RESEARCH ARTICLE SUMMARY

SOCIAL NEUROSCIENCE

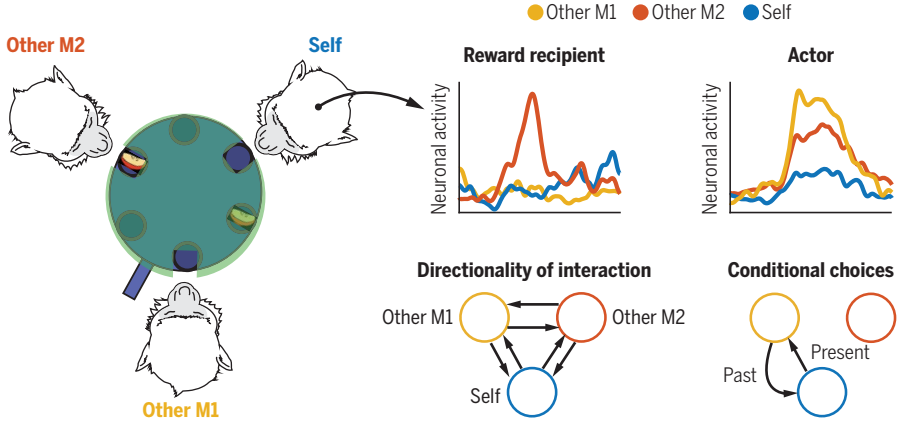
Social agent identity cells in the prefrontal cortex of interacting groups of primates

Raymundo Báez-Mendoza*, Emma P. Mastrobattista, Amy J. Wang, Ziv M. Williams*

INTRODUCTION: Social groups play a foundational role in the behavior of many animal species. During group interactions, an individual's behavior can affect not only the well-being of others but also how others respond in return. Therefore, representing both the identities of others as well as their actions and outcomes is necessary for the ability to interact successfully within groups. Without these combined representations, it would not be possible to engage effectively with others or to understand how one's actions affect particular group members. It would also not be possible to form mutually beneficial affiliations, avoid exploitation by others, or understand how the behaviors of specific individuals within a group interrelate.

RATIONALE: Most primates, including humans, live in social groups wherein an individual's success relies on the ability to interact effectively with others. Rhesus macaques, in particular, are known to form nonkin interactions and long-lasting alliances. They also engage in mutually beneficial behavior based on reciprocity between individual group members. Yet how neurons in the primate brain precisely represent the interactive behavior of groups or resolve the basic problem of coding for multiple agents remains largely unknown. In this study, we developed a three-agent paradigm using small groups of interacting Rhesus macaques in combination with single-neuronal recording and stimulation techniques to begin addressing these questions.

RESULTS: Groups of adult male rhesus macaques performed a three-agent task in which each individual could offer, in sequence, a food reward to one of the other group members using a rotary table. During these group interactions, we found that the primates reciprocated past offers of reward and retaliated when they did not receive a reward from another. We also observed that the primates formed mutually beneficial affiliations that reflected the reputation and past behavior of other group members. These results, therefore, together suggested that the primates kept track of their interactions with specific individuals within their groups and responded adaptively to the behavior of others.



A three-agent task in rhesus macaques reveals a rich representation of group behavior and agent identity in the dmPFC. (Left) Three monkeys sat around a rotary table apparatus that allowed them to allocate food to each other. Simultaneously, neuronal activity was recorded from their dmPFC. (Top right) Individual neurons represented the specific group members offering (actor) and receiving a reward (recipient). (Bottom right) Neurons in the dmPFC collectively encoded detailed information about specific interactions within the group, the directionality of those interactions, the past behavior of other group members, and their influence on the animals' own decisions.

As the primates performed the task, we obtained single-neuronal recordings from the dorsomedial prefrontal cortex (dmPFC; Brodmann's area 24) in an area proposed to play a role in social behavior and its dysfunction. Collectively, these neurons encoded information about the choices and reward outcomes of different group members, providing, in combination, a highly detailed account of the group's interactions. These neurons tracked the others' behaviors across spatial locations, reflecting the social context of the animals' interactions and the agents involved. They also reliably represented interactions between other individuals, even when those interactions did not involve the recorded animals themselves, thus explicitly linking the identities of others with their specific behaviors.

Finally, by following the group's behavior over time, we find that neurons in the dmPFC reliably tracked prior interactions and integrated information about the past behavior of other agents to influence the animals' own actions. Modeled together, these neurons reliably predicted the animals' own upcoming decisions to reciprocate or retaliate in response to the behavior of individual group members. Conversely, disrupting neuronal activity in the dmPFC diminished the animals' ability to engage in agent-specific behavior and, therefore, their capacity to form mutually favorable interactions.

CONCLUSION: By following the social behavior of small groups of three rhesus macaques, we find neurons in the dmPFC that code for the agency identity of others and that can therefore link the identities of others with their specific behaviors. By encoding both the current and past actions and outcomes of specific group members, these neuronal ensembles may allow animals to track the behavior of other individuals. In combination with other core areas involved in social cognition, these neurons could form a detailed representation of multiple interactions and together construct a comprehensive "map" of the group's dynamics. By further integrating information about these dynamics to inform upcoming decisions, these populations could therefore crucially enable the formation of agent-specific interactions necessary for the effective social behavior of groups. ■

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RESEARCH ARTICLE

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Social agent identity cells in the prefrontal cortex of interacting groups of primates

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The ability to interact effectively within social groups is essential to primate and human behavior. Yet understanding the neural processes that underlie the interactive behavior of groups or by which neurons solve the basic problem of coding for multiple agents has remained a challenge. By tracking the interindividual dynamics of groups of three interacting rhesus macaques, we discover detailed representations of the groups' behavior by neurons in the dorsomedial prefrontal cortex, reflecting not only the other agents' identities but also their specific interactions, social context, actions, and outcomes. We show how these cells collectively represent the interaction between specific group members and their reciprocation, retaliation, and past behaviors. We also show how they influence the animals' own upcoming decisions and their ability to form beneficial agent-specific interactions. Together, these findings reveal prefrontal neurons that code for the agency identity of others and a cellular mechanism that could support the interactive behavior of social groups.

Social groups play a foundational role in the behavior of most animal species. To interact effectively within social groups, individuals must be able to represent not only the identities of other group members but also their specific behaviors (*1*, *2*). Without such representations, it would not be possible to understand how the actions and outcomes of specific individuals relate or how one's actions affect specific group members (*3*). It would also not be possible to develop mutually beneficial affiliations and avoid exploitation by others (*1*, *4*, *5*). Understanding how neurons in the brain represent the behavior of specific individuals or their interaction within groups, however, has remained a challenge. Although prior investigations have revealed neurons in temporal regions that respond to the specific identities or facial features of others (*6*–*9*), they do not reveal how neurons encode another's behavior or their interaction. Other studies, by comparison, have identified neurons in associative brain regions that respond to another's behavior (*10*–*15*) but do not reveal how neurons represent their specific identities or group interactions.

Most primates live within social groups in which an individual's success relies on the ability to interact effectively with conspecifics (*1*, *4*, *16*). Rhesus macaques, in particular, can recognize different individuals (*6*, *17*) and form nonkin interactions and long-lasting alliances (*18*–*20*). They also engage in mutually beneficial behavior based on reciprocation between specific individuals and keep track of others' behavior (*19*, *20*). By studying the group behavior of rhesus macaques, we can therefore begin to characterize how neurons in the primate brain represent interactions within small social groups and to explore how neurons code for the specific identities and behaviors of others.

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Three-agent group interaction task in rhesus macaques

We devised a three-agent task in which three adult male rhesus macaques sit at a turntable and each of which could offer a food reward to either of the other two monkeys over successive trials (Fig. 1, A and B). For each successive trial, one of the primates was assigned to be the "actor" and could use a handle on the turntable apparatus to offer a food reward to one of the other two agents ("recipient"). Further, the primate assigned to be the actor would alternate in a pseudo-random fashion from trial to trial (Fig. 1C). Thus, for example, monkey 1 could be the actor in one trial and may offer a reward to monkey 2. On the subsequent trial, monkey 2 could be the actor and may reciprocate that same offer of a reward to monkey 1 or, instead, offer a reward to monkey 3.

Next, to further dissociate the actor's movements from the specific individual receiving a reward, we set the apparatus such that either a clockwise or counterclockwise handle movement allowed the actor to offer a reward to the same animal on different trials (Fig. 1D, left, and fig. S1). To further limit the possibility that animals used simple conditioned responses, the trials also alternated such that the monkey receiving a reward may be different from the monkey offering a reward as the actor in the next trial (Fig. 1D, middle). Finally, to dissociate the location of reward from the specific monkey receiving it, we alternated the physical locations of the primates in relation to one another halfway through the session (Fig. 1D, right).

Therefore, taken together, the nature of this task aimed to mimic some of the basic ethological features that define interactions between primates within groups (e.g., offering and receiving reward or grooming and being groomed) but in a way that could be studied in a neurophysiologic setting. More importantly, it allowed us to examine interactions between specific individuals within the group (e.g., did monkey 1 or 2 receive a reward, and, if so, was a reward given to them by monkey 2 or 3). All trial conditions were controlled in an automated fashion, and all events were recorded and analyzed offline at millisecond resolution (*21*). For each new session and day, a different triad of monkeys was selected from a possible four communally housed adult male macaques. The group performed an average of 105 ± 8.7 (mean ± SEM) trials per session for a total of 22 sessions.

Tracking agent-specific interactions within the primate groups

Behaviorally, the primates reciprocated past offers of reward, suggesting that they kept track of their interaction with specific individuals in their group. Because the actors had to choose between two possible agents, we could examine the interaction between specific group members. Here, we find that the animals were significantly more likely than chance to reciprocate an offer of reward from another animal (9.2 ± 4.0% above chance; signed-rank test, $Z = 2.3$, $P = 0.01$; Fig. 1E, left, and fig. S2A). Therefore, if monkey 1 gave a reward to monkey 2 on a particular trial, for example, monkey 2 would be more likely to offer a reward to monkey 1 on a subsequent trial (*16*, *22*).

The animal's behavior also reflected the specific type of interaction with the other group members. Whereas reciprocation of reward reflects a mutually positive interaction, retaliation reflects a negative one. For example, if monkey 1 gave a reward to monkey 2 in the previous trial, monkey 3 retaliated against monkey 1 by offering a reward to monkey 2 in the next trial (Fig. 1E, middle). Here, we find that the primates were significantly more likely to retaliate than expected by chance (10.2 ± 4.2%; signed-rank test, $Z = 2.30$, $P = 0.01$; Fig. 1E, middle, and fig. S2A). Moreover, when considering both positive and negative interactions together (i.e., "tit-for-tat" strategy in which the current actor gives back to the previous actor if it received reward and withholds reward if they had not received reward) (*16*), we find that the

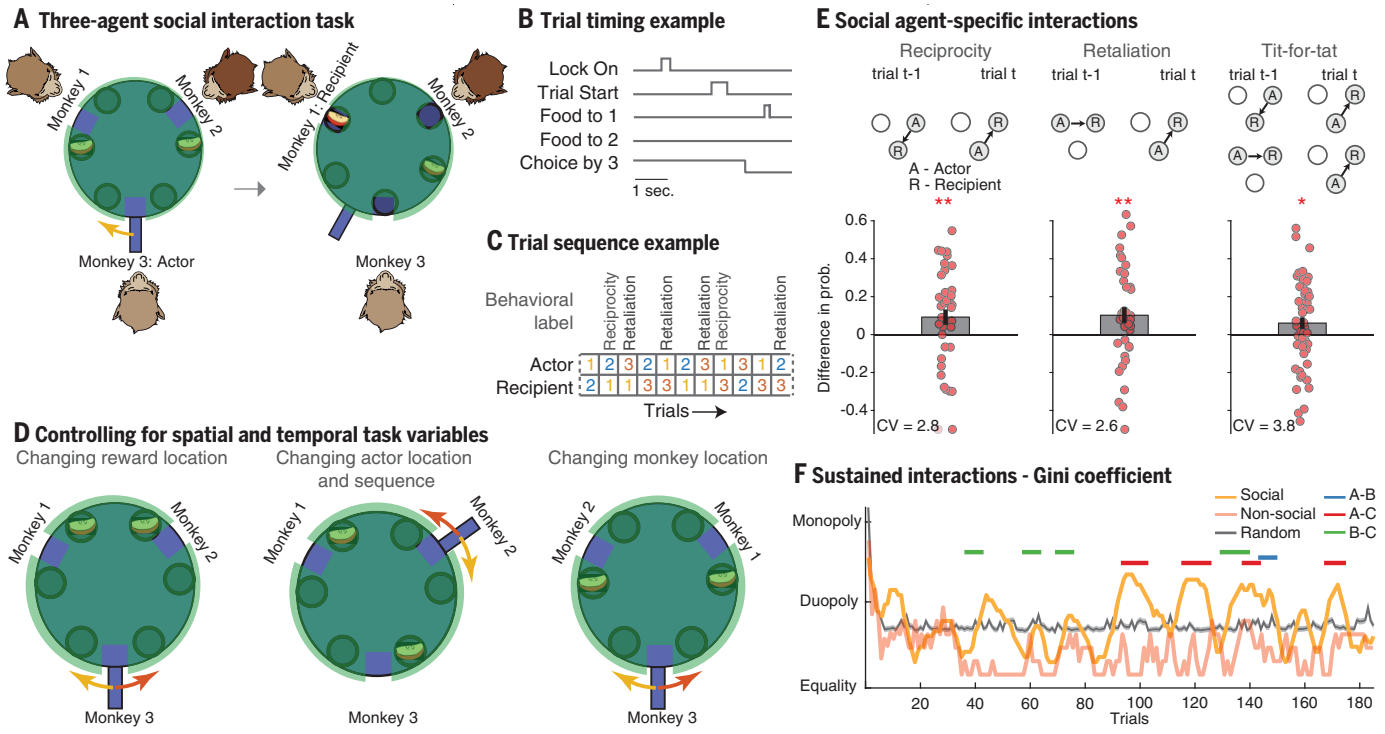

Fig. 1. Three-agent task for testing partner-specific interactions in rhesus macaques. (**A**) Groups of three monkeys sat around a custom-made turntable apparatus that allowed them to interact with each other through food allocation. All monkeys could observe the initial food location through a transparent cover (shown in green), the actor's choice, and the reward recipient. Turntable movement, together with food location, determined the reward recipient (fig. S1). (**B**) Example timing of events for the trial shown in (A). In this trial, monkey 3 (referred to here as "choice by 3") offered a reward to monkey 2 (referred to here as "food to 2"). (**C**) The animals interacted with each other over multiple trials, with the actor on each trial being selected in a pseudo-random fashion. The actor could engage in reciprocity or retaliation based on what the previous actor chose. (**D**) Control measures were used to dissociate the identities of the different agents from variables such as the direction of movement (left), the role of each agent (middle), or the monkeys' spatial locations (right). (**E**) Illustration of trial combinations in which the animals displayed reciprocation, retaliation, and tit-for-tat behavior. Arrows show to whom the actor offered a reward. The animals displayed reciprocation, retaliation, and tit-for-tat behavior with specific individuals at probabilities that were significantly higher than expected from chance (*P < 0.05, and **P < 0.01; CV, coefficient of variation). Bars are the probability of reciprocating compared with not reciprocating ± SEM. Each point depicts an individual's probability within a particular session (fig. S2). (**F**) Gini coefficient illustrates the distribution of reward (dark orange) during a representative session. The highlighted horizontal lines illustrate transient duopolies (permutation test, P < 0.05). For comparison, the distributions of reward expected from chance (gray) and in a representative nonsocial session (light orange) are displayed separately.

animals were more likely than chance to display this behavior (6.1 ± 3.0%; signed-rank test, Z = 1.98, P = 0.023; Fig. 1E, right, and fig. S2A). All animals showed similar reciprocity and retribution across groups [all tests: Z > 1.65, P < 0.04; (*21*)]. These results therefore suggest that the animals kept track of not only whom they interacted with but also how.

The monkeys' behavior did not reflect simple conditioned responses. An important feature of the task was that either a clockwise or counterclockwise movement by the actor could deliver the reward to the same individual on different trials [fig. S1; (*21*)]. Moreover, the pseudo-random sequence in which the role of actor was assigned meant that there was no guarantee that the reward recipient would be the actor on the next trial [Fig. 1C; (*21*)]. Here, we find that the animals were significantly more likely to reciprocate past offers of reward to a specific individual when the offer occurred one or two trials back (7.1 ± 3.2%; signed-rank test, Z = 2.04, P = 0.02). By contrast, the monkeys displayed no evidence of "win-stay-lose-switch" behavior (i.e., simply responding to receipt of reward independently of the specific agent offering it; signed-rank test, Z = 0.4, P = 0.68), together suggesting that the animals responded to the past actions of specific individuals within the group rather than simply the last location from which they received a reward.

Social context dependency and specificity of group interactions

To further confirm that the monkeys kept track of their interactions with specific individuals in the group, we switched their physical seating positions in relation to one another halfway through the session. Using this manipulation, we found that none of the primates displayed a systematic reward assignment preference to a particular location either before or after the switch (signed-rank test, Z = 0.32, P = 0.74). More notably, they continued to display reciprocity with specific animals that had offered them reward on past interactions regardless of seating arrangement (signed-rank test, Z = −0.89, P = 0.37; before versus after change).

Next, we examined the influence that the history of past interactions and social context played in the animal's behavior. Prior studies have shown that the past behavior or "reputation" of specific individuals and their social dominance status can markedly influence how group members interact with them (*23*–*25*). Here, we find that difference in the other's reputation based on past interactions (i.e., how likely they were to reciprocate over the past 20 trials) had a significant effect on the animal's choices [odds ratio (OR) = 1.54, t = 9.2, P = 3.5 × 10^{-20}; fig. S2C]. Furthermore, all animals developed transient duopolies (i.e., consistent runs of reciprocation) at probabilities that were significantly higher than expected from chance (permutation test, P < 0.05; Fig. 1F). Although social dominance did not have an independent effect on the animal's choices

(i.e., on the current trial; reciprocity, $Z = 0.41$, $P = 0.68$; retaliation, $Z = -0.061$, $P = 0.95$; tit-for-tat, $Z = 0.68$, $P = 0.49$; Wilcoxon rank-sum test; fig. S2B), it did play a role when considering the animals' past interactions (i.e., whether past interactions were with a more dominant or subordinate animal; OR = 1.14, $t = 2.1$, $P = 0.035$; fig. S2C).

We also confirmed the social-context dependency of the animals' behavior by replacing the other two primates with distinct inanimate totems while yoking trials from past sessions [fig. S2E; (*21*)]. Here, we find that replacing the other group members with totems led to a loss of reciprocation (signed-rank test, $Z = 0.42$, $P = 0.34$; fig. S2F) and tit-for-tat behavior (signed-rank test, $Z = 1.05$, $P = 0.15$). Together, these results suggest that the animals kept track of who they previously interacted with and that their choices were dependent on the social context of their interaction.

Finally, we used two additional ethological metrics to evaluate the animals' interactions (fig. S3). Consistent with prior field studies demonstrating that primates are more likely to look at the individuals they interact with (*25*–*29*), we find that the monkeys look first [58.9 ± 4.4% versus 50% chance; $\chi^2(1) = 5.35$, $P = 0.021$] and longer (42.6 ± 3.4% versus 57.3 ± 3.5%, nonrecipient versus recipient; $t_{17} = 2.12$, $P = 0.049$, paired t test) at the monkey receiving reward (fig. S3, A to C). We also examined whether differences in facial expressions may have affected the animals' choices. Of the trials tested ($n = 450$), we find that the most common facial expression displayed by the animals (when they were potential recipients of reward) before the actor's choice was affiliative (83.8%, $n = 78$; fig. S3D). These expressions, however, did not alter the overall likelihood that the actor would reciprocate with reward to the expressing monkey [$\chi^2(1) = 1.36$, $P = 0.24$] or that the actor would retaliate [$\chi^2(1) = 0.53$, $P = 0.46$] or engage in tit-for-tat strategy [$\chi^2(1) = 0.004$, $P = 0.94$; fig. S3E].

Single neuronal representations of individuals receiving reward

Based on these findings, we next investigated the relationship between neuronal activity and the real-time interaction dynamics between animals in these groups. Together, we recorded from 521 neurons in the primates' dorsomedial prefrontal cortex (dmPFC; Brodmann's area 24) along the dorsal anterior cingulate sulcus (fig. S4A)—an area previously implicated in social cognition in both monkeys (*10*, *30*–*32*) and humans (*33*–*35*). Only units with a high degree of signal-to-noise ratio, adequate refractory period, and stable waveform morphology were used (Fig. 2A, inset, and fig. S4, B and C). Here, for neuronal analysis, we defined the primate from which neuronal activity was recorded as "self" and the other two agents as "other monkey 1" and "other monkey 2" (Fig. 2A).

We first asked whether certain neurons in the population responded to the reward outcome of specific individuals within the group. Because each recorded animal interacted with two other agents, we could importantly examine not only whether another monkey received a reward but also which specific monkey received it. Focusing on the reward period, we found that 19.9% ($n = 104$) of the neurons displayed a change in their activity when any of the other animals received a reward [two-way analysis of variance (ANOVA) with post hoc testing corrected for repeated comparison across the three agents, $P < 0.01$; (*21*)]. More notably, 9.6% ($n = 50$) of neurons displayed a significant change in their activity only when a specific other individual received reward (i.e., the neurons "preferred" the other monkey; Fig. 2D, top, and fig. S5A), a proportion that was significantly higher than expected by chance given the number of neurons recorded (permutation test, $P < 0.0001$; Fig. 2B, bottom). Figure 2, B and C, illustrates representative neurons recorded from the same animal that responded distinctively to reward received by oneself, any other agent, or a specific-other agent as well as their population dynamic.

Neurons that responded to receipt of reward by specific other agents were largely distinct from those that responded to the animal's own receipt of reward. Overall, 26.4% ($n = 138$) of the neurons displayed a change in their firing activity when reward was received by the recorded animal itself. However, most of these displayed little response to the other's reward, with only 14 neurons displaying a change in their activity to both self-reward and specific-other reward [$\chi^2(1) = 9.7$, $P = 0.001$; Fig. 2B, bottom], results that were largely consistent across statistical analyses (table S1). The responses of these neurons to receipt of reward, by comparison, did not reflect more generalized processes such as a negative reward prediction error. Because any of the three agents could function as actors, we could dissociate signals that reflected another agent's observed receipt of reward from its expectancy (i.e., the animals had no expectancy of reward and therefore held no reward prediction error when they were the actor) (*36*). Consistently, we found that neurons responding to another specific agent's reward displayed no difference in response based on whether a putative negative reward prediction error was present ($n = 50$; rank-sum test, $Z = 0.86$, $P = 0.38$; Fig. 2D, bottom), confirming that they responded selectively to the specific agents receiving reward.

Specificity of neuronal responses to social context and identity

The responses of these neurons to receipt of reward by other specific agents were also robust to differences in their physical locations. It could be argued, for example, that neurons that responded to the other agents may have simply encoded the location of reward rather than the specific agents receiving it. Therefore, to control for this possibility, we switched the locations of the other two animals halfway through the sessions as the primates continued to perform the task. However, we find that only four of the neurons that displayed selectivity to the agents receiving reward also displayed selectivity to reward location [$\chi^2(1) = 23.7$, $P = 1.13 \times 10^{-6}$]. More notably, the neurons that displayed selective responses to particular agents before the switch continued to show similar responses to those same agents afterward (rank-sum test, $Z = 2.86$, $P = 0.004$; Fig. 2E, right, and fig. S5B). Figure 2E, left, illustrates the responses of one such neuron before versus after the switch, with the vertex of the triangle representing maximal neuronal activity for a specific monkey.

We also considered the possibility that these neurons may have responded to lower-level sensory features such as the others' faces (*7*, *37*) independently of their social interaction. For example, simply looking at the other agents may have elicited similar responses. Therefore, to test for this, we examined a separate intertrial control period in which no task was performed but in which the primates gazed freely at the other two monkeys (*21*). We find, however, that even when directly viewing the other animals under this control, only 6.1% ($n = 15$ of 244) of the neurons distinguished between which specific agent the primates were looking at (i.e., based on the recorded animal's eye positions; Fig. 2F). More notably, only two of these neurons overlapped with those that responded to the specific agents receiving reward [$\chi^2(1) = 21.6$, $P = 3.4 \times 10^{-6}$], and the degree to which the recorded animal's gaze modulated these neurons' activities was negligible (rank-sum test, $Z = -4.89$, $P = 9.7 \times 10^{-7}$; Fig. 2F). Therefore, unlike interconnected areas such as those in the temporal lobe (*8*, *9*, *38*, *39*), neurons in this area did not reflect information about the others' faces.

Finally, to confirm that neuronal responses to the other agents reflected the social context of their interaction, we recorded from an additional 403 neurons while the recorded primates performed the nonsocial control (*12*). As before, the two other animals were replaced with distinct inanimate totems while we yoked the distribution of reward from a past session (fig. S2E). Unlike the main task, however, we find that 0.6% ($n = 3$) of the neurons changed their activity based on which specific totem was given reward and at a proportion significantly lower from that observed before [$\chi^2(1) = 40.6$, $P = 1.8 \times 10^{-6}$; Fig. 2G, inset]. Moreover, these differences in neuronal response were not associated with

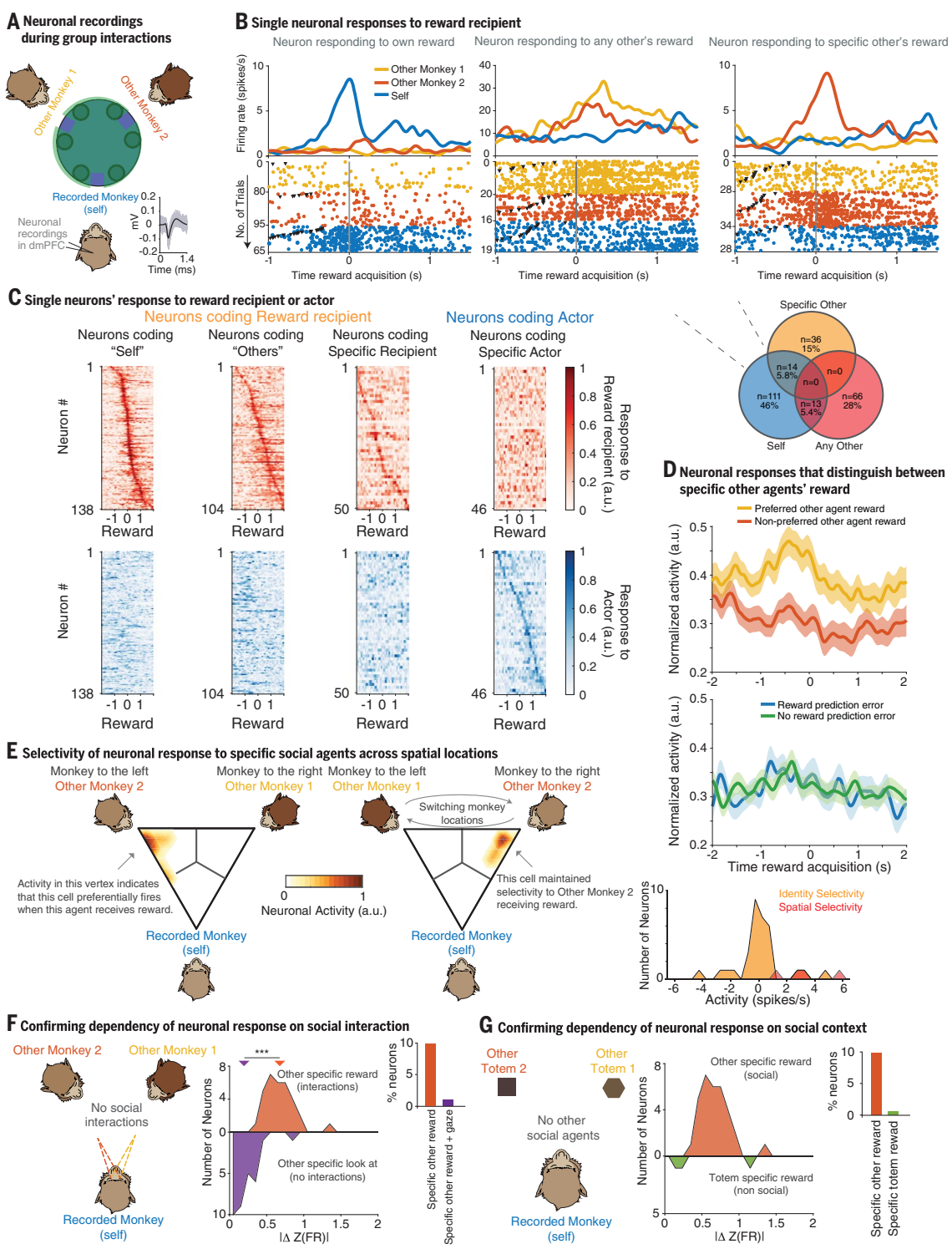

Fig. 2. Selectivity of neurons to specific social agents during group interactions. (**A**) The monkey undergoing neuronal recordings from the dmPFC within each session was referred to as "self" and the two other monkeys as "other monkey 1" and "other monkey 2." Recorded neurons displayed stable waveform morphology (inset; fig. S4). (**B**) Peri-event time histogram and raster examples of neurons that displayed changes in their activities when particular agents within the group received a reward. The inverted black triangles mark when the actor chose. Venn diagram of neurons that displayed response selectivity to reward recipient agency. (**C**) Heatmap of single neurons' responses to reward recipient (top, red) and actor (bottom, blue) aligned to the timing of reward acquisition. Only neurons with significant modulation are shown (ANOVA, $P < 0.01$). (**D**) (Top) Normalized population activity of neurons encoding "specific-other-reward" to the preferred and the nonpreferred other monkey. (Bottom) The same neuronal population as above but parsed by the absence or presence of a possible reward prediction error for "self." (**E**) The locations of other monkey 1 and other monkey 2 were switched halfway in the session to test the selectivity of neuronal responses to specific agents independently of their spatial locations. Heatmap of neuronal activities on a ternary plot before and after the switch of a representative neuron. Here, each vertex represents maximal neuronal activity for a particular monkey. The color code provides the density of activity across trials. The particular neuron displayed here responded almost exclusively to receipt of a reward by other monkey 2 both before and after switching its location relative to the recorded animal. Shown on the right is a histogram of neurons that retained a preferential response to a specific agent ($n = 34$, orange) and neurons ($n = 4$, red) that signaled both reward receipt and location. a.u., arbitrary units. (**F**) To test that neuronal responses were not explained by looking at others' faces, we tracked the recorded animals' eye positions during an intertrial period (left). The middle panel shows the distribution of neurons' activity displaying social agent–specific reward responses based on whether others received reward (top, orange) or whether the recorded animal looked at others during the intertrial period (bottom, blue; normalized to the preferred animal). The proportion of cells is shown on the right (***$P < 0.0001$). IΔ Z(FR)I, absolute difference in Z-scored firing rate. (**G**) The primates performed the same task but in the absence of social agents to test the effect of social context on neuronal responses (left). The middle panel shows the distribution of the absolute normalized difference in firing rates of individual-specific reward neurons based on social agents (orange) or nonsocial agents (green). The proportion of neurons relative to the total number of recorded neurons on each task is shown on the right.

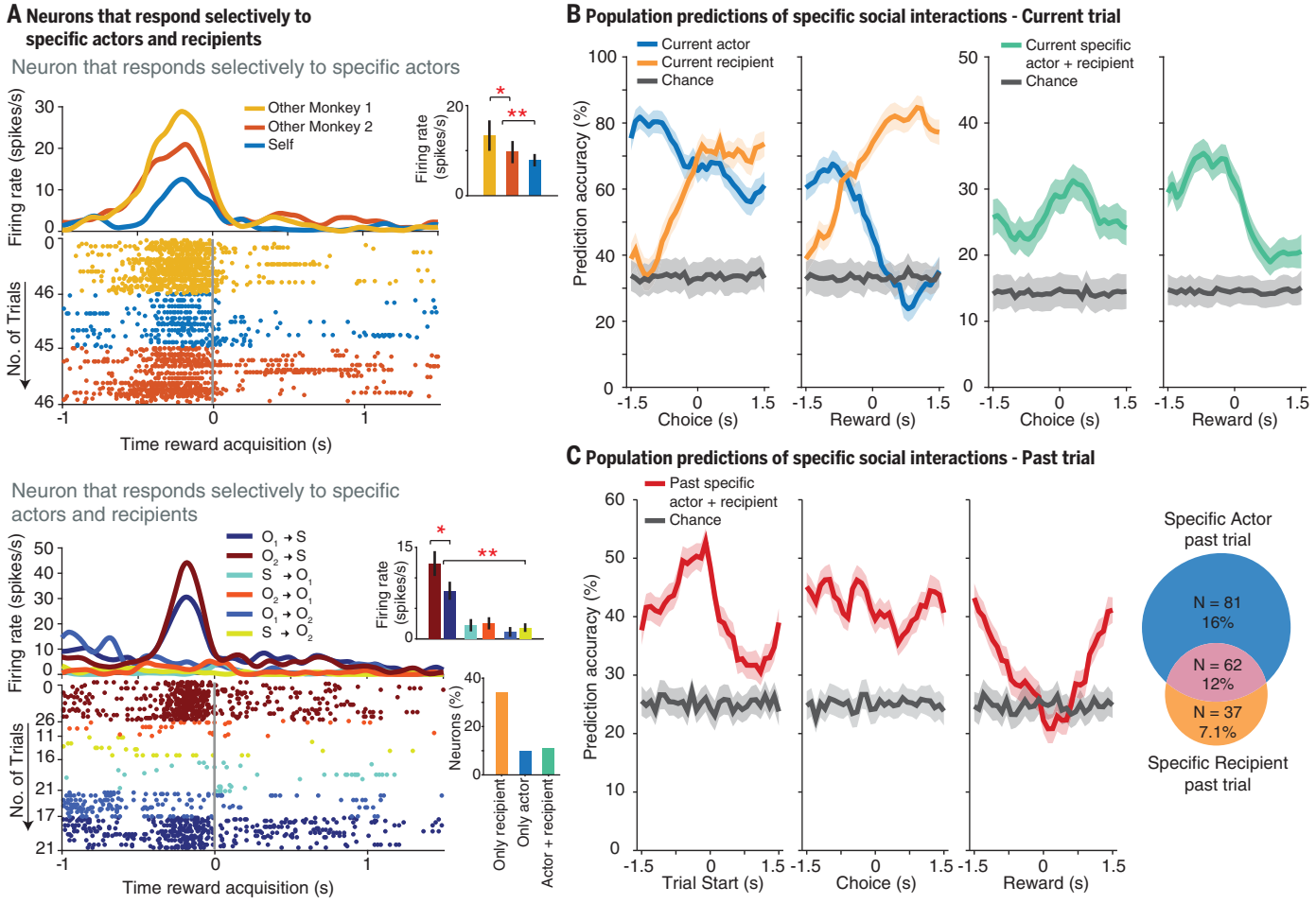

Fig. 3. Neural population predictions of specific interactions within the group. (**A**) (Top) A neuron that displayed a change in its activity based on whether other monkey 1 or other monkey 2 was the actor. (Bottom) A neuron that displayed a change in its activity based on whether other monkey 1 or other monkey 2 was the actor but only when they specifically offered a reward to the recorded. The insets show the average firing rate for each condition during a 1-s time window centered at 0.3 s before the reward was acquired; the error bars represent SEM. The lower inset shows the proportions of neurons encoding specific agent receiving a reward, the specific actor offering a reward, and the combination of the specific actor and recipient across all possible interaction types. *P < 0.05; **P < 0.01. (**B**) (Left) Decoding performance for specific actor and recipient, separately. (Right) Decoding performance for specific interactions in which both the actor and recipient of reward were decoded on a trial-by-trial basis. Multiclass one-versus-all decoders were trained with 80% of trials and tested on the remaining 20% of trials (1-s window advanced in 0.1 s intervals). The colored curves indicate mean prediction accuracy on test trials (±95% confidence interval). (**C**) (Left) Decoding performance for the combination of specific actor and reward recipient in the previous trial when the recorded animal is the actor in the current trial and, therefore, planning its choice. (Right) Venn diagram of the number of neurons displaying selectivity for the specific actor (blue) and the specific recipient (orange) in the past trial.

a change in mean neuronal activity (rank-sum test, $P > 0.5$) and, as noted above, we observed no change in behavioral reaction and movement times to suggest a difference in engagement or attention. Lastly, 0% (n = 0 of 83) of neurons were modulated when a specific other monkey received reward, but when no actor offered it (reward dissociation control; see Materials and methods), together suggesting that the activities of these neurons were indeed dependent on the social context of the animals' interactions.

Neuronal representations of agent-specific actions and interactions

For the primates to effectively interact within these groups, it was necessary for them to know not only who received the reward but also who was the actor that offered it. In our task, any of the three primates could be the actor on a given trial (if they were not the actor on the previous trial) and, in turn, could offer a reward to either of the other two agents. Thus, for example, other monkey 1 may be the actor in one trial and could choose to offer a reward to other monkey 2, or other monkey 2 may be the actor and could choose to offer a reward to other monkey 1. Here, we find that 8.8% (n = 46) of the neurons distinguished between whether other monkey 1 or other monkey 2 was the actor (Figs. 2C and 3A), meaning that they responded differently based on which agent offered reward. Moreover, when considering their group interactions, we find that 11.1% (n = 58) of neurons changed their activity based on which specific animal the actor offered reward to (fig. S5, C and D). Figure 3A, bottom, illustrates such a representative cell, which displays a difference in activity based on whether other monkey 1 or other monkey 2 offered reward to the recorded animal but displays little or no difference in activity for any other interaction.

Next, given these observations, we asked whether and to what degree these neural populations were predictive of interactions within the group and the identities of the specific agents involved on a per-trial basis. Here, we trained multiclass decoders on the

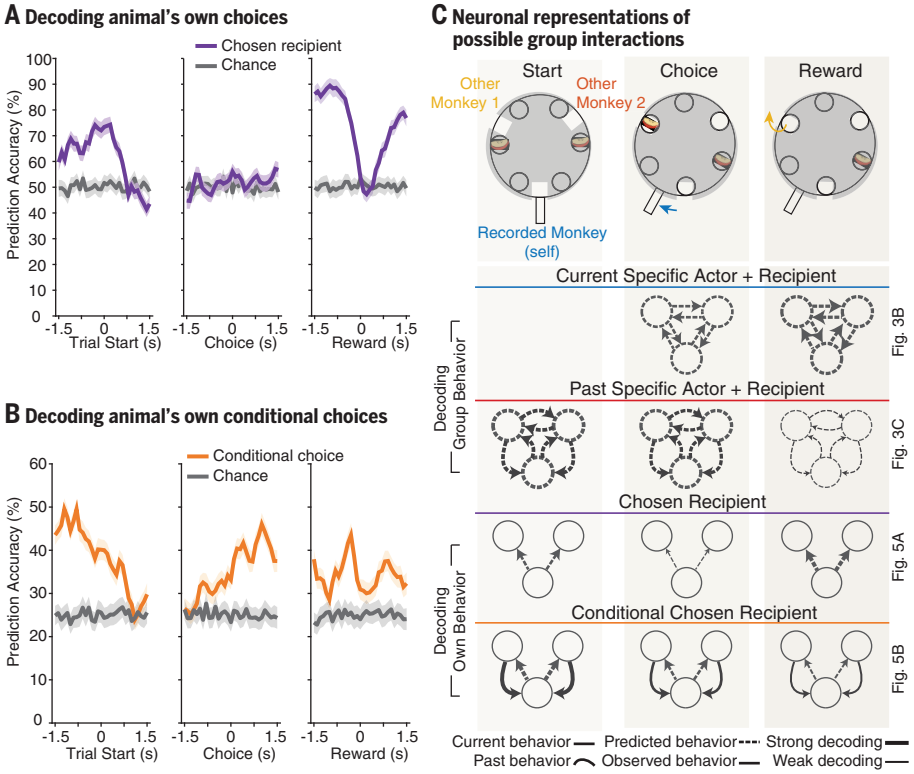

Fig. 4. Dependency between past interactions and predictions of upcoming choices. (**A**) Neuronal responses accurately predicted the animal's own upcoming choices before making its motor selection. (**B**) The animal's past interactions modulated neuronal predictions of the animal's upcoming choice. By considering both the other monkeys' choices and the recorded animals' current choice combinations, the curves here reflect neuronal population predictions contingent on the other's past actions. (**C**) Summary of decoding results. Each column corresponds to one distinct epoch and each row to the relevant information decoded. The arrows reflect the actor (circle) offering a reward to another agent. Each set of arrows reflects the possible combinations of current and past behavior, predicted and observed behavior, and the relative strengths of decoding. Thus, for example, thick arrows indicate that those specific interactions could be highly accurately decoded from the neural population response, whereas thin arrows indicate that decoding accuracy for those interactions was poor when compared with chance. The relevant figures for each panel are shown on the right to allow for ease of comparison.

neuronal responses of 80% of matched trials from all recorded cells and tested the model's performance in the held-out sample [performed in 1-s windows advanced in 0.1-s intervals; (*21*)]. We find that the identity of the specific actor could be decoded with an accuracy of 81.7 ± 2.9% (mean ± 95% CI) before choice selection (Fig. 3B, left), meaning that these neurons could be used to predict which specific agent offered reward. As the trial progressed, however, prediction accuracy increased for the specific identity of the reward recipient, with a decoding accuracy of 70.1 ± 2.8% once the actor made its choice. More notably, both the actor (72.8 ± 3.1%) and the recipient of reward (72.75 ± 3.3%) could be accurately decoded even when confining our analyses to interactions between other monkey 1 and other monkey 2 (i.e., excluding the recorded animal as the agent; fig. S6A).

Collectively, the activities of these neurons held detailed representations about specific interactions within the group. Peak decoding accuracy for agent-specific interactions was 35.4 ± 0.78% and significantly higher than chance shortly before reward was acquired (chance is 16.6%, given the number of possible actor-recipient combinations; $P < 0.01$, permutation test; Fig. 3B, right). The highest decoding performances were for interactions that specifically resulted in reward for the recorded animals (52%), meaning that they were predictive of who specifically offered a reward to them. Decoding accuracy for the agent to whom the recorded animals offered reward was slightly lower at 44%. Similar decoding performances were also observed for "mixed-selectivity" neurons (*40*) that encoded information about both the specific actor and recipient of reward [fig. S6, B and C; (*21*)] as well as when comparing decoding performances across spatial locations [fig. S7A; (*21*)]. Decoding accuracy for more basic sensorimotor variables such as movement direction ($P > 0.2$, permutation test; fig. S7B) or the direction of gaze ($P > 0.2$, permutation test), conversely, was at chance. The activities of these neurons, therefore, appeared to hold detailed information about which specific individuals in the group interacted with whom.

Effect of past interactions on neuronal responses and upcoming decisions

Last, we asked how the neural population responses may relate to the animal's own decisions. To interact effectively, the actor had to take into consideration past interactions with other agents when making decisions. Here, we find that 15.2% ($n = 79$) of the neurons displayed a difference in response on the current trial (t) based on who was the specific actor on the prior trial (t-1; $P < 0.01$), whereas 6.7% ($n = 35$) displayed a difference in response based on the past trials' specific recipient of reward (Fig. 3C, right). From all population neurons, we could decode information about past (t-1) interactions within the group on trials (t) in which the monkey was the current actor with an accuracy of 52.8 ± 1.9% [null hypothesis (H_0) = 25% chance; $P < 0.01$, permutation test; Fig. 3C, left]. When further accounting for the actor's own current decisions, these neural populations could predict the animal's upcoming choices contingent on the other agent's past actions with an accuracy of up to 49.5 ± 1.0% (H_0 = 25% chance, permutation test, $P = 0.005$; Fig. 4B). In other words, the activities of these neurons could be used to accurately predict whether the recorded animal will reciprocate or retaliate in response to the other's past choices (i.e., rather than simply based on any receipt of reward, irrespective of which social agent offered it). Overall, peak decoding accuracy for whom the recorded animals will offer a reward before their motor responses was 74.3 ± 1.4% and significantly higher than chance (H_0 = 50% chance; Fig. 4A). Figure 4C further illustrates these decoding performances across the different group interactions and how they relate the animal's own choices. Taken together, these dmPFC neurons therefore appeared to predict the animal's upcoming decisions based on past interactions with specific agents in its group.

Effect of stimulation on agent-specific interactions

Next, based on these observations, we asked whether and what causal role the dmPFC may have played in the animals' decisions during these group interactions. As noted above, the primates reciprocated past offers of reward from specific individuals to enact mutually beneficial interactions. They also displayed evidence of retaliation against individuals who did not, behaviors that are often naturally seen within primate groups (*41*–*43*). Therefore, to

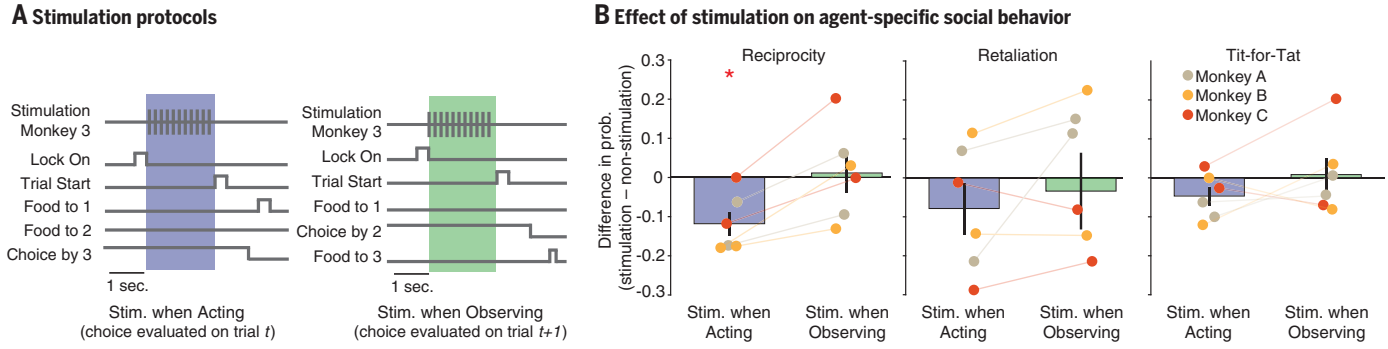

Fig. 5. Effect of stimulation in the dmPFC on group interactions and its selectivity. (**A**) Brief event-triggered electrical stimulation was delivered bilaterally to the dmPFC (200 Hz, 0.1 mA over 2 s, given between locking of the apparatus and trial start) as the primates performed the same task as before. Stimulation was given either when the animal was the actor (blue background) or when they were the observer (green background) for control comparison. (**B**) The bar plot provides the mean difference in probability of reciprocating, retaliating, or using the tit-for-tat strategy on stimulated versus nonstimulated (baseline) trials ± SEM. Each point depicts individual sessions color coded by the animal receiving stimulation. Additional controls used to confirm that stimulation did not affect more basic motoric behavior or cognitive processes such as attention are described in the main text. For specific comparisons, *$P < 0.05$.

further study this question, we used event-triggered stimulation delivered bilaterally to the dmPFC (200 Hz, 0.1 mA over 2 s; from lock on to trial start; Fig. 5A) as the primates performed the same task as before. To allow for control comparison, stimulation was given to the animals on randomly interleaved trials divided equally between those in which the stimulated primate was the actor and observer (*21*).

Before proceeding with the main task, we confirmed that stimulation did not have nonspecific effects on the animals' motoric behavior. Overall, we find that the animals displayed similar reaction times (signed-rank test, $Z = 0.07$, $P = 0.94$) and a similar likelihood of selecting one direction over another (signed-rank test, $Z = 0.04$, $P = 0.96$) when comparing stimulated versus nonstimulated trials. We also confirmed that stimulation did not disrupt the monkeys' ability to make appropriate choices. Here, in a separate control task, we allowed the animals to deliver reward to themselves by moving the turntable handle [i.e., without other agents; fig. S1D; (*21*)] but find that stimulation did not affect the animals' performances (100% correct performance for both stimulated, $n = 27$, and nonstimulated, $n = 24$, trials). Next, we considered the possibility that stimulation might affect their memory of past events or more complex strategic behaviors by evaluating the animals' likelihood of enacting win-stay-lose-switch strategies. These canonical strategies represent decisions in which the animal repeated the last choice made on the prior trial if they received a reward irrespective of who offered it (*21*). However, we again find that stimulation did not affect the animals' likelihood of enacting this strategy ($F_{2,15} = 0.67$, $P = 0.52$; fig. S8A). Lastly, we verified that stimulation did not affect the animals' likelihood of looking at particular animals after receiving reward ($F_{2,119} = 0.145$, $P = 0.86$, for stimulation condition; fig. S8B), together confirming that the effect of stimulation was specific.

Finally, based on these findings, we considered the primates' interactions with the other group members. Evaluating the primates' behavior on trials in which they were the actor during the main task, we find that stimulation led to an 11.8% drop in their likelihood of reciprocating past offers of reward from another specific agent ($F_{2,15} = 4.8$, $P = 0.02$). In other words, stimulation diminished their propensity to offer reward to the specific agent from which they received a reward on a previous trial, an effect that was consistent when examined across the different agents (post hoc test, $P = 0.013$; Fig. 5B). By contrast, stimulation had little effect on the animal's likelihood of retaliating in response to past negative interactions or using tit-for-tat strategy ($F_{2,15} = 0.43$, $P = 0.65$; $F_{2,15} = 0.91$, $P = 0.42$; respectively, Fig. 5B) and had no effect on response variability (rank-sum test, $P > 0.2$ for reciprocity, retaliation, and both strategies) to suggest a generalized disruption of behavior. More notably, stimulating when the animal observed the others' choices did not affect the animal's likelihood of reciprocating past offers of reward (post hoc test, $P = 0.80$), together suggesting that stimulation had a temporally selective effect on the primates' ability to enact mutually positive interactions with specific agents in their groups.

Discussion

Most animals, including humans, live within social groups in which they interact with many other group members. The basic cellular processes that precisely underlie group behavior or by which neurons represent specific group interactions, however, have remained poorly understood. Here, we identify neurons in the primate dmPFC that responded selectively to the actions and outcomes of specific group members. By recruiting different subsets of cells to represent the specific actions and outcomes of each individual, these neural populations encoded information not only about the behavior of individuals but also about the directionality of the interactions between them, even when the recorded animals themselves were not involved. Together, these findings identify cells in the primate dmPFC that encode the "agency identity" of others, meaning that they encode information about the behavior of specific individuals. Such computations are essential for effective social behavior.

Another notable finding is that many of the neurons encoded information not only about the actions and outcomes of specific individuals within the group but also about their past behaviors. Moreover, neural predictions of the animal's own upcoming decisions were modulated by the other agents' past actions, suggesting that the animal's upcoming decisions to reciprocate or retaliate were influenced by past interactions with specific group members. Consistent with these observations, stimulation of the dmPFC had a selective effect on the animal's ability to reciprocate past favorable interactions with specific individuals while having little effect on other aspects of its decisions, social viewing preferences, or motoric responses. That stimulation of the dmPFC affected social choices, but not social orienting behaviors, indicates potentially different parallel systems underlying these behaviors. Together, they also suggest that neuronal activity in this area is necessary for mediating mutually

beneficial interactions with specific individuals within these social groups.

Collectively, these findings begin to elucidate the neuronal computations that underlie social group interactions and the role that the dmPFC may play in this process. They also identify neurons capable of encoding the actions, outcomes, and past behavior of specific agents. Given its broad connectivity with temporal regions such as the fusiform gyrus and amygdala that are known to respond to the identities and facial features of others (*6*, *37*, *44*), the dmPFC may be particularly well suited for holding representations of specific group members and mediating mutually favorable interactions. Moreover, the rich representation of agency-specific action and reward recipient in dmPFC could be potentially used for monitoring the consequence of social actions between specific group members, a hypothesized function of the medial prefrontal cortex (*36*, *45*, *46*). Together with other areas proposed to be involved in social cognition (*47*, *48*), the dmPFC may play a core role in orchestrating the interactive social behavior of groups.

Materials and methods

Animals

All procedures were performed under approval by the Massachusetts General Hospital institutional review board and were conducted in accordance with Institutional Animal Care and Use Committee (IACUC) guidelines. Four adult male *Macaca mulatta*, weighing 10 to 13 kg, were included in the study. The animals were singly housed, in the same room, together with other adult male macaques. All animals lived in these settings for more than 2 years and were highly familiar with each other. For each day of testing, three of the four primates were selected for task performance. They were brought individually to a separate neurophysiology room. They were then seated in primate chairs around a custom-made apparatus that allowed them to interact with each other under controlled settings (below). All animals were kept on 80% fluid restriction from ad libitum consumption. The fluid was supplemented through task performance (fruit consumption) based on weight.

Task apparatus

The three monkeys sat in primate chairs that were equally spaced around a custom-made turntable apparatus that allowed them to interact with each other through the allocation of food (Fig. 1, A and B, and fig. S2E). The apparatus consisted of two 35-cm-diameter disks made of transparent acrylic superimposed on each other. The bottom disk had six food wells that were each 2.5 cm in diameter and positioned 12.5 cm away from the center, spaced in 60° intervals. The top disk had three equidistant 3-cm square openings that allowed the animals to retrieve food from the wells. The bottom disk was attached to a 20-cm-diameter bearings turntable, which in turn was attached to a pedestal. The bottom disk had a round 8-cm-long handle that the actor could use to move the turntable either clockwise or counterclockwise. The turntable was made in-house.

Turning the handle allowed the actor to align one of the six food wells with a specific opening such that they could offer a food reward to one of the other two agents (Fig. 1D and fig. S1). Further, by using this apparatus, all three monkeys could determine who the agent was and which specific agent received reward. More importantly, it allowed us to evaluate interactions that were salient to the animals (e.g., offering and receiving reward) and in a way that can be studied under neurophysiologic settings.

The precise timing of the agent's choices and retrieval of food were acquired with infrared-based receivers and emitters (Adafruit). Eye positions were recorded and sampled at 125 Hz via an infrared camera (ISCAN). All behavioral data were acquired at 1-kHz resolution and simultaneously synchronized to the neuronal recordings (MAP, Plexon). Validation of all trial events was also separately made using an overhead video system (Kinect 2, Microsoft).

Behavioral task

For each new session and day, three monkeys were placed in primate chairs (Crist instruments) situated around the turntable. The chairs had an opening that allowed them to perform the task with the right arm. Before starting each trial, two of the wells were baited with a food reward, and the handle was placed in front of the acting animal's arm. The turntable disk was held in place with a linear actuator (Actuonix) under the control of a microcontroller (Arduino). Each trial started with an auditory tone (0.5 s long, Adafruit) coupled with the release of the turntable through disengagement of the actuator. After this, the agent allocating food on a particular trial (actor) moved the turntable using the handle to offer food to one of the other two agents (recipients). The moment the actor moved the handle, an infrared (IR) receiver-emitter (Adafruit) captured the start of choice execution. The recipient monkey then picked up the food from the apparatus, triggering a separate IR event captured by another IR receiver-emitter and concluding a single trial. Therefore, there was a variable delay between the actor's choice and when the recipient collected the food reward.

To ensure that reward allocation was salient to all three monkeys, food delivered to the animals consisted of precut apple cubes measuring about 0.125 cm^3. Individual monkeys consumed on average 150 g of apple per session. To dissociate movement direction from the specific monkey receiving the reward, we set the turntable such that either a clockwise or counterclockwise movement allowed the actor to offer a reward to the same animal on different trials. Thus, on half of the trials, a food reward would be placed on the turntable such that a clockwise movement would provide a reward to monkey 1 sitting on its left (Fig. 1A). On other trials, by comparison, the food would be placed so that the same movement would provide a reward to monkey 2 sitting to its right (Fig. 1D and fig. S1).

To further limit the possibility of simple conditioned responses to receipt of reward, the trials alternated such that the monkey receiving reward would not necessarily be the primate offering reward as the actor in the next trial (Fig. 1D, right; further examples are shown in fig. S1). We pseudo-randomized the turn order for each agent following these two rules: An agent could not be the actor two trials in a row, and all agents had to be actors at least once every five trials. The monkeys were given 20 s to provide a response. If they did not, we proceeded to the next trial with the proviso that the next actor would not be the same as the previous actor. On average, the monkeys did not respond, i.e., move the handle, on only 5.9% of the trials.

Finally, to dissociate the location of reward from the specific monkey receiving it, we swapped the physical locations of the two nonrecorded animals halfway through a session (Fig. 1D, middle). This manipulation, therefore, allowed us to test the role of an animal's physical location in the group's behavior as well as in neuronal responses.

Social context control

To evaluate the effect that social context had on the animal's behavior, in separate sessions, we had the animals perform the same task as before but with no other animals present. Here, the primate being recorded was seated with two different monkey-shaped totems placed on top of the other primate chairs. These totems were monkey-shaped figures (30 cm tall; Gund) and had cartoon-like facial features. The totem sitting to the left of the acting monkey had a red shirt to further distinguish it from the other totem. During these nonsocial controls, the reward was allocated by the totems based on trials that were "yoked" from their conspecifics on previous sessions. Here, movement of the turntable by the totems was controlled using a semiautomated system outside the view of the recorded animal (Arduino). We conducted an average of 145.8 ± 15.3 (mean ± SEM) trials per session in eight sessions of the social context control.

Self-reward control

The self-reward control was used to further confirm that neuronal responses reflected the

social context of the animals' interactions rather than simply the actor's choice selections. In these trials, each monkey could move the turntable to retrieve reward for themselves in the presence of the other animals (fig. S1D). Thus, the recorded animals observed and experienced being both the agent of their own reward and the agent of someone else's reward in a social context.

Reward-dissociation control

A reward-dissociation control was used to further confirm that neuronal responses reflected the agency of the other's actions (i.e., which specific social agent offered reward to whom). In this control, all three monkeys were placed in their chairs but, instead of allowing the actor monkey to reach and perform the action, the turntable was moved automatically. Therefore, instead of the monkey performing an action, rewards occurred probabilistically as if the acting monkey had "acted" (i.e., thus dissociating action from receipt of reward).

Eye calibration and gaze

To calibrate the eyes' position, we aligned their horizontal and vertical positions to four fixed locations along the food wells, each spaced 25 cm apart from each other. For each new session, we then validated these corresponding spatial locations with horizontal and vertical positions derived from the eye tracking system by pseudo-randomly rotating food into each of the four wells, that is, akin to how eye tracking systems are often calibrated using four-point orientation with a horizontal screen (*12*). For the primary analyses, eye fixations were defined as eye velocity below 25% of its statistical SD for longer than 0.1 s (*12*, *49*). Relative looking times were defined as the total time the animal fixated at the reward recipient versus the nonrecipient, starting at the choice time and up to 3 s after the other monkey received reward.

Dominance hierarchy measurements

To assess the animal's relative hierarchical rank, we first performed a food priority test in which the animals sat in front of each other in their chairs and both could reach for a food item (*50*). Dominant monkeys reached for the food first. Supplemented by observations of the veterinary staff (*51*, *52*), we observed a consistent linear transitive hierarchy across the four monkeys, denoted here as A > B > C > D.

Single-neuronal recordings

We implanted microelectrode arrays (FMA-32, MicroProbes for Life Sciences) targeting the dorsal anterior cingulate sulcus of the dmPFC bilaterally (two per hemisphere) under stereotactic guidance (David Kopf Instruments; fig. S4) in three monkeys. These monkeys were selected based on their ability to consistently interact with each other and participate in the task over prolonged durations, as detailed below. The mean location of electrode implantation was +32.2 interaural and +3.5 lateral from the midline (*53*). Each array consisted of 36 microelectrodes, two of which were used for reference and two for ground. A craniectomy followed by a durotomy exposing both hemispheres allowed a dorsal approach to implant the electrode arrays in the dmPFC. Electrode leads and their connectors were secured to the skull with the aid of titanium screws (Synthes) and dental acrylic (Jet dental). Each animal was also implanted with a head-restraining device (Crist Instruments) to enable both eye movement and neuronal recordings. Recordings began 2 weeks after surgical recovery. Neuronal data was amplified (2000 to 10,000 times), band-pass filtered (0.3 to 10 kHz), digitized (40 kHz), and stored using a data acquisition system (MAP, Plexon).

A minimum threshold of three standard deviations was used to differentiate neural signals from background noise (i.e., underlying activity not selected as putative units). Putative units were further isolated based on four primary criteria: (i) the units needed to display spikes with a peak-to-trough 0.3 to 0.5 ms long, (ii) their interspike interval had to be larger than 2 ms, (iii) the unit's waveform morphology had to be consistent throughout the session recording, and (iv) the units needed to be separated based on the first three principal components. Only well-isolated units with $L_{ratio} < 0.2$ and isolation distance > 15 were included in the data analyses (fig. S4C) (*54*, *55*). Single-unit isolation and selection was performed in Offline sorter (Plexon). Overall, we recorded neuronal activity in 44 experimental sessions over a period of 90 days.

Neural stimulation

Stimulation was delivered to the dmPFC using low-impedance electrodes (100 to 500 kilohms) implanted in the same area of the dmPFC. Stimulation consisted of a 2-s-long alternating rectangular positive-to-negative pulse sequences at 200 Hz and 0.1 mA. The pulse duration was 0.002 s with cathodal phase leading (STG4008-16mA, Multichannel Systems). These are similar parameters to those used in clinical settings for deep-brain stimulation (*10*, *56*, *57*). Here, stimulation started when the apparatus was first locked and ended at the start of the trial, that is, the time at which the actor could first make their choice (Fig. 5A). Before proceeding with the main tasks, we performed test stimulations to ensure that stimulation did not elicit a motoric response or apparent sensory percept. Using the self-reward control described above, we also ensured that stimulation did not affect their ability to make objectively appropriate turntable movements.

During stimulation sessions, there were three types of trials: (i) trials in which no stimulation was given, that is, sham stimulation, (ii) trials in which stimulation was given when the animal was the actor, and (iii) trials in which stimulation was given when the animal was not the actor but was observing the others. For each session, we ensured that the animals had at least 60 trials for each of these trial types. The electrical stimulation was performed in a pseudo-random fashion.

Behavioral analysis

Evaluating for agent-specific interactions

Several behavioral metrics were used to evaluate whether the animals kept track of their interaction with other individuals in their group. As described previously (*22*), reciprocity was defined as trials in which the current actor offered reward to the agent that had given reward to them on the previous trial. Thus, for example, if monkey 1 offered reward to monkey 2 on trial *t*-1, then monkey 2 would offer reward to monkey 1 on trial *t*. Retaliation, or spite, was defined as trials in which the current actor chose not to offer reward to the monkey if that monkey had not offered them reward on the previous trial (*22*). Tit-for-tat behavior was defined by the combination of reciprocation and retaliation on trial *t-1*. Thus, the actor would offer reward to an agent if they received reward from them the previous trial but would not offer reward to them if they did not. Finally, win-stay-lose-shift or Pavlov behavior was defined as repeating the animal's last choice if they had received reward and changing their choice if they did not. Like reciprocity, retaliation, and tit-for-tat behavior, win-stay-lose-shift behavior requires them to attend to the task and keep past outcomes in memory. However, it does not require them to attend to the specific agents involved (*5*). The animals' choices in relation to each of these strategies were compared using a Wilcoxon signed-rank test ($P < 0.01$).

Evaluating for interaction between specific group members

The Gini coefficient describes, in a single metric, the distribution of wealth within a group and can therefore efficiently quantify the formation of consistent runs of interaction between their members (*58*). In our task, the Gini coefficient illustrates transient duopolies (i.e., runs of repeated reciprocation between two agents, and, thus, wealth accumulation between a specific monkey pair), monopoly (i.e., only one individual receives reward from both other monkeys), or equality (i.e., all animals receive the same number of rewards). To identify significant runs of reciprocation, we simulated each session with a Bernoulli process (2000 repetitions) and labeled the presence of significant deviations, as tested by a permutation

test, as runs of reciprocation ($P < 0.05$). To illustrate the transient formation of duopolies, we estimated the Gini coefficient with a time horizon of eight trials back.

Evaluating the effects of past history and dominance

To further quantify the degree to which agent-specific features such as past behavior or dominance affected the animal's decisions, we fitted a logit model (GLM 1) that took into account the influence that past interactions and dominance had on the animals' preferences. For past interaction, we considered three complementary metrics: (i) the animal's short-term choice history as defined by the other's choices within the past two trials, (ii) their intermediate-term choice history as defined by the difference in the others' "reputation" over the past 20 trials, and (iii) their long-term choice history as defined by the difference in the others' reputation from the previous session (GLM 1):

$$Y_t = \beta_0 + \beta_1 HiGave_{t-1} + \beta_2 HiGave_{t-2} + \beta_3 \Delta Reputation + \beta_4 \Delta ReputationLastSession$$

Here, the dummy variables $HiGave_{t-1}$ and $HiGave_{t-2}$ were 1 if the higher-ranking monkey gave the actor a reward one or two trials back, respectively. To further take into account the intermediate-term effect of choice history, we defined an individual's reputation as the boxcar moving average of reciprocity choices over the past 20 trials, as described previously (*59*). The $\Delta Reputation$ term was the difference in reputations between the other monkeys. Finally, to consider the long-term effect of the other animal's choice history, the term $\Delta ReputationLastSession$ was defined as the difference in the final reputation of the other animals from the previous session.

Next, to further address the relationship between differences in reputation and the session's time course, we created a second model (GLM 2) with differences in reputation terms covering a time course from four trials back up to 15 trials back. We defined, as for GLM 1, an individual's reputation as the boxcar moving average of reciprocity choices, but here we estimated this over the last four ($\Delta Reputation_{[t-4,\,t-1]}$), five, and up to 15 trials back and tested them simultaneously. The potential recipients' reputation was then compared for each term in GLM 2:

$$Y_t = \beta_0 + \beta_1 \Delta Reputation_{[t-4,t-1]} + \beta_2 \Delta Reputation_{[t-5,t-1]} + \ldots + \beta_{12} \Delta Reputation_{[t-15,t-1]}$$

Social communication and choice

A high-resolution time aligned audio-video setup and custom-programmed graphical user interface was used to quantify and analyze the animals' facial expressions and vocalizations. To examine the potential relation between facial expressions or vocalizations and the animals' choices, the recorded animals were videotaped during performance of the standard task (n = 450 trials). Labeling of the animal's facial expressions started 5 s before the start of each trial and up to 10 s after a choice was made. The behavioral labels were defined as follows:

i. Neutral: Resting or observing without overt expression.

ii. Lip smacking or affiliative: Protrusion of the lips and contraction of the muscles surrounding the mouth.

iii. Threat or agonist behavior: Opening of the mouth accompanied by direct stare, with or without showing teeth.

iv. Vocalization: Opening of the mouth accompanied by an audible call.

v. Eating movement: Chewing or moving food from or to the cheeks.

Next, the choices made by each animal were tracked on a trial-by-trial basis to determine whether the presence of a particular facial expression by the potential recipient led to a higher likelihood of reciprocating reward. Overall, the monkeys displayed overt facial expressions (i.e., a non-neutral expression) before the choice was made in 20.6% of the trials. Of these, the animals lip smacked, which is an affiliative behavior, in 83.8% of the trials (n = 78), whereas they displayed a threatening or agonist-type behavior in the remaining 16.1% (n = 15). They displayed only three overt vocalizations across trials.

Evaluating variability in choices with stimulation

To quantify the degree to which stimulation may have simply disrupted the animal's choice selections (i.e., irrespective of whom they interacted with), we calculated the coefficient of variation on trials in which stimulation was and was not given and evaluated the difference between conditions with a rank-sum test.

Neuronal analysis

Single-neuronal analysis

In the first step of our analyses, we explored the relationship of neuronal activity to reward recipient and actor of each task-related activation using two-way ANOVA ($P < 0.01$). The factors and their levels were as follows: reward recipient (self, other #1, and other #2) and actor (self, other #1, and other #2), and the interaction between both factors. We followed this with a Holm post hoc test, which corrects for multiple comparisons. We classified each neuron's activity depending on the results of the post hoc test, as follows. Neurons reflected self-reward when only the factor reward was significant and mean firing rate during own trials was higher than during any of the conspecific's trials. Likewise, a neuron reflected any other reward when activity was higher when any of the conspecifics received reward compared with own reward. Critically, a neuron reflected a specific other's reward when activity was higher during this conspecific's reward retrieval compared to self-reward and to the other conspecific's reward. We used the same method to classify a neuron as coding action but applied to the actor factor. Neurons coded actor for reward when the statistical interaction actor*reward was significant. These neurons revealed coding of reward for an animal only when either that animal or a conspecific performed the action that led to reward. To classify these neurons, we used the same method described above applied to both factors. Finally, to evaluate whether and to what degree neurons reflected who specifically offered or received reward in the prior trial, we used a similar classification approach based on a two-way ANOVA. The factors, however, were now related to what had occurred in the past trial. We used a chi-square test to compare the number of neurons in different categories ($P < 0.05$). For illustration, a heatmap of single neuronal responses were obtained by normalizing each neuron's activities by the maximum minus minimum of neuronal responses across all task conditions (Fig. 2C). Only neurons that displayed significant modulation are shown (ANOVA, $P < 0.01$).

Next, for statistical validation, we fitted a generalized linear model with a Poisson distribution to the activity of each neuron to assess neuronal encoding of agent-specific reward-related. We defined the following GLM 3:

$$FR_i = \beta_0 + \beta_1 SelfActor + \beta_2 OtherActor + \beta_3 SelfRecipient + \beta_4 OtherRecipient$$

where the variable *Self Recipient* was defined as 1 when the recorded animal received a reward in trial i, and −0.5 if any other monkey received the reward. Thus, the β_3 coefficient captured whether the neuronal activity was related to the reward receipt of the recorded animal or any other agent: it was negative if the activity was higher when any other agent received a reward, and positive if the activity was higher when self received a reward. The variable *OtherRecipient*, on the other hand, was defined as −1 if other monkey 1 was the reward recipient, 1 if other monkey 2 was the reward recipient, and 0 otherwise. The β_4 coefficient, thus, captured if the neuronal activity was related to the identity of the other agent, with the sign indicating for which animal the activity was higher: A negative sign indicates higher activity during other monkey 1 trials, whereas a positive sign indicates higher activity during other monkey 2 trials. The same logic was extended to the variables

SelfActor and *OtherActor*. Neurons reflected *self-reward* when the coefficient $\beta_3 SelfRecipient$ was positive and significant [t test; $P < 0.01$, false discover rate (FDR) corrected], and the $\beta_4 OtherRecipient$ was not significant. Likewise, neurons reflected *any other reward* when only the coefficient $\beta_3 SelfRecipient$ was negative and significant, and the $\beta_4 OtherRecipient$ was not significant. Finally, neurons encoding specific other's rewards showed a significant $\beta_4 OtherRecipient$ coefficient, of which the sign indicated for which other agent the neuronal activity was higher. We used the same method to classify a neuron as coding action but applied it to the actor-related variables: *SelfActor* and *OtherActor*. A neuronal response was classified only if the model fit was significant as determined by the deviance test ($P < 0.01$). To further consider the potential effect that relative rank (between the actor and the recipient) had on neuronal response, we tested GLM 4:

$$FR_i = \beta_0 + \beta_1 SelfActor + \beta_2 OtherActor + \beta_3 SelfRecipient + \beta_4 OtherRecipient + \beta_5 ActorRecipientRelativeRank$$

Given that our original GLM 3 is a reduced model of GLM 4, we determined whether GLM 4 was the better model with the deviance test. Overall, 54.8% of neurons incorporated information about the social rank of the animals receiving reward.

Finally, we considered the potential effects of reward expectancy on neuronal response. Because the recorded animal might have expected to receive reward but did not when other monkey (e.g., other monkey 1) gave reward to other monkey (e.g., other monkey 2), a neuronal response to a specific other's reward could be confounded with a negative reward prediction error-like signal, particularly because the dmPFC has been shown to contain signals related to prediction errors (*36*). To dissociate this alternative explanation, we contrasted the neuronal responses when the specific other received reward when the self was the actor versus when the other agent was the actor with a rank-sum test. Critically, when the recorded animal was the actor, it did not expect to receive reward on that trial; hence, when the other agent received reward there was no reward prediction error. By contrast, when the other agent (e.g., other monkey 2) was the actor, the recorded animal might have expected to receive reward, and if it had not received a reward, it would then generate a negative reward prediction error-like signal.

Population decoding

We used multiclass one-versus-all support vector machine (SVM) classifiers with a linear kernel to quantify the information contained in dmPFC neuronal population activity (*60*). The SVM classifiers were trained on a subset of data to find linear boundaries that provided the best separation between patterns of transformed neuronal population activity defined by a grouping variable (for example, whether reward recipient was self, other monkey 1, or other monkey 2). The classifier was thus trained to map the neuronal signals and the behavioral conditions. SVM classification is biologically plausible: A neuron pool could perform a linear classification by comparing its inputs with a stored vector of synaptic weights (*61*).

We aggregated trial-by-trial firing rates of independently recorded dmPFC neurons, that is, by creating pseudo-populations. The dataset was conformed of 1-s time windows that were advanced in 0.1-s intervals starting 2 s before and ending 2 s after an event. We used all recorded neurons that met inclusion criteria for a minimum trial number, without preselection, with the exception of the analyses of pure- and mixed-selectivity neurons. We divided the dataset into 80% for training the multiclass SVM algorithm and 20% for testing the model's predictions. To construct the training and testing datasets, we randomly selected the trials that would constitute each dataset and averaged the corresponding neuronal activity in 25 equally populated bins for each condition to obtain a balanced dataset. Importantly, the training and testing datasets were balanced for each condition. This procedure was repeated 200 times and averaged to obtain a parametric estimate of the accuracy of each decoder and to perform a permutation test. The performance of the classifier was evaluated by comparing the classifier predictions on the test data with the labels for the test data.

We report the proportion of test repetitions that were labeled correctly as prediction accuracy. In all classification cases, chance performance was determined by randomly shuffling the training labels and reporting the proportion of test repetitions that were labeled correctly. Average chance prediction accuracy was similar to the theoretical chance prediction accuracy in all cases given that we used balanced and equally populated bins for each tested condition. The plotted prediction accuracy is aligned to the center of the analyses window, whereas the reported timing of changes in accuracy including peak (or maximum) accuracy reflect the center of this time window.

Eye position analysis

To control for the possible effects of gaze or "lower-level" sensory features related to the identities of the other social agents, we also tracked the recorded animal's eye position. First, we detected the animal's eye fixations during an intertrial control interval in which no task was performed. During this period, the animals did not perform a task and were free to look at their conspecifics. We defined a fixation when eye velocity was below 25% of its statistical SD for longer than 0.4 s as described previously (*49*). Second, we contrasted single neuronal activity while gazing at other monkey 1 or other monkey 2 in the first 0.4 s of eye fixation using a Wilcoxon rank-sum test. We defined a neuron as distinguishing between specific agents if the test was significant, and a chi-square test was used to compare the number of neurons that displayed a response.

Spatial location analysis

To evaluate the effect that spatial location had on the neuronal response, we swapped the physical locations of the two nonrecorded animals halfway through the trials (Fig. 1D, middle). We then contrasted the neuronal responses to the location of the other monkeys, either to the monkey to its left or its right independent of identity, before and after switching the animal's positions with a two-way ANOVA ($P < 0.05$). We provide a ternary plot to visualize the relation between neuronal activity related to the agents' identity and their spatial location. Any given location in the triangle is determined by the magnitude of response when each of the three monkeys received a reward. Each side of the triangle corresponds to one of these magnitudes, and each vertex represents a maximal response when a specific animal received a reward in relation to the other two monkeys. Thus, for example, activity localized to the left-upper vertex before the switch in Fig. 2E indicates that the neuron only responded when a reward was given to the monkey in that location. The color code provides the density of activity across trials.

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SUPPLEMENTARY MATERIALS

science.org/doi/10.1126/science.abb4149
Figs. S1 to S8
Tables S1 and S2
MDAR Reproducibility Checklist

View/request a protocol for this paper from *Bio-protocol*.

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