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Neuronal reference frames for social decisions in primate frontal cortex

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Social decisions are crucial for the success of individuals and the groups that they comprise. Group members respond vicariously to benefits obtained by others, and impairments in this capacity contribute to neuropsychiatric disorders such as autism and sociopathy. We examined the manner in which neurons in three frontal cortical areas encoded the outcomes of social decisions as monkeys performed a reward-allocation task. Neurons in the orbitofrontal cortex (OFC) predominantly encoded rewards that were delivered to oneself. Neurons in the anterior cingulate gyrus (ACCg) encoded reward allocations to the other monkey, to oneself or to both. Neurons in the anterior cingulate sulcus (ACCs) signaled reward allocations to the other monkey or to no one. In this network of received (OFC) and foregone (ACCs) reward signaling, ACCg emerged as an important nexus for the computation of shared experience and social reward. Individual and species-specific variations in social decision-making might result from the relative activation and influence of these areas.

Social cohesion depends on vicarious identification with members of one's group. In social situations, we are aware of our actions and their consequences, but also consider those of others, especially those with whom we might interact[1]. We also estimate the internal states of others, perhaps by simulation[2], which in turn shapes our future actions. Social situations can drive observational learning[3], and other-regarding preferences influence neural computations that ultimately result in cooperation, altruism or spite[4,5]. Disruptions of neural circuits involved in other-regarding processes may underlie social deficits attending neuropsychiatric conditions like autism[6]. Human imaging and clinical studies have found critical links between social deficits and abnormal brain activity in frontal cortex and its subcortical targets[7].

Neural circuits involved in reinforcement learning and decision-making are crucial for normal social interactions[8]. Critical nodes include ACC[9–11], the OFC[12–17] and subcortical areas, such as the dopaminergic ventral tegmental area, substantia nigra[18,19], the striatum[20,21], the lateral habenula[22] and the amygdala[23]. Neuroimaging studies in humans report activation of some of these areas by both giving rewards and receiving rewards[24–28], and lesions to some of these areas result in impaired social decision-making[7]. These findings suggest that a generic circuit for reward-guided learning and decision-making mediates social decisions[8]. Despite this evidence, and the clear clinical relevance of understanding the neurobiology of social decision-making, precisely how neurons in any of these areas compute social decisions remains unknown, largely because of difficulties in implementing social interactions while simultaneously studying neuronal activity and controlling contextual variables. Single-unit recording studies in nonhuman animals, such as macaques, making social decisions of similar complexity to those made by humans would help to address this gap.

We implemented a reward-allocation task in pairs of rhesus macaques while recording from single neurons in three critical nodes in the decision-making network, namely the ACCg, ACCs and OFC. Our study capitalized on monkeys' willingness to engage with a social partner via an interposed computer system while simultaneously controlling the sensory and reward environment. We specifically matched choices for the reward outcomes directly received by the actor monkey (decision maker) and controlled for potential secondary acoustic reinforcement effects associated with delivering juice to the recipient monkey. In these conditions, we found regional biases in the encoding of social decision outcomes with respect to self and another individual. In this network of received (OFC) and foregone (ACCs) reward signals, ACCg emerged as an important nexus for the computation of shared experience and social reward.

RESULTS

Summary of behavior in the reward-allocation task

On half of the trials, termed choice trials, actor monkeys chose between visual stimuli that led to juice being delivered either to themselves (self reward), to the recipient monkey (other reward) or to neither monkey (neither reward). Offers appeared in pairs of three types, which defined self:neither trials, self:other trials and other:neither trials (**Fig. 1**). On the other half, termed cued trials, monkeys observed a single cue that indicated that self, other or neither rewards would be delivered by the computer.

Actor monkeys performed the reward-allocation task well (**Fig. 2a**), as indicated by the low mean number of incomplete trials per session (4.6 ± 0.2% (s.e.m.); Online Methods), even when the actors had no chance of obtaining juice rewards themselves, which was the case for other:neither choice trials and for other and neither cued trials (7.4 ± 0.3%).

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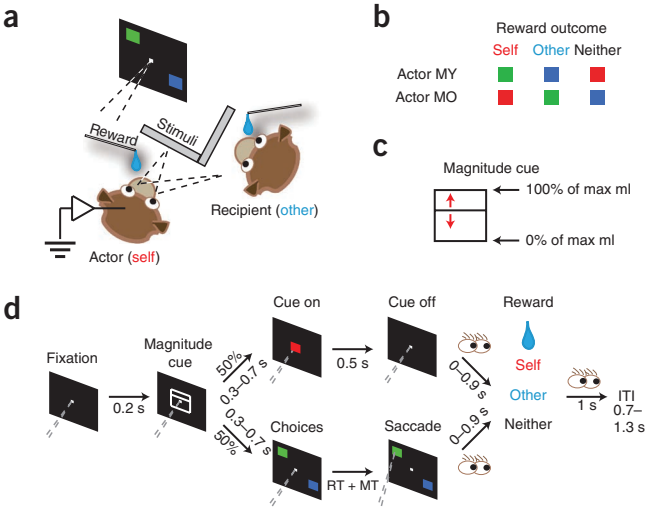

Figure 1 Reward-allocation task. (**a**) Experimental setup for an actor and a recipient monkey. (**b**) Stimulus-reward outcome mappings for reward delivered to actor (self), recipient (other) or no one (neither), shown separately for each actor. (**c**) Magnitude cue used to indicate juice amount at stake for each trial (see **d**). The position of the horizontal bisecting line specified the percentage of maximum reward that was possible. (**d**) Task structure (see Online Methods). Top fork, cued trials; bottom fork, choice trials. Dashed gray lines show the angle of the actor's gaze, converging on the fixation point. Eye cartoons indicate times at which the actor could look around. ITI, inter-trial interval; MT, movement time; RT, reaction time.

Actor monkeys also made significantly fewer errors when they made active decisions (choice trials) than when there was no choice (cued trials) or when there was no reward at stake for themselves ($P < 0.0001$, Welch two-sample t test). These findings suggest that monkeys find it rewarding to actively choose what to do and can be motivated to work without direct reinforcement.

Reaction times often serve as a proxy for motivation in incentivized tasks[29–33]. Reaction times for making different choices demonstrate that actors discriminated the reward types and had orderly preferences amongst them[29,33]. Actors were fastest to choose self rewards, followed by other rewards and neither rewards (**Fig. 2b**). Self versus other reaction times differed by a mean of 39 ms ($P < 0.0001$, Welch two-sample t test); other versus neither reaction times differed by a mean of 20 ms ($P < 0.0001$). The ordered reaction times by monkeys making choices in the reward allocation task suggest that rewarding self is more reinforcing than rewarding the recipient, which is in turn more reinforcing than rewarding no one[33].

Finally, actor monkeys shifted gaze to the recipients more frequently following juice delivery to them than after juice delivery to themselves or to neither monkey, consistent with greater interest in the actions of the other monkey when he was rewarded (**Supplementary Fig. 1**). Taken together, these observations support the conclusion that the actor monkeys were acutely aware of the difference between self, other and neither reward outcomes[33].

We quantified decision preferences by calculating a contrast ratio based on actors' choices (equation (1), Online Methods). Consistent with our previous reports[33,34], actors preferred self rewards over other or neither rewards, but preferred other over neither rewards (**Fig. 2c**). On self:neither and self:other trials, actor monkeys almost always chose to reward self (preference index, mean ± s.e.m.: self:neither, −0.99 ± 0.00; self:other, −0.99 ± 0.00; significantly different from zero: both $P < 0.0001$, one sample t test; **Fig. 2c**). In contrast, on other:neither trials, actors preferred to allocate rewards to the recipient monkey (0.17 ± 0.01, $P < 0.0001$, one sample t test; **Fig. 2c**). We observed similar choice preferences for each actor individually (**Supplementary Fig. 2**).

We previously found that the preference to allocate reward to the other monkey is enhanced by greater familiarity between the two animals and is abolished if the recipient is replaced with a juice collection bottle[33]. We also observed that reward withholding is reduced when actor monkeys are dominant toward recipients, and that the variability and the degree of preferences often depend on the identity of the recipients[33]. Furthermore, we found that actor monkeys prefer to deliver juice to themselves than to both themselves and the recipient simultaneously, perhaps reflecting the competitive nature of simultaneously drinking juice, a resource controlled outside of experimental sessions to motivate performance and often monopolized by

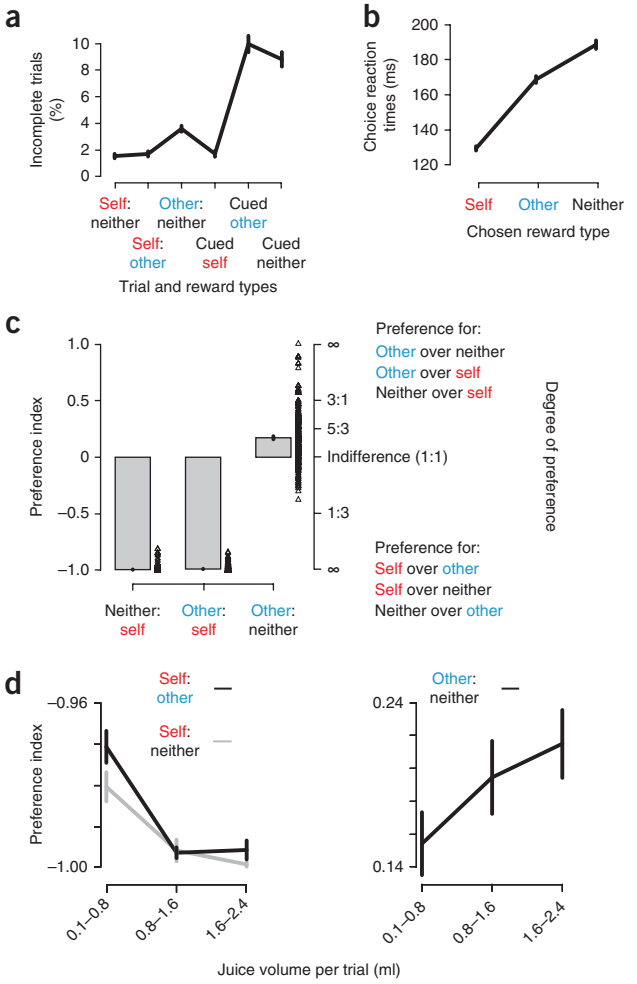

Figure 2 Behavior in the reward-allocation task. (**a**) Proportions of incomplete trials (mean ± s.e.m.) (see Online Methods) during the reward-allocation task. (**b**) Choice reaction times (ms) from trials in which rewards were chosen for self, other or neither (mean of session medians ± s.e.m.). (**c**) Choice preferences (preference index, mean ± s.e.m.) as a function of reward outcome contrasts. Data points next to each bar show the biases for individual sessions. The degree of preference axis on the right shows the range of preference indices in ratio terms. (**d**) Choice preferences (mean ± s.e.m.) as a function of reward magnitude on 219 single-unit sessions collected with the magnitude cue.

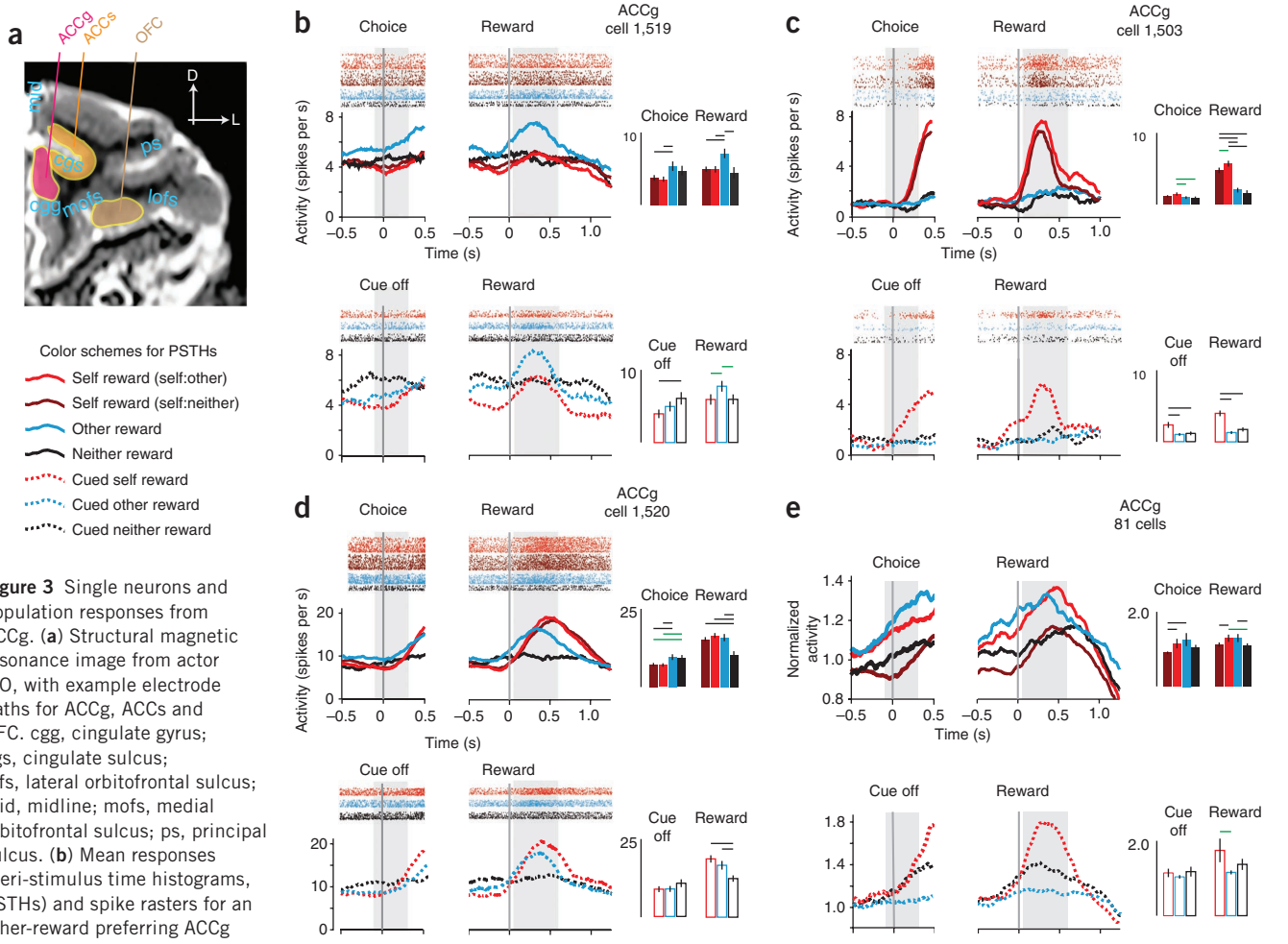

Figure 3 Single neurons and population responses from ACCg. (**a**) Structural magnetic resonance image from actor MO, with example electrode paths for ACCg, ACCs and OFC. cgg, cingulate gyrus; cgs, cingulate sulcus; lofs, lateral orbitofrontal sulcus; mid, midline; mofs, medial orbitofrontal sulcus; ps, principal sulcus. (**b**) Mean responses (peri-stimulus time histograms, PSTHs) and spike rasters for an other-reward preferring ACCg neuron on choice trials (upper, solid traces) and cued trials (lower, dashed traces). Data are aligned to choice/cue offset (left) and reward onset (right) for each reward outcome. Bar histograms on right show mean ± s.e.m. activity from the two epochs (gray regions). Color codes for PSTH traces and histograms are shown below. (**c**) PSTHs and spike rasters for a self-reward preferring ACCg neuron. (**d**) PSTHs and spike rasters for a shared self and other reward–preferring ACCg neuron. (**e**) Normalized choice/cue epoch and reward epoch responses for 81 ACCg neurons. Data in **c**–**e** are presented as in **b**. In all bar histogram insets, the horizontal lines above different conditions indicate significance differences (black, $P < 0.05$ by paired t test; green, $P < 0.05$ by bootstrap test).

dominant monkeys living in pairs with subordinate monkeys in their home cages[33] (M.L.P., unpublished observation). Finally, exogenously increasing oxytocin levels in the CNS amplifies actors' preference to allocate reward to the other monkey over no one[34]. Taken together, these patterns of behavior endorse the fundamentally social nature of the reward-allocation task.

We also found that preferences scaled with the magnitude of juice on offer. With larger amounts of juice at stake, actors became more motivated to receive rewards (self:neither and self:other, slope significantly different from zero: both $P < 0.001$, type II regression) and to allocate rewards to the other monkey over no one (other:neither, $P < 0.05$) (**Fig. 2d**). These findings suggest that both direct and vicarious reinforcement processes that motivate social decisions are magnified by reward magnitude[25–27].

Differential encoding of social decision outcomes

We recorded the activity of single neurons in ACCg ($n = 81$), ACCs ($n = 101$) and OFC ($n = 85$) from two actor monkeys (**Fig. 3a**) during the reward-allocation task, and analyzed the data for both a choice/cue epoch and a reward epoch (Online Methods; data for individual monkeys are shown in **Supplementary Fig. 3**). Overall, we found notable similarities in activity and functional classes across the choice and reward epochs (**Supplementary Fig. 4**). We examined single-neuron and population responses from ACCg (**Fig. 3**), ACCs and OFC (**Fig. 4**), followed by further quantifications in each region (**Fig. 5**).

ACCg contained neurons selective for allocating rewards to another individual, receiving rewards or both. One class of ACCg neuron (**Fig. 3b**) preferentially responded when actors chose to allocate reward to recipients. On choice trials, this example neuron discharged more strongly when the actor chose other rewards (7.12 ± 0.66 (mean and s.e.m.), spikes per s) compared with self rewards on either self:neither or self:other trials (4.95 ± 0.36 and 4.93 ± 0.45 spikes per s, respectively; both $P < 0.01$, Welch two sample t test), and also preferred other rewards over neither rewards (4.44 ± 0.79 spikes per s, $P < 0.05$). This neuron did not differentiate self from neither rewards ($P = 0.97$, Welch two sample t test). On cued trials, this neuron only weakly preferred other over self or neither rewards (both $P = 0.08$, Welch two sample t test; **Fig. 3b**).

In contrast, another class of ACCg neuron (example neuron in **Fig. 3c**) responded selectively for choosing self rewards. The example neuron discharged more when the actor chose to reward himself on self:neither and self:other trials (4.77 ± 0.38 and

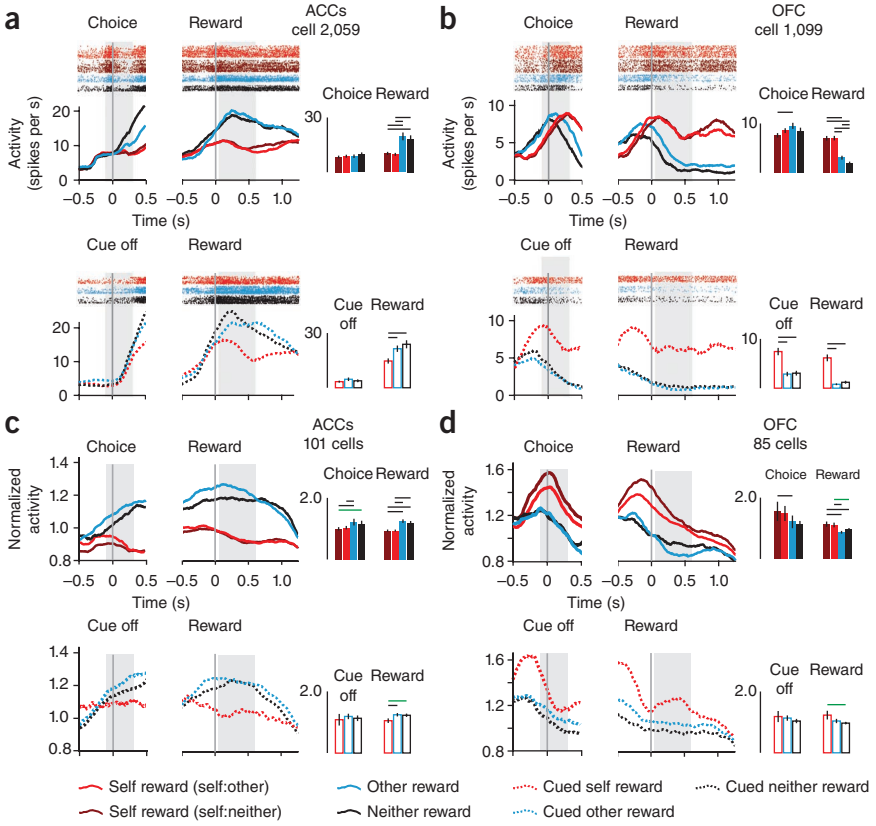

Figure 4 Single neurons and population responses from ACCs and OFC. (**a**) PSTHs and spike rasters for a single ACCs neuron preferring forgone rewards. Data are aligned to choice/cue offset (left) and reward onset (right) for each reward outcome. Bar histograms on right show mean ± s.e.m. activity from the two epochs (gray regions). (**b**) PSTHs and spike rasters for a single OFC neuron preferring self reward. (**c**) Normalized reward epoch responses of 101 ACCs neurons. (**d**) Normalized choice/cue epoch and reward epoch responses of 85 OFC neurons. In all panels, data are presented as in **Figure 3**.

5.70 ± 0.41 spikes per s, respectively) compared with choosing other and neither rewards (2.02 ± 0.32 and 1.60 ± 0.39 spikes per s, respectively) (all $P < 0.0001$, Welch two sample t test; **Fig. 3c**). Moreover, it showed stronger responses when the actor monkey received rewards in self:other than in self:neither context, but this effect did not reach statistical significance ($P = 0.10$, Welch two sample t test). On cued trials, this neuron preferred self over other or neither rewards (both $P < 0.0001$, Welch two sample t test). For both choice and cued trials, the response did not differentiate other and neither rewards (both $P > 0.23$, Welch two sample t test).

Finally, a third class of ACCg neuron (example neuron in **Fig. 3d**) responded equivalently to both received rewards (self:neither, 15.28 ± 0.70 spikes per s; self:other, 16.47 ± 0.81) and allocated rewards to other (15.81 ± 1.16 spikes per s) (both $P > 0.64$, Welch two sample t test), but responded significantly less to neither rewards (10.17 ± 1.23 spikes per s, other versus neither and self versus neither, both $P < 0.005$). Similarly, on cued trials, this neuron preferred other over neither rewards ($P < 0.05$, Welch two sample t test), but did not differentiate between self and other rewards ($P = 0.27$).

Notably, the fact that the solenoid valves controlling juice delivery (including one for neither rewards that only produced clicks) were placed outside the experimental room, as well as the white noise played inside the room, during sessions rules out a simple explanation that other reward–specific (**Fig. 3b**) and shared self/other reward responses (**Fig. 3d**) were merely sensory responses to the sounds of the reward-delivery mechanism.

To contrast population coding of decision and reward information in various conditions, we computed a normalized activity bias between each pair of outcomes, expressed as a proportional modulation in mean firing rates normalized by baseline firing rate. In the ACCg population, the mean normalized activity bias for other over neither rewards (other versus neither) was 0.21 ± 0.10 (s.e.m.), a 21% difference, which was significant ($P < 0.05$, paired t test; **Figs. 3e** and **5a**). Similarly, the bias for self (from self:other) over neither rewards was 0.20 ± 0.12 ($P = 0.09$, paired t test). Notably, the population showed equivalent responses for self rewards (self:other) and other rewards (0.01 ± 0.12, $P = 0.96$, paired t test). On the other hand, it showed a significant bias for self rewards when the actors were presented with a choice between rewarding themselves and recipients compared with when the actors were presented with a choice between rewarding themselves and no one (self:other versus self:neither, 0.17 ± 0.08, $P < 0.05$, paired t test), suggesting that ACCg is particularly sensitive to a reward context involving an option to reward another individual. Thus, the ACCg population showed an equivalent preference for other and self rewards, and preferred both over neither rewards.

On cued trials, however, a notably different pattern emerged. The population responded strongly to self rewards, but barely responded to other rewards (0.59 ± 0.32, $P = 0.07$, paired t test; **Fig. 3e**). Furthermore, the population responded no differently to other and neither rewards (0.22 ± 0.14, $P = 0.14$, paired t test).

Taken together, these results indicate that ACCg, as a population, encodes both giving and receiving rewards. At the population level, neuronal activity selective for allocating rewards to another individual was specific to active decisions (**Fig. 3e**), similar to what has been reported by functional magnetic resonance imaging of human ventral striatum during voluntary versus forced charitable donations[25]. The confluence of neurons selectively responsive to self, other and both (self and other) rewards in ACCg suggests that this area contains the information necessary to mediate the vicarious reinforcement processes that appear to motivate actors to give to recipients.

Figure 4a shows a typical ACCs neuron that fired more strongly preceding other and neither rewards than self rewards. On choice trials, this neuron discharged more strongly when the actor monkey chose not to reward himself (other rewards, 19.64 ± 2.15 spikes per s; neither rewards, 18.19 ± 2.03) compared with when he chose to reward himself directly (self:neither, 10.31 ± 0.86 spikes per s; self:other, 9.79 ± 0.81) (all $P < 0.001$, Welch two sample t test). The example neuron responded equivalently to self rewards in self:other and self:neither contexts ($P = 0.66$, Welch two sample t test), and responded equivalently to other and neither rewards ($P = 0.62$), consistent with encoding 'foregone' rewards. On cued trials, this neuron responded equivalently to other and neither rewards ($P = 0.39$, Welch two sample t test), but responded less to self rewards (both $P < 0.005$), resembling the responses to active decisions.

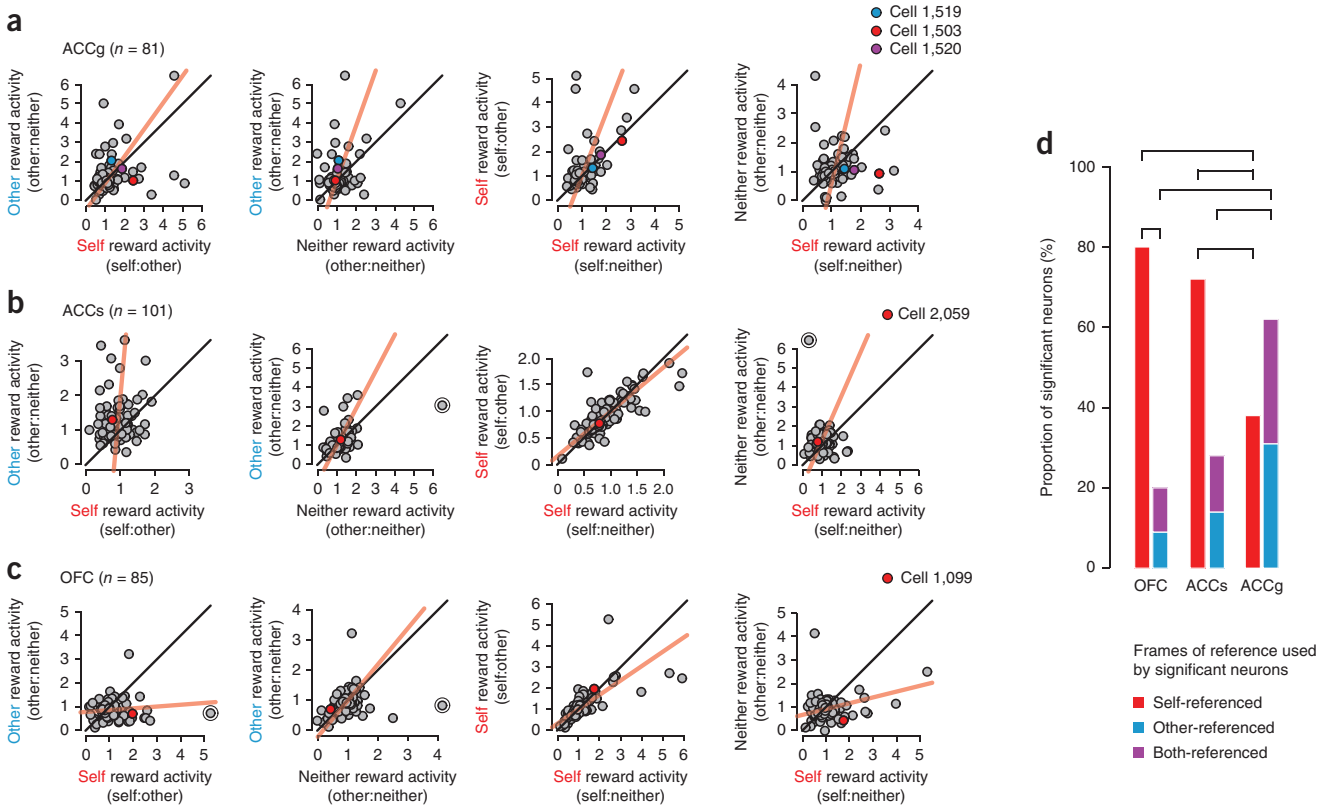

Figure 5 Population biases for self, other and neither rewards. (**a**–**c**) Scatter plots show mean normalized reward epoch responses (proportion of modulation relative to baseline) of individual neurons (from left to right) between self (self:other) and other rewards, between other and neither rewards, between self rewards from self:neither and self:other contexts, and between self (self:neither) and neither rewards for ACCg (**a**), ACCs (**b**) and OFC (**c**) populations. Regression lines (type II) are shown in red (the circled data points are excluded from the regression). Unity lines are shown in black. The example neurons from **Figures 3** and **4** are indicated on the scatter plots. (**d**) Proportion of neurons (out of significantly classified neurons) from OFC, ACCs and ACCg using self-referenced, other-referenced and both-referenced frames to represent reward outcomes. Inset shows color codes used in the bar graph. Bars indicate significant differences in proportions ($P < 0.05$, χ^2 test).

Figure 4b shows a typical OFC neuron that preferentially encoded juice rewards received by the actor. On choice trials, this neuron discharged substantially more for self rewards than for the alternatives on both self:neither and self:other trials. Activity for self rewards did not differ between the two self reward contexts (7.00 ± 0.47 and 7.03 ± 0.46 spikes per s, respectively; $P = 0.97$, Welch two sample t test), but it exceeded the cell's activity for other and neither rewards (3.06 ± 0.40 and 1.85 ± 0.42 spikes per s, respectively; both $P < 0.0001$). On cued trials, this neuron responded most strongly to self rewards than to both other and neither rewards (both $P < 0.0001$, Welch two sample t test), but it did not respond differently between other and neither rewards ($P = 0.25$) (**Fig. 4b**).

The ACCs population showed a strong and equivalent response bias for foregone rewards (self versus other, activity bias = 0.31 ± 0.07; self versus neither, activity bias = 0.25 ± 0.08, both $P < 0.005$, paired t test; **Figs. 4c** and **5b**). The population did not differentiate other from neither rewards (0.06 ± 0.06, $P = 0.31$, paired t test). Unlike ACCg, the population did not respond differentially to self:other and self:neither contexts (differed by 0.003 ± 0.02, $P = 0.90$, paired t test). We found similar patterns on cued trials: responses to self rewards were substantially reduced compared with other rewards (0.19 ± 0.09, $P < 0.05$, paired t test) and neither rewards (0.18 ± 0.10, $P < 0.08$) (**Fig. 4c**). These results indicate that, during social interactions, ACCs neurons predominantly signal foregone rewards.

The OFC population predominantly encoded self rewards compared with other and neither rewards. The bias for self over other rewards was 30% (0.30 ± 0.09, $P < 0.005$, paired t test). For self versus neither rewards, the bias was also significant (0.17 ± 0.08, $P < 0.05$, paired t test; **Figs. 4d** and **5c**). Population activity for other and neither rewards did not differ (0.08 ± 0.06, $P = 0.20$, paired t test; **Figs. 4d** and **5c**). Unlike ACCg, the population did not respond differentially to self:other and self:neither contexts (differed by 0.06 ± 0.07, $P = 0.39$, paired t test). On cued trials, the self reward bias was not present compared with other rewards (0.19 ± 0.16, $P = 0.24$, paired t test) and was only weakly present over neither rewards (0.26 ± 0.15, $P < 0.08$). On cued trials, the population did not distinguish other rewards from neither rewards ($P = 0.33$, paired t test; **Fig. 4d**). These results indicate that OFC neurons predominantly encode rewards received by the actors and that this information was encoded more faithfully during active decision-making.

Neuronal reference frames for social decisions

Neuroimaging and scalp-recording studies in humans can only study neuronal activity at an aggregate level. Our single-unit recording data therefore provide a unique opportunity to quantify the frame of reference in which individual neurons in ACCg, ACCs and OFC encode social decisions. To do this, we classified cells from each area on the basis of an analysis of variance (ANOVA) of neuronal activity of individual neurons with reward outcome (self, other or neither), trial type (choice or cued) and reward magnitude (small, medium or large) as factors (Online Methods). Reward epoch responses differed

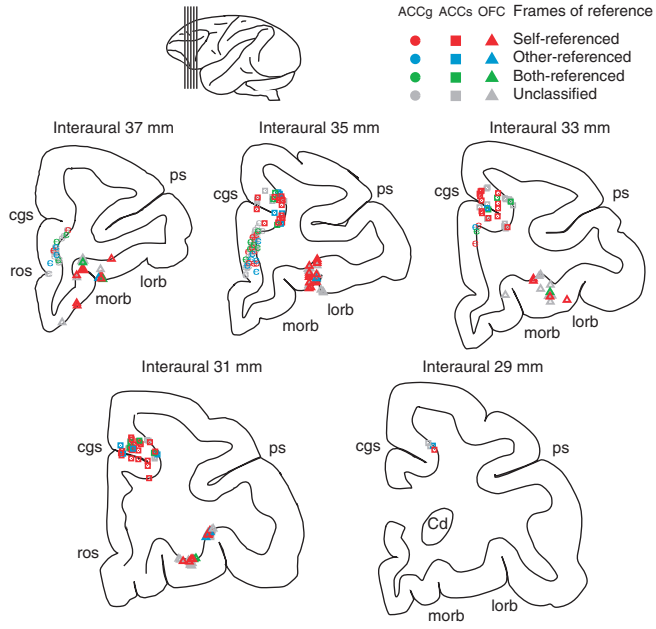

Figure 6 Anatomical projections of recorded locations of all ACCg, ACCs and OFC cells. Recording sites were transformed from chamber coordinates into interaural coordinates. The interaural coordinates of individual cells from both monkeys were then projected onto standard stereotaxic maps of rhesus monkeys[50], with a 2-mm interaural spacing in the anterior-posterior dimension. Cells are shown on coronal slices and color-coded for the types of frames of reference used, as specified in **Supplementary Table 1** (see box). The lateral view of the brain (inset) shows the locations of the coronal sections. Cd, caudate; cgs, cingulate sulcus; lorb, lateral orbitofrontal sulcus; morb, medial orbitofrontal sulcus; ps, principal sulcus; ros, rostral sulcus.

significantly ($P < 0.05$) for a large number of neurons from all areas in a manner that depended on reward outcome (ACCg, 57%; ACCs, 72%; OFC, 57%), trial type (ACCg, 36%; ACCs, 52%; OFC, 45%) and reward volume (ACCg, 12%; ACCs, 25%; OFC, 24%) (**Supplementary Table 1**). Furthermore, we observed marked similarities in reward outcome coding across the choice/cue and reward epochs (**Supplementary Fig. 4**).

On the basis of the statistical significance of the ANOVA during the choice/cue and reward epochs, we identified individual neurons as self-referenced (modulation referenced to self rewards, preferring either self or foregone rewards), other-referenced (modulation referenced to other rewards), both-referenced (modulation referenced to both self and other rewards, but not neither rewards) or unclassified (Online Methods). We considered the proportion of different cell types among the classified neurons based on this scheme. In OFC, 80% ($n = 36$ of 45 neurons) were self-referenced, whereas only 9% (4 of 45) were other-referenced and 11% (5 of 45) were both-referenced (both $P < 0.0001$, χ^2 test; **Fig. 5d**). In ACCs, 72% (51 of 71) were self-referenced, whereas only 14% (10 of 71) were other-referenced and 14% (10 of 71) were both-referenced (both $P < 0.0001$, χ^2 test; **Fig. 5d**). In contrast, ACCg contained similar proportions that were self-referenced (38%, 12 of 32), other-referenced (31%, 10 of 32) and both-referenced (31%, 10 of 32) ($P > 0.79$, χ^2 test; **Fig. 5d**). Notably, ACCg contained a significantly higher proportion of neurons (>60%) that were sensitive to the reward outcome of the recipient monkey (other-referenced and both-referenced) than either OFC or ACCs (both $P < 0.005$, χ^2 test; **Fig. 5d**). ACCg also contained a significantly smaller proportion of self-referenced neurons than either OFC or ACCs (both $P < 0.005$, χ^2 test). Finally, we found similar results when we repeated the analysis and included trial-by-trial choice reaction times as covariates (**Supplementary Fig. 5**).

To test whether different neuronal frames of reference (self-, other- and both-referenced) were anatomically segregated, we used principal component analysis on recording coordinates to identify the major axis with the largest dispersion in three-dimensional space. We then projected neurons to that axis to test differential distributions in individual monkeys separately (**Fig. 6**). We did not observe any systematic anatomical clustering among different frames of reference; self-, other- and both-referenced neurons in ACCg, ACCs and OFC were intermingled (all $P > 0.56$, Wilcoxon rank sum test).

Next, we examined whether differential encoding of self, other and neither rewards was also present before making a decision. We found very little evidence for systematic signals early in the trial just after target onset (50–250 ms after target onset). In ACCg, only zero, three and one cells were classified into self-, other- and both-referenced classes, with only 12% of neurons showing significant effect of reward type. In ACCs, only one, two and three cells belonged to each category, with only 22% of the neurons showing significant reward type effects. Similarly, in OFC, only two, two and four cells belonged to each category, with only 28% of the neurons showing significant reward type effects. Thus, in our reward allocation task, signals in ACCg, ACCs and OFC appear to emerge around the time of choice and reward delivery.

When we examined the reward magnitude sensitivities of individual neurons, we found the population in ACCs to be most sensitive (**Supplementary Figs. 6** and **7**). Furthermore, signal-to-noise in neuronal responses to specific reward outcomes were largely consistent with the preferred neuronal encoding scheme in each region (**Supplementary Fig. 8**). None of our findings were driven by whether or not actors looked at recipients (**Supplementary Fig. 9**).

Finally, we examined whether session-to-session variation in prosocial tendencies on other:neither trials (**Fig. 2c**) could be explained by variability in the responses of ACCg neurons, the population most sensitive to other's rewards. We split recording sessions on the basis of actors' choices on other:neither into two categories: more prosocial (higher other over neither choices relative to the median preference index) and less prosocial (lower other over neither choices relative to the median preference index). Actors tended to be more prosocial on recording sessions when other-referenced and both-referenced ACCg neurons showed less variability in spiking during the reward epoch ($P < 0.05$, bootstrap test; **Fig. 7a**).

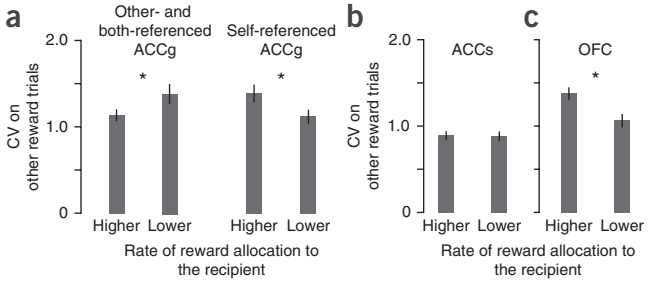

Figure 7 Prosocial behavior and the fidelity of neuronal responses on other:neither trials. (**a**) ACCg. (**b**) ACCs. (**c**) OFC. Coefficients of variation in firing rate (CV; Online Methods) during the reward epoch on other reward trials are plotted as a function of whether actors were more or less prosocial on other:neither trials on the basis of median split (higher: preference index greater than median; lower: preference index less than median). *$P < 0.05$, bootstrap test.

In contrast, we found that self-referenced ACCg neurons generated more variable responses during the reward epoch in which actors were more prosocial ($P < 0.05$, bootstrap test). ACCs neurons did not show any systematic relationship between response variance and behavior ($P = 0.47$, bootstrap test; **Fig. 7b**). Notably, OFC neurons showed a similar pattern as self-referenced ACCg neurons ($P < 0.005$, bootstrap test; **Fig. 7c**). These findings suggest a strong link between prosocial behavior and the fidelity of social reward signals carried by those neurons that incorporate the experience of others into their responses. This could be a result of enhanced attention to the recipient or other processes known to influence signal-to-noise in cortical neurons.

DISCUSSION

Our findings strongly endorse the hypothesis that distinct frontal regions contribute uniquely to social decisions by differentially processing decision outcomes with respect to actors (self) and their partners (other). The finding that OFC neurons selectively encode self reward is consistent with previous results implicating this area in representing the subjective value of rewards[12,13], but extend those results by demonstrating that such value signals are encoded egocentrically. Encoding of foregone rewards by ACCs neurons, on the other hand, is consistent with previous data implicating this area in error monitoring and behavioral adjustment[35–37]. For example, foregone reward signaling by ACCs might be used to learn from observation, rather than direct experience, and adjust ongoing behavior during social interactions. Furthermore, mirroring of self and other rewards by ACCg neurons is consistent with previous studies linking this area to specifically social functions, such as shared experience and empathy[38].

Our findings are consistent with those of a previous study examining the effects of lesions in these same brain regions (Online Methods), which found that ACCg, but not OFC or ACCs, contributes causally to the use of visual social information to guide behavior[9]. Specifically, ACCg lesions completely abolished typical hesitation to retrieve food when confronted with social stimuli[9]. Our findings also agree with previous findings that lesions in ACCs impair the use of reward history to guide decisions adaptively[10]. The differences between ACCs and ACCg that we observed support and extend the finding that learning from experience is mediated by ACCs, whereas learning from feedback from another individual is mediated by ACCg[8]. Specifically, in a learning task in which human subjects monitored their history of correct responses as well as the advice given to them by a confederate, blood oxygen level–dependent (BOLD) activation in ACCs tracked reward learning rate, whereas BOLD activation in ACCg tracked social learning rate based on advice from the confederate[8]. In our study, we propose that ACCs tracked foregone rewards relative to self, whereas ACCg tracked reward outcomes of another individual in a more complex manner.

Notably, the ACCg population also responded more strongly when monkeys chose self reward when the alternative was allocating reward to the other monkey compared with the response when monkeys chose self reward when the alternative was rewarding no one. In contrast, neither the OFC neuronal population response nor the ACCs neuronal population response was sensitive to social context when monkeys rewarded themselves. Sensitivity to social context in ACCg endorses a specialized role for this area in computing social decisions, even when one acts selfishly.

It is worthwhile to note that a small number of ACCs and OFC neurons, although much less in proportion compared with ACCg (**Fig. 5d**, **Supplementary Table 1** and **Supplementary Fig. 5**), were classified as either other- or both-referenced. This observation supports the idea that a small number of ACCs and OFC neurons do carry information about rewards allocated to another individual. What is notable is that the majority of OFC and ACCs neurons (80% and 72%, respectively) did not carry such other-regarding information (other- or both-referenced), whereas the majority of ACCg neurons did (62%). This endorses a fundamentally social role for neurons in ACCg.

A prior study showed that OFC neurons modulate their activity when a monkey receives juice reward together with another individual[39], suggesting that value signals in OFC are sensitive to social context. In that study, OFC neurons responded differentially as a function of whether the subject monkey received juice rewards alone or together with another monkey[39]. Our current study builds on and extends those findings in three important ways. First, we used a free-choice task that allowed us to infer the subjective value of rewards delivered to self, other and no one. Notably, even in a social context, OFC neurons were selective for self reward, the most preferred outcome. Second, we compared the responses of OFC neurons to responses of neurons in ACCg and ACCs recorded in identical task conditions, allowing us to examine regional differences in the encoding of social reward information in primate frontal cortex. Third, when we compared responses of ACCg neurons on free-choice and cued trials, we found that responses to rewards delivered to the recipient monkey were largely absent when actors passively observed the event rather than actively choosing it. Taken together, these findings indicate that social context can affect the encoding of reward information in all three areas; OFC appears to evaluate personally experienced rewards, ACCs evaluates reward information that is not directly experienced, and ACCg multiplexes information about the direct experience of reward and vicarious reinforcement experienced by allocating reward to another individual.

It is noteworthy that ACCs neurons showed much less modulation by actors' received reward outcomes compared with OFC neurons, as ACCs neurons often show substantial modulation to received reward in nonsocial settings[11]. ACCg, on the other hand, contains neurons that compute reward signals in both other and self frames of reference. Together, our findings suggest that, as in sensory and motor systems[40], identifying the frames of reference in which reward outcomes are encoded may be important for understanding the neural mechanisms underlying social decision-making[8].

Accumulating evidence endorses a special role for the medial-frontal cortex in representing information about another individual[8,41–44]. For instance, perceived similarity while observing others is correlated with hemodynamic response in the subgenual ACC[44]. Furthermore, a group of neurons in the primate medial-frontal cortex selectively responds to observing actions performed by other individuals[41]. Such other-referenced signals, however, are not limited to the medial wall of the frontal cortex. Neurons in the dorsolateral prefrontal cortex (DLPFC) track the behavior of a computer opponent in an interactive game[45], and BOLD responses in DLPFC and ventromedial prefrontal cortex during observational learning track observed action and observed reward prediction errors, respectively[46]. In addition, BOLD activity in anterior frontal areas tracks preferences to donate to charity[24]. Brain networks involved in mentalizing[47], vicarious pain perception[48] and empathy[49] therefore seem to be critical for mediating social interactions, suggesting that other-regarding cognition is orchestrated by a distributed network of frontal cortical areas.

Social and emotional behaviors are highly idiosyncratic among individuals. Understanding the neural mechanisms that drive such

individual differences remains one of the most pressing issues in neuroscience. We hypothesize that the differential activation of neurons in ACCg, ACCs and OFC contribute to individual and, perhaps, species differences in social function.

METHODS

Methods and any associated references are available in the online version of the paper.

Note: Supplementary information is available in the online version of the paper.

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AUTHOR CONTRIBUTIONS

S.W.C.C. and M.L.P. designed the study and wrote the paper. S.W.C.C. and J.-F.G. performed the experiments and S.W.C.C. analyzed the data.

COMPETING FINANCIAL INTERESTS

The authors declare no competing financial interests.

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ONLINE METHODS

General and behavioral procedures. All procedures were approved by the Duke University Institutional Animal Care and Use Committee, and were conducted in compliance with the Public Health Service's Guide for the Care and Use of Laboratory Animals.

Two actor (MY and MO) and five recipient monkeys (*Macaca mulatta*) participated. For all monkeys, a sterile surgery was performed to implant a head-restraint prosthesis (Crist Instruments) using standard techniques[11]. Six weeks after surgery, monkeys were trained on a standard, center-out, oculomotor task for liquid rewards. Actor monkeys were then trained on the reward-allocation task (**Fig. 1**) in the presence of a recipient. Subsequently, a second surgery was performed on actors to implant a recording chamber (Crist) providing access to the ACCs, ACCg and OFC. All surgeries were performed under isoflurane anesthesia (1–3%, vol/vol), and the recording chambers were regularly cleaned, treated with antibiotics and sealed with sterile caps.

Horizontal and vertical eye positions were sampled at 1,000 Hz using an infrared eye monitor camera system (SR Research Eyelink). Stimuli were controlled by PsychToolBox and Matlab (MathWorks). Actors and recipients sat in primate chairs (Crist), 100 cm from one another at a 45° angle (**Fig. 1a**). Actors (both males) and recipients (four males, one female) were unrelated and were not cagemates. Different pairs were selected depending on the availability of recipient monkeys. Actors were housed in a colony with 12 other male rhesus macaques, some of which were pair-housed. All of the male monkeys resided in this colony room, and the one female monkey resided in the adjacent colony room with other females. Of the total seven actor-recipient pairs that we tested, the actor monkey was dominant over the recipient in six cases. Furthermore, three pairs could be classified as 'more familiar' with one another because their cages faced each other, as defined previously[33]. Based on these relationships, we would expect a mixture of prosocial and competitive preferences, as we previously found that dominant actors are slightly less competitive than subordinates, but pairs in which the actor is less familiar with the recipient are slightly less prosocial than when they are more familiar.

In the experimental setup, each monkey had his own monitor, which displayed identical visual stimuli. Both the actor and recipient monkeys had their own tube from which juice drops were delivered. To prevent monkeys from forming secondary associations of solenoid valve clicks or the sound of the recipient drinking the juice reward with respect to different reward types, the solenoid valves that delivered the juice rewards were placed in another room and white noise was also played in the background. Experimenters were unable to hear solenoids anywhere inside the recording room. Our control of the acoustic environment explicitly rules out a simple explanation that both-referenced reward encoding found in ACCg is a product of such secondary sensory associations. Critically, a separate solenoid (also placed in another room) was designated for neither rewards; it produced clicks, but delivered no fluid.

The face region of the recipient, with respect to the gaze angle of the actor (horizontal and vertical eye positions), was determined empirically before the experiments. The frequency with which actors looked at recipients was computed from number of gaze shifts to the recipient's face (±8.5° from the center of the face)[33,34]. We used a large window to capture gaze shifts that were brief in duration and large in magnitude and often directed at varying depths (for example, eyes and mouth; **Fig. 1a**).

Monkeys performed the task to obtain drops of cherry- or orange-flavored juice. Actors began a trial by shifting gaze (±2.5°) to a central stimulus (0.5° × 0.5°), and maintained fixation (200 ms). For 219 single-unit sessions, the reward magnitude at stake (0.1–2.4 ml) on each trial was cued by the position of a horizontal bisecting line (200 ms), indicating the percentage of the maximum possible volume. There were two kinds of trials, termed choice trials and cued trials. Following a variable delay (300, 500 and 700 ms), choice and cued trials were presented at equal probabilities, randomly interleaved. On choice trials, two visual targets (4° × 4°) appeared at two random locations 7° eccentric in the opposite hemifield. Actors shifted gaze to one target (±2.5°) to indicate a choice in the maximum allowed time of 1.5 s (from stimulus onset). The pair of stimuli appearing on a given trial was drawn from the set of three stimuli (**Fig. 1b**), pseudorandomly selected. On cued trials, actors maintained fixation (±2.5°) while a cue (4° × 4°) appeared centrally (500 ms). Cues indicating rewards for the actor, recipient or neither monkey occurred with equal frequency, pseudorandomly determined (**Fig. 1b**). Reward onset was followed by a 0–900-ms delay from the time of either making a choice or cue offset. Actors were free to look around during this delay and for 1 s after reward delivery. Reward delivery was followed by an intertrial interval of 700, 1,000 or 1,300 ms. After making an error (see below), both monkeys received visual feedback (a white rectangle, 10° × 10°) followed by a 5-s time out before the next trial.

Recording procedures. All recordings were made using tungsten electrodes (FHC). Single electrodes were lowered using a hydraulic microdrive system (Kopf Instruments or FHC). Single-unit waveforms were isolated and action potentials were collected using a 16-channel recording system (Plexon).

To guide the placement of recording tracks and localize recording sites, we acquired structural magnetic resonance images (MRI; 3T, 1-mm slices) of each actor's brain. Detailed localizations were made using Osirix viewer. In addition to MRI guidance, we confirmed that electrodes were in ACCg, ACCs or OFC by listening to gray matter– and white matter–associated sounds while lowering the electrodes. ACCg neurons were recorded from Brodmann areas 24a, 24b and 32, ACCs neurons (dorsal and ventral banks) were recorded from 24c and 24c', and OFC neurons were recorded from 13m and 11 (based on standard anatomical references[51,52]; **Figs. 3a** and **6**).

Single-unit recordings were made from two actor monkeys while each was engaged in a reward-allocation task with a recipient monkey in 267 sessions. A total of 81 ACCg neurons (MY, 45; MO, 36), 101 ACCs neurons (MY, 39; MO, 62) and 85 OFC neurons (MY, 46; MO, 39) were included in the study. Neurons were selected for recording based solely on the quality of isolation. For a small subset of the data (18%; ACCg, 0%; ACCs, 25%; OFC, 27%), data were collected in a task with a fixed reward size (typically 1.0 ml per successful trial; identical to **Fig. 1d** except without the magnitude cue). For the majority of the cells (82%, $n = 219$), data were either collected in a task with the magnitude cue (ACCg, 100%, $n = 81$; ACCs, 60%, $n = 61$; OFC, 42%, $n = 36$; **Fig. 1d**) or both with and without the magnitude cue (that is, two or more consecutive blocks per cell; ACCg, 0%; ACCs, 15%, $n = 15$; OFC, 31%, $n = 26$). We combined the two types of data in our analyses unless otherwise specified.

Data from each cell consisted of firing rates during 440 ± 13 (±217) (median ± s.e.m. (±s.d.)) trials. A trial was considered incomplete if the monkey failed to choose a target on choice trials (choice-avoidance error) or to maintain fixation after cue onset on cued trials (forced-choice avoidance error). Such trials were not included in the neural analysis. The monkeys performed the task well, as evidenced by a high percentage of correct trials even on trials in which they did not receive juice reinforcement (**Fig. 2a**).

Data analysis. Choice preference indices were constructed as contrast ratios[33,34].

$$\text{Preference Index} = \frac{R_A - R_B}{R_A + R_B} \quad (1)$$

R_A and R_B were the frequency of making particular choices. For self:other trials, R_A and R_B were number of choices to reward other and self, respectively. For other:neither trials, R_A and R_B were number of choices to reward other and neither, respectively. Finally, for self:neither trials, R_A and R_B were number of choices to reward neither and self, respectively. Indices therefore ranged from −1 to 1, with 1 corresponding to always choosing to allocate reward to other on other:neither trials and self:other trials, and always choosing not to reward self on self:neither trials. An index of −1 corresponds to the opposite, generally stated as choosing not to allocate reward to the other monkey or choosing to reward oneself. Values of 0 indicate indifference. For constructing neuronal preferences, we simply substituted the choice frequency with neuronal firing rates associated with making specific decisions. Response times, the time from the onset of choices to movement onset, were computed using a 20° s^{-1} velocity threshold criterion[33,34].

Spike rates were computed during the reward epoch (50–600 ms from reward onset) as well as the choice/cue epoch (−100–300 ms from making a choice or cue offset). For the population analyses, we normalized reward firing rates to the average baseline rates for each reward outcome (300-ms interval before fixation onset). Using marginally different time windows and different normalization methods all resulted in similar conclusions. Coefficients of variation were

calculated for each neuron on the basis of the s.d. (σ) and mean (μ) using the spike rates (spikes per s) from the reward epoch:

$$\mathrm{CV} = \frac{\sigma}{\mu} \quad (2)$$

In OFC and ACCs populations, the two self rewards (that is, self rewards chosen from self:neither and self:other trials) were largely indifferent (**Figs. 4** and **5b**,**c**), and we combined them by taking means for the coefficient of variation analysis. In contrast, the population of ACCg neurons responded more strongly to self rewards obtained from a social context (self:other) compared with when there was no reward stake for the other monkey (self:neither); thus, we considered the two self rewards separately in ACCg (see **Figs. 3** and **5a**).

ANOVA was used to classify the reward response selectivity of individual neurons from each area and performed per individual cells. Two-factor ANOVA was used to classify the selectivity of reward outcome (self, other or neither) and trial type (choice or cued) for all neurons. Three-factor ANOVA was used to classify the selectivity of reward volume (binned into small, medium, large) for the 82% of cells from all areas that were collected in the task with a magnitude cue. Statistical significance for each reward type was computed by Tukey HSD test. Finally, we excluded three OFC cells when our analyses involved using the data from neither rewards because these cells were recorded on very rare sessions in which the monkeys either never chose the neither reward option or did so fewer than four times. Across all analyses, using slightly different epoch durations for neuronal data analyses led to similar results.

Classification of cell types by significant reward specificity. Based on Tukey HSD tests from the one-way ANOVA on reward outcome (self, other, or neither) for both the choice/cue epoch and reward epoch responses, we classified cells into the following categories: self-referenced, other-referenced, both-referenced and unclassified. These categories do not imply functional roles, but indicate that firing rates were significantly different based on reward outcomes. We refer to a neuron as self-referenced if the responses of the neuron were significantly different ($P < 0.05$) between self and other rewards as well as between self and neither rewards, but not different between other and neither rewards. We refer to a neuron as other-referenced if the responses of the neuron showed significant differences in firing rates between self and other rewards as well as between other and neither rewards, but not different between self and neither rewards. Finally, we refer to a neuron as both-referenced if the responses of the neuron showed significant differences in responses between self and neither rewards as well as other and neither rewards, but not different between self and other rewards. Neurons that did not fall into one of these categories were considered as unclassified. Applying slightly different criteria or differently configured ANOVA did not change the overall proportional trends of these classes.

Reward magnitude analysis. We examined reward magnitude modulation in 219 neurons (that is, 82% of all neurons collected with the magnitude cue; 81 ACCg, 76 ACCs and 62 OFC neurons). We performed a linear regression on the activity (spikes per s) of individual neurons across unbinned reward sizes. We fit the data using the reward epoch activity separately for self, other and neither reward outcomes and obtained fitted slopes (that is, reward magnitude sensitivity in spikes per s per ml) for each reward outcome. For examining the relationship between the reward magnitude sensitivity across actors' received and foregone reward outcomes, we compared the average signed slopes from all received rewards (self rewards on choice and cued trials) and all foregone rewards (other and neither reward on choice and cued trials) in individual neurons.

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