



Neural populations in macaque anterior cingulate cortex encode social image identities

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The anterior cingulate cortex gyrus (ACCg) has been implicated in prosocial behaviors and reasoning about social cues. While this indicates that ACCg is involved in social behavior, it remains unclear whether ACCg neurons also encode social information during goal-directed actions without social consequences. To address this, we assessed how social information is processed by ACCg neurons in a reward localization task. Here we show that neurons in the ACCg of female rhesus monkeys differentiate the identities of conspecifics in task images, even when identity was task-irrelevant. This was in contrast to the prearcuate cortex (PAC), which has not been strongly linked to social behavior, where neurons differentiated identities in both social and nonsocial images. Many neurons in the ACCg also categorically distinguished social from nonsocial trials, but this encoding was only slightly more common in ACCg compared to the PAC. Together, our results suggest that ACCg neurons are uniquely sensitive to social information that differentiates individuals, which may underlie its role in complex social reasoning.

Processing information with respect to social context is a fundamental component of social cognition^{1–3}. In humans and nonhuman primates, this ability allows individuals to navigate social interactions and learn about their environment from others^{4,5}. To date, it remains unclear whether social information processing relies on unique computations or distinct neural circuits, or whether it employs general functions that also mediate complex behavior in nonsocial contexts^{6,7}. Given the prevalence of social information in daily life, it is important to understand the underlying neural codes governing its use.

In primates, the medial frontal cortex, particularly the anterior cingulate cortex gyrus (ACCg), has consistently been implicated in social information processing^{8–11}. Neuroimaging in humans has found activation in the ACCg when participants estimate the probability that a social partner is trustworthy¹², the similarity of others' political beliefs or preferences to their own¹³, or the volatility of information coming from a confederate⁴. In monkeys, neurons in a specific region of the ACCg, situated in area 32, rostral to the corpus callosum, encode the receipt of reward for both themselves and others¹⁰, and

lesions that include this region reduce the tendency to form prosocial preferences⁹. Encoding of social variables is less prevalent more caudally and dorsally in ACC¹⁰, suggesting that this region of ACCg plays an important role in producing socially appropriate behavior that takes others into account. However, compared to self-guided goal-directed choices, these types of social decisions typically have added complexity, such as ambiguity about the states, beliefs, or actions of others. Overlapping regions of ACCg are also activated when making nonsocial decisions in complex environments, for instance when humans adapt their behavior based on uncertain evidence¹⁴, or when monkeys make decisions that weigh costs versus benefits¹⁵. Since the ACCg is implicated in both social reasoning and more general cognitive control processes, one possibility is that its involvement in social situations relates to the complexity of these tasks rather than their social nature. Here, we aimed to study ACCg involvement in goal-directed behaviors of similar complexity that vary only in the involvement of social versus nonsocial information.

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A natural social cue that can guide decisions is directed gaze^{2,16,17}. Observing another individual attending to an object or location in the environment can shift one's attention toward the same direction, a behavior called gaze following. Gaze following can impact future decisions related to the information in the focus of shared attention^{18,19}, and is a conserved tendency across primate species found in both adult and infant humans as well as monkeys^{17,20–22}. This behavior is also altered in some cases of neurodivergence. For example, the ability to follow a sender's gaze can be affected in individuals with autism²³. Whether gaze following deficits represent unique alterations in social processing or are part of larger deficits in attentional, orienting, or salience detection mechanisms is unclear.

To better understand whether unique neural processes are engaged by social cues that inform directed eye movements, we developed a reward localization task in which rhesus monkeys use direction of a social cue or a nonsocial cue to select a visual target to get a reward. This task allowed us to determine whether ACCg neurons respond to social information in the absence of potential social outcomes (e.g., prosocial influences). In addition, our task varied whether the cues contained information about the rewarded target's location. To determine whether encoding of social information is unique to the ACCg, we contrasted neural responses to those in the prearcuate cortex (PAC), area 8A, in and around the frontal eye fields. This region is not strongly implicated in social cognition, but rather in visual attention and planning upcoming eye movements^{24,25}, which are also important aspects of the task. Our results show that neurons in both regions differentiate social from nonsocial cues. However, the ACCg, but not PAC, showed a bias toward distributed encoding of social identity information over nonsocial image identities. This occurred despite social identity being irrelevant to solving the task. These results add to the growing body of literature implicating the ACCg in uniquely processing social information and suggest that identity encoding could underlie its role in complex social reasoning.

Results

Task performance

Previous research has shown that monkeys can follow the gaze of conspecifics¹⁷. Here we tested whether monkeys could use an image of a conspecific's directed gaze to select a rewarded target. We used image sets, each consisting of 5 unique images of the same monkey's face gazing to the left, right, or forward. Directional images within each set included two pairs of images that each had an identical monkey head with the eye region manipulated to direct the gaze left in one

image and right in the other. We assessed whether there were differences between this socially guided behavior and the same behavior guided by nonsocial cues in the form of arrows (Fig. 1). There were four different trial blocks that occurred repeatedly in pseudorandom order. One block contained all nonsocial image sets, and the others contained image sets of 2 monkey faces each. The block structure was implemented to encourage monkeys to learn all image sets, and to test whether blocks with social images differed from nonsocial blocks. Each block included right, left, and nondirectional images counterbalanced and randomly selected. To begin each trial, monkeys had to hold a touch-sensitive bar and fixate a point on the task screen until an image appeared for 1000 ms. Subjects could freely view the image if they continued to hold the bar. Then two identical green squares were shown on the right and left, and monkeys had to choose the correct target to receive a fruit juice reward (Fig. 2). If the image did not indicate a direction, the squares were different colors (red and purple) and the monkey had to select the purple square to receive a reward. To make a choice, monkeys fixated the desired square and simultaneously released the bar. Data include 31,953 trials over 39 sessions for Monkey N, and 24,641 trials over 30 sessions for Monkey J.

Given that the visual guides (i.e., eye gaze and arrow direction) conveyed the same information, we predicted that monkeys should be able to use either cue type to perform the task. We found that both monkeys performed significantly better than chance (> 50%) for both types of visual guides (Fig. 3). Interestingly though, they both performed worse when using social guides, compared to nonsocial guides. A logistic regression analysis including context, information source (directional cue or target color), and gaze direction, found a significant main effect of context in Monkey N ($t_{1,31953} = -2.49$, $p < 0.05$), and a trend toward significance in Monkey J ($t_{1,24641} = -1.85$, $p = 0.065$), with better performance on nonsocial trials in both cases. Given Monkey J's high performance overall, the difference between animals is likely a ceiling effect. Despite this asymmetry, however, performance was greater than chance in both contexts, demonstrating that monkeys can use gaze information from static social images to guide choice behavior.

Gaze behavior

Our task design allowed the monkeys to freely view the visual guides, so we quantified their natural viewing behavior to determine whether attending to a stimulus increased their ability to gather information and make better choices. In general, monkeys spent the most time looking at either the eyes or arrows of the visual guides, or at the cued

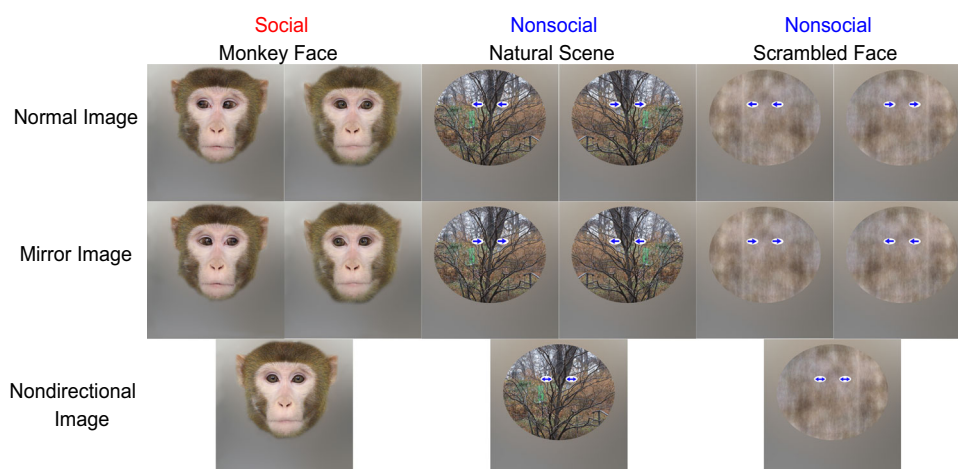


Fig. 1 | Visual guides. Example image sets for different types of visual guides. Top row: Visual guides with the same monkey gazing left or right (social), a natural scene with arrows pointing left or right (nonsocial), and a scrambled monkey image

with arrows pointing left or right (nonsocial). Middle row: The same visual guides as the top row, but with eye gaze or arrow directions reversed. Bottom row: examples of visual guides of each type that do not give any directional information.

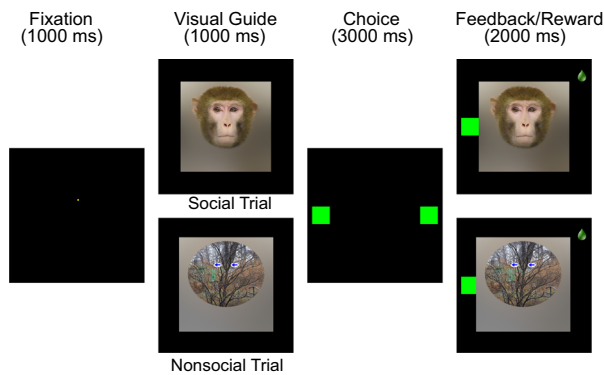


Fig. 2 | Behavioral task. Each trial required monkeys to fixate a point on the screen for 1000 ms to begin. They were then shown either a social (top) or nonsocial (bottom) visual guide. Following visual guide presentation, two identical green squares appeared (or one purple and one red square on nondirectional trials; not shown). Monkeys were given a juice reward if they choose the target indicated by the visual guide.

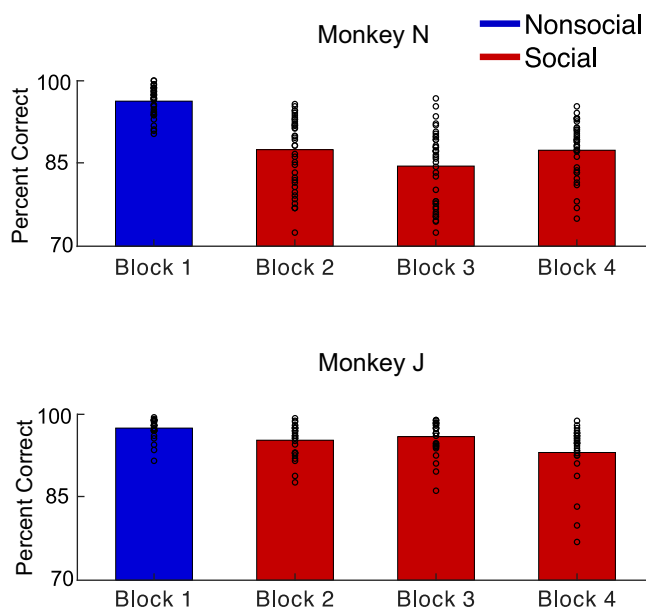


Fig. 3 | Behavioral performance across blocks. Percent of trials in which the correct target was selected for Monkey N and Monkey J. Block 1 (blue) includes all nonsocial trials and Blocks 2-4 (red) are social trials. Bars show the overall accuracy across sessions ($n = 39$, 30 sessions Monkeys N, J). Dots indicate block-wise accuracies in each session.

target location (Fig. 4). To determine whether performance was predicted by the amount of time monkeys looked at the discriminative region of the visual guides, we quantified the total time on each trial that their gaze fell within an ellipse with a horizontal radius of 5 and vertical radius 2.5 visual degrees, centered on the eyes or arrows, during correct and incorrect trials for both contexts. Multiple linear regressions determined whether gaze durations varied with performance (correct vs incorrect), context (social vs nonsocial), information source (directional cue vs nondirectional), and the interaction of these parameters (Fig. 5). We found a main effect of performance for both subjects (monkey N: $t_{31953} = 4.54$, $p < 0.001$, monkey J: $t_{24641} = 4.81$, $p < 0.001$), with longer gaze times on correct trials. In addition, there were effects of information source (monkey N: $t_{31953} = -2.76$, $p < 0.01$, monkey J: $t_{24641} = -2.74$, $p < 0.01$), with longer gaze times on nondirectional trials in both animals. This is likely because monkeys could

anticipate the rewarded target location on directional trials, and sometimes moved their eyes in anticipation, as in Fig. 4, whereas direction information was not available on nondirectional trials until the targets appeared. For monkey N, there were also interaction effects of performance \times context ($t_{31953} = -3.49$, $p < 0.001$), information source \times context ($t_{31953} = -4.69$, $p < 0.001$), and a three-way interaction ($t_{31953} = 3.46$, $p < 0.001$) performance \times information source \times context, such that the longest gaze times were for correct responses to non-informative social images. In Monkey J, there was an interaction effect of performance \times information source ($t_{1,24641} = 3.13$, $p < 0.005$), where gaze duration was longer for correct responses on informative trials. However, we did not find consistent effects of social vs nonsocial context, suggesting that the type of visual guide had little impact on gaze duration. Together, these data show that there are idiosyncrasies in how monkeys attend to each stimulus, but both monkeys looked at the stimulus longer during nondirectional trials, and correct performance consistently accompanied longer viewing times.

Neurophysiology

We recorded 101 and 114 neurons from ACCg and 102 and 126 from the PAC in subject N and J, respectively (Fig. 6a, b). To quantify neural encoding in this task, we fit the firing rate of each neuron in 200 ms sliding windows with a multiple regression model (Methods). Most neurons that encoded context did so between the onset of the visual guide and 500 ms post onset in both ACCg (6 neurons Monkey N, 16 neurons Monkey J) and PAC (8 neurons Monkey N, 17 neurons Monkey J) (Fig. 7). A small number of neurons in the ACCg encoded context before image onset, which was possible because the cues appeared in blocks, so monkeys could anticipate seeing a social or nonsocial image (2 neurons Monkey J only). To assess the tendency for neurons to respond more to social vs nonsocial cues, we calculated the average regression weight on the context predictor in the first 500 ms following stimulus onset for each neuron. Positive weights indicated greater firing rates for social stimuli, while negative indicated greater firing rates for nonsocial stimuli. Within the ACCg, similar proportions of neurons had positive and negative weights (50% Monkey N, 56% Monkey J, positive beta weights), and binomial tests confirmed that ACCg had no bias toward stronger responses for a particular context ($p = 0.83$). Within the PAC, there was also no overall bias toward stronger responses for a particular context (binomial test, $p = 0.42$). In Monkey J, there were similar proportions of neurons that responded to each context (52% positive). In Monkey N, a smaller proportion of selective neurons responded more for social images (13% positive), but a binomial test showed that this was not statistically significant ($p = 0.07$).

Next, we assessed response latencies in both regions. We found that in PAC, but not ACCg, neurons that had higher firing rates for social contexts tended to have shorter latencies than those responding more to nonsocial contexts (Wilcoxon rank sum: PAC, $Z_{\text{pos-neg}} = -2.33$, $p = 0.021$, ACCg, $Z_{\text{pos-neg}} = -1.02$, $p = 0.31$). The reason for faster PAC responses to social cues is unclear, but it underscores that PAC neurons are differentially responsive to social and nonsocial images. Finally, we found no significant difference in latencies between regions ($Z_{\text{pos-neg}} = 1.19$, $p = 0.23$).

Since there were not strong differences in how ACCg and PAC encoded social context, we assessed encoding of other variables in the task. To do this, we collapsed the sliding regression into four 1000 ms epochs, and found the number of neurons with significant encoding at any point in each epoch. During the fixation epoch, before the visual guide was presented, there was very little information encoded in either region, as expected (Fig. 8). When the visual guide appeared, the most common variable encoded by ACCg was context (10% overall, 20.2% of task-responsive neurons), followed by information source (7%, 13.8% of task-responsive neurons), followed by target location (3%, 6% of task-responsive). In addition, several ACCg neurons significantly

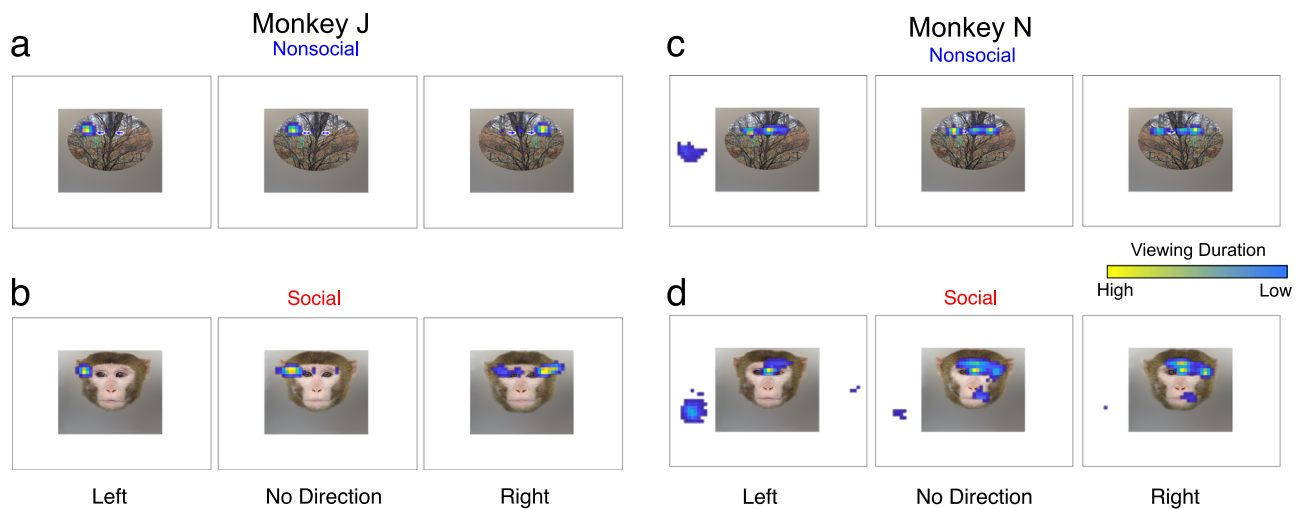


Fig. 4 | Examples of viewing behavior. Heatmaps display normalized viewing duration across all sessions for Left, No Direction, and Right visual guides. **a, c** Nonsocial visual guide. **b, d** Social visual guide.

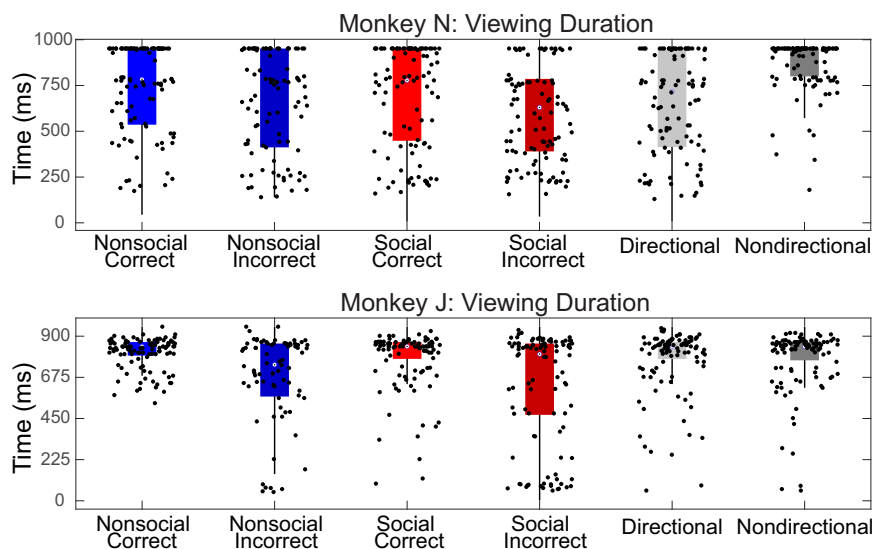


Fig. 5 | Gaze duration across task conditions. Viewing duration during visual guide presentation for correct and incorrect trials separated by social (red) and nonsocial (blue) context, also separated by information source (directional or nondirectional). Each box includes the 25th to 75th percentiles, centered on the

median; whiskers include the full range of the data. Analyses were performed on all trials, and points show 100 representative trials, selected by downsampling the total trials in each condition. The maximum time was the duration of the visual guide presentation (1000 ms).

differentiated one or more social identities (Fig. 8a, red bars). Significance for the social identity regressors meant that a neuron responded to all image variations showing the same monkey in the visual guide. Pooled together, neurons differentiating one or more image identities constituted 14.0% of neurons in ACCg (30 neurons, 27.5% of task responsive neurons). In the subsequent epochs surrounding choice and feedback, encoding of information source and target location increased, while encoding of image identities decreased (Fig. S1).

To determine whether these responses are unique to ACCg, we contrasted our results with neurons in the PAC, whose function is more related to visual attention and planning²⁵. Overall, larger proportions of PAC neurons encoded task-relevant information (Fig. 6, right). The most prevalent encoding in PAC during the visual guide epoch was target location (19%), followed by information source (18%), followed by the interaction between target location and information source (14%), which captured the fact that target location is not known on

trials in which the eyes or arrows are uninformative (Fig. 8b). The prevalence of information about the location of targets is consistent with PAC's role in visuospatial attention and planning upcoming saccades. Compared to ACCg, location information was encoded by significantly more task-responsive neurons in PAC during the visual guide epoch (target location 44/203 neurons in PAC, 7/109 neurons in ACCg, binomial test uncorrected $p = 2.1 \times 10^{-5}$, corrected $p = 6.4 \times 10^{-5}$; interaction of target location and information source 33/203 PAC, 3/109 ACCg binomial test uncorrected $p = 1.2 \times 10^{-5}$, corrected $p = 3.6 \times 10^{-5}$). Target location encoding increased in both regions during the choice epoch (Fig. S1). On the other hand, context encoding was slightly more common in ACCg during the visual guide epoch, when considered against the proportion of task-responsive neurons (25/203 neurons PAC, 22/109 neurons ACCg, binomial test uncorrected $p = 0.019$, corrected $p = 0.059$). However, we interpret this effect with caution because there were not differences in the overall proportions of neurons encoding context (10.2% ACCg, 11.0% PAC). In addition, we

observed PAC neurons that were sensitive to image identities. Together, neurons with selectivity for one or more images accounted for 23.7% of neurons in PAC (54 neurons, 26.6% task-responsive). Among these, however, there appeared to be a preference for nonsocial image identities, rather than social, the opposite pattern of that found in ACCg neurons. Therefore, we investigated this pattern in more detail in subsequent analyses below.

First, however, we ensured that differences in sensitivity to social and nonsocial identities were not related to variability in behavior between the different cue types. Our behavioral analyses found that accuracy was lower on social trials, so we performed the same multiple regressions described above using only correct trials and found qualitatively similar results (Fig. S2). In particular, comparable percentages of neurons differentiated one or more image identities (17.2% and 21.9% ACCg and PAC, compared with 14.0% and 23.7% reported above),

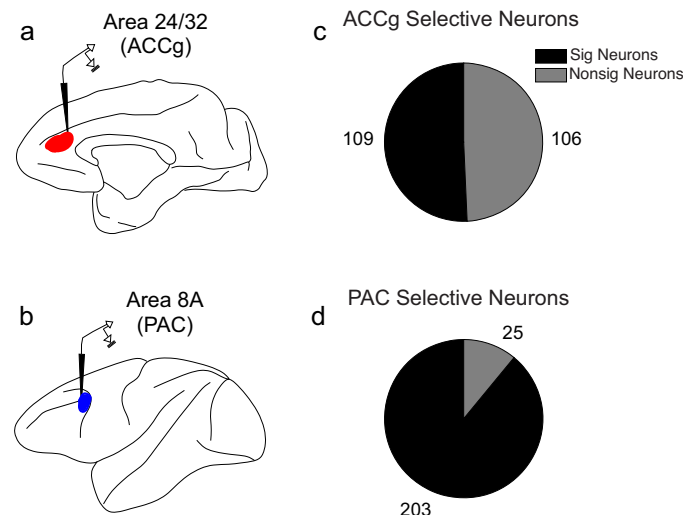


Fig. 6 | Neuron recording summary. **a** Target location in the ACCg. **b** Target location in the PAC. **c, d** Number of neurons across both monkeys that were selective for one or more task variables (black) in the ACCg and PAC.

with the same pattern of preferential encoding of social identities in ACCg but not PAC. Therefore, identity encoding appears to be unaffected by accuracy in this task. Other behavioral results showed that the amount of time that the monkey viewed the discriminative region of the cues (eyes/arrows) was variable, and for one monkey differed between social and nonsocial cues. We therefore regressed firing rates on the viewing durations calculated above. Here, we found that 55/215 (25.6%) neurons in ACCg and 80/228 (35.1%) neurons in PAC had firing rates that correlated with viewing duration. If identity encoding is unrelated to viewing duration, we would expect identity neurons to have these correlations at the same rate as the general neuron population. Such was the case. Out of 30 identity coding neurons in ACCg, only 9 had correlations with viewing duration (30%, binomial test against population prevalence $p = 0.54$) and out of 54 identity coding neurons in PAC, 21 correlated with viewing duration (38.9%, binomial test $p = 0.57$). Therefore, correlations between firing rate and viewing duration were no more common in identity coding neurons than the rest of the neurons, indicating that these correlations are not driving the identity coding that we report.

Next, to quantify the tendency of ACCg to respond selectively to different social identities and PAC to differentiate nonsocial images, we performed a post-hoc analysis. Binomial tests compared the proportion of neurons significant for one or more social identity regressors during the visual guide epoch to the proportion significant for nonsocial identity regressors, separately for both areas. To correct for the fact that there were more unique social images than nonsocial images, we normalized the neuron proportions by computing the average number of significant neurons per nonsocial image and multiplying this by the total number of social images. We found that a higher proportion of ACCg neurons were sensitive to social images (binomial test, $p \leq 9.5 \times 10^{-6}$, Fig. 9a) and this was consistent in each monkey's data tested separately (Monkey N, $p = 4.4 \times 10^{-5}$, Monkey J, $p = 0.012$). We assessed the location of significant neurons to determine whether social identity neurons were anatomically clustered in the ACCg, however, we did not observe a clear pattern (Fig. 10).

In contrast to ACCg, PAC neurons selective for image identities were not biased toward social cues, and if anything suggested a bias in the opposite direction. Overall, a higher proportion of PAC neurons were sensitive to unique nonsocial images compared to social (Fig. 9b),

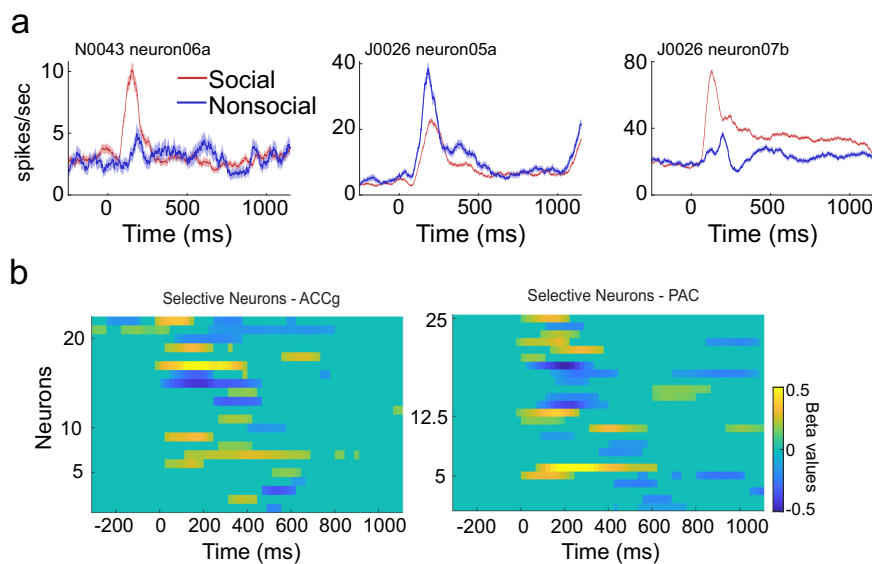


Fig. 7 | Neurons encoding social versus nonsocial contexts. **a** Example responses of three ACCg neurons encoding social/nonsocial context during the visual guide period. Lines show mean firing rates, shading shows \pm SEM. **b** Coefficient weights for context for all neurons that demonstrated selectivity in a multiple regression

during visual guide presentation in the ACCg (left) and PAC (right). Positive betas (warm colors) indicate stronger responses for social context, while negative betas (cool colors) represent stronger responses for nonsocial context.

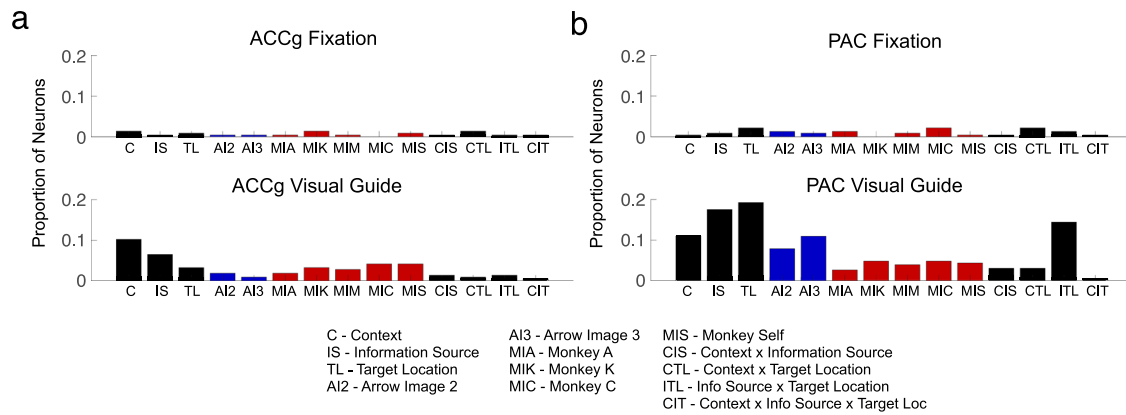


Fig. 8 | Single unit encoding in ACCg and PAC. Proportions of neurons in ACCg ($n = 101, 114$ Monkey N, J) **a** and PAC ($n = 102, 126$ Monkey N, J) **b** whose firing rates varied significantly with task variables in two epochs. Red bars indicate neurons significant for regressors that identified a social identity. Blue bars show neurons significant for regressors that similarly identify a nonsocial image.

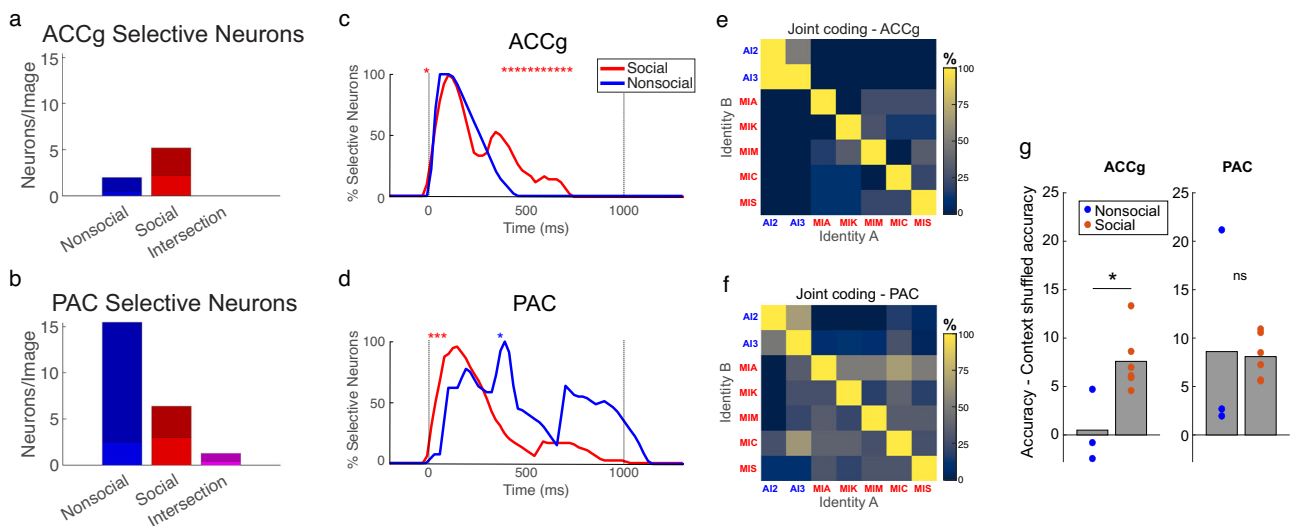


Fig. 9 | ACCg neurons selective for social identities. **a, b** Number of neurons per image sensitive to social identities only (red), nonsocial identities only (blue), or both (purple) in the ACCg **a** and PAC **b**. Lighter bar segments indicate the neurons contributed by Monkey N and darker segments indicate neurons from Monkey J. **c, d** Time course of responses relative to the appearance of the visual guide among significant neurons of each type in the ACCg **c** and PAC **d**. Y-axes are the percent of neurons with selectivity for each image type. Permutation tests determined significance for differences between social and nonsocial percentages. * one-sided $p < 0.05$. **e, f** Percent of neurons selective for identity A that are also selective for identity B in ACCg **e** and PAC **f**. Abbreviations for image identities are as shown in Fig. 8 (red = social, blue = nonsocial). Total identity selective neurons in panels **a–f**: 30 ACCg, 54 PAC. **g** Decoding accuracies (percent) for each identity (dots) above accuracies obtained when identities were shuffled within social and nonsocial contexts (see Fig. S4). Decoding was done with pseudopopulations from each subject and region ($n = 101, 114$ ACCg, and $102, 126$ PAC, Monkeys N, J respectively). Gray bars show the mean across images of each type. Comparison of social versus nonsocial decoding accuracy was assessed with two-sided Wilcoxon rank-sum tests on $n = 9$ images, * $p = 0.048$.

but this was driven by Monkey J (Monkey N, binomial test $p = 0.45$, Monkey J, $p = 1.7 \times 10^{-14}$). Since more than one identity regressor might significantly explain neuron firing (i.e., a neuron may respond to a subset of images), we quantified the number of neurons that reached significance for more than one image identity (Fig. S3). Among ACCg neurons sensitive to social identities, 73.1% (19/26) responded to one identity and 26.9% (7/26) responded to more than one identity. This is similar to identity-sensitive cells recorded from the primate amygdala that respond to some, but not all monkey faces²⁶, and is consistent with distributed encoding of social identities. Critically, no ACCg neuron was selective for both a social and a nonsocial image ('intersection', Fig. 9a, b). Only PAC neurons responded to images of both types. This could be clearly seen by examining joint coding of image identities (Fig. 9e, f). Joint coding was defined as a neuron with significant regression coefficients for two (or more) identities. In PAC, small

proportions of neurons jointly coded many different image pairs, but in ACCg, joint coding was only found among images of the same type (social or nonsocial; Fig. 9e, f, Fig. S3). Moreover, joint coding among social images was spread among pairs of identities and not consistently found among particular pairs, suggesting that there was no underlying feature or grouping of identities that the test monkeys were detecting to cause a neuron to respond to both. We also assessed the time course of encoding each image type. Identity selective neurons responded with similar time courses in ACCg, regardless of the type of image, but social identity neurons continued to be active significantly longer during stimulus presentation (Fig. 9c). On the other hand, PAC neurons responded to social images slightly earlier than nonsocial images (Fig. 9d). This is consistent with our finding that neurons in PAC that responded to social over nonsocial contexts tended to respond earlier. Together, these data could suggest that

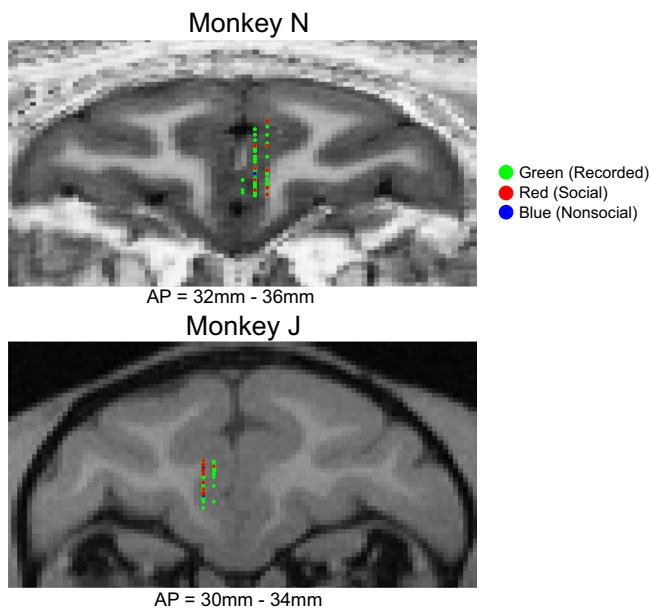


Fig. 10 | Neuron Locations. Coronal MR images through the prefrontal cortex. Images show the mid-point, in the anterior-posterior (AP) dimension, of the recording field in each subject, with all recorded neurons projected onto this slice. Note that this results in some recording locations appearing to fall slightly outside of gray matter boundaries. Colored dots represent recorded neurons (green = all recorded neurons; red = neurons that were significant for social image identity; blue = neurons significant for nonsocial image identity).

social information reaches the PAC faster than information from other sources, suggesting a distinct circuit.

Overall, these results are consistent with distributed coding of social identities among ACCg neurons, meaning that individual identities should be decodable from neural populations. To test this, we used linear discriminant analysis (LDA) to classify each of the 9 image identities in the task from pseudopopulations of ACCg neurons and PAC neurons. We found that image identities were decoded above chance in each group of neurons, but because neurons also distinguished social and nonsocial contexts categorically, the classifiers frequently confused images of the same type (Fig. S4a–d). To determine if identities were decodable above and beyond the social or nonsocial context, we established a control condition in which image identities were shuffled within their respective contexts. This within-context shuffling mimics what we would expect if neurons differentiated social from nonsocial cues, but did not differentiate unique identities (Fig. S4e–h). We subtracted classification rates obtained from the shuffled data from those obtained from real data, and found that only social identities were decodable from ACCg populations (Fig. 9g). Comparison of corrected accuracies revealed significantly higher decoding of social versus nonsocial identities in ACCg (Wilcoxon ranksum test $p = 0.048$). On the other hand, all images were decodable from PAC neurons, and there were no differences between social and nonsocial image types (Wilcoxon ranksum test $p = 0.55$). This is expected, given that neurons in PAC distinguished all image types, whereas neurons in ACCg only distinguished different social identities. Together, this supports the conclusion that neurons in ACCg are particularly sensitive to the identities of conspecifics.

Discussion

Social interactions are important to our daily lives, and the ability to track an agent's identity is a fundamental component of normal social interactions. Here, we found that a small but significant proportion of neurons in the ACCg were sensitive to the identity of conspecifics in social images, but not identities of nonsocial images. As a population,

ACCg neurons encoded social, but not nonsocial identities. This occurred in a task where social or nonsocial images played identical roles in guiding behavior, and where the identity of the monkeys had no relevance to accurate performance. The task did not involve social interactions, decisions about the other animal, or future social consequence of choices the actor monkey made. Therefore, these results indicate that identity coding happens incidentally in ACCg. Moreover, similar selectivity was not found in a frontal region more involved in visuospatial attention, the PAC. In PAC, neurons differentiated images of either type, and were not biased toward social cues. This suggests that the tendency to encode images of a particular monkey, rather than a familiar image in general, is a specialization of the ACCg that may underlie its role in more complex social tasks. In particular, it suggests that ACCg may be involved in parsing and/or tracking the identities of social partners.

Our results are in line with other recent evidence showing that ACC processes social identities^{18,27}. For instance, in monkeys engaging in a 3-way prisoners dilemma task where they had to choose which partner to give a reward to, the animals tracked the decisions of each partner and used this information to decide how to interact with them¹⁸. Neurons on the dorsal bank of the ACC sulcus encoded information about partner identities as well as their past behaviors, two pieces of information that could be used to make socially-relevant choices. However, our study provides an important contrast, showing that neurons that respond selectively to social identities are not sensitive to the identity of nonsocial images when making identical decisions, with no social consequences. Together, these studies support the notion that the social identity coding we observe in ACC is directly linked to social decision making.

Our results stand in contrast to a recent study, which found that fewer ACC neurons responded to social images compared to nonsocial images that were paired with different amounts of reward²⁸. Similar to our study, task demands were equated for social and nonsocial conditions. However, unlike our task, potential rewards differed among image types, with the nonsocial images predicting different reward amounts and social images predicting the same amount. Since ACC is known to strongly encode reward expectations^{29–31}, this could explain our contrasting results. In addition, the regions of ACC that neurons were recorded from differed across studies. In the present study, neurons were recorded more rostrally, in the pregenual ACCg (Fig. 10). This is the same area that has previously been reported to differ from neighboring ACC regions in its tendency to encode socially-relevant information¹⁰. Consistent with this, there was no clear specialization for social cues reported in a more caudal region of ACC²⁸. Taken together, these findings suggest functional localization of social information processing to the pregenual ACCg.

In humans, multivoxel activity patterns in a similar region of ACC also differentiates the unique identities of human photos²⁷. Similar to our study, social images were used to convey task information, but unique identities were associated with different degrees of accuracy of the information they provided. In that case, the same region of ACC tracked confidence in the advisor, again suggesting that identity encoding is important for guiding future behavior. In our task, there was no difference in the predictive ability of different social (or nonsocial) images, and in fact monkey identity was entirely incidental to the task. Despite this, neurons in the ACCg still differentiated identities when they were social in nature. This suggests that responding to social identities may be an automatic function of the ACCg that occurs even when it is not relevant to ongoing behavior. Other aspects of our results are consistent with the idea that monkeys attend to task-irrelevant features of the social cues, such as identity. For instance, both monkeys were slightly but consistently less accurate when using social guides. It is possible that the actor monkeys attended to other visual features of the images that contribute to a recognizable identity, and this may have distracted them from performing as proficiently on

social trials. We ensured that all images in the task were highly familiar and that only the region of the eyes or arrows could be used to locate the target in order to minimize these effects. However, it remains possible that social cues carry more inherent meaning or intrinsic value³² that is absent from the nonsocial cues, and this results in distraction and the slight differences in behavior that we observed. Indeed, we cannot determine how the test monkeys interpreted the social cues, beyond the target selection rules that they learned in the task. Despite this, it is unlikely that the identity coding we observed in ACCg was driven by nonspecific effects of attention, valuation, or otherwise heightened level of engagement with the social images, because responses differed from those in PAC. If identity encoding were due to a general feature of how the monkeys interpreted or responded to the images, rather than a function specific to ACCg, then we would expect to have seen similar results in PAC neurons. Regardless, further work is needed to determine the nature of social value and how it relates to social image processing in ACCg.

In broader studies of social cognition, the ACCg in both monkeys and humans has been found to play an important role in social decision-making. For example, the trust game^{12,33} and ultimatum game³⁴ require participants to track individual identities or other schema that can be used as a basis for making judgements when interacting with their partner(s). Additionally, monkeys with circumscribed lesions to the ACCg cannot learn from vicarious reward delivered to a conspecific⁹. And similarly, monkeys that watched partners perform a task were able to perform the same task significantly better compared to not observing a partner, and this ability was also linked to activity in the ACC^{35,36}. Therefore, there is strong evidence that ACC, and ACCg in particular, is important for social decision-making.

In contrast to ACCg, PAC primarily encoded location information during the visual guide epoch, which is consistent with a role in visuospatial attention and planning upcoming eye movements. One of our subjects (Monkey N) even performed preemptive saccades toward target locations before the choice epoch (Fig. 4), consistent with the idea that the monkeys begin anticipating the location they will respond to once the information is presented in the cue. We also found that some neurons in PAC were sensitive to social image identities, but these were intermixed with similar or greater proportions (in the case of monkey J) of neurons sensitive to the identity of nonsocial images. Some PAC neurons even responded to more than one image type. This suggests that PAC parses unique features of similar trials but doesn't preferentially encode social identities like ACCg. Similarly, we found that many PAC neurons also distinguished social versus nonsocial contexts. This is in line with previous studies showing that these neurons can encode more abstract, contextual information^{25,37}, in addition to more concrete spatial or attentional information. Although we made efforts to match the size and location of the arrows to the eyes, contextual differences could still be driven by features of the task, such as the need to recall the rules of how to interpret eyes or arrows.

An important limitation of our study is that we used only female monkeys, and it's not clear whether males would respond to social images in a similar manner. Previous studies have shown that dominance as well as the sex of the monkey can play a role in social behavior and decision-making³². We suspect that these effects would be limited in our task, since it was designed to remove any social interaction or social decision-making, and instead focus on target selection for self-reward. Nonetheless, future studies will be needed to understand if there are any links to sex or dominance in ACCg activity related to social identities.

Overall, there is a growing body of literature implicating the ACCg, along with other regions, in a putative circuit for social decision-making^{6,38-40}. Our study expands on this by showing that the ACCg is uniquely sensitive to the identity of social images when using eye gaze

to infer target information. An important component of social interactions is the ability to interpret gaze and this aspect of our study could have implications for understanding impaired gaze following and social functioning in neurodivergent individuals⁴¹. Of note, there are direct unidirectional connections between the ACCg and PAC, particularly the frontal eye fields^{42,43}, which may provide a circuit by which social information directs one's own gaze. Beyond gaze, identity coding is important for myriad social behaviors, including pair bonding and group-level dynamics, and understanding how ACCg neurons interact with wider social-brain circuits will help reveal mechanisms that produce complex socially-appropriate behavior.

Methods

Subjects

We trained two female rhesus macaques (*Macaca mulatta*), aged 6 and 9 years and weighing approximately 5.7 and 6.8 kg at the time of recording (Monkey J and N, respectively). Monkeys were socially housed with at least one companion monkey in their home cage with visual access to other monkeys in the colony. Each subject underwent cranial surgery to implant a head positioner for accurate eye-tracking and to minimize movement during neural recording, as well as a unilateral recording chamber positioned over either the left (Monkey J) or right (Monkey N) hemisphere. Surgical anesthesia was induced with ketamine (10 mg/kg IM) and maintained with 1–5% inhaled isoflurane. Monkeys were intubated and all surgical procedures were performed using sterile technique. Monkey N had an acrylic headpost while Monkey J had a titanium headpost. Chamber dimensions were 35.19 mm × 27.14 mm, and placement was calculated using images obtained from a structural MRI scan at 3T for each subject. The chambers were positioned to allow access to both ACCg (areas 24/32) and the PAC (area 8A). All procedures were in accordance with the National Institute of Health guidelines and recommendations from the Icahn School of Medicine at Mount Sinai Animal Care and Use Committee.

Behavioral task

Subjects were trained using positive reinforcement to sit head-fixed in a primate chair that allowed postural adjustments. During training and testing sessions, the chair was placed in a testing rig facing a computer monitor. A touch-sensitive bar was affixed to the front of the chair within the monkeys' reach. Eye movements were tracked with an infrared tracking system (ISCAN). Behavioral interfaces were controlled with NIMH MonkeyLogic software⁴⁴. To begin each trial, monkeys held the bar and fixed their gaze within 2° visual angle of a fixation cue for 1000-ms. The fixation cue was located at 5° above the origin to place the eyes in the center of the discriminative cues that were subsequently presented. Visual guides were approximately 10° × 10° in size. Following visual guide presentation, two identical green squares, 2° × 2° in size, were shown to the right and left. To discourage any reflexive actions (e.g., the monkeys responded as soon as the visual cue turned off) the start of the choice epoch was offset by steps of 250-ms between 0 and 1 s (i.e., 0-ms, 250-ms, 500-ms, 750-ms, 1000-ms). Once they made a choice, the unchosen square disappeared, and the visual guide reappeared along with their selected choice. Correct choices resulted in fruit juice reward; incorrect selections resulted in a 6-s timeout.

Two types of visual guides defined two different contexts, social and nonsocial. Social images were monkey faces and nonsocial images were arrows on a complex background. There were 9 image sets in total – 3 nonsocial sets, and 6 social sets. Each image set included otherwise identical images that indicated left, right, or neither direction. Each social image was a forward-facing monkey face with neutral expression and gaze directed to the left or right, or forward-facing gaze (see Fig. 1). Monkey faces were manipulated photographs of animals from our colony, including the test monkeys. Because our goal

was to test social images as a category, we included a mix of sexes, familiarities, and ranks, but did not power the image set to systematically test for effects of any of these variables. Images included 3 male and 3 female demonstrator monkeys. Some of monkeys in the images were housed in the same room as the test monkey and others were housed in separate rooms. The nonsocial images included pairs of arrows pointing to the left or right, or bidirectional arrows, set in white circles of approximately the same size and location as the monkey eyes, placed on a complex background. Backgrounds were either a natural scene, (i.e., trees in a park), or scrambled pixels of the monkey faces. The former was included because they are recognizable, natural images whereas the latter match the monkey faces in low level visual statistics. For all directional images (both social and nonsocial), images were digitally manipulated to flip, horizontally, the eye gaze or arrow background, while holding everything else constant. This was done to make sure that the monkeys only used gaze direction or arrow direction to select the target, and no other defining landmarks in the images. For nondirectional trials (i.e., eyes looking forward or double-headed arrows), the images did not indicate the correct target, so the targets consisted of a red and purple square instead of identical green squares, and the purple square was always correct. These trials were included to assess whether neurons encoded informative and non-informative visual guides similarly.

Images belonging to the same set were defined as having the same identity. For social cues, a set included a total of 5 unique images: 3 different photographs of the same monkey (gaze right, gaze left, gaze forward), with each of the averted gaze images duplicated and one copy manipulated to invert the gaze direction. For nonsocial cues, there were likewise 5 unique images: the same background was presented in native and mirrored orientation, each with left and right arrows, and a native image was presented with bidirectional arrows. In total, across 9 image sets, there were 45 unique images used in the task. Trials occurred in blocks. Monkeys finished a block by completing 25 trials correctly, at which point a new block was pseudorandomly selected, with the constraint that blocks never repeated sequentially. Sessions were completed after approximately 800 correct trials.

Statistics and reproducibility

No statistical methods were used to predetermine sample size. Practical and ethical constraints limit the number of subjects in non-human primate studies. Two subjects are included because it is the smallest number with which we can demonstrate reproducibility. To this end, our main statistical results were verified in each subject's data and reported separately. The numbers of neurons recorded were based on anticipated effect sizes based other studies of cognitive variables in prefrontal neurons. Analyses included all sessions in which at least one well isolated neuron was recorded (6 and 0 sessions excluded from Subject N and J respectively). All completed trials from each session were included. Neurons with overall firing rate <1Hz were excluded because low firing rate neurons are difficult to characterize with the statistical methods employed here. Trials were presented to the monkeys in random order within the block structure described above. Neurons were not screened for response properties, and any well isolated neuron in one of the target regions was recorded. The investigators were not otherwise blinded during experiments because data were automatically logged by the behavioral interface and data acquisition system. All analyses were carried out with Matlab version 2021b (MathWorks).

Behavioral analysis

Behavioral analyses were carried out separately for each subject. To quantify task performance, we used a logistic regression to predict correct or incorrect target selection from context (i.e., social versus nonsocial), information source (i.e., directional guide versus target

color), cued direction (i.e., left versus right), and the interactions between these predictors.

Since monkeys freely viewed the visual guides, we also assessed how task variables influenced the amount of time they viewed the discriminative parts of the cues on each trial. To do this, we quantified the amount of time that the monkeys' eyes fell within an ellipse with horizontal radius of 5° and vertical radius of 2.5°, centered on the eyes or arrows in the visual guide, and used a multiple regression analysis with the parameters above, with the addition of performance (i.e., correct trials versus incorrect trials), to predict viewing time. All test statistics were based on two-tailed significance thresholds.

Neurophysiological recording

We used standard methods for acute neurophysiological recording (see ref. 45). Briefly, in each recording session, we simultaneously recorded from 3 to 12 tungsten microelectrodes (FHC, Inc) or 16-channel linear arrays (V-probes, Plexon). A guide tube was placed to penetrate dura for each probe. Since Monkey N had an acrylic headpost, we placed an empty guide tube positioned outside the recording field for ground. Monkey J had a titanium headpost, which was used for grounding. Each recording day, electrodes were manually lowered with custom-built microdrives to a target depth. We calculated target depths stereotaxically using 3 T structural MRI images. Once lowered to desired depth, fine adjustments were made to isolate waveforms from single neurons. We recorded from all well-isolated neurons in target areas, resulting in a random sampling of neurons. Waveforms were acquired and digitized using an acquisition system (Ripple Neuro) and saved for off-line analysis. Single units were isolated offline with manual cluster cutting, performed using Offline Sorter (Plexon). Isolated units with overall firing rates less than 1Hz were excluded from further analysis.

Neurophysiological analysis

To capture dynamics of encoding across a trial, we fit a multiple regression model (Eq. 1) to the firing rates of each neuron in sliding 200 ms windows. Model predictors were context (social versus nonsocial), information source (directional guide versus target color), cued direction (left versus right), the interactions between all predictors, and a matrix of image identities coded as one-hot vectors, using one social and one nonsocial image as an uncoded reference.

$$\hat{FR} = \beta_{\text{context}} + \beta_{\text{InfoSource}} + \beta_{\text{GazeDirection}} + \beta_{\text{Interaction}} + \beta_{(1-9)} \text{Identity}(1 - 9) \quad (1)$$

We analyzed neural activity during four trial epochs: fixation, visual guide on, choice, and feedback. All analysis epochs were chosen a priori, based on task events. The first window in each epoch started 200 ms before the onset of the relevant event, then analysis windows were stepped forward by 20 ms. This process was repeated through 1200 ms after epoch onset. To establish a two-tailed significance criterion, we ran this same sliding regression over the fixation epoch, when nothing was present on screen and selected a criterion that resulted in $\leq 5\%$ false discovery rate for information source and cued direction, which could not be anticipated at this time. With this criterion, significant encoding was defined as $p < 0.0005$ for Monkey J and $p < 0.003$ (two-tailed) for Monkey N, each for 4 consecutive time windows. A significant coefficient on an identity regressor meant that the neuron statistically differentiated that identity from the reference identity, not that the neuron responded uniquely to that identity, since neurons were often significant for more than one identity regressor. Therefore, we refer to such neurons as sensitive to, selective for, or differentiating identities, and the population that contains these neurons as encoding identities in a distributed manner.

We quantified the observed difference between neurons selective for social and nonsocial identity using a binomial test. The number of

selective neurons per nonsocial image was multiplied by the total number of social images to normalize our groups. The binomial test was then used to compare the probability of observing the proportion selective social neurons to nonsocial neurons.

To capture differences in encoding probability between social and nonsocial visual guides, we performed a permutation test. We randomized neurons sensitive to either social or nonsocial information using 10,000 permutations. We selected time bins that were greater than 95% of permutations for social>nonsocial and for nonsocial>social.

Decoding analyses

Four pseudopopulations were created, one for each subject and brain area. For each pseudopopulation, we matched the number of trials of each image identity by finding the minimum number of trials (n) of any identity across all sessions and randomly selecting n trials that included each identity for the analysis. Trials were selected without regard to the direction indicated by the cue (left, right, or non-directional) or whether the cue was the native or mirrored version, so the trials included random mixes of these variables. We performed the full analysis on 50 different runs of this trial selection procedure and averaged the results of all runs. For decoding, each neuron contributed a vector of normalized firing rates, averaged over a 500 ms window starting 200 ms after the appearance of the cue. Linear discriminant analysis (Matlab 2021b function `fitcdiscr.m`) classified image identities (1 to 9), using leave-one-trial-out cross-validation. We used two different shuffling procedures to establish significance. First, all identity labels were shuffled. This removed any information about identity, but also about social versus nonsocial context. Since our data showed that neurons differentiate contexts categorically, the decoders could improve accuracy by relying on context signals, for example improving the rate of random classification from 1/9 to 1/6 for a social image or 1/3 for a nonsocial image. Therefore, we also used a within-context shuffle procedure that scrambled the image labels within social and nonsocial contexts. This shuffling did not disrupt information that the neurons carried about social versus nonsocial contexts but scrambled any information about unique identities within each context. For each shuffle procedure, we ran the shuffle 10 times in each of the 50 runs. Two-sided non-parametric tests (Wilcoxon rank-sum) assessed significance.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The behavioral and neural data generated in this study have been deposited in the figshare database under accession code <https://doi.org/10.6084/m9.figshare.25447075>.

Code availability

Custom code to reproduce results is available at <https://doi.org/10.6084/m9.figshare.25447075>.

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Author contributions

J.S. and E.L.R. designed the study and wrote and revised the manuscript. J.S. collected and curated the data and conducted analyses. E.L.R. supervised data collection and analysis.

Competing interests

The authors declare no competing interests.

Additional information

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