Neuronal activity in the orbitofrontal cortex of monkeys choosing between three options varying on three dimensions

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Numerous human and animal studies have shown that neurons in orbitofrontal cortex (OFC) encode economic decision variables including the value of individual offers, the chosen good, and the chosen value. However, most previous studies examined binary choices between options that varied on two dimensions. Thus, it remains unclear whether and how the neuronal population in OFC can accommodate more complex choices including choices between multiple options. Here we examined trinary choices between offers that varied on three dimensions (juice flavor, quantity, probability). We recorded from the OFC of two monkeys and we analyzed the spiking activity of $N = 1,466$ cells. We found that different groups of cells encoded the value of individual offers, the chosen juice and the chosen value. Importantly, the activity of offer value cells integrated the juice quantity and the animal's risk attitude, and thus reflected the subjective nature of value. Previous studies had not addressed this issue. In summary, our results confirm and generalize previous findings. They thus advance our understanding of the neuronal mechanisms of value computation and value comparison underlying economic choices.

Keywords: economic choice; orbitofrontal cortex; trinary choice; risky choice; subjective value; neurophysiology

Choice involves a process of computing the subjective value (SV) of an option and comparing the SVs of each alternative [8][10][2]. Converging evidence from human[3], monkey[8], and rodent[5] studies have shown that neurons in orbitofrontal cortex (OFC) (i.e., offer value cells) encode an offer's SV, while chosen value and chosen juice cells reflect the comparison of SVs during choice. These neurons sufficiently represent the mental stages of value computation and value comparison during economic choice.[7] It also appears that OFC can integrate multiple attributes during SV formation [9][1].

However, it remains poorly understood whether the OFC decision circuitry generalizes to multinary options involving multiple dimensions. Economic choice was largely studied using binary offers. Previous work[8] has shown that offer value cells may represent subjective value, but they actually do not show whether they *encode* value. Furthermore, behavioral studies of multinary choice have reported anomalies such as choice overload[4] and decoy effects[11] that violate rationality assumptions. Thus, understanding the decision mechanism in OFC during trinary choice may pave the way to address these behavioral anomalies. Hence, this study aims to assess: (a) whether offer value cells can flexibly compute the an offer's SV that varied across multiple dimensions; and (b) whether the OFC neural circuitry can accommodate the computation and comparison of SVs during trinary choice.

Choice task. We developed a behavioral paradigm of trinary choices. Monkeys were presented with at most three offers that varied on three dimensions, namely juice flavor, quantity, and the probability of juice delivery. Offers were represented as incomplete pies (**Fig 1A**). Each session has 500-600 trials. We collected behavioral and electrophysiological recordings across 247 sessions (121 for Monkey E; 127 for Monkey G). We recorded in central OFC.

Logistic analysis. The logistic model [6] can be written as:

$$Pr(J) = \frac{V_J^{\eta}}{\sum_{I=A,B,C} V_I^{\eta}} \quad (1)$$

where J is the juice type, $Pr(J)$ is the probability of choosing juice J, and η measures choice accuracy. We defined the SV as $V_J = \rho_J p_J^{\gamma} q_J$, where q_J is the quantity, p_J is the probability, ρ_J is the relative value, and γ is the risk attitude. We fitted the model using maximum likelihood. For each session, we obtained estimates for parameters ρ_A, ρ_B, γ, and η.

Neuronal analysis. We defined a large number of candidate variables that OFC neurons might potentially encode. This included: offer quantity (q_J), offer probability (p_J), offer expected quantity ($p_J q_J$), offer value ($V_J = \rho_J p_J^{\gamma} q_J$), J chosen ($= 1$ if J was chosen; 0 otherwise), and got J ($= 1$ if J was received; 0 otherwise). We also defined variables chosen q_J, chosen p_J, chosen $p_J q_J$, chosen V_J, and received value. We defined several 0.5 s time windows aligned with offer onset, go signal, and juice delivery. A neuronal response is defined as the activity of one cell in one time window. We regressed each response on each variable. If the regression slope is nonzero, the variable is said to explain the response. We constructed a population table summarizing the explanatory power of different variables across time windows. Variable selection analysis identified a small subset of variables with the highest explanatory power.

Results. We recorded 1,466 neurons (919 from Monkey E; 547 from Monkey G) in OFC. Monkeys chose offers with the highest SV (**Fig 1B-C**). Choice was variable as the SVs were closer to the center of the simplex (**Fig 1C**). Choices were fairly separable, but not entirely, suggesting that monkeys were not randomly choosing.

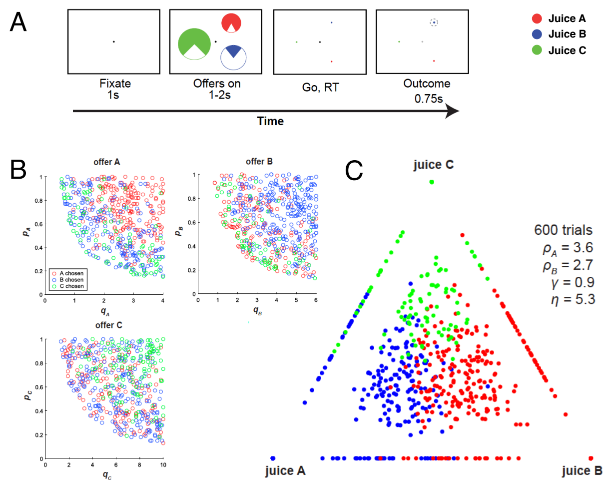

Figure 1: **(A)** *Choice task.* Monkeys chose between three options that varied for flavor, quantity, and probability. Pie colors represented juice flavor, the circle radius represented quantity, and the filled angle represented probability. During the trial, offers are shown after fixation. Saccade targets are then turned on, and monkeys indicated their choice with a saccade. Monkeys either received the juice or not, conditional on the probability. **(B)** *Example session, offer distributions.* The three plots refer to juices A,B, and C. The two axes denote probability and quantity, each data point is a trial, the colors are the chosen juice. **(C)** *Example session, joint distribution of SVs.* In the simplex, data are normalized by the sum of the SVs. Each data point is a trial. Points in the triangle are trinary choices while points along the edge are binary choices. Vertices represented the juice type. Colors represented the chosen juice. Points closer to the vertex of J have higher SVs that favor juice J; points closer to the center have more equal SVs.

Neuronally, example cell activities (**Fig 2A-D**) suggest that OFC neurons selectively respond to various stages of the decision process. Indeed, population analysis (**Fig 2E**) revealed a clear distinction between time windows preceding and following the trial outcome. Variables related to received juice dominated during the late time windows (post-juice 1,2); the variables *A, B, C Chosen* dominated during *pre-juice*, which follows eye movement but precedes trial outcome; *chosen value* dominated during the first two time windows where the decision process takes place. Variable selection analysis revealed that the best subset of variables during the pre-outcome time windows are the triplet of offer values; chosen value; the triplet of chosen juice; chosen probability; and chosen position. The best subset during the post-outcome time windows are got juice and the triplet of received juice. Notably, the fact that *offer values* explained neuronal responses better than the competing variable of *offer expected quantity* suggests that OFC neurons encode the subjective values that reflect the animal's juice preference and risk attitudes.

Overall, our findings show that: (a) the OFC decision circuit fairly generalizes to trinary choice; (b) that the circuit reflects the mental stages of value computation, value comparison, and the trial outcome; and (c) the activity of offer value cells in reflect the subjective nature of value.

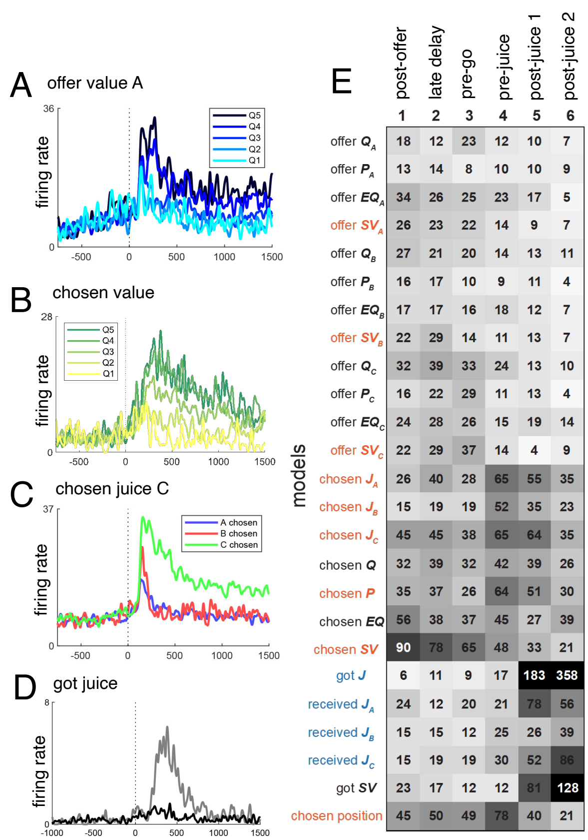

Figure 2: **(A)** *Example cell encoding offer value A*. Trials were divided in into quantiles according to *offer value A* (V_A). Cell activity increased as a function of V_A. **(B)** *Cell encoding chosen value*. Trials were also grouped in quantiles. **(C)** *Cell encoding chosen juice*. Trials were divided in three groups according to the juice the monkey chose. **(D)** *Cell encoding got juice*. Trials were divided in two groups conditional on juice delivery. **(E)** *Population analysis*. Cell activity was analyzed in six 0.5s time windows. Each entry is the number of neuronal responses best explained by the corresponding variable. The number of responses are also indicated in greyscale. Orange text denotes the best subset of k variables with the highest explanatory power during the first four time windows. Blue text denotes the best subset during the last two time windows.

Acknowledgments

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