Supporting Information

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SI Experimental Procedures

Animals. The monkeys who participated in this study were part of a minicolony of four adult female rhesus macaques (*Macaca mulatta*) housed in the same animal room for more than 4 y. The monkeys lived in interconnected cages that permitted direct physical interaction but also allowed to isolate the monkeys when needed through a system of sliding partitions. When isolated, the monkeys could nevertheless communicate visually and vocally at all times. Monkeys were isolated during the experimental phases to facilitate handling and monitoring of fluid intake. The partitions were removed for 2–3 h per day, allowing the monkeys to interact freely. A clear social hierarchy was present. To quantify precisely the rank of each animal, three observers (two animal caretakers and one experimenter) rated independently the frequency and nature of interactions for all possible monkey dyads (i.e., three per monkey). The behavior of each member of a dyad was rated on five different dimensions using a −5 to +5 rating scale: proximity (escape ↔ approach), gaze (averted ↔ staring), grooming (groomer ↔ groomee), food access (low priority ↔ high priority), and conflict (victim ↔ aggressor). This process resulted in 15 ratings per monkey, which were summed and averaged across the three observers to obtain a global social-rank score. Hereafter, the monkeys are referred to according to their position in the hierarchy, as Mo1 to Mo4 in descending order of social rank. Social-rank scores are shown in Fig. 5*C*.

Two monkeys (Mo2 and Mo4) learned and performed the behavioral task and were used for single-unit recordings in the orbitofrontal cortex. They also served as each other's passive partner on days in which they were not being recorded as the active participant. A third monkey (Mo1) participated only as passive partner. Mo3 did not participate in this study.

Surgery and Recording Site Verification. All experimental procedures were conducted in compliance with local authorities on Animal Care (Direction Départementale des Services Vétérinaires, Lyon, France) and the European Community standards for the care and use of laboratory animals [European Community Council Directive (1986), Ministère de l'Agriculture et de la Forêt, Commission Nationale de l'Expérimentation Animale]. Animals were prepared for chronic recording of single neuron activity during a single sterile surgery performed under isoflurane anesthesia. Standard procedures were followed for implantation of a head-restraint post and chronic recording chamber to allow descending wire microelectrodes into the brain. In monkeys Mo2 and Mo4, the chamber was implanted over the frontal lobe of the left and right hemisphere, respectively (ML = 9.0 mm and AP = 32.5 mm). Monkey Mo1, who was not recorded from, had a head post and a recording chamber implanted over a different brain region. The monkeys were then left to recover with the proper antibiotic coverage, and pain-relievers were given as needed. Confirmation of electrode track localization within area 13 was obtained postmortem in monkey Mo2 and through anatomical MRI reconstruction in monkey Mo4 (Fig. 1*B*).

Behavioral and Electrophysiological Procedures. Experiments were conducted in a semidark room. The monkeys were seated in a primate chair, the two passive partners facing the active monkey at a distance of 72 cm and separated by 30 cm. Each monkey had a feeder tube place near its lips to deliver finite quantities of water, using a gravity-based solenoid device (Crist Instruments). A photocell-activated response lever was placed within reach of the active monkey's hand and its eye position was monitored using a custom-built infrared video eye tracker (100-Hz sampling rate). Reward prediction cues were presented on a 19-inch LCD monitor positioned horizontally between the active monkey and its partners. The active monkey was trained to fixate the visual cue and rewards were delivered at the end of the trial on the conditions (*i*) that fixation was maintained within a 10°-wide tolerance window centered on the cue and (*ii*) that the manual lever was released as soon as the luminance of the cue was dimmed. To facilitate learning of the association between a given cue shape and the current trial's reward contingency, two white LEDs were placed above the partners' head and two red LEDs were fixated on their feeder tubes. The trial's rewarded partner was designated by the illumination of the corresponding white LED just before fixation-point onset, and the delivery of the reward was accompanied by the illumination of the corresponding red LED.

Single-neuron activity was recorded extracellularly with tungsten microelectrodes (Frederick Haer; 1–2 MΩ at 1 kHz), amplified using a Neurolog system (Digitimer), and digitized for online spike discrimination using the MSD software (Alpha-Omega). Once a single unit was isolated, we used manual testing (waving objects in front of the monkey's eyes, providing free rewards), and presented stimuli on the computer monitor to identify cells that were visually responsive. This step was our prerequisite to begin formal data acquisition given that the reward cues were visual shapes, but we did not attempt to map the spatial extent of their receptive field nor their tuning to specific visual features. It was sufficient that the neurons exhibited some sensitivity to centrally presented stimuli.

Behavioral control, visual display, and data storage were under the control of a PC running the REX system (1).

Reward Conditions. Monkeys performed two types of trials. Self-only reward trials were trials in which only the active monkey was rewarded. In contrast, joint-reward trials were trials in which both the active monkey and one partner were rewarded. Both trial types unfolded essentially in the same manner. A trial was initiated when the active monkey's hand contacted the response lever. After a delay of 500 ms, a white spot appeared at the center of the monitor, which the monkey had to foveate. The central spot was replaced 300 ms later by a reward-condition cue. This cue was presented for a variable duration (1,000–2,500 ms), after which it dimmed, prompting the monkey to release the lever. If the monkey released the bar with a reaction time ≤400 ms, a green circle appeared, indicating that the response was correct and the active monkey was rewarded with a drop of water after a 1,000- to 1,600-ms delay. Joint-reward trials had two additional features: (*i*) at the beginning of the trial, one of the passive monkeys was designated as the partner by illuminating the corresponding LED 200 ms before fixation point onset; (*ii*) the partner was rewarded midway through the reward delay interval, 500–800 ms after the active monkey's response. If the monkeys broke fixation during the presentation of the bright cue or responded too early or too late, the trial was aborted and no reward was delivered. The unpredictable luminance switch and the short reaction time window ensured that the monkey would have to devote attentional and motor resources to the task, the amount of which could be pitted against the expected value of the reward.

The reason for delivering the partner's reward first was made after pilot testing showed that when the active monkey received the reward first, it disengaged from the task and no longer paid attention to the partner, hence little or no behavioral effect was observed. The behavior changed and the partner's reward became

more relevant when it was delivered first and the active monkey was still waiting for its own reward and remained focused to the task.

In this experiment we used two types of trials blocks. (*i*) The *nonsocial* block contained self-only reward trials and the shape of the reward-condition cue specified the size of the active monkey's reward: 0.8 mL (small), 1.6 mL (medium), or 3.2 mL (large). (*ii*) The *social* block contained a mixture of self-only reward and joint-reward trials and the shape of the cue specified the identity of the reward recipients: actor only (A), actor and partner 1 (A+P1), actor and partner 2 (A+P2). Reward size was fixed at 1.6 mL for both the active monkey and the partner. Within each block, trials with different reward conditions were randomly interleaved. It could be argued that in the social block, the information contained in the reward cue was fully redundant with that provided by LED illumination. However, in other block types used during training and recording sessions, where different combinations of reward sizes and recipient identity were tested, the outcome could not be predicted by the illumination (or absence of illumination) of the partner LED. Therefore, for simplicity—and to avoid confusing the animals—we maintained the partner-designation procedure before reward-cue onset throughout all experiments.

Nonsocial and *social* blocks were alternated during the same recording sessions. Data collection on a given block was stopped once the monkey had performed 20 correct trials per reward condition. Block order was balanced across sessions. Time and motivation allowing, the same block could be performed more than once. The two block types were run once or twice for each neuron (20 trials per condition; i.e., 60 trials per block) depending on our ability to hold the cells. Thus, we have about the same number of sessions with the following block orders: AB, BA, ABAB, and BABA.

To keep motivation as constant as possible from one day to the next, we let the monkey work for approximately the same amount of water each day, regardless of whether neurons were successfully isolated or not. The partners were also maintained under fluid control. Because the amount of water they obtained during the testing session was limited, extra fluid was given at the end of each day to maintain proper water balance. Because the experiment was carried out over a period of several months, the daily amount of water could be adjusted individually if needed to maintain an optimal motivation level.

Data Analysis. Behavioral data consisted in a measure of performance (mean percentage of correct response) and reaction times. We also examined the distribution of eye positions to infer how monkeys allocated their attention across the workspace in the different task epochs. Statistical analyses of behavioral performance were carried out on the testing sessions that yielded the single-unit data.

Single-unit data were analyzed as follows. We focused on cue-related activity, since it is at this juncture that neuronal activity is most likely to contain information about the monkey's cognitive appraisal and anticipation of the different reward outcomes, and since it is the epoch in which behavior is most stable and invariant across conditions. Indeed, following lever release, the behavior was unconstrained and more variable in terms of where the animal looked at and what it attended to; hence, neural activity could not be unambiguously related to discrete events such as reward anticipation and consumption. Statistical analyses were conducted on successfully completed trials, with a minimal requirement of 20 trials per condition for inclusion in the analyses. We first identified task-responsive neurons. For each event of interest, we compared mean pre-event activity (−300 to 0 ms) and mean postevent activity (50–450 ms) using *t* tests. Raster and peristimulus time histograms were then inspected individually to eliminate spurious responses (generally, low firing rates with random, isolated bursts of activity). In a second step, reward-condition effects were tested on the task-responsive neurons by comparing the mean firing rates in the same postevent epoch using one-way ANOVA. These comparisons were computed on both single-unit and population activity. Population activity was analyzed and represented as normalized firing rate. To preserve as much as possible the original "envelope" of each cell's peristimulus activity, we used a simple normalization procedure that consisted in computing, for each neuron and for each experimental condition, a spike density function (sdf) by convolving individual spikes with a Gaussian kernel of $\sigma = 16$ ms. Each sdf was then normalized (sdfnorm) in the following way: sdfnorm = (sdf − minrate)/(maxrate − minrate); minrate and maxrate being defined, respectively, as the minimum and maximum value across all spike density functions computed for a given neuron in the interval (−500 ms:1,000 ms) relative to the event of interest.

Data were analyzed separately for each monkey. When no difference was found in the proportion of cells and in population activity curves, the data from the two monkeys were combined. A specific analysis was conducted to quantify the modulation of cue-related activity as a function of reward size and social context. For each neuron, two simple indices were computed. The reward-size effect in the *nonsocial* block was represented by the index $SZ = (l - s)/(l + s)$, with l and s defined as mean postcue activity for large and small reward cues, respectively,. The social context effect in the social block was represented by the index $SC = (a - p)/(a + p)$, with a defined as mean activity for the actor only (A) cue, and p as the mean activity for the actor and partner 1 (A+P1) and actor and partner 2 (A+P2) cues.

Behavior. ***Performance.*** We computed the percentage of correctly completed trials and mean manual reaction time for each reward condition in the *nonsocial* and *social* blocks. Behavioral data were obtained for 47 sessions in monkey Mo2 and 45 sessions in monkey Mo4 during which we collected single-unit data. The proportion of correct responses varied systematically across the different reward conditions. These data are shown in Fig. 2*B*. Reaction times did not prove to be a very sensitive measure of performance. Reaction times were slower for small than for medium and large rewards in the *nonsocial* block for monkey Mo2 (respectively 345, 315, and 317ms for the small, medium, and large rewards, S > M and S > L, $P < 0.01$) but no significant differences were found in monkey Mo4 (respectively 317, 325, and 326 ms, not significant). There was no effect of reward condition on reaction times in the *social* block for either monkey. The lack of sensitivity of reaction time to reward condition may be because of the fact that we used a stringent reaction-time criteria (≤400 ms), which might have constrained the monkeys to respond with short reaction times and small variance.

Because we used the percentage of correct responses as main behavioral measure, the question arises as to the nature of the errors that were made and whether their distribution differed between social conditions. We analyzed error trials on the entire dataset (~20,000 trials). Error trials were of different types: "early" errors, when the monkey let go of the lever before dimming of the cue, and "late" errors, when the monkey failed to release the lever within the 400-ms reaction time limit. Early errors could be caused by a deliberate decision to abort the ongoing trial or, in contrast, by excessive haste in responding. Because the interval from cue-onset to cue-dimming was variable, thus making the go signal unpredictable, we have no clear boundaries for the assignment of early errors to either of these two possible causes. Late errors also could occur for two different reasons: the monkey released the lever but the response latency fell just over the imposed reaction time limit because of lack of preparedness or inattention (late-response errors), or the monkey never released the lever and maintained pressing it until the start of a new trial, thus expressing its rejection of the reward offer (no-response errors).

Error trials we therefore classified as follows: (*i*) early response, (*ii*) late response, and (*iii*) no-response. Although early and late responses each accounted for ~20% of all error trials, no-response errors were by far the most frequent type and represented ~60% of

all errors. Similar proportions of the three error types were found in both the *nonsocial* and the *social* block and in both monkeys. In the *nonsocial* block, no-response errors are more frequent by a ratio of ~3:1 for small compared with medium or large reward trials (Fig. S1*A*) (small reward: 43% and 40% for Mo2 and Mo4, respectively, vs. medium-large rewards 15–11% and 12–13% for Mo2 and Mo4, respectively). In the *social* block, a proportionally larger frequency of no-response errors are made on joint-reward trials ("A+P1" – "A+P2": 25–22% for Mo2, 31–25% for Mo4) compared with self-only reward trials ("A": 11% for Mo2, 9% for Mo4). Thus, the frequency of no-response error is the main factor accounting for differences in performance across social contexts and reward conditions.

Eye movements. The distribution of gaze positions in the *social* block was computed for several intervals bounded by key event transitions: (*i*) end of intertrial pause, (*ii*) manual lever contact, (*iii*) reward-condition cue onset, (*v*) cue dimming/lever release, (*v*) partner reward delivery (on joint-reward trials), (*vi*) actor reward delivery, (*vii*) trial end. The interval between events *ii* and *iii* contained fixation point onset in self-only reward trials and partner LED illumination and fixation point onset in joint-reward trials. The data shown in Fig. 2*C* shows the horizontal and vertical distribution of eye positions over the workspace (1° resolution, 10 ms per sample). Because the different intervals had different durations, eye-position samples were summed across each interval and normalized such that values of 0 and 100 represent the local minima and maxima, respectively.

From lever contact to cue-onset, gaze is mainly distributed around three zones: the center of the video monitor, partner 1's face, and partner 2's face. The three areas of interest appear very clearly on self-only trials [Fig. 2*C*, *Top*, just after lever touch as the monkey experienced the onset of the fixation target but was also expecting the potential designation of a partner (which, by definition, did not occur on these trials)]. In contrast, on joint-reward trials (*Middle* and *Bottom*), the monkey's gaze was clearly biased toward the designated partner and the fixation target. After cue onset, and up until the monkey responded, the monkey looked exclusively at the center of the screen to detect the dimming of the cue. The most informative epoch is that which immediately follows the manual response. On self-only reward trials, the monkey kept looking at the screen center until the delivery of its own reward (even though at this stage, reward was no longer contingent upon continuous fixation). On joint-reward trials, the monkey also gazed at the partner, but never at the other monkey, and this well before the partner's reward was delivered. This observation suggests that the monkey was aware of, and showed a keen interest in, perceiving the partner's reward outcome. It also confirms that the monkey's eye movements reflect its awareness of the reward contingencies and were not simply driven by attention to exogenous stimuli.

Working for No Reward? The behavioral task used in the present experiment is only superficially similar to studies of "low-cost" altruism, in which a monkey is offered the choice between getting food for itself versus getting food for itself and a partner. Such low-cost altruism is very rare among monkeys and apes (2–4). Here, the monkey could choose to accept or refuse performing joint-reward trials, but the latter option did have a cost because monkeys were under fluid restriction and defecting on such trials meant giving up rehydration opportunities. As part of the training process, we also experimented with different combinations of actor and partner rewards. To test whether monkeys would work in a purely altruistic manner, we used a block configuration composed of four reward conditions, two in which the designated partner, but not the active monkey, received a reward, and two in which both the active monkey and the partner received a reward. All rewards were of the same size. The results were without appeal: the offer to work only for the benefit of the partner was systematically rejected [Mo2 (mean of 30 sessions): other only = 3%, both = 67%; Mo4 (mean of 21 sessions): other only = 4%, both = 72%]. As soon as the association between the cue's shape and the reward outcome was learned, the monkeys refused to perform such trials. The sharing partner's social status had no effect on the results, as the monkeys behaved no more altruistically toward the high (P1) than toward the low (P2) status partner. Note that there was little to be gained by abandoning an ongoing trial because it did not allow the monkey to get faster to the next trial (the timeout period ensured that total trial duration was the same for abandoned and correctly completed trials). Nevertheless, it appears that the active monkey estimated that the effort of attending to the cue and producing fast reaction times was not justified in the absence of compensation, and that the incentive value of procuring a reward to the partner was null.

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2. Colman AD, Liebold KE, Boren JJ (1969) A method for studying altruism in monkeys. *Psychol Rec* 19:401–405.
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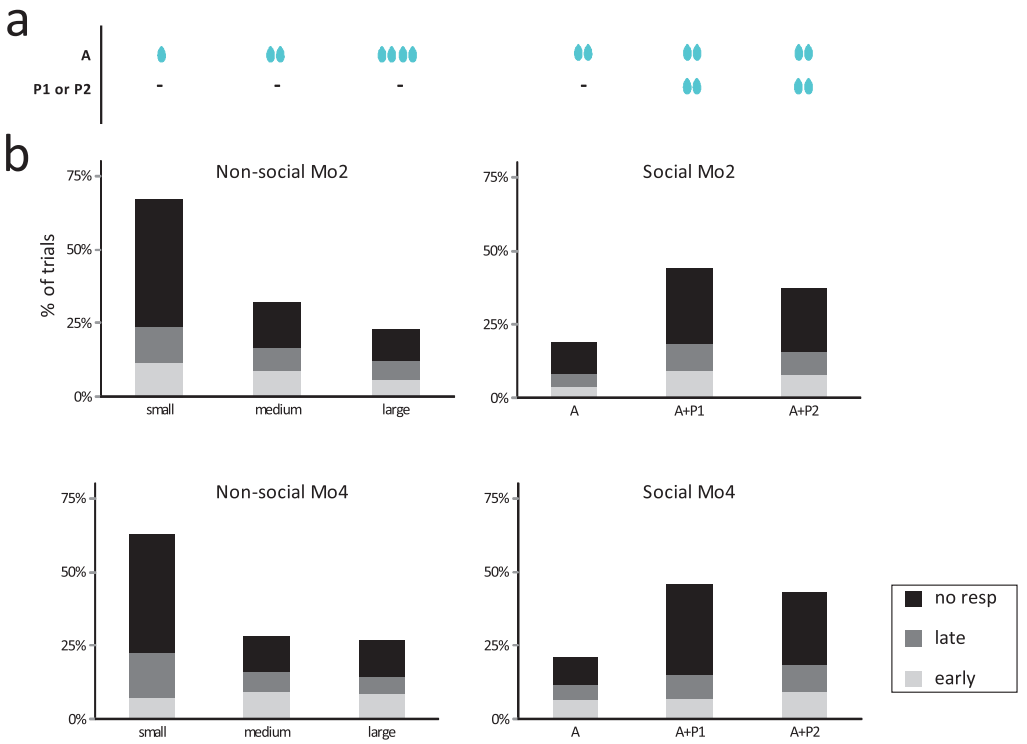

Fig. S1. Error trials distribution in the different reward conditions (related to Fig. 1). (*A*) Reward schedules for actor (A) and partners (P1 or P2) on *nonsocial* and *social* blocks. (*B*) Percentage of early responses, late responses, and no-response errors on *nonsocial* (*Left*) and on *social* (Right) trials block for Mo2 (*Upper*) and Mo4 (*Lower*).

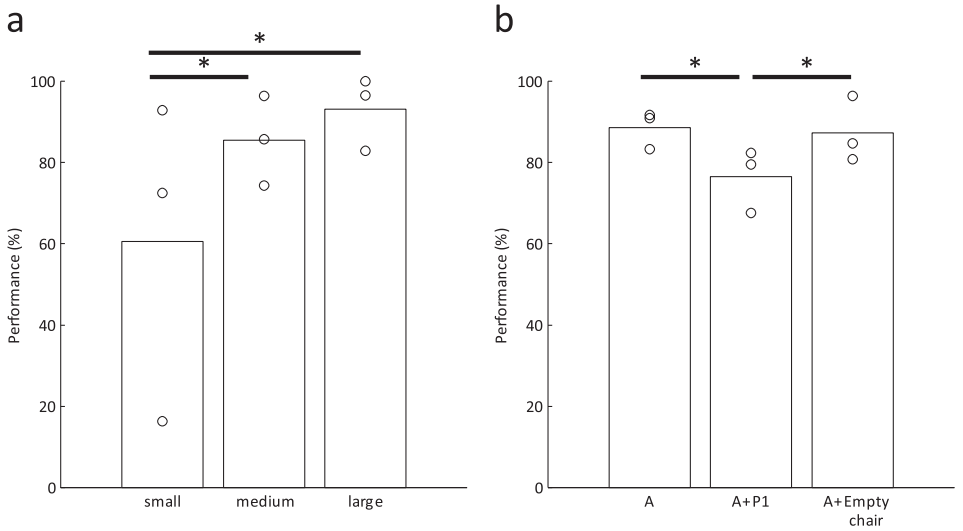

Fig. S2. Percentage of correct responses of monkey Mo4 on three "empty partner chair" control sessions (related to Fig. 2). (*A*) *Nonsocial* trial block, showing a standard reward-size effect on performance. (*B*) *Social* block with the monkey facing partner 1 on one side and an empty monkey chair. On "A + empty chair" trials, juice was delivered from the absent partner's dispenser even though no one was there to collect it. The asterisks and horizontal lines indicate significant pair-wise comparisons ($P < 0.05$ or better).

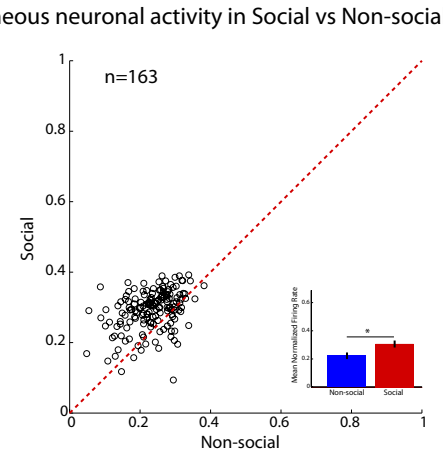

Fig. S3. Spontaneous activity of OFC neuronal population (related to Fig. 3). Scatter-plot shows mean normalized firing rate for each neuron in the two blocks. *Inset* bar graph shows mean normalized activity of all neurons recorded from Mo2 and Mo4 in the interval from end of a trial *t* and beginning of trial *t* + 1 for *nonsocial* and *social* blocks (*$P < 0.01$).

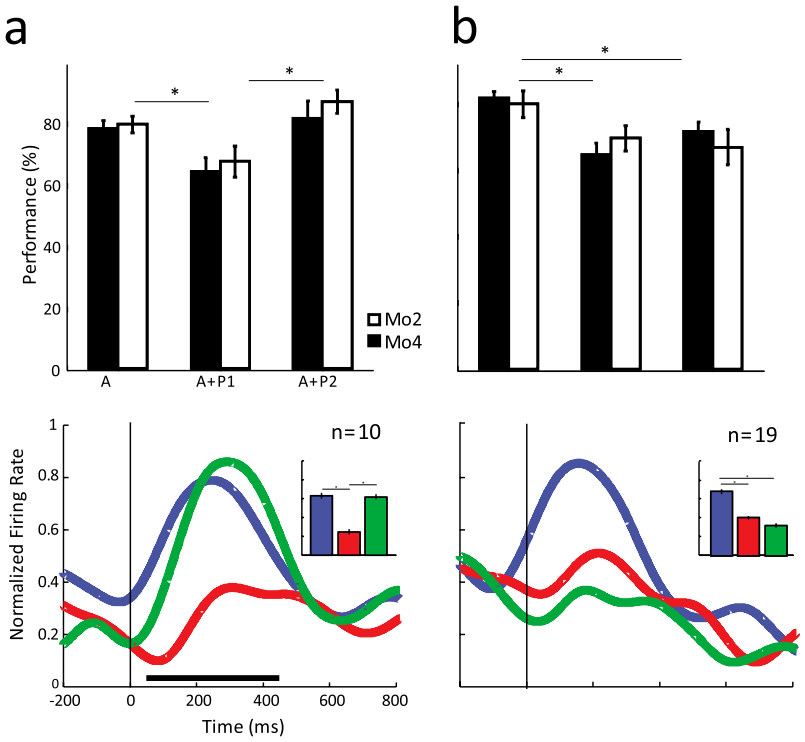

Fig. S4. Effect of social preference on reward value (related to Fig. 3). (*A*) Behavior (*Upper*) and neuronal subpopulation activity (*Lower*) recorded when partner 2 was preferred over partner 1. (*B*) Behavior (*Upper*) and neuronal subpopulation activity (*Lower*) recorded when no social preference was found for partner 2. The two cell subpopulations were drawn from the up-modulated population shown in Fig. 2. Of the 29 cells showing up-modulated responses with reward value, 10 fell in the first behavioral subclass and 19 in the second subclass. This analysis was not conducted on the down-modulated population because we found only 4 cells recorded on sessions with significant social bias effect. *Insets* show the mean activity in the time window indicated by the thick horizontal bar. The asterisks and horizontal lines indicate significant pair-wise comparisons ($P < 0.05$ or better).

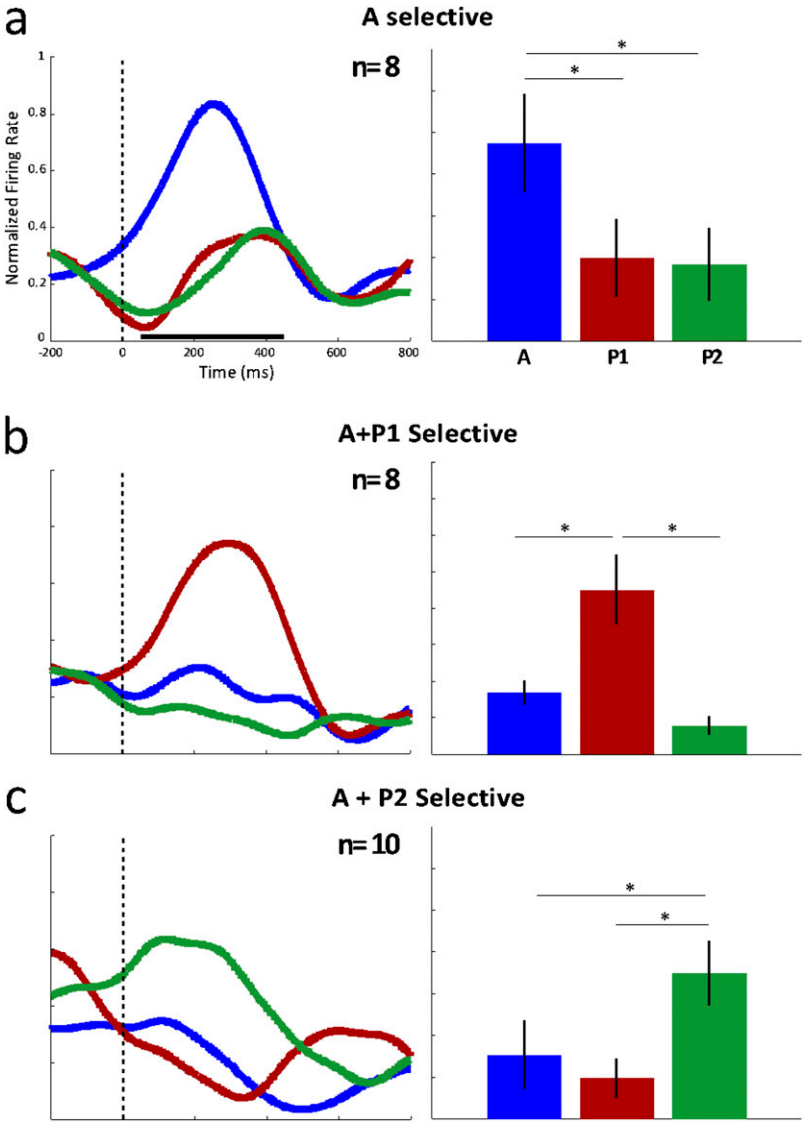

Fig. S5. Population activity of three subsets of neurons which responded to the reward cue in the *social,* but not in the *nonsocial* block (related to Fig. 3). These cells were not considered as coding directly for motivation. These neurons were selective for a given reward cue, with a response peak signaling a reward to self-only (A), a joint reward with partner 1 (A+P1), or a joint reward with partner 2 (A+P2). (*A–C*, *Left*) Normalized population spike density curves; (*Right*) the mean discharge rate in the time window indicated by thick horizontal bar below the spike density curves. The asterisk and thin horizontal lines indicate significant pair-wise comparisons ($P < 0.01$).