

Article

Electrophysiological signatures of inequity-dependent reward encoding in the human OFC

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SUMMARY

Social decision making requires the integration of reward valuation and social cognition systems, both dependent on the orbitofrontal cortex (OFC). How these two OFC functions interact is largely unknown. We recorded intracranial activity from the OFC of ten patients making choices in a social context where reward inequity with a social counterpart varied and could be either advantageous or disadvantageous. We find that OFC high-frequency activity (HFA; 70–150 Hz) encodes self-reward, consistent with previous reports. We also observe encoding of the social counterpart's reward, as well as the type of inequity being experienced. Additionally, we find evidence of inequity-dependent reward encoding: depending on the type of inequity, electrodes rapidly and reversibly switch between different reward-encoding profiles. These results provide direct evidence for encoding of self- and other rewards in the human OFC and highlight the dynamic nature of encoding in the OFC as a function of social context.

INTRODUCTION

We often cannot help but compare our own outcomes with those of others: did our sibling get a bigger piece of cake, our friend a better price on her car, or our colleague a higher bonus? Comparing rewards is a part of social life, and individuals' satisfaction with their own outcomes often varies as a function of the outcomes obtained by comparable others.¹ Inequity aversion, the preference for fair reward distribution among individuals, is observed widely in human society,² with human children as young as 3 years old reacting to unequal distributions of rewards,³ as well as in other primates.^{4,5} Navigating decisions involving inequity relies on the interplay of reward valuation and social cognition. A wealth of functional neuroimaging and lesion evidence has pointed to the involvement of the human orbitofrontal cortex (OFC) in both value-based decision making and social cognition. Here, we addressed how the OFC links both processes by conducting intracranial recordings in neurosurgical patients performing a social decision-making task.

Historically, lesion studies point to a critical role for the OFC in social functioning. Lesions in humans lead to impairments in social judgments and social behaviors, including disinhibition, inappropriate actions, and misinterpretation of others' moods.^{6–10}

Patients with orbitofrontal damage struggle with theory of mind¹¹ and exhibit reduced responses to socially charged stimuli while retaining normal autonomic responses to other sensory stimuli.¹² Furthermore, human neuroimaging studies show OFC activation during social tasks.^{13–16}

The role of the OFC in individual value-based decision making is well established with converging evidence from lesion, neuroimaging, and electrophysiological studies.¹⁷ The OFC encodes various valuation-related variables such as probability, reward magnitude, expectations, and regret.^{18–22} Notably, the medial OFC (mOFC; ventromedial PFC [vmPFC]) computes options' subjective value.^{23–28} This suggests that the OFC integrates multiple parameters to compute a common neural-reward currency, facilitating decision making between options with different attributes^{23,29} (note that other studies do not report a common currency coding at the neuron level^{30,31}).

Despite extensive research on the role of the human OFC in both social functioning and value-based decision making, and despite the clinical relevance of understanding the neural mechanisms of social valuation, little is known about the fine-scale neuronal processing of social information and its influence on valuation mechanisms. Single-neuron primate literature provides some answers. In one study, macaque monkeys worked



to collect rewards either only for themselves or for themselves and a monkey partner. Value-coding neurons (e.g., neurons increasing their firing rate with the magnitude of reward) decreased their discharge rate when monkeys were working to obtain rewards for themselves and a partner vs. when they worked for self-rewards only, in line with the behavioral finding that monkeys preferred working in the non-social context. Furthermore, neuronal activity was found to track the identity of the partner monkey.³² The primate OFC thus contains key neuronal mechanisms for the evaluation of social information. However, in another study where monkeys chose between a reward for themselves, a reward to another monkey, or no reward at all, the OFC only encoded the monkey's own reward, regardless of the social context.³¹ In humans, intracranial electroencephalogram (iEEG) provides the rare opportunity to examine neural mechanisms at a "mesoscale" level of analysis lying between the extensive anatomical coverage of fMRI and the temporal resolution of single-unit recordings.³³ Here, we leverage iEEG to investigate how the OFC processes monetary decisions in different inequity-defined social contexts. We focus on high-frequency activity (HFA; 70–150 Hz), as recent studies have found a relationship between HFA and decision-making computations in humans.^{20,22,26,34} HFA is an index of non-oscillatory neural activity reflecting information processing linked to multiunit activity in the infragranular cortical layers and to dendritic potential in supragranular layers.^{35–37} HFA is also linked to the BOLD signal in fMRI,³⁸ allowing us to connect the two literatures. HFA modulation is present in a variety of cognitive processes depending on cortical activation, including memory, attention, language, and motor control. In addition, we also examined theta activity (4–8 Hz), known to be involved in social decision making and fairness evaluations in scalp EEG studies.^{39–41}

We collected intracranial recordings from 10 neurosurgical patients with electrodes implanted in the OFC while they played a repeated trial dictator game. In dictator games, a single player (the "dictator") decides how to split different pots of money between themselves and a social counterpart. Dictator games have been widely used in behavioral and neural research to study social decision making.^{42,43} Here, we leverage two important features of the task. First, its non-strategic nature makes it easy to understand and ensures that when the game is repeated, the choices are independent since one does not need to anticipate the social counterpart's behavior. Second, its simplicity enables variation in important choice features, such as the set of possible payoffs.⁴⁴

In our task, on each trial, patients chose between two money allocations for themselves and an anonymous social counterpart ("other"): an equitable option that appeared on all trials (\$10 for themselves; \$10 for other) and an inequitable option varying from trial to trial. The inequitable option could be advantageous ("advantageous inequity," higher payoff for the patient than for the social counterpart) or disadvantageous ("disadvantageous inequity," lower payoff for the patient). We also manipulated several reward-related variables in the task by changing the inequitable option's payoffs across trials (see table in [STAR Methods](#)).

Based on the OFC's involvement in social functioning and reward valuation, we hypothesize that the OFC plays a role in so-

cial decision making. We examine three potential, non-exclusive ways in which OFC activity could demonstrate its involvement in social decision making.

- (1) Does the OFC encode rewards related to the social counterpart in addition to self-related rewards?
- (2) Is the OFC sensitive to the type of inequity present in a trial (advantageous vs. disadvantageous)?
- (3) Does the type of inequity influence the encoding of self- and other-related rewards? In other words, is reward encoding inequity dependent? Past research shows that activity in reward-sensitive brain regions is influenced by factors beyond objective reward value, such as outcome distribution^{45,46} and social context³² (note that by context we mean "the set of experimental factors that affect how a particular feedback stimulus is evaluated"⁴⁷). Here, we test whether advantageous and disadvantageous inequities affect reward-related variable encoding.

RESULTS

Social decision-making behavior in neurosurgical patients

We recorded intracranial signals from 10 adult patients (5 female, mean age = 35.6, SD = 10.45, 8 right-handed, 1 ambidextrous) undergoing intraoperative neurosurgical treatment for refractory epilepsy. As electrode placement and treatment decisions are made solely by the clinical team, the number and location of electrodes varied across patients. We recorded from a total of 144 electrodes, of which 134 (136 bipolar pairs) were included in the final dataset as artifact-free, OFC electrodes (for details, see [STAR Methods](#)).

Testing occurred in a 15–20 min session. In each trial, patients chose between two allocations of money for themselves and another anonymous social counterpart.⁴³ [Figure 1B](#) illustrates the experimental paradigm. Trials started with a fixation cross, followed by the game presentation screen. Patients chose between two allocations: a fixed, equitable option that did not vary across trials (\$10 for themselves; \$10 for other) and an inequitable option that varied across trials. Inequitable options were either advantageous (i.e., higher payoff for the patient than for other; for example, \$12 for themselves and \$8 for other) or disadvantageous (i.e., lower payoff for the patient than for other; for example, \$8 for themselves and \$14 for other). For a list of the variables used in the analyses, please refer to the table in the [STAR Methods](#).

Overall, patients chose the equitable option on 47.9% of the trials (SD = 8%, 29.4%–61.3%). In disadvantageous trials, patients had a strong preference for the equitable option (89%, SD = 14%, 51%–100%), even though it meant forgoing higher payoffs for themselves. In advantageous trials, they overall avoided the equitable option (7.7%, SD = 6.7%, 0%–22.5%). While there are other behavioral strategies reported in the literature (i.e., inequity minimizing, self-payoff maximizing), overall, patients in this study were consistent in their choices to minimize disadvantageous inequity.⁴⁸ To further examine the effect of inequity on choice behavior, we used a logistic linear mixed-effect model with fixed effects of inequity type (advantageous vs. disadvantageous), unsigned inequity (the absolute difference

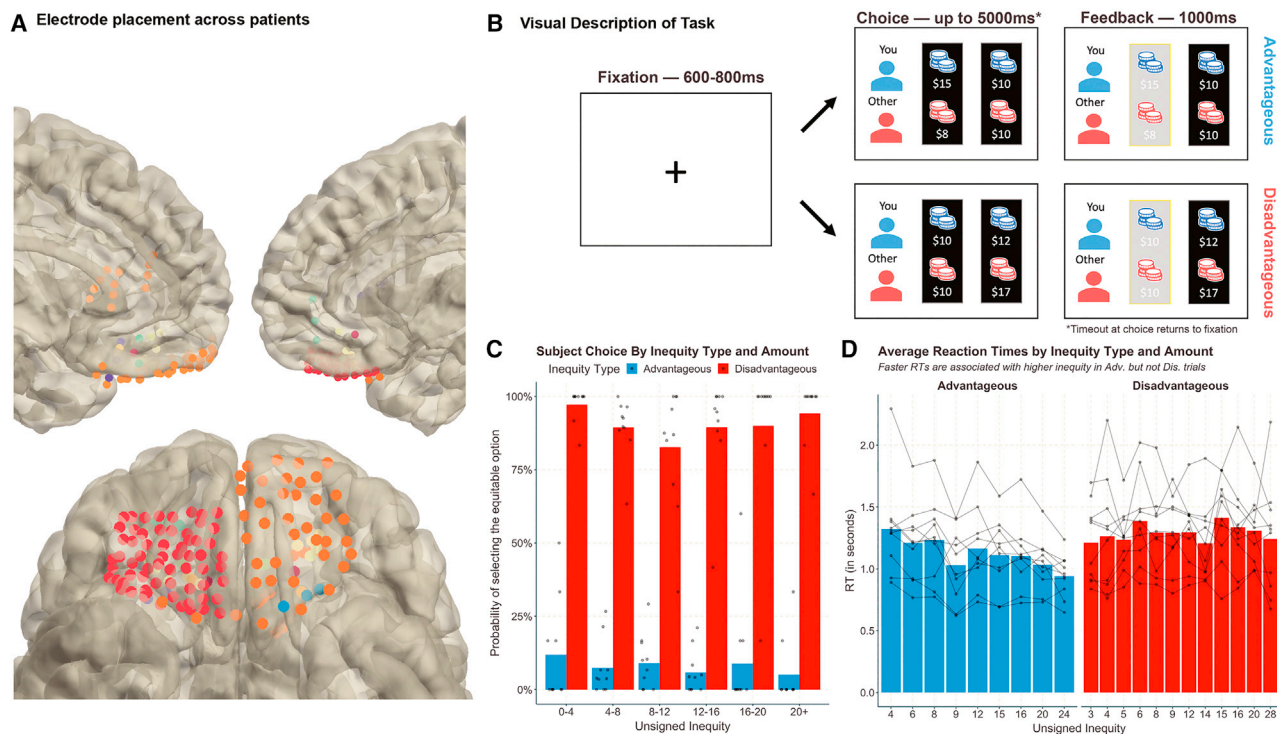


Figure 1. Experimental approach

(A) Anatomical reconstruction showing placement of all 144 electrodes in OFC across all 10 patients. Each color corresponds to a patient.

(B) Patients ($n = 10$) chose between two allocations of money for themselves and an anonymous other player: an equitable option that appeared in all trials (\$10 for themselves and \$10 for the other player) and a second inequitable option that varied from trial to trial. Depending on the values of the inequitable option, patients encountered two types of inequities: advantageous inequity, in trials in which the inequitable option presented a higher payoff for the patient than for the other player (see example in the top row), and disadvantageous inequity, in trials in which the inequitable option presented a lower payoff for the patient than for the other player (see example in the bottom row).

(C) Patient choices were affected by the inequity type. Red bars denote the probability of selecting the equitable option in a disadvantageous trial, while the blue bars represent the probability of selecting the equitable option in an advantageous trial. Black dots denote individual subjects' average choices. Patients avoided selecting the inequitable option when the inequity was not in their favor. When inequity was advantageous, they tended to select the inequitable option, yet they were more reluctant to do so the higher the inequity.

(D) Reaction times were modulated by both inequity type and unsigned inequity. In advantageous trials, denoted by the blue bars, the log-scaled reaction times decreased as the amount of inequity increased. In disadvantageous trials, denoted by the red bars, there was no association between unsigned inequity and the log-scaled reaction times. The black dots and lines represent subject averages. These effects were consistent across patients.

between one's offer and the other player's offer within the inequitable option), and their interaction, as well as self-offer (the amount offered for themselves in the inequitable option) as a controlling factor, and a random effect of patient. Patients were more likely to choose the equitable option in disadvantageous vs. advantageous trials (inequity type, odds ratio [OR] = 238.3, 95% confidence interval [CI] [99.4, 570.8], $p < 0.001$) and with higher amounts of unsigned inequity (OR = 1.2, 95% CI [1.1, 1.3] $p < 0.001$). The interaction between inequity type and unsigned inequity was also significant (OR = 0.81, 95% CI [0.75, 0.88], $p < 0.001$). By breaking down this interaction, we found that bigger inequity amounts were associated with more equitable choices in advantageous trials (OR = 1.1, 95% CI [1.01, 1.21], $p = 0.002$) but not in disadvantageous trials (OR = 0.81, 95% CI [0.94, 1.04], $p = 0.645$), suggesting some advantageous inequity aversion for higher inequities.

To examine the effect of inequity on patients' reaction times, we ran a similar multiple linear mixed-effects regression on the log-

scaled reaction times. Disadvantageous trials (vs. advantageous) and higher unsigned inequity amounts were associated with shorter reaction times (respectively: $\beta = -0.26$, $t = -6.169$, $p < 0.001$; $\beta = -0.006$, $t = -2.20$, $p = 0.03$; $\beta = -0.008$, $t = -3.57$, $p < 0.001$). The interaction between inequity type and unsigned inequity was also significant ($\beta = 0.007$, $t = 2.471$, $p < 0.001$). By breaking down this interaction, we found that bigger inequity amounts were associated with faster reaction times in advantageous trials ($\beta = -0.006$, $t = -2.225$, $p = 0.03$) but not in disadvantageous trials ($\beta = 0.002$, $t = 1.148$, $p = 0.25$). This behavioral effect was consistent across subjects (Figures 1D and S2). For full behavioral and reaction time (RT) results, see Table S1.

Social decision variables encoded in OFC via HFA

Considering the OFC's role in decision making and reward evaluation, we predicted it would encode self-reward information. Additionally, given its involvement in social processing, we hypothesized that it would also encode reward information for

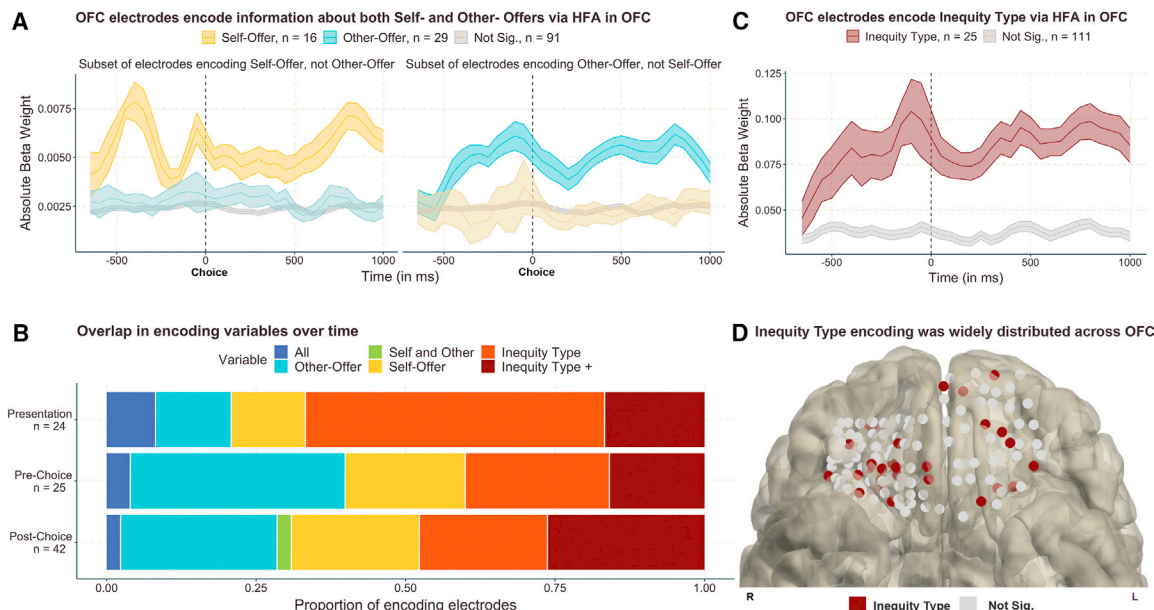


Figure 2. Social decision variables encoded via OFC via HFA

(A) HFA in OFC electrodes encoded reward-related variables pertaining to both the self and the other player. In the left and right plots, the y axis represents the absolute value of the average beta weights from the regression predicting HFA as a function of self-offer and other-offer, respectively. Left plot shows all electrodes significantly encoding the self-offer ($n = 16$, yellow), the average beta weight for those same electrodes when other-offer was used as a predictor (not significant, blue), and the average beta weights for all electrodes that did not significantly encode self-offer or other-offer ($n = 91$, gray). The right plot similarly shows the average absolute value of beta weights for electrodes significantly encoding other-offer ($n = 29$, blue), those same electrodes when self-offer was used as a predictor (not significant, yellow), and the average beta weights for all electrodes that did not significantly encode other-offer or self-offer ($n = 91$, gray). The shaded portions for each line show the standard error of the mean. The dashed vertical line ($t = 0$) indicates the time at which patients made a choice between the two options.

(B) Social decision-making variables were broadly encoded in OFC electrodes across the three task epochs (presentation, pre-choice, and post-choice; see STAR Methods). The x axis shows the proportion of encoding electrodes that encoded at least one variable, respective to each epoch. Self-offer and other-offer were encoded robustly across all three epochs, but rarely did the same electrode encode both those variables during the same epoch (3.6% of encoding electrodes across all epochs, including those that also encoded inequity type). Inequity type was also robustly encoded across all three epochs and was frequently encoded along with either self-offer or other-offer, denoted “inequity type +”. Finally, 2.9% of encoding electrodes encoded all three variables within a single epoch.

(C) Inequity type was encoded via HFA in the OFC. The figure plots the average absolute value of the beta weights across all electrodes that significantly encoded inequity type ($n = 25$, red) and across electrodes that did not encode inequity type ($n = 111$, gray). The dashed vertical line ($t = 0$) indicates the time at which patients made a choice between the two options. The shaded portions for each line show the standard error of the mean.

(D) Anatomical localization of electrodes encoding inequity type (dark red dots; gray dots represent non-encoding electrodes). See Figures S3 and S4 for localization for other variables.

the social counterpart. Following the approach laid out in Saez et al.,²² we tested our hypothesis that these reward-related, social decision-making variables were encoded using HFA in the OFC. Briefly, our regression approach extracted temporal intervals where a variable of interest (self-offer, other-offer, etc.) correlated with the HFA above a permuted null distribution (see STAR Methods for full details). In all analyses, we used false discovery rate (FDR) correction to account for the number of electrodes.

As predicted, we found that electrodes encoded self-offer across all three epochs of the task (overall 13% of unique OFC electrodes across task; by epoch, presentation: 5%, pre-choice: 4%, post-choice: 10%; Figures 2A and 2B). Furthermore, as hypothesized, we found that other-offer was similarly encoded across many electrodes (overall 22% of unique OFC electrodes across task; by epoch, presentation: 5%, pre-choice: 10%, post-choice: 15%; see Figures 2A and

2B) though rarely within the same electrode as self-offer (Figure 2B). These results were not driven by a few patients: self-offer encoding was found in 4 patients and other-offer in 9 patients (see Table S2).

To address potential confounding effects of the moderate correlation between self-offer and other-offer (correlation $[corr] = 0.24$; Figure S1), we conducted additional analyses using a conservative residual approach. To test for the encoding of self-offer, we first ran a single regression to test the relationship between other-offer and HFA and obtained the residuals by calculating the difference between the actual HFA and the predicted HFA based on other-offer. Finally, we tested whether self-offer significantly predicted these residuals above a permuted null distribution. Likewise, we tested whether other-offer significantly predicted the HFA residuals based on self-offer. The results (Table S3) confirm the encoding of both self-offer and other-offer in HFA.

Next, we examined if inequity type (e.g., whether the inequitable option was advantageous or disadvantageous to the patient) was also encoded in the OFC via HFA. Using a similar approach as with self- and other-offers, we found many electrodes significantly encoded inequity type across all three task epochs (21% of unique OFC electrodes across task; by epoch, presentation: 13%, pre-choice: 8%, post-choice: 15%; [Figures 2B and 2C](#)). Additionally, we found that a single electrode frequently encoded inequity type along with either self-offer or other-offer (see [Figure 2B](#)). Here, too, the results were not driven by a few patients: encoding electrodes were found in 9 out of 10 patients ([Table S2](#)).

Importantly, in our design, advantageous options have higher self-offers (mean = 20.1, range = 11–30) compared with disadvantageous options (mean = 8.5, range = 3–15). It is possible that the electrodes encoding inequity type are actually high vs. low self-offers. To test this, we classified trials as either high or low and tested whether high self can explain the HFA activity in the 51 electrode-epoch pairs previously identified as encoding inequity type. We found that this is not the case: the difference in the amounts offered for the self in the two types of inequities cannot fully explain our inequity type findings (see [STAR Methods](#) for details). Furthermore, a multivariate analysis controlling for self-offer and self-chosen confirmed the correlation between HFA activity in the OFC and inequity type ([Table S3](#)).

Inequity-dependent reward-encoding results

Based on the predominance of the inequity type effect, we hypothesized that inequity type would moderate how self-offer and other-offer were encoded in the HFA. For example, self-offer might be encoded less strongly in disadvantageous trials compared with advantageous trials, perhaps reflecting a devaluation of the offer in the face of large disadvantageous inequity as reported in the behavioral literature.¹ Since testing interaction terms within a permutation framework is still a subject of debate in the statistical literature^{49–52} (see [STAR Methods](#) for details), we opted for the following approach. We ran regressions predicting the HFA using each predictor in advantageous and disadvantageous trials separately. We then calculated the difference in R² lines, summed them across bins, and took the absolute value as our permutation statistic. This statistic is small whenever either regressor poorly predicts the HFA in both inequity types, as well as when the regressor predicts well the HFA in both inequity types; it is large when the R² values are high in only one inequity type. Notably, we permuted this test statistic in two separate ways: first by permuting the regressor within the two inequity types and then by permuting the inequity type labels. We FDR corrected for the number of electrodes for both permutations. We qualified an electrode as inequity-dependent encoding if it passed both permutation tests. We found that many electrodes encoded self-offer (24% of OFC electrodes across task; by epoch, presentation: 10%, pre-choice: 12%, post-choice: 1%) and other-offer (28% of OFC electrodes across task; by epoch, presentation: 12%, pre-choice: 11%, post-choice: 14%) in an inequity-dependent manner. This inequity-dependent encoding was found in 9 patients across variables ([Table S2](#)). While for some electrodes, encoding of a variable was stronger in advantageous than in disadvantageous trials, for others the pattern was reversed. In addition, we found

that many of these inequity-dependent electrodes significantly encoded reward variables in one inequity type but not in the other (see exemplar electrode in [Figure 3A](#)). An electrode's preferred inequity type was consistent within a trial. Only one electrode switched from encoding in the advantageous trials to encoding in the disadvantageous trials over the course of a trial ([Figure 3C](#)).

To ensure that these inequity-dependent results for self-offer were not driven by any correlation with other-offer, we additionally ran all regressions of the residuals of the HFA after regressing out the effect of other-offer. The pattern of results was robust to this variation ([Table S3](#)).

We then evaluated alternative explanations that might be driving this effect. First, we considered the possibility that our inequity-dependent results could be driven by the encoding of the chosen and unchosen options, as previous studies in non-human primates have shown that OFC neurons encode chosen and foregone values.^{21,53} In our task, patients were consistent in choosing the inequitable option (self-offer and other offer, whose values varied from trial to trial) in instances of advantageous inequity and the equitable option (always \$10 for themselves and \$10 for the other player) in instances of disadvantageous inequity. Let us now consider an electrode encoding self-chosen, that is, the patient's payoff from the chosen option. As a result of our patients' consistent choice behavior and the task design, in advantageous trials, this electrode would encode self-offer. In disadvantageous trials, on the other hand, this electrode would not show any significant encoding because self-chosen is always the same. As a result, this electrode might be misinterpreted as “encoding self-offer in advantageous trials only.” Similarly, electrodes that appear to encode self-offer only in disadvantageous trials might in fact be encoding self-unchosen, that is, the foregone self-offer. To test whether our findings are better explained by different sets of electrodes encoding chosen and unchosen options rather than inequity-dependent encoding of self-offer, we did the following. We focused on the 26 electrode-epoch pairs that we identified as significantly encoding self-offer in advantageous trials only. Using a single regression, we then tested whether self-chosen was encoded across all trials. If there was either no significant time bin or only 1 significant time bin, we concluded that the self-chosen explanation does not provide any additional explanatory power over the inequity-dependent encoding of the self-offer explanation (this is because for an electrode to be marked as significant in the inequity-dependent encoding, at least two significant bins are needed to pass the permutation test). If two bins or more were significant in the regression analysis, we concluded that self-chosen could explain our results. This approach is very liberal in favor of the self-chosen explanation: we counted in favor of the self-chosen explanation any electrode-epoch pair that could potentially reach significance. We found that out of 26 electrode-epoch pairs that significantly encoded self-offer in advantageous inequity, 12 could in theory be explained by self-chosen across both inequity types, but the 14 others could not be explained by self-chosen at all.

We repeated the same process for the electrode-epoch pairs encoding self-offer only in disadvantageous trials and tested whether their activity is better explained by self-unchosen in all

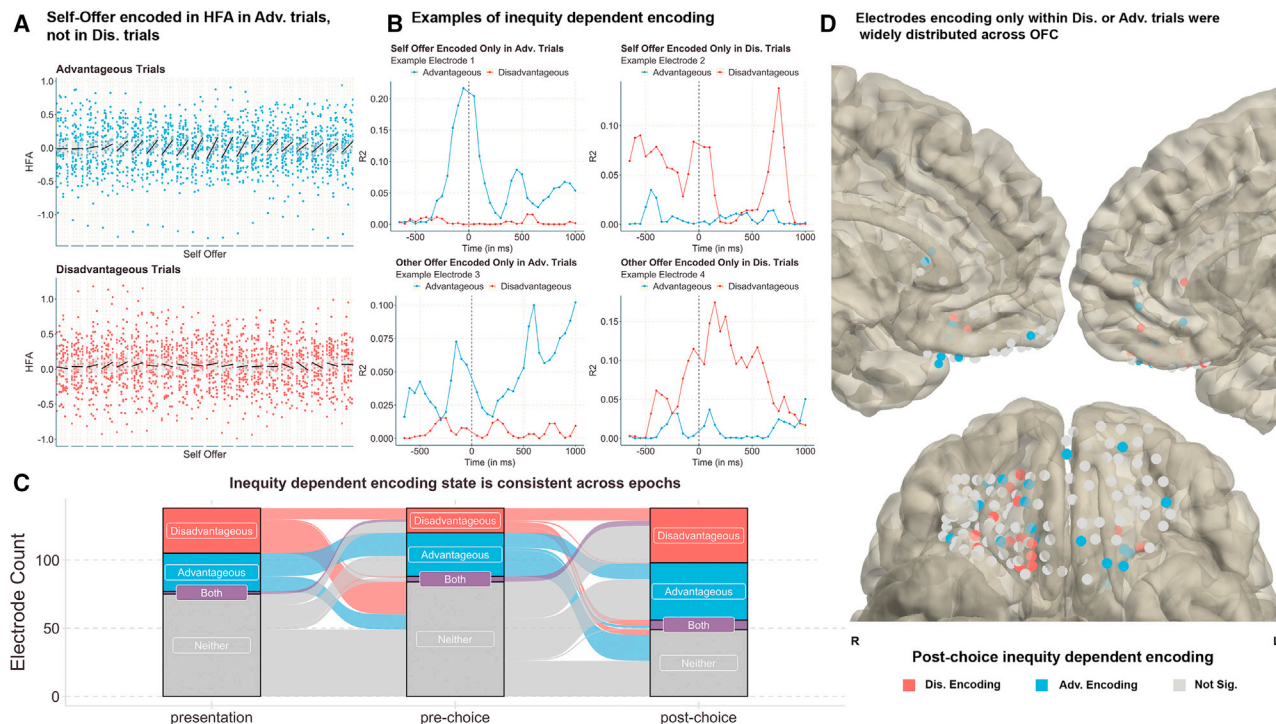


Figure 3. Inequity-dependent reward encoding

(A) Example of an electrode encoding self-offer in advantageous trials but not in disadvantageous trials. The top plot shows the individual regressions across each time bin (50 ms), with the x axis showing the self-offer values presented across trials and the y axis showing the HFA baselined to 200 ms before trial onset, and each dot represents an advantageous trial. The bottom plot is as above but for the disadvantageous trials. While self-offer was significantly encoded in advantageous trials, no such relationship was detected for disadvantageous trials. Shading around regression lines in each subplot represent 95% confidence intervals.

(B) Time course of encoding in example electrodes. Each subplot shows the R2 from the individual regression for both advantageous (blue lines) and disadvantageous (red lines) trials for example electrodes. The top and bottom plots show example electrodes that encoded self-offer and other-offer, respectively. The left and right plots show encoding in advantageous and disadvantageous trials, respectively. The vertical dashed line ($t = 0$) indicates the time at which patients made a choice between the two options.

(C) Inequity encoding type across epochs. The y axis represents the number of electrodes that encoded a particular reward-related variable, and the facets show how this count changed across the three task epochs. Electrodes that encoded task variables (self-offer, other-offer, max, and minimum [min]) in advantageous trials tended to not encode task variables in disadvantageous trials in different epochs. An electrode was marked as “both” if there was no evidence of it using inequity-dependent reward-encoding and the summed R2 across bins was in the top 5% of the null distribution for both advantageous and disadvantageous trials. Otherwise, the electrode was marked as neither.

(D) Anatomical localization of inequity-dependent reward-encoding electrodes in the post-choice epoch (blue/red/gray dots represent electrodes encoding only in advantageous/disadvantageous/none conditions).

trials. We found that out of 24 electrode-epoch pairs that significantly encoded self-offer in advantageous inequity, 11 could in theory be explained by self-foregone, but the others were not. Taken together, these results suggest that self-chosen and self-foregone by themselves cannot fully explain the inequity-dependent encoding finding.

Third, it is possible that these inequity-dependent encodings could be driven by a “unified” encoding of a different predictor. By “unified” we mean that the predictor was encoded across both inequity types similarly. For example, self-offer is identical to maximum value in advantageous trials, meaning that electrodes that seem to be encoding self-offer in only advantageous trials might instead be encoding maximum value across all trials. To address this possibility, we tested each inequity-dependent electrode that encoded either self-offer in advantageous trials or other-offer in disadvantageous trials to see if those electrodes

also significantly encoded maximum (max) value across both inequity types. In total, there were five inequity-dependent-encoding electrodes whose behavior could also be explained by the unified encoding of max value. These electrodes were excluded from the remaining inequity-dependent analyses. The same process was conducted to see if minimum value unified encoding could explain self-offer encoding in disadvantageous trials and other-offer encoding in only advantageous trials. None of these electrodes’ responses were significantly predicted by minimum value encoding across both inequity types.

Anatomical distribution of social reward encoding

We examined the relationship between anatomical organization within the OFC and the encoding of self-offer, other-offer, and inequity type. We tested this by predicting the test statistic from our electrode-specific linear models (see [STAR Methods](#) for

details) from each of the three averaged MNI coordinates of the bipolar-referenced electrodes. We found a modest effect of electrode location within our inequity-dependent analyses. Specifically, the *y* coordinate (anterior/posterior axis) predicted the magnitude of the inequity-encoding effect across all predictors ($p = 0.03$, $\beta = 0.001 \pm 0.0005$, $t = 2.161$, $df = 1,603$, linear mixed-effect model), indicating a higher likelihood of inequity-dependent encoding with more anterior electrode placement. However, this result does not survive multiple comparisons correction. Furthermore, there were no effects of anatomical localizations along the *x* (lateral/medial) axis or the *z* (superior/inferior axis) axis.

In addition, to refine our anatomical analyses, we used the human Brainnetome Atlas to classify electrodes into distinct OFC subregions.⁵⁴ We included all subregions within the orbital group of the Brainnetome Atlas and regions in the superior and middle frontal group that included Brodmann area 10, as well as subgenual area 32 from the cingulate group, resulting in a total of 12 subregions. For each variable of interest (self-offer, other-offer, and inequity type in the unified analyses and self-offer and other-offer in the split analyses), we fitted the log transform of the variable's test statistic with a one-way mixed-effects model with the Brainnetome region as the fixed factor and epoch and patients as random factors. These analyses can be interpreted similarly to the commonly used repeated-measures ANOVA, with the advantages of the mixed-effects approach.⁵⁵ Here, the ANOVA test of interest was the main effect of region. This effect was not significant for any variable in the unified analyses (self-offer: $F(7, 263.79) = 1.95$, $p = 0.063$; other-offer: $F(7, 331.47) = 1.44$, $p = 0.190$; inequity type: $F(7, 220.93) = 1.14$, $p = 0.338$), nor in the split analyses (self-offer: $F(7, 141.39) = 1.35$, $p = 0.232$; other-offer: $F(7, 261.50) = 0.90$, $p = 0.508$). These results indicate that the variables' strength of encoding did not differ across the different subregions of the OFC. These are consistent with the findings that HFA encoding of different reward-related variables is distributed across the OFC and the vmPFC.²²

Theta encoding

The analyses presented above were also conducted for activity in the theta band, as theta activity has been found to be a marker of fairness in scalp EEG studies. Overall, the theta and HFA results were similar. We found that self-offer was encoded in 12.5% of OFC electrodes (in 8 patients), other-offer was encoded in 6% of OFC electrodes (in 3 patients), and inequity type was encoded in 15% of OFC electrodes (7 patients). There was minimal overlap between theta and HFA encoding: the proportion of theta electrode-epoch pairs encoding a given variable that also encoded this variable in HFA ranged from 9% to 19%, depending on the variable (Table S4). This provides support that these two frequency bands provide independent information on reward encoding.

The inequity-dependent encoding analysis also yielded similar results to what we found in the HFA analyses. 35% of OFC electrodes encoded self-offer and 38% encoded other-offer in an inequity-dependent manner. This inequity-dependent encoding was found in 9 patients across variables. Again, there was minimal overlap between theta and HFA inequity-dependent encoding: among the electrode-epoch pairs showing some inequity-dependent encoding for a variable in HFA, only 9%–15% showed the

same type of encoding in theta, depending on the variable (Table S4).

DISCUSSION

The role of the OFC in value-based choice is well established, but its role in human social decision making is less clear. We conducted a human intracranial study on social decision making and inequity processing. Patients played a repeated dictator game, making choices between allocations of money for themselves and a social counterpart: one fair, equitable option and one inequitable option—either advantageous or disadvantageous. Our focus was on HFA, an index of local cortical computation^{35,56} that captures value-based computations in non-social tasks.^{19,22} We demonstrate that HFA in the OFC encodes variables related to social reward and provide further evidence for inequity-dependent encoding, an encoding pattern by which the OFC can rapidly adapt to changing social contexts.

Behavior

Patients exhibited a clear preference for minimizing disadvantageous inequity at the expense of their own payoff, regardless of the size of the inequity. They showed less concern for minimizing advantageous inequity and instead prioritized maximizing their own payoff in advantageous trials. We observed a slight effect of inequity size in advantageous trials, where larger inequities led to more equitable choices, indicating aversion to “extreme” advantageous inequities. RT analysis supported these findings. Patients had shorter RTs in disadvantageous vs. advantageous trials, suggesting they were less conflicted in disadvantageous trials.⁵⁷ In disadvantageous trials, small and big amounts of inequity elicited similar RTs, suggesting similar (low) levels of conflict. In contrast, in advantageous trials, bigger inequities were associated with longer RTs, suggesting increased conflict. Overall, these results show an aversion to disadvantageous inequity regardless of its size and a lesser aversion to extreme advantageous inequities. These findings align with previous research demonstrating stronger responses to disadvantageous inequity, despite aversion to both disadvantageous and advantageous inequities.^{2,58}

OFC encodes social variables in addition to self-related variables

We found that the human OFC, in addition to encoding self-offer, also encodes variables relevant to their social counterpart: 22% of OFC electrodes tracked the value of other-offer. This number was lower when examining theta activity (6%), suggesting that while some social information might be encoded redundantly in the two frequency bands, the overlap is not total. This evidence demonstrates the encoding of other reward in the human OFC, extending the findings that HFA in the human OFC encodes self-related reward variables in a non-social decision-making task.^{20,22,26,34}

The HFA results complement the non-human primate literature using single-neuron recordings. Previous findings indicated that OFC neurons only encode rewards for oneself, while other brain regions, like the anterior cingulate gyrus, encode both self- and other rewards.^{31,32} In our study, we demonstrate that the human OFC encodes both self- and other rewards. These divergent

findings may stem from differences in defining social context across studies. For example, in Chang et al.'s paradigm, the actor monkey and its partner could never receive rewards in the same trial, and in Azzi et al.'s study, both monkeys were always rewarded with the same amount of water. This discrepancy could also be due to methodological differences between human and animal study procedures (e.g., extensive training in animal studies, use of secondary reinforcers in human studies). Additionally, differences between HFA and single-neuron activity should be considered, as they are not directly comparable. HFA reflects summed multiunit activity, while single-neuron activity represents specific neuronal responses.^{35,59} Lastly, these results may highlight species differences in the extent to which humans and non-human primates encode and perceive rewards related to social counterparts.

Inequity type is encoded in the OFC

We found that the OFC was sensitive to the type of inequity (advantageous vs. disadvantageous) presented in the trial: 21% of our sample's OFC electrodes encoded inequity type, an effect observed in 9 of our 10 patients. Similar results were obtained in the theta band, with 15% of electrodes encoding inequity type in 7 patients, in line with the scalp EEG literature's findings that theta is a neural signature of fairness.⁴⁰ It is worth emphasizing that inequity type was not explicitly mentioned in the game instructions nor was it signaled in the trial display (i.e., with a different background color). The predominance of the effect confirms the importance of fairness considerations in valuation and decision making. Furthermore, this variable represents an example of social context encoding in the OFC, one that is relevant to our patients' behavior but does not explicitly include reward values.

Inequity-dependent encoding of reward-related variables

The prominent inequity type effect and our behavioral findings prompted investigation of whether inequity type modulates the encoding of other reward-related variables. We examined the encoding of different variables separately in advantageous and disadvantageous trials and found substantial numbers of OFC electrode encoded variables in an inequity-dependent way. Based on the findings that self-reward can be devalued in the face of disadvantageous inequity,⁶⁰ we hypothesized that inequity type might increase or decrease encoding of reward-related variables. Instead, we found that the relationship between HFA and reward variables was increased in advantageous vs. disadvantageous trials for certain electrodes but was diminished for others. In other words, depending on the type of inequity, electrodes rapidly and reversibly switched between different reward-encoding profiles. The pattern of encoding was observed in 9 out of 10 patients and was found for theta band activity as well. Furthermore, we observed that many inequity-dependent electrodes significantly encoded reward variables only in one inequity type but not the other. This suggests that inequity type might turn on and off reward encoding in distinct populations of OFC electrodes, although we cannot rule out that some encoding is happening in non-significant electrodes and that we are unable to observe it. Overall, these findings show that different social contexts can modulate reward-related variable encoding.

Conclusion

In our study, we investigated the involvement of the OFC in social decision-making processes. Our findings revealed that the OFC not only encodes reward variables associated with self-related outcomes but also encodes those related to a social counterpart. In addition, we found that the OFC is sensitive to the type of inequity, distinguishing between advantageous and disadvantageous situations. Furthermore, we observed that depending on the type of inequity, OFC electrodes presented different reward-encoding profiles. This inequity-dependent encoding could allow the OFC to flexibly and rapidly adapt valuation computations to different contexts. Social state-dependent encoding may not be specific to inequity. The value of our daily decisions often relies on the social context in which they occur—having a glass of wine at dinner among friends is deemed an acceptable choice, while doing so in the middle of a lecture is not. Future research is needed to uncover how other social contexts, such as social distance between individuals^{61,62} or the cooperative vs. competitive nature of an interaction,⁶³ are encoded in the brain.

Limitations of the study

Although the current study provides valuable insights into the role of the OFC in social decision making, some limitations must be acknowledged. First, our study was conducted on patients with epilepsy undergoing clinical evaluation, raising the question of the generalizability of our findings. To address this, we undertook extensive efforts to only test patients fully alert and cooperative and excluded electrodes near seizure foci or contaminated by artifacts.

A second limitation relates to the task design: some variables of interest were correlated. These collinearities could have been mitigated through a more controlled study design. For instance, self- and other-offers could have been fully orthogonalized, and self-offer could have been balanced with inequity type to ensure similar ranges of values in both advantageous and disadvantageous trials. We controlled for collinearity using complementing statistical approaches; however, future studies would benefit from carefully balanced study designs. Furthermore, while the inequitable option was pseudo-randomly presented on the left- and right-hand sides, the option that was most attractive to disadvantageous inequity minimizers was more frequently presented on the left-hand side (69.1% of trials). As our patients mostly employed a strategy to minimize disadvantageous inequity, they mostly selected the left-hand side option ($70.4\% \pm 8\%$ of trials). This side bias is unlikely to undermine the inequity-dependent encoding results because (1) our analyses focused exclusively on variables related to the presentation of offers, not on patients' choice, (2) the inequitable option was presented as frequently on the left as it was on the right, and (3) we found evidence of encoding both self-offer and other-offer in both inequity types—in other words, even though the inequitable option was rarely selected in disadvantageous trials, we still find evidence of electrodes encoding this value (Figure 3B). A better controlled experimental design for these elements would minimize confounding variables and provide stronger conclusions.

A third limitation of the study arises from the challenge of incorporating choice behavior into our analyses due to the lack of variance in choice. In most trials, patients selected the equal

option when facing disadvantageous inequity and the unequal option when facing advantageous inequity. This limitation prevented us from investigating questions related to choice behavior, such as identifying the neural activity that accompanies or predicts altruistic decision making. Furthermore, the collinearity between choice and inequity type may raise concerns regarding the interpretation of certain findings. While we made rigorous efforts to address this concern with a variety of complementary tests, future studies would benefit from eliciting diverse behaviors. The homogeneity of choices in our sample may be attributed to the sample size ($n = 10$), which falls within the higher range for iEEG studies¹⁹ but is smaller compared with behavioral and neuroimaging studies on inequity aversion. Moreover, the use of hypothetical rewards and hypothetical social counterparts may have influenced participants' choices. These considerations suggest that our results may not generalize to individuals who disregard inequity to either maximize their own payout or maximize the payout of both participants.⁶⁴

Finally, it is important to note that while we examine the role of the OFC in social decision making, the study does not have a non-social condition. As a result, our data cannot determine if the encoding of self-related rewards differs between social and non-social contexts or if there are specific aspects of social settings influencing OFC activity. However, our findings demonstrate that the OFC encodes social information (other-offer, inequity type) and that the encoding of reward-related variables is influenced by the type of inequity.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.celrep.2023.112865>.

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AUTHOR CONTRIBUTIONS

I.S. and M.H. designed the experiment; R.T.K. and J.J.L. supervised data collection; I.S., J.J.L., D.M., and B.R.S. collected the data; D.M. and B.R.S. analyzed the data; D.M., B.R.S., I.S., M.H., and R.T.K. interpreted the data; D.M. and B.R.S. wrote the manuscript; and M.H. and R.T.K. supervised the project.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
Matlab 2020b	MathWorks Inc.	https://www.mathworks.com/products/matlab.html
Fieldtrip Toolbox	Oostenveld et al. ⁶⁵	https://www.fieldtriptoolbox.org/
R 4.0.3	R core Team ⁶⁶	https://www.r-project.org/
Tidyverse	Wickham et al. ⁶⁷	https://www.tidyverse.org/
Afex	Singmann et al. ⁶⁸	https://cran.r-project.org/web/packages/afex/index.html
LME4	Bates et al. ⁶⁹	https://cran.r-project.org/web/packages/lme4/index.html
FreeSurfer 6.0	Dale et al. ⁷⁰	https://surfer.nmr.mgh.harvard.edu/
Brainnetome atlas	Fan et al. ⁵⁴	https://atlas.brainnetome.org/
Custom scripts	This paper	https://zenodo.org/badge/latestdoi/514342754

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Robert T. Knight (rtknight@berkeley.edu).

Materials availability

This study did not generate any new reagents.

Data and code availability

- All data reported in this paper will be shared by the [lead contact](#) upon request.
- Original code has been deposited on Zenodo and is available for public download (Zenodo: <https://zenodo.org/badge/latestdoi/514342754>). DOIs are listed in the [key resources table](#).
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Patients

We recorded intracranial signals from 10 (5 female) adult patients (mean age = 36.6 years, SD = 10.45, age range = 25–58 years) who were undergoing intraoperative neurosurgical treatment for refractory epilepsy. Each patient was implanted with subdural grids, strips and/or depth electrodes to localize the seizure onset zone for subsequent surgical resection. We selected patients with electrodes implanted in the OFC/vmPFC (range, average, overall). The position of these electrodes was dictated solely by the patient's clinical needs. The cohort consisted of 4 unilateral cases (1 left, 3 right) and 6 bilateral cases. Patient recordings took place at four hospitals: the University of California, San Francisco (UCSF, N = 1) Hospital, the Stanford School of Medicine (N = 1), the University of California Irvine Medical Center (UCI, N = 7) and the University of California, Davis (Davis, N = 1). All patients provided written informed consent as part of the research protocol approved by each hospital's Institutional Review Board and by the University of California, Berkeley. Patients were tested when they were fully alert and cooperative.

METHOD DETAILS

Behavioral task

We investigated social preferences using a modified Dictator task in which patients chose between two allocations of money for themselves and an anonymous social counterpart ("Other"). [Figure 1B](#) illustrates the experimental paradigm. Trials started with

a fixation cross ($t = 0$), followed by the game presentation screen ($t = 750$ ms). At that time, patients were given up to 5 s to choose between two allocations: a fixed, EQUITABLE option that did not vary across trials (\$10 for themselves; \$10 for the other player), and an INEQUITABLE option, that varied across trials. The inequitable option was either advantageous (i.e., with a higher payoff for the patient than for the social counterpart, for example, \$12 for themselves; \$8 for Other) or disadvantageous (i.e., with a lower payoff for the patient than for the social counterpart, for example, \$8 for themselves; \$14 for Other). In addition, as a control we included catch trials ($n = 24$) in which the second allocation was also equitable and either dominated the fixed \$10/\$10 option (for example \$14 for themselves; \$14 for Other, $n = 12$) or was less valuable than the fixed \$10/\$10 option (for example \$4 for themselves; \$4 for Other, $n = 12$). These catch trials were excluded from the neural analyses. Once a choice was made (using the left or right arrow keys on the keyboard), the chosen allocation was highlighted for 1000ms, after which a new trial started. If the patient did not choose within the allotted time limit, a timeout occurred and the game moved on to the following trial. Timeouts were infrequent ($4\% \pm 1\%$ of trials across patients) and were excluded from the analysis. The location of the equitable and non-equitable allocations (left/right) was randomized across trials. The specific offers given for each trial are included in the Zenodo repository along with the custom scripts (see “Data and Code availability”).

Patients were instructed that there was no wrong or right way to play the game, and that they should play according to their own preferences. Due to IRB limitations, we were unable to pay patients according to their decisions in the game, but we asked them to make decisions as if they were playing with real money. Patients completed a training session prior to the game in which they played a few rounds under the experimenter’s supervision until they felt confident that they understood the task. The game itself was composed of 228 trials. A full experimental run typically lasted approximately 20 min. Stimulus presentation was operated by pygame.

Data acquisition

Electrophysiological data were recorded using Tucker-Davis Technologies (Stanford, and UCSF), Nihon-Kohden (UCI) or Natus (Davis) systems. Data processing was identical across all sites: channels were amplified $\times 10000$ and analog filtered (0.01–1000 Hz) with > 2 kHz digitization rate. The photodiode’s input was recorded in the electrophysiological system as an analog input. This signal was used to synchronize the behavioral and electrophysiological data.

QUANTIFICATION AND STATISTICAL ANALYSIS

Data preprocessing

Offline, continuous data were downsampled to 1KHz, low-pass filtered at 200Hz, and notch-filtered at 60Hz and its harmonics up to 300 Hz to remove line noise (Butterworth, 4th order, 2 Hz bandwidth). The data was then demeaned and detrended, before being re-referenced, using a common average reference for grids and strips, and a bipolar reference to an adjacent electrode for depth electrodes. We visually identified and removed channels with poor contact or excessive noise throughout the recording. In addition, each dataset was visually inspected with a neurologist in order to remove electrodes exhibiting epileptic activity and noisy epochs (such as epochs with a spread of epileptic activity from the primary epileptic site). HFA was extracted using a band-pass-Hilbert approach⁷¹ to extract HFA, 20-Hz-wide sub-bands spanning from 70 to 150 Hz in 5 Hz steps (70–90, 75 to 95, ... up to 130 to 150 Hz). Finally, we segmented the continuous EEG data into three epochs. Presentation is defined as trial onset until 750ms, pre-choice is defined from 650ms until button press, and post-choice is defined from button press until 1000ms. Each epoch was baselined using the first 200ms preceding trial onset. Data preprocessing was carried out in MATLAB (MathWorks) using the Fieldtrip Toolbox.⁶⁵ Data analysis was carried out in R⁶⁷ using custom scripts (Zenodo: <https://zenodo.org/badge/latestdoi/514342754>) and the tidyverse package.⁶⁷

Anatomical reconstructions

We used an anatomical data processing pipeline⁷² to localize electrodes from a pre-implantation MRI and a post-implantation CT scan. The MRI and CT images were aligned to a common coordinate system and fused with each other using a rigid body transformation. We then compensated for brain shifts caused by the implantation surgery. A hull of the patient brain was generated using the Freesurfer analysis suite.⁷⁰ Electrodes were then classified by a neurologist according to the anatomical location within each subject’s anatomical space. Only electrodes confirmed to be in the OFC/vmPFC were included in the analysis. Out of these 144 OFC electrodes, 134 were artifact-free and included in subsequent analyses (range 2–60 per patient, mean 13.4 electrodes). For illustration purposes, we converted patient-space electrodes into Montreal Neurological Institute (MNI) coordinates using volume-based normalization. Figure 1 shows all OFC/vmPFC used in the analysis.

	Variable Name	Qualitative Description	Quantitative Description
Primary Variables Of Interest	Self-Offer	The amount of money offered for oneself in the inequitable offer. (<i>The amount offered for the self in the equitable option is always \$10, and was not analyzed</i>)	–
	Other-Offer	The amount of money offered for the social counterpart in the inequitable offer. (<i>The amount offered for the counterpart in the equitable option is always \$10, and was not analyzed</i>)	–
	Inequity Type	A binary variable denoting whether the trial included an inequitable option where the self could receive a higher payout than the social counterpart OR where the social counterpart could receive a higher payout than oneself	<i>If Self-Offer > Other-Offer, Advantageous else Other-Offer > Self-Offer, Disadvantageous</i>
Secondary Variables of Interest	Max	The maximum value of the inequitable option	<i>max(Self-Offer, Other-Offer)</i>
	Min	The minimum value of the inequitable option	<i>min(Self-Offer, Other-Offer)</i>
	Unsigned Inequity	The absolute value of the difference in potential payout within the inequitable option	<i>abs(Self-Offer - Other-Offer)</i>
	Signed Inequity	The difference in potential payout within the inequitable option	<i>Self-Offer - Other-Offer</i>

Table: Definition reward-related variables used across the analyses.

FRD correction

For all the analyses presented below, we used FDR correction to account for the number of electrodes we ran analyses on ($n = 136$). This is a conservative approach. The results presented are not corrected for the number of epochs and variables.

Social decision variables encoding in the OFC via HFA

To determine if a given electrode was encoding one of our task-related variables (see table in the [STAR Methods](#)), we employed a regression approach where the dependent variable was defined as the analytic amplitude of the HFA time series extracted via Hilbert transform.²² We then divided HFA time series into three event-related epochs to account for inter-trial latencies: presentation (0–750ms after trial onset), pre-choice (0–650ms before choice), and post-choice (0–1000ms after choice). We used a 200-ms baseline to remove any pre-stimulus differences in baseline amplitude and averaged HFA activity using a 200ms rolling window at 50ms increments. To identify task-selective channels, we performed separate linear regressions of average HFA activity on each reward-related regressor of interest.

We calculated the encoding window in individual regressors/electrodes by taking the longest stretch of time in which all time points showed significant encoding ($p < 0.05$). False-positive rate was determined using a permutation strategy, where the test statistic was the sum of the F statistics across the encoding window. This approach is insensitive with respect to time of task-related activation and to the direction of encoding (i.e., HFA increases or decreases). For each regressor-HFA regression, we shuffled the relationship between behavioral labels and HFA activity 1,000 times. The resulting distribution was taken as the null for that regressor-electrode combination.

It is important to note that in our design, Advantageous options are associated with higher Self-Offers (mean = 20.1, range = 11–30) than Disadvantageous options (mean = 8.5, range = 3–15). It could thus be that electrodes we identified as encoding Inequity Type are in fact encoding high vs. low Self-Offers. To test this alternative explanation, we created a new dummy variable, High Self-Offer, and used the mean of Self-Offer (mean = 14.29) to classify trials as either High or Low. We chose the mean of Self-Offer rather than the median because the mean separated the trials in sets very similar to Advantageous and Disadvantageous trials. We then tested whether High Self can explain the HFA activity in the 51 electrode-epoch pairs that were previously identified as significantly encoding Inequity type, using a single regression per time bin (the first step of the regression + permutation approach used for testing Inequity Type). If there was either no significant bin, or only 1 significant bin, we concluded that High Self cannot explain the significant encoding of Inequity Type, because at least two significant bins are needed to pass the permutation test. If two bins or more were significant in the regression analysis, we concluded that High Self could explain our Inequity results. This approach favors the High Self explanation: we counted in favor of the High Self-explanation any electrode that could potentially reach significance. We found

that out of 51 electrode-epoch pairs that significantly encoded Inequity Type, 21 could in theory be explained by High Self, but the 30 others cannot. These results suggest that the difference in the amounts offered for the Self in the two types of inequities cannot fully explain our inequity type findings.

State-dependent inequity encoding

To test if electrodes encoded reward variables in one Inequity Type but not the other, we took a similar approach used for unified encoding. We ran each predictor-electrode separately for advantageous-type trials and disadvantageous-type trials. Advantageous-type trials were defined as trials where within the varying option, the Self-Offer was higher than the Other-Offer. Disadvantageous trials were defined conversely, where the Other-Offer was higher than the Self-Offer in the variable option. As above, we took a permutation approach. For each variable-electrode pair, we shuffled the relationship between behavioral labels and HFA activity 1,000 times. To simultaneously capture 1) encoding of a reward-related variable in one Inequity Type and 2) a *lack* of evidence for encoding of a reward-related variable in the corresponding Inequity Type, we defined the test statistic for the permutation test as the absolute difference in R² values between the two regressions, across the entire epoch. Note that unlike in the unified encoding analyses, this method does not filter to only include significant stretches of encoding. This allows us to avoid testing separately for encoding in the advantageous trials and then again in the disadvantageous trials but doesn't allow us to capture specific time windows of encoding within an epoch. We then FDR corrected across all 136 electrodes.

We then performed a second permutation test on the electrodes that survived our first test of state-dependent encoding. The first test calculates the chance one would see a given reward-related variable encoded in exactly one Inequity Type by chance. In the second permutation, we test the likelihood of seeing encoding of a given reward-related variable in only one-half of the trials by shuffling the Inequity Type labels. The test statistic was calculated as above, resulting in a second null distribution for each regressor-electrode pair. Electrode-regressor pairs were classified as using state-dependent encoding only if the regression was significant ($p < 0.05$) by both permutation strategies. We highlight that this is a conservative approach as we FDR corrected for all 136 electrodes in both tests.

Alternative hypotheses

To confirm that our state-dependent inequity results could not be better explained by differences in noise between the two inequity types, we performed a secondary analysis that compared the residuals between inequity types for each regression across all time bins. Within state-dependent inequity encoding electrodes, we took the residuals from each time bin in each epoch and performed a t test between the two inequity types. If the confidence interval of the difference in means did not include 0, we excluded this electrode's epoch from the inequity-dependent analyses. We found that differences in noise between the two conditions were rare, happening in only 1.5% of electrode-epoch pairs, suggesting that the state-dependent inequity encoding is not driven by differences in noise in the underlying neural signal.

Our second alternative hypothesis was that the state-dependent inequity encoding analysis might actually be detecting unified encoding a different variable, whereby "unified" we mean that the predictor was encoded across both inequity types similarly. For example, instead of an electrode encoding Self-Offer only in Advantageous trials, instead that electrode might be encoding Max Value in both Advantageous and Disadvantageous trials. To evaluate this possibility, we took all the electrodes that encoded Self-Offer in a state-dependent manner and tested to see if they also encoded Max value across all trials, using the regression and permutation approach described above. In total, there were five state-dependent encoding electrodes whose behavior could also be explained by the unified encoding of Maximum Value. These electrodes were also excluded from the remaining state-dependent analyses. The same process was conducted to see if Minimum Value unified encoding could explain Self-Offer encoding in Disadvantageous trials and Other-Offer encoding in only Advantageous trials. None of these electrodes' responses were significantly predicted by Minimum value encoding across both inequity types.

Anatomical analyses

To determine if the effects of our above analyses were localized to a specific region of the OFC we used linear mixed-effects modeling. Specifically, we averaged the MNI coordinates of the bipolar-referenced electrodes for each MNI axis. We then tested if the MNI coordinate predicted the test statistic, using a different model for each MNI axis, each with a random effect of subject. See the above methods for the definition of the test statistic. We ran these analyses for both the unified and state-dependent encoding analyses first grouped across all predictors, and then separately for each of our main predictors (Self-Offer, Other-Offer, Inequity Type).

In order to refine the regional analysis, we also used the human Brainnetome Atlas.⁵⁴ OFC electrodes were classified into 12 subregions: we included all subregions within the Orbital group of the Brainnetome atlas, regions in the Superior and Middle Frontal group that included Brodmann area 10, as well as subgenual area 32 from the Cingulate group. Following the approach used by Golan et al.,⁵⁵ for each one of our variable of interest (Self-Offer, Other-Offer and Inequity Type in the Unified analyses, and Self-Offer and Other-Offer in the Split analyses), we fitted the log transform of the variable's test statistic with a one-way mixed-effects model with the fixed factor of Brainnetome region, and the random factors of epoch and patients. Bipolar electrodes were classified according to the Brainnetome location of the first electrode of each pair. This analysis was implemented using the *afex*⁶⁸ and *LME4* package⁶⁹ of the R language.⁶⁶ The results of this analysis can be interpreted similarly to the more commonly used repeated-measures ANOVA, with the advantages of the mixed-effects approach. The main effect of Region was tested using Type III ANOVA with Kenward-Roger approximation for degrees of freedom implemented by the *afex* R package.⁶⁸