the magenta circle the goalie eye position. The green rectangle indicates the physical location of the kicker and the magenta rectangle indicates the physical location of the goalie.

**DISCUSSION:**

This study reported on two interactive paradigms, both featuring pairs of nonhuman primates responding to each other’s behaviors and modifying each other’s behavioral environment in real-time. The ‘face-off’ paradigm was used to examine the effects of neuropeptide treatment on social dominance, whereas the ‘penalty kick’ paradigm was leveraged to investigate how primate mSTS contributes to strategic competition. While the neurobiological questions motivating these studies are very different, both behavioral paradigms aim to improve upon the existing experimental designs in social neuroscience by providing the subjects with a more dynamic and evolving decision space. In the following sections, the potential applications, theoretical impact, and limitations to these two paradigms will be discussed.

**Experiment 1. Modulation of Spontaneous Social Interaction and Flattening of Dominance Hierarchy with Oxytocin and Vasopressin:**

The current study shows that treating a group of male macaque monkeys intranasally with aerosolized OT relaxes their spontaneous social interactions with others and flattens the preexisting status hierarchy among monkeys. These results lend further support to the positive link between OT and social behavior observed in a variety of animals, from rodents44-49 to nonhuman primates14,28,50-55. In contrast, the functional involvement of the OT system in human behavior, especially the effect of acute OT administration, remains highly controversial56-60. This substantial disparity between animal and human OT research may be deeply rooted in the fact that OT often has task- or stimulus-specific effects in humans61-65, and it can interact with individual traits such as gender, personality, attachment styles, and psychopathology66-69, making it difficult to compare across studies70-71. In this study, we chose to exclusively examine naturalistic social interactions among adult male macaque monkeys belonging to a small, stable, hierarchical group. This unique combination of a task-free paradigm and a closed social group may have contributed to the detectability of OT effects.

Additionally, using the same paradigm, we also found that the intranasal delivery of aerosolized AVP reproduces the effects of OT with greater efficacy and that all behavioral effects are replicated when OT or AVP is injected focally into the ACCg. As most cortical areas in primates, including the ACCg, lacks OT receptors but is rich in AVP receptors72, these results indicate that exogenous OT may shape social behavior partially through nonspecific binding with AVP receptors. These findings bear important implications for the future use of OT in basic as well as translational research, and further highlight the importance of using flexible, naturalistic behavioral paradigms to investigate the neurobiology of nonapeptides.

It is worth noting that the otherwise unconstrained paradigm presented here does require placing monkey pairs in respective primate chairs, thus limiting their ability to avoid or retreat from each other. However, because the monkeys’ heads are unconstrained, they can still look away or turn away from each other. While this set-up may have, to some extent, inflated the naturally existing tension among monkeys, it is necessary to induce quantifiable confrontational and avoidant behaviors, especially given the time constraint that is faced when conducting behavioral testing post neuropeptide inhalation in multiple monkey pairs.

**Experiment 2. Examination of Strategic Competition with a Virtual Soccer Game:**

Like perceptual decision making73-74 and neuroeconomics75-78, most prior research on social decision making has employed binary choice tasks (*i.e.*, two-alternative forced choice [2AFC] tasks) (for examples, see Rilling *et al.*79, Sanfey *et al*.80, Lee81, and Haroush and Williams82). By contrast, we presented a continuous choice space, necessitating behavioral modifications in real-time in response to the behavior of other agents. The strategies monkey players displayed in this task parallel the multidimensional dynamics of real-life competitions among humans, such as chess, poker, and soccer34-37,83,84. Furthermore, naturally motivated by competition, all monkeys learned this task very quickly (the average number of training trials administrated before recording: kicker = 1,550 trials in 8.5 days, goalie = 3,800 trials in 12.5 days), and the strategies of pairs of players evolved together throughout time, supporting the idea of an evolving decision space where the action of one player exerts immediate impact on the other and *vice versa*.

It remains controversial whether macaques or other nonhuman primates possess a full, multilevel theory of mind (ToM). It is unclear, for example, whether monkeys are able to understand and exploit the false beliefs of others85-86. In addition, studies of ToM in nonhuman primates often have trouble distinguishing behaviors arising from true understanding and reasoning from those simply acquired through reinforcement learning and deployed according to simple rules. The ease with which the penalty kick paradigm evokes complex, flexible, strategic behaviors affords researchers the rare opportunity of side-stepping the controversy surrounding ToM and directly investigating the neurobiology of strategic decision making without overtraining monkeys.

Neuroimaging studies have indicated that the human TPJ uniquely contributes to ToM or to mentalizing in a social context87-92. Prior neurophysiological recordings in STS have linked it to social perception39-43 but, until now, there was no established experimental paradigm to examine neurophysiological signals associated with ToM in nonhuman primates. Using this behavioral paradigm, we found that in mSTS, a subregion of monkey STS that shares the most similar functional connectivity with the human TPJ29, neurons multiplex various abstract, nonperceptual signals associated with strategic social interactions. These findings lend support to the hypothesis that mSTS is the simian homolog of the human TPJ and endorse the idea that multilevel intentional reasoning in humans has its origins in abstract computations that contribute to strategic social interactions in nonhuman primates93-94.

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