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Economic Choices under Simultaneous or Sequential Offers Rely on the Same Neural Circuit

Abbreviated title: Same neural circuit for two choice tasks

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30 Abstract

31 A series of studies in which monkeys chose between two juices offered in variable amounts
32 identified in the orbitofrontal cortex (OFC) different groups of neurons encoding the value of
33 individual options (*offer value*), the binary choice outcome (*chosen juice*) and the *chosen value*.
34 These variables capture both the input and the output of the choice process, suggesting that the
35 cell groups identified in OFC constitute the building blocks of a decision circuit. Several lines of
36 evidence support this hypothesis. However, in previous experiments offers were presented
37 simultaneously, raising the question of whether current notions generalize to when goods are
38 presented or are examined in sequence. Recently, Ballesta and Padoa-Schioppa (2019)
39 examined OFC activity under sequential offers. An analysis of neuronal responses across time
40 windows revealed that a small number of cell groups encoded specific sequences of variables.
41 These sequences appeared analogous to the variables identified under simultaneous offers, but
42 the correspondence remained tentative. Thus in the present study we examined the relation
43 between cell groups found under sequential versus simultaneous offers. We recorded from the
44 OFC while monkeys chose between different juices. Trials with simultaneous and sequential
45 offers were randomly interleaved in each session. We classified cells in each choice modality
46 and we examined the relation between the two classifications. We found a strong
47 correspondence – in other words, the cell groups measured under simultaneous offers and
48 under sequential offers were one and the same. This result indicates that economic choices
49 under simultaneous or sequential offers rely on the same neural circuit.

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58 Significance Statement

59 Research in the past 20 years has shed light on the neuronal underpinnings of economic
60 choices. A large number of results indicates that decisions between goods are formed in a
61 neural circuit within the orbitofrontal cortex (OFC). In most previous studies, subjects chose
62 between two goods offered simultaneously. Yet, in daily situations, goods available for choice
63 are often presented or examined in sequence. Here we recorded neuronal activity in the primate
64 OFC alternating trials under simultaneous and under sequential offers. Our analyses
65 demonstrate that the same neural circuit supports choices in the two modalities. Hence, current
66 notions on the neuronal mechanisms underlying economic decisions generalize to choices
67 under sequential offers.

68 **Introduction**

69 Neurophysiology experiments where monkeys chose between different juice types identified in
 70 the OFC different groups of cells encoding individual *offer values*, the binary choice outcome
 71 (*chosen juice*) and the *chosen value* (Padoa-Schioppa and Assad, 2006). Similar results were
 72 obtained in monkeys choosing between juice bundles (Pastor-Bernier et al., 2019), in mice
 73 (Kuwabara et al., 2020), and in humans using fMRI (Hare et al., 2008; Howard et al., 2015). The
 74 variables encoded in OFC capture both the input and the output of the choice process, and the
 75 corresponding cell groups are computationally sufficient to generate binary decisions (Rustichini
 76 and Padoa-Schioppa, 2015; Song et al., 2017; Zhang et al., 2018). In monkeys, mild electrical
 77 stimulation of this area biases choices in predictable ways (Ballesta et al., 2020). Furthermore,
 78 lesions in humans (Camille et al., 2011; Yu et al., 2018), high current stimulation in monkeys
 79 (Ballesta et al., 2020) or optogenetic inactivation in mice (Gore et al., 2019; Kuwabara et al.,
 80 2020) dramatically increases choice variability. The circuit dynamics is consistent with a
 81 decision process (Rich and Wallis, 2016), and trial-by-trial fluctuation in the activity of each cell
 82 group correlates with choice variability (Padoa-Schioppa, 2013). Taken together, these results
 83 suggest that the cell groups identified in OFC constitute the building blocks of a neural circuit in
 84 which economic decisions are formed. One caveat is that current notions on this circuit emerge
 85 mostly from studies in which two options were presented simultaneously. Yet, in most daily
 86 situations, options available for choice appear or are examined in sequence. Moreover, some
 87 scholars have argued that choices under sequential or simultaneous offers rely on qualitatively
 88 different mechanisms (Kacelnik et al., 2011; Hunt et al., 2013; Hayden and Moreno-Bote, 2018).

89 To shed light on the mechanisms underlying choices under sequential offers, we recently
 90 recorded from the OFC of monkeys choosing between different juices offered sequentially
 91 (Ballesta and Padoa-Schioppa, 2019). Consistent with previous observations (McGinty et al.,
 92 2016; Hunt et al., 2018), neuronal responses in any time window depended on the presentation
 93 order (i.e., on what juice the animal was offered at that time). However, an analysis of neuronal
 94 responses across time windows revealed that different groups of cells encoded different
 95 patterns of variables, referred to as “sequences”. Across a large population of neurons, we
 96 identified 8 such sequences. We also noted that these sequences presented analogies with the
 97 cell groups previously identified under simultaneous offers. For example, some sequences
 98 represented the value of specific juices, while other sequences presented binary responses.
 99 These observations suggested that the two sets of cell groups recorded under sequential and
 100 under simultaneous offers might in fact be one and the same. If this hypothesis was confirmed,
 101 notions on the decision mechanisms acquired under simultaneous offers would apply to a much
 102 broader domain of choices than previously recognized.

103 To test this hypothesis, we recorded the activity of neurons in OFC while monkeys chose
 104 between different juices. In each session, choices under simultaneous offers and choices under
 105 sequential offers were pseudo-randomly interleaved. In the analysis, we first separated trials
 106 with the two choice tasks (modalities) and classified each cell in each choice task. We then
 107 considered the whole population and compared the results of the classification obtained for the
 108 two choice tasks. We envisioned three possible scenarios: (1) the two choice tasks could
 109 engage different neuronal assemblies (different populations); (2) the two tasks might engage the
 110 same neuronal population but individual neurons might have different roles in the two tasks
 111 (independent classification); or (3) the same groups of neurons might support decisions in the
 112 two choice tasks (corresponding classifications). Statistical analyses provided strong evidence
 113 for the last hypothesis. Thus our results indicate that choices under sequential offers and
 114 choices under simultaneous offers rely on the same decision circuit.

115 Materials and Methods

116 All the experimental procedures adhered to the *NIH Guide for the Care and Use of Laboratory*
 117 *Animals* and were approved by the Institutional Animal Care and Use Committee (IACUC) at
 118 Washington University.

119 Animal subjects and choice tasks

120 Two adult male rhesus monkeys (*Macaca mulatta*; monkey J, 10.0 kg, 8 years old; monkey G,
 121 9.1 kg, 9 years old) participated in this study. Before training and under general anesthesia, we
 122 implanted on each animal a head restraining device and an oval chamber (axes 50x30 mm).
 123 Chambers were centered on stereotaxic coordinates (A30, L0), with the longer axis parallel to
 124 coronal planes, allowing bilateral access to OFC with coronal electrode penetrations. Structural
 125 MRI scans (1 mm sections) obtained before and after surgery were used to locate OFC and
 126 guide neuronal recordings. During the experiments, monkeys sat in an electrically and
 127 acoustically insulated enclosure (Crist Instrument Co), with their head fixed and pink noise in the
 128 background. A computer monitor was placed in front of the animal at 57 cm distance. The gaze
 129 direction was monitored at 1 kHz using an infrared video camera (Eyelink, SR Research). The
 130 behavioral task was controlled using custom-written software (<https://monkeylogic.nimh.nih.gov>)
 131 (Hwang et al., 2019) based on Matlab (v2016a; MathWorks Inc).

132 In each session, the animal chose between two juices labeled A and B (A preferred) offered in
 133 variable amounts. Each session included trials with two choice modalities, referred to as Task 1
 134 and Task 2 (**Fig.1AB**). The two tasks were nearly identical to those used in previous studies
 135 (Padoa-Schioppa and Assad, 2006; Ballesta and Padoa-Schioppa, 2019), and trials with the two
 136 tasks were pseudo-randomly interleaved. In both tasks, offers were represented by sets of
 137 colored squares displayed on the computer monitor. For each offer, the color indicated the juice
 138 type and the number of squares indicated the quantity. Each trial began with the animal fixating
 139 a large dot in the center of the monitor. After 0.5 s, the initial fixation point changed to a small
 140 dot or a small cross; the new fixation point cued the animal to the choice task used in that trial.
 141 In Task 1 (**Fig.1A**), cue fixation (0.5 s) was followed by the simultaneous presentation of the two
 142 offers. After a randomly variable delay (1-1.5 s), the center fixation disappeared and two
 143 saccade targets appeared near the offers (go signal). The animal indicated its choice with an
 144 eye movement. It maintained peripheral fixation for 0.75 s, after which the chosen juice was
 145 delivered. In Task 2 (**Fig.1B**), cue fixation (0.5 s) was followed by the presentation of one offer
 146 (0.5 s), an inter-offer delay (0.5 s), presentation of the other offer (0.5 s), and a wait period (0.5
 147 s). Two colored saccade targets then appeared on the two sides of the fixation point. After a
 148 randomly variable delay (0.5-1 s), the center fixation disappeared (go signal). The animal
 149 indicated its choice with a saccade, maintained peripheral fixation for 0.75 s, after which the
 150 chosen juice was delivered. Central and peripheral fixation were imposed within 4-6 and 5-7
 151 degrees of visual angle, respectively.

152 For any given trial, q_A and q_B indicate the quantities of juices A and B offered to the animal,
 153 respectively. An "offer type" was defined by two quantities [q_A , q_B]. On any given session, we
 154 used the same juices and the same sets of offer types for the two tasks. For Task 1, the spatial
 155 configuration of the offers (left/right) varied randomly from trial to trial. For Task 2, trials in which
 156 juice A was offered first and trials in which juice B was offered first were referred as "AB trials"
 157 and "BA trials", respectively. The terms "offer1" and "offer2" indicated, respectively, the first and
 158 second offer, independently of the juice type and amount. In Task 2, the presentation order
 159 varied pseudo-randomly and was counterbalanced across trials for any offer type. The spatial

location (left/right) of saccade targets varied randomly and independently of the presentation order. The juice volume corresponding to one square (quantum) was set equal for the two tasks and remained constant within each session. It varied across sessions (70-100 μ l) for both monkeys. The association between the initial cue (small dot, small cross) and the choice modality (Task 1, Task 2) varied across sessions, in blocks.

In Task 2, AB trials and BA trials were analyzed separately (see below). A power analysis indicated that comparing neuronal responses across tasks would be most effective if the number of trials for Task 2 was $\sqrt{2}$ times that for Task 1. Thus in most sessions we set the number of trials for Task 2 equal to 1.5 times that for Task 1.

Prior to this study, monkey J had participated in experiments using Task 2 and had no exposure to Task 1. For the current study, the animal was first trained with Task 1 alone and then with the two tasks randomly interleaved. Monkey G had participated in different experiments using simultaneous offers (Task 1) or sequential offers (Task 2). For the current study, the animal was trained to perform the two choice tasks randomly interleaved.

Across sessions, we used the following juices (colors): lemon Kool-Aid (bright yellow), grape juice (bright green), cherry juice (diluted to 3/4 with water or no dilution, red), peach juice (diluted to 3/4 with water, rose), fruit punch (diluted to 1/3 with water, magenta), apple juice (diluted to 1/2 with water, dark green), cranberry juice (diluted to 1/3 with water, pink), peppermint tea (bright blue), kiwi punch (dark blue), watermelon Kool-Aid (lime) and slightly salted water (0.65 g/l concentration, light gray).

Behavioral analysis

Choices in the two tasks were analyzed separately with probit regressions. For Task 1, we used the following model:

$$\begin{aligned} \text{choice } B &= \Phi(X) \\ X &= a_0 + a_1 \log(q_B/q_A) \end{aligned} \quad (1)$$

where $\text{choice } B = 1$ if the animal chose juice B and 0 otherwise, Φ was the cumulative function of the standard normal distribution, and q_A and q_B were the quantities of juices A and B offered. From the fitted parameters, we derived measures for the relative value of the juices $\rho_{\text{Task1}} = \exp(-a_0/a_1)$ and the sigmoid steepness $\eta_{\text{Task1}} = a_1$.

For Task 2, we used the following probit model:

$$\begin{aligned} \text{choice } B &= \Phi(X) \\ X &= a_2 + a_3 \log(q_B/q_A) + a_4 (\delta_{\text{order,AB}} - \delta_{\text{order,BA}}) \end{aligned} \quad (2)$$

where $\delta_{\text{order,AB}} = 1$ for AB trials and 0 otherwise, and $\delta_{\text{order,BA}} = 1 - \delta_{\text{order,AB}}$. Thus AB trials and BA trials were analyzed separately but assuming that the two sigmoids had the same steepness. From the fitted parameters, we derived measures for the relative value $\rho_{\text{Task2}} = \exp(-a_2/a_3)$, the sigmoid steepness $\eta_{\text{Task2}} = a_3$, and the order bias $\varepsilon = 2 \rho_{\text{Task2}} a_4/a_3$. The order bias was defined such that $\varepsilon < 0$ ($\varepsilon > 0$) indicated a bias in favor of offer1 (offer2). We also defined the relative values specific to AB trials and BA trials as $\rho_{AB} = \exp(-(a_2+a_4)/a_3)$ and $\rho_{BA} = \exp(-(a_2-a_4)/a_3)$. Of note, the order bias was defined such that $\varepsilon \approx \rho_{BA} - \rho_{AB}$.

199 In some cases, one or both choice patterns presented complete or quasi-complete separation
 200 (i.e., the animal split choices for ≤ 1 offer types). In these cases, the fitted steepness (η) was
 201 high and unstable. We identified outlier sessions using an interquartile criterion. Defining IQR as
 202 the interquartile range, values below the first quartile minus $1.5 \times \text{IQR}$ or above the third quartile
 203 plus $1.5 \times \text{IQR}$ were identified as outliers and removed from the behavioral analysis (**Fig.1D-F**).
 204 This criterion excluded 14/115 sessions for monkey J and 51/191 sessions for monkey G.
 205 Including all sessions in the analysis did not substantially change the results. Importantly, data
 206 from all sessions were included in the neuronal analyses.

207 Neuronal recordings

208 Neural recordings focused on area 13m in the central orbital gyrus (Ongur and Price, 2000). We
 209 recorded from both hemispheres of monkey J (left: AP 31:35, ML -8:-10; right: AP 31:35, ML
 210 6:10) and both hemispheres of monkey G (left: AP 31:36, ML -7:-12; right: AP 31:36, ML 4:9).
 211 Tungsten single electrodes (100 μm shank diameter; FHC) were advanced remotely using a
 212 custom-built motorized micro-drive (step size 2.5 μm). Typically, one motor advanced two
 213 electrodes placed 1 mm apart, and 1-2 such pairs of electrodes were advanced unilaterally or
 214 bilaterally in each session. Each electrode would usually record the activity of 1-2 cells (average
 215 1.25 cells/electrode). Amplified signals (gain: 10,000) were filtered (high-pass cutoff: 300 Hz;
 216 low-pass cutoff: 6 kHz; Lynx 8, Neuralynx), digitized (frequency: 40 kHz) and saved to disk
 217 (Power 1401, Cambridge Electronic Design). Spike sorting was performed off-line (Spike 2 v6,
 218 Cambridge Electronic Design). Only cells that appeared well isolated and stable throughout the
 219 session were included in the analysis.

220 Neuronal classification within task modality

221 For each neuron, trials from Task 1 and Task 2 were first analyzed separately using the
 222 procedures developed in previous studies (Padoa-Schioppa and Assad, 2006; Ballesta and
 223 Padoa-Schioppa, 2019). For Task 1, we defined four time windows: post-offer (0.5 s after offer
 224 onset), late-delay (0.5-1 s after offer onset), pre-juice (0.5 s before juice onset) and post-juice
 225 (0.5 s after juice onset). A "trial type" was defined by two offered quantities and a choice. For
 226 Task 2, we defined three time windows: post-offer1 (0.5 s after offer1 onset), post-offer2 (0.5 s
 227 after offer2 onset) and post-juice (0.5 s after juice onset). A "trial type" was defined by two
 228 offered quantities, their order and a choice. For each task, each trial type and each time
 229 window, we averaged spike counts across trials. A "neuronal response" was defined as the
 230 firing rate of one cell in one time window as a function of the trial type. Neuronal responses in
 231 each task were submitted to an ANOVA (factor: trial type). Neurons passing the $p < 0.01$ criterion
 232 in at least one time window in either task were identified as "task-related" and included in
 233 subsequent analyses.

234 Following previous work (Padoa-Schioppa and Assad, 2006; Padoa-Schioppa, 2013), neurons
 235 in Task 1 were classified in one of four groups *offer value A*, *offer value B*, *chosen juice* or
 236 *chosen value*. Each variable could be encoded with positive or negative sign, leading to a total
 237 of 8 cell groups. For the classification, we proceeded as follows. Each neuronal response was
 238 regressed against each of the four variables defined in **Table 1**. If the regression slope b_1
 239 differed significantly from zero ($p < 0.05$), the variable was said to "explain" the response. In this
 240 case, we set the signed R^2 as $sR^2 = \text{sign}(b_1) R^2$; if the variable did not explain the response, we
 241 set $sR^2 = 0$. After repeating the operation for each time window, we computed for each cell the
 242 $\text{sum}(sR^2)$ across time windows. Neurons explained by at least one variable in one time window,
 243 such that $\text{sum}(sR^2) \neq 0$, were said to be tuned; other neurons were labeled "untuned". Tuned

cells were assigned to the variable and sign providing the maximum $|sum(sR^2)|$, where $|\cdot|$ indicates the absolute value. Indicating with “+” and “-” the sign of the encoding, each neuron was thus classified in one of 9 groups: *offer value A+*, *offer value A-*, *offer value B+*, *offer value B-*, *chosen juice A*, *chosen juice B*, *chosen value+*, *chosen value-* and *untuned*.

Neuronal classification in Task 2 followed the procedures described by Ballesta and Padoa-Schioppa (2019). Under sequential offers, neuronal responses in OFC were found to encode different variables defined in relation to the presentation order (AB or BA). Specifically, the vast majority of responses were explained by one of 11 variables defined in **Table 1**. These included one binary variable capturing the order (*AB | BA*), six variables representing individual offer values (*offer value A | AB*, *offer value A | BA*, *offer value B | AB*, *offer value B | BA*, *offer value 1*, and *offer value 2*), three variables capturing variants of the chosen value (*chosen value*, *chosen value A*, *chosen value B*) and a binary variable representing the binary choice outcome (*chosen juice*). Each of these variables could be encoded with a positive or negative sign. Most neurons appeared to encode different variables in different time windows. In principle, considering 11 variables, 2 signs of the encoding and 3 time windows, neurons might present a very large number of variable patterns across time windows. Remarkably, however, the vast majority of OFC neurons presented one of 8 patterns. These patterns are referred to as sequences and defined in **Table 2**. Thus we classified each cell as encoding one of these 8 sequences. For each cell and each time window, we regressed the neuronal response against each of the variables predicted by each sequence. If the regression slope b_i differed significantly from zero ($p < 0.05$), the variable was said to explain the response and we set the signed R^2 as $sR^2 = \text{sign}(b_i) R^2$; if the variable did not explain the response, we set $sR^2 = 0$. After repeating the operation for each time window, we computed for each cell the $sum(sR^2)$ across time windows for each of the 8 sequences. Neurons such that $sum(sR^2) \neq 0$ for at least one sequence were said to be tuned; other neurons were untuned. Tuned cells were assigned to the sequence that provided the maximum $|sum(sR^2)|$. As a result, each neuron was classified in one of 9 groups: *seq #1*, *seq #2*, *seq #3*, *seq #4*, *seq #5*, *seq #6*, *seq #7*, *seq #8* and *untuned*.

271 Comparing classification across choice task

We aimed to ascertain the relation between the classifications obtained for Task 1 and Task 2. To do so, we used statistical analyses for categorical data (Agresti, 2019). First, we constructed a 9x9 contingency table in which rows and columns represented, respectively, the cell classes defined in Task 1 and Task 2, and each entry indicated the number of neurons with the corresponding classifications. Second, to estimate whether the cell count obtained for any particular pair of classes departed from chance level, we computed a table of odds ratios. For each location (i, j) in the contingency table, $X_{i,j}$ indicated the number of cells classified as class i in Task 1 and as class j in Task 2. We defined:

$$280 \quad a_{1,1} = X_{i,j} \quad (3)$$

$$a_{1,2} = \sum_{n \neq j} X_{i,n}$$

$$a_{2,1} = \sum_{m \neq i} X_{m,j}$$

$$281 \quad a_{2,2} = \sum_{m \neq i, n \neq j} X_{m,n}$$

282 The corresponding odd ratio (OR) was defined as:

$$OR_{i,j} = (a_{1,1}/a_{1,2})/(a_{2,1}/a_{2,2}) \quad (4)$$

The OR was calculated for each entry of the contingency table. We thus obtained a 9x9 table. For each entry (i, j) , $OR_{i,j} = 1$ was the chance level. Conversely, $OR_{i,j} > 1$ ($OR_{i,j} < 1$) indicated that the number of neurons classified as (i, j) was higher (lower) than expected by chance based on the number of cells in class i and the number of cells in class j . To assess whether departures from chance level were statistically significant, we used the two-tailed Fisher's exact test, separately for each entry.

To compare the across-tasks table to some benchmark, we created two within-task tables. For each choice task and each trial type, we randomly divided trials in two sets (1 and 2). Pooling trial types, we obtained two complete sets of trials (set 1 and set 2). This procedure ensured that each set had the same number of trial types. For Task 1 data, we repeated the cell classification procedure described above separately for each trial set. We thus generated the within-task contingency table and the table of OR s comparing the results obtained for sets 1 and 2. We repeated these operations for Task 2 data. To assess whether the two within-task tables of OR s and the across-tasks table of OR s differed significantly from each other, we used the Breslow-Day test (Breslow and Day, 1980). In essence, this test examines the homogeneity of OR s, with the null hypothesis that different strata are statistically identical. In our case, the null hypothesis was that for each location in the OR table, the three measures (two within-task and one across-task) were statistically identical. The Breslow-Day test is ultimately a Chi-squared test. Its statistic has an asymptotic Chi-squared distribution with $k-1$ degrees of freedom. Here the test was conducted entry by entry, with d.f. = 2, and $p < 0.01$ identified statistical significance.

Following the results presented in this study, we proceeded with a comprehensive ('final') classification based on the activity recorded in both tasks. For each task-related cell, we calculated the $sum(sR^2)$ for the eight variables in Task 1 ($sum(sR^2)_{Task1}$) and eight sequences in Task 2 ($sum(sR^2)_{Task2}$) as described above. We then added the corresponding $sum(sR^2)_{Task1}$ and $sum(sR^2)_{Task2}$ to obtain the $sum(sR^2)_{final}$. Neurons such that $sum(sR^2)_{final} \neq 0$ for at least one class were said to be tuned; other neurons were untuned. Tuned cells were assigned to the cell class that provided the maximum $|sum(sR^2)_{final}|$.

311 Selective activity range

In each task, neurons respond to the encoded variables in multiple time windows. The strength of the encoding, referred to as selectivity, varies across windows and from cell to cell. Thus for each cell and for each task, one might identify the time window with maximum selectivity. We examined whether there was a systematic relationship between the maximum selectivity window measured for any given cell in the two tasks. To do so, we first defined the activity range (AR). For each cell and each time window, we performed the linear regression

$$fr = b_0 + b_1 EV \quad (9)$$

where fr was the firing rate, EV was the encoded variable and b_0 and b_1 were the fitted parameters. Indicating the minimum and maximum of EV respectively as EV_{min} and EV_{max} , we computed $\Delta EV = EV_{max} - EV_{min}$. The activity range was defined as $AR = |b_1 \Delta EV|$, where $|\cdot|$ indicates the absolute value. We also defined the selective activity range as:

$$SAR = P \times N \times AR \quad (10)$$

where $P = 1$ if the response passed the ANOVA criterion and 0 otherwise and $N = 1$ if the slope of the encoded variable differed significantly from zero and 0 otherwise.

Results

Two monkeys chose between different juices offered in variable amounts. Offers were represented by sets of colored squares displayed on a computer monitor, and animals indicated their choice with an eye movement. In each session, trials with two choice modalities were randomly interleaved. In one modality (Task 1), two offers were presented simultaneously (**Fig.1A**); in the other modality (Task 2), two offers were presented in sequence (**Fig.1B**). A cue presented at the beginning of the trial indicated to the animal the choice modality for that trial. The two juices used in each session were labeled A and B, with A preferred, and we indicated the quantities offered in any given trial with q_A and q_B . For Task 2, trials in which juice A was offered first and trials in which juice B was offered first were referred to as AB trials and BA trials, respectively. The first and second offers were referred to as offer1 and offer2, respectively.

Comparing choices across tasks

Our data set included 306 sessions from two monkeys (115 from J, 191 from G). Sessions included 216-880 trials (mean $\pm$ std = 590 ± 160). For each session, we analyzed trials with the two choice tasks separately using probit regressions (see **Methods**). For Task 1 (simultaneous offers), the probit fit provided measures for the relative value ρ_{Task1} and the sigmoid steepness η_{Task1} . For Task 2 (sequential offers), the probit fit provided measures for the relative value ρ_{Task2} , the sigmoid steepness η_{Task2} and the order bias ε (**Fig.1C-F**). Intuitively, the relative value was the quantity ratio q_B/q_A that made the animal indifferent between the two juices, the sigmoid steepness was inversely related to choice variability, and the order bias (measured in Task 2) was a bias favoring the first or the second offer. Specifically, $\varepsilon < 0$ indicated a bias favoring offer1 and $\varepsilon > 0$ indicated a bias favoring offer2.

The experimental design gave us the opportunity to compare choices across tasks. Our analyses revealed several phenomena. First, the relative values measured in the two tasks were very similar and highly correlated across sessions ($r > 0.90$; **Fig.1D**). At the same time, ρ_{Task1} and ρ_{Task2} presented some differences. Specifically, relative values in Task 2 were generally higher than in Task 1 ($p < 10^{-10}$, t test), and this effect increased with the relative value. Second, sigmoids measured in Task 2 were significantly shallower compared to Task 1 ($p < 10^{-25}$, t test; **Fig.1E**). In other words, presenting offers in sequence substantially increased choice variability. Third, in Task 2, animals showed an order bias favoring offer2 (**Fig.1F**). This effect was highly significant ($p < 10^{-25}$, t test) but quantitatively modest (mean(ε) = 0.26 uB) compared to relative values, which typically ranged between 1 and 4 uB (mean(ρ) = 2.26 uB).

These three behavioral phenomena – larger choice variability, preference bias and order bias – were likely due to the higher cognitive demands imposed by Task 2 (see Discussion). Importantly, these effects were relatively small and essentially orthogonal to the main question addressed in this study, concerning the relation between cell groups recorded in the two choice tasks. Thus for the analyses of neuronal activity presented in the rest of this study, we examined responses of each neuron in each task in relation to variables defined based on the relative value measured in the same task, ignoring the order bias (see **Table 2**).

366 Neuronal classification in each choice task

367 Previous studies of choices under simultaneous offers identified in OFC different groups of cells
 368 encoding individual offer values, the binary choice outcome and the chosen value (Padoa-
 369 Schioppa and Assad, 2006). Similarly, recent work on choices under sequential offers identified
 370 different groups of cells encoding different decision variables (Ballesta and Padoa-Schioppa,
 371 2019). Our goal was to ascertain whether the two sets of cell groups correspond to each other.
 372 To do so, we recorded and analyzed the activity of 1,526 cells (672 cells from monkey J and
 373 854 cells from monkey G). In the analysis, our general strategy was to classify cells separately
 374 in each task according to the same criteria used in previous work, and to then compare the
 375 results of the two classifications at the population level. Thus we divided trials with Task 1 and
 376 Task 2 and proceeded in steps.

377 For Task 1 trials, we defined four 500 ms time windows aligned with the offer presentation (post-
 378 offer, late-delay) and the juice delivery (pre-juice and post-juice). A “trial type” was defined by
 379 two offers and a choice. For Task 2 trials, we defined three 500 ms time windows aligned with
 380 the two offers (post-offer1, post-offer2) and with the juice delivery (post-juice). A “trial type” was
 381 defined as two offers in a particular order and a choice. For each task, each trial type and each
 382 time window, we averaged spike counts across trials. In each task, a neuronal response was
 383 defined as the firing rate of one cell in one time window as a function of the trial type. Neuronal
 384 responses were submitted to an ANOVA (factor: trial type). Neurons presenting a significant
 385 modulation ($p < 0.01$) in at least one task and at least one time window were identified as task-
 386 related and included in subsequent analyses. In total, 645/1,526 (42%) cells met this criterion.
 387 Further analyses were restricted to this population.

388 While inspecting individual responses, we made three observations. First, replicating several
 389 previous studies, responses in Task 1 appeared to encode one of the variables *offer value*,
 390 *chosen juice* or *chosen value* (**Fig.2**). Second, confirming the results of our recent study on
 391 sequential offers, neurons in Task 2 appeared to encode different variables in different time
 392 windows. Across time windows, particular sequences of variables were most frequent. For
 393 example, in the three time windows under consideration, the neuron in **Fig.2C** encoded
 394 variables *offer value B | BA*, *offer value B | AB* and *chosen value B*. These variables define
 395 sequence #3 in **Table 2**. In the same time windows, the cell in **Fig.2F** encoded variables –
 396 *AB|BA*, *AB|BA* and *chosen juice B*. These variables define sequence #5. Similarly, the cell in
 397 **Fig.2I** encoded variables *offer value 1*, *offer value 2* and *chosen value*, which define sequence
 398 #7. Third and most important, there appeared to be a reliable correspondence between
 399 neuronal responses recorded in the two tasks. In principle, neurons tuned in one task could be
 400 untuned in the other task. That is, different cell assemblies in OFC could support choices in the
 401 two tasks. In contrast, neurons were typically tuned in both tasks or not at all. Furthermore, the
 402 variable encoded in Task 1 corresponded to specific sequences encoded in Task 2. For
 403 example, neurons encoding *offer value A* in Task 1 typically encoded sequence #1 in Task 2;
 404 neurons encoding *offer value B* in Task 1 typically encoded sequence #3 in Task 2; neurons
 405 encoding *chosen juice A* in Task 1 typically encoded sequence #5 in Task 2; etc. The three
 406 example cells in **Fig.2** illustrate this point.

407 For a statistical analysis, we classified neurons in Task 1 and Task 2 following the same
 408 procedures of previous studies (Padoa-Schioppa, 2013; Ballesta and Padoa-Schioppa, 2019).
 409 For Task 1, we regressed each response against each variable. Each regression provided a
 410 slope and the R^2 . If the slope differed significantly from zero ($p < 0.05$) the variable was said to
 411 explain the response. If the slope was statistically indistinguishable from zero, we set $R^2 = 0$. We

considered the signed sR^2 , where the sign was obtained from the regression slope, summed it over time windows, took the absolute value, and assigned each neuron to the variable providing the maximum $|sum(sR^2)|$ (see **Methods**). Task-related cells not explained by any variable in any time window were labeled “untuned”. For Task 2, we used a very similar procedure, except that, for any of the 8 sequences, different variables were examined in different time windows (**Table 2**). Again, each neuron was assigned to the sequence providing the maximum $|sum(sR^2)|$, where sR^2 is the signed R^2 and the sum is across time windows.

Matching classifications across choice tasks

To compare the results across tasks, we constructed a contingency table where rows represented classes in Task 1, columns represented classes in Task 2, and in each entry quantified the cell count. We envisioned three possible scenarios illustrated in **Fig.3**. (1) The table might be concentrated on the first row and first column (**Fig.3A**), indicating that the two tasks engage different neuronal populations; (2) the table might present a uniform distribution (**Fig.3B**), indicating that the two tasks engage the same neuronal population but the role of individual neurons differs across task; or (3) the contingency table might be concentrated on the diagonal (**Fig.3C**), indicating that individual neurons have the same role in the two choice tasks.

Fig.4A illustrates the cell counts actually measured in the experiments. The vast majority of neurons were either non-task related ($881/1,526 = 58\%$), or tuned in both tasks ($490/1,526 = 32\%$). Importantly, different groups of cells accounted for different numbers of neurons. Thus to compare each cell count to chance level, we computed for each entry the odds ratio (OR ; see **Methods**). We thus obtained a table of OR s (**Fig.4B**). For each entry, $OR=1$ was chance level; conversely, $OR>1$ or $OR<1$ indicated that the cell count was above or below that expected by chance, respectively. For each entry, a Fisher’s exact test ($p<0.01$) assessed whether departure from chance was statistically significant (**Fig.4C**). Inspection of **Fig.4B** reveals that cell counts were significantly above chance for all entries on the diagonal. Conversely, the vast majority of off-diagonal entries ($69/72$) was at or below chance level. In conclusion there was a strong correspondence between the class identified for any given cell in Task 1 and that identified for the same cell in Task 2.

We noted that a few off-diagonal entries in **Fig.4B** were significantly above chance. We conducted two analyses to assess the significance of this observation. First, we examined this finding could be explained by the correlation between different variables defined in **Table 1**. This correlation and the intrinsic variability of neuronal firing rates likely induced some misclassification. We thus expected that instances for which OR_{ij} was significantly >1 would occur only when the variables indexed by i and j were highly correlated with each other. To test our hypothesis, we generated the correlation matrix C , separately for each task. For Task 1, entry $C_{m,n}$ in this matrix was simply the correlation between variables m and n , which did not depend on the time window. For Task 2, since each sequence included different variables in different time windows, we computed the correlation matrix separately in each time window using the relevant variables. We then calculated the mean correlation matrix across time windows. The correlation matrices obtained for the two tasks were similar, and we averaged them to obtain the average correlation matrix, referred to as table Z . Of note, table Z was symmetric by construction (**Fig.5A**). Inspection of it reveals that correlations between specific pairs of variables were particularly high. For example, variables *offer value A+* and *chosen value A* were highly correlated ($r = 0.69$). Similarly, variables *offer value B+* and *chosen value B* were highly correlated ($r = 0.63$). To assess the relation between OR table and Z table, we plotted them against each other entry by entry (excluding the diagonals; **Fig.5B**). The two tables were highly

458 correlated (Pearson: $r = 0.75$, $p = 4 \cdot 10^{-11}$). Furthermore, significant departure from chance level
 459 in the OR table ($OR_{ij} > 1$) occurred only when the variable correlation was particularly high
 460 ($Z_{ij} > 0.5$).

461 Second, to compare the results in **Fig.4B** to some benchmark, we generated equivalent OR
 462 tables separately for each choice task. For Task 1, we divided trials randomly in two sets (set 1
 463 and set 2; see **Methods**). We analyzed the two sets of trials separately and thus obtained two
 464 independent classifications. We repeated this operation for each cell in the population, and
 465 generated a contingency table (not shown) and a table of ORs (**Fig.6A**) where rows and
 466 columns corresponded to set 1 trials and set 2 trials, respectively. We repeated this analysis for
 467 data from Task 2 and obtained an equivalent OR table (**Fig.6B**). Since the two sets of trials
 468 were interleaved and the criterion used to separate them was arbitrary, we expected the OR
 469 tables to concentrate on the diagonal. Conversely, non-zero off-diagonal entries should capture
 470 noise in the classification procedures due to the correlation between encoded variables (**Fig.5A**)
 471 and to trial-to-trial variability in spike counts. To assess whether the table in **Fig.4B** (across
 472 tasks) differed significantly from the tables in **Fig.6AB** (within task) we used a Breslow-Day test
 473 (see **Methods**). **Fig.6C** illustrates the results of this analysis. In essence, classifications across
 474 tasks were as consistent as classifications within tasks (all $p \geq 0.01$).

475 In all previous analyses, neurons were classified based on the activity recorded in multiple time
 476 windows. For a control, we repeated the analysis of **Fig.4** using only one time window for each
 477 task. We then matched time windows across tasks. Indicating with $[x, y]$ the pair formed by time
 478 windows x (Task 1) and y (Task 2), we examined the three pairs [post-offer, post-offer1], [post-
 479 offer, post-offer2] and [post-juice, post-juice]. In general, the results based on a single time
 480 window were similar to those based on multiple windows, albeit noisier. For example,
 481 considering the time window pair [post-offer, post-offer1], all the diagonal entries in the OR table
 482 were significantly above chance (along with a few off-diagonal entries). The two other pairs of
 483 time windows provide similar pictures. These findings confirmed that there was a strong
 484 correspondence between the cell classification in the two choice tasks.

485 Taken together, our results indicated that the cells groups identified under sequential offers are
 486 equivalent to those identified under simultaneous offers. Building on this finding, we proceeded
 487 with a comprehensive classification based on both choice tasks, by summing the R^2 across all
 488 seven time windows (see **Methods**). Henceforth, we may refer to the different groups of cells
 489 using the standard nomenclature – *offer value*, *chosen juice* and *chosen value* – independently
 490 of the choice task. In total, the final classification resulted in 235 *offer value* cells, 168 *chosen*
 491 *juice* cells and 233 *chosen value* cells.

492 Matching maximum selectivity windows across choice tasks

493 To complement the results described above, we examined whether there was some
 494 correspondence between the time windows in which any given neuron was most selective in
 495 Task 1 and in Task 2. To address this issue, we defined for each cell, each task and each time
 496 window the selective activity range (SAR), which captured the strength of the encoding (see
 497 **Methods**). For each cell and each task, the maximum selectivity window (MSW) may be defined
 498 as the time window for which SAR was maximal. Because neurons often responded similarly in
 499 different time windows (e.g., post-offer1 and post-offer2 in Task 2), we used a soft definition and
 500 identified as MSW any time window such that $SAR / \max(SAR) > 0.6$.

To compare the *MSWs* identified for each cell in the two tasks across the population, we generated a contingency table where rows and columns represented time windows in the two tasks and each entry indicated the number of cells with corresponding *MSWs* (**Fig.7A**). We also computed the corresponding table of odds ratios (**Fig.7B**), and the p values obtained from Fisher's exact tests (**Fig.7C**). The results indicated that time windows for which neurons were maximally selective in the two tasks were systematically related across the population. Specifically, cells for which *MSW* = post-offer in Task 1 typically had *MSW* = post-offer1 and/or *MSW* = post-offer2 in Task 2. Similarly, cells for which *MSW* = post-juice in Task 1 typically had *MSW* = post-juice in Task 2. This finding supports the understanding that individual neurons have similar functions in the two choice tasks.

511 Discussion

The past 20 years witnessed enormous progress in the understanding of the cognitive and neural underpinnings of economic choices. An extensive body of work demonstrates beyond reasonable doubt that subjective values are explicitly represented at the neuronal level (Padoa-Schioppa, 2007; Kable and Glimcher, 2009; O'Doherty, 2014; Perkins and Rich, 2021). Furthermore, substantial evidence links economic decisions to neuronal activity in the OFC. Neurons in this area represent different decision variables in a categorical way (Hirokawa et al., 2019; Onken et al., 2019). In particular, when monkeys (or mice) choose between juices, different groups of cells encode individual offer values, the binary choice outcome and the chosen value (Padoa-Schioppa and Assad, 2006; Kuwabara et al., 2020). These variables capture both the input and the output of the choice process, suggesting that the cell groups identified in OFC might constitute the building blocks of a decision circuit. The population dynamics (Rich and Wallis, 2016), correlations between neuronal and behavioral variability (Padoa-Schioppa, 2013), the effects of lesion (Camille et al., 2011; Yu et al., 2018) or inactivation (Gore et al., 2019; Kuwabara et al., 2020), and computational modeling (Rustichini and Padoa-Schioppa, 2015; Song et al., 2017; Zhang et al., 2018) support this proposal. These and corroborating results set the stage for a detailed understanding of the decision mechanisms. One important caveat is that current notions came primarily from studies in which two offers were presented simultaneously. Yet, in many daily choices, offers appear or are examined sequentially, and some authors suggested that choices under sequential offers may rely on fundamentally different mechanisms (Kacelnik et al., 2011; Hunt et al., 2013; Hayden and Moreno-Bote, 2018). Thus the purpose of this study was to assess whether choices under sequential and simultaneous offers engage the same neural circuit. In a previous study, we recorded from the OFC under sequential offers. Through an analysis of neuronal responses across time windows, we identified different groups of neurons encoding different sequences of decision variables (Ballesta and Padoa-Schioppa, 2019). Importantly, since any choice task engages only a subset of neurons, it remained unclear whether choices under sequential or simultaneous offers rely on the same neuronal population, or whether the functional role of any given cell would be preserved across choice modalities. In the present study, we alternated two choice tasks on a trial-by-trial basis. In a nutshell, we found a strong correspondence between the cell groups previously identified in the two conditions. In other words, choices under sequential or simultaneous offers appear to rely on the same neural circuit. This result indicates that notions emerging from studies of choices under simultaneous offers generalize to a much broader domain of choices than previously recognized.

An interesting question is whether the neuronal populations described here might also subserve foraging choices such as those made by an animal that could continue to exploit the current food patch or leave it in search of better but riskier opportunities. Such choices are sometimes

548 construed as “yes-or-no” and distinguished from binary choices of the sort examined in our
 549 experiments (Kolling et al., 2012; Hayden and Moreno-Bote, 2018). However, what appears as
 550 a yes-or-no choice could also be construed as a binary choice between two offers – one
 551 unambiguous (the current patch) and one more ambiguous (a probability distribution over other
 552 possible patches and times necessary to reach them). In economics, the value of the latter offer
 553 is often referred to as an opportunity cost. The question of how the brain treats patch-leaving
 554 choices – as yes-or-no or binary – remains open. If patch-leaving choices are treated as binary,
 555 it seem reasonable to assume that the neuronal populations identified in our studies play the
 556 same role when choices are about leaving a food patch. Conversely, if the brain treats patch-
 557 leaving choices as qualitatively different, such choices might rely on different neuronal
 558 mechanisms. These intriguing questions remain open for future research.

559 Alternating the two tasks within each session gave us the opportunity to compare choices in a
 560 controlled way. We thus discovered three interesting phenomena. Under sequential offers, (a)
 561 choices were more variable, (b) relative values were higher (preference bias), and (c) choices
 562 were biased in favor of the second offer (order bias). The last observation confirms previous
 563 reports (Krajbich et al., 2010; Ballesta and Padoa-Schioppa, 2019; Rustichini et al., 2021). At
 564 the cognitive level, these phenomena may be understood as follows. The difference in choice
 565 variability (a) may be interpreted noting that choices under sequential offers were cognitively
 566 more demanding because they required holding in working memory the value of offer1,
 567 comparing the values of two goods when only offer2 was visible, remembering the chosen juice
 568 for an additional delay, and mapping that choice onto the appropriate saccade target. Each of
 569 these mental operations could contribute choice variability. Along similar lines, the preference
 570 bias (b) may reflect the higher cognitive demands of Task 2. In particular, we note that when the
 571 two offer targets appear on the monitor, information about the two values is no longer on display
 572 on the monitor. If at that point the animal has not finalized its decision, or if it has failed to retain
 573 in working memory the decision outcome, it makes sense to choose the target associated with
 574 the more valuable juice (juice A), especially if the value difference between the two juices is
 575 large. Finally, the order bias (c) may be interpreted noting that decisions in Task 2 were made
 576 shortly after offer2 appeared on the monitor, when that offer was perceptually most salient. Thus
 577 a choice bias favoring offer2 is not surprising. The neuronal origins of choice biases including
 578 the phenomena documented here remain an important and open question for future work.

579

580 Figure legends

581 **Figure 1.** Experimental design and behavioral performance. **(AB)** Experimental design. In each
 582 session, a monkey chose between two juices labeled A and B (A preferred). Trials with two
 583 choice modalities, referred to as Task 1 and Task 2, were randomly interleaved. At the
 584 beginning of each trial, the animal fixated a large dot in the center of the monitor. After 0.5 s, the
 585 fixation point changed to either a small dot or a cross; this cue indicated to the animal the task
 586 used in that trial. In Task 1 (simultaneous offers), two offers appeared on the left and right sides
 587 of the fixation point. The animal maintained fixation for a randomly variable delay, at the end of
 588 which the fixation point was extinguished and two saccade target appeared by the offers (go
 589 signal). The animal indicated its choice with a saccade and maintained peripheral fixation until
 590 juice delivery. In Task 2 (sequential offers), the two offers were presented in sequence and
 591 spaced by an inter-offer delay. Two saccade targets matching the colors of the two offers
 592 appeared on the two sides of the fixation point. After a variable delay, the fixation point was
 593 extinguished (go signal). The animal indicated its choice with a saccade and maintained
 594 peripheral fixation until juice delivery. For each offer, the color indicated the juice type and the
 595 number of squares indicated the juice amounts. Thus in the trials shown here, the animal chose
 596 between 1 drop of juice A and 3 drops of juice B. The left/right configuration in Task 1, the
 597 presentation order in Task 2 and the left/right position of the saccade targets in Task 2 varied
 598 randomly from trial to trial. In both tasks, fixation breaks prior to the go signal lead to trial
 599 abortion. The same offer types were used for both tasks. **(C)** Example sessions. The percent of
 600 B choices (y-axis) is plotted against the log quantity ratio (x-axis). Each panel includes data
 601 points for Task 1 (gray circles) and for Task 2 (red and blue triangles for AB trials and BA trials,
 602 respectively). Sigmoids were obtained from probit regressions (**Eq.1** and **Eq.2**). The panel
 603 indicates the relative value (ρ) and sigmoid steepness (η) measured in each task, and the order
 604 bias (ϵ) measured in Task 2. A choice bias favoring offer2 ($\epsilon > 0$) corresponds to the blue sigmoid
 605 displaced to the right of the red sigmoid. **(D)** Comparing the relative value (ρ) across choice
 606 tasks. Relative values measured in Task 1 (x-axis) are plotted against those measured in Task
 607 2 (y-axis). Each data point represents one session. Gray ellipses indicate 90% confidence
 608 intervals. The two measures were highly correlated. However, relative values were generally
 609 higher in Task 2 than in Task 1, and this effect increased with ρ (the main axis of the ellipse is
 610 rotated counterclockwise compared to the identity line). **(E)** Comparing the sigmoid steepness
 611 (η) across choice tasks. Sigmoids in Task 2 were consistently shallower (lower η ; higher choice
 612 variability) compared to Task 1. **(F)** Distribution of order bias measured across sessions. A small
 613 triangle indicates the mean. Animals presented a consistent bias favoring offer2. In panels DEF,
 614 results from both monkeys were pooled (N = 241 sessions; 65 outliers removed, see **Methods**).
 615 Statistical tests and p values are indicated in each panel. The sessions shown in panel C is
 616 highlighted in cyan in panels DE.

617 **Figure 2.** Three example neurons. **(A-C)** Example 1, *offer value B + (seq #3)* cell. Panel A
 618 illustrates the choice pattern. Panel B illustrates the neuronal response measured in Task 1
 619 (time window: post-offer). Each data point represents one trial type, and the firing rate (y-axis) is
 620 plotted against variable *offer value B*. The gray line is from a linear regression. In C, the three
 621 panels illustrate the neuronal responses measured in Task 2 (time windows: post-offer1, post-
 622 offer2, post-juice). Each data point represents one trial type, red and blue colors are for AB and
 623 BA trials, and gray lines are from linear regressions. In the three time windows, this cell seemed
 624 to encode variables *offer value B | BA*, *offer value B | AB*, and *chosen value B*, respectively, all
 625 with a positive slope. This pattern of responses corresponds to *seq #3* (see **Table 2**). **(D-F)**
 626 Example 2, *chosen juice B (seq #6)* cell. Same conventions as in example 1. In panel E (Task 1,
 627 post-juice time window), firing rates are plotted against the variable *chosen juice*. In the three

time windows defined for Task 2, the cell seemed to encode variables AB / BA , $-AB / BA$ and *chosen juice B*, respectively. This pattern of responses corresponds to *seq #6* (see **Table 2**).
(G-I) Example 3, *chosen value + (seq #7)* cell. Same conventions as in example 1. In panel H (Task 1, post-offer time window), firing rates are plotted against the variable *chosen value*. In the three time windows defined for Task 2, the cell seemed to encode variables *offer value 1*, *offer value 2* and *chosen value*. This pattern of responses corresponds to *seq #7* (see **Table 2**).

Figure 3. Comparing classification across tasks, possible results. In this cartoon, rows and columns represent different cell groups defined for Task 1 and Task 2, respectively. For each entry, the gray shade indicates the number of cells classified according to the corresponding groups in the two tasks (or the corresponding odds ratio). The three panels illustrate three possible scenarios. **(A)** Separate populations. Task 1 and Task 2 might recruit different groups of neurons. **(B)** Independent classification. The two tasks might recruit the same neurons but the role of any cell in one task might be unrelated to that in the other task. **(C)** Consistent classification. Task 1 and Task 2 might recruit the same neurons and each cell might have the same functional role in the two tasks.

Figure 4. Neuronal classification is consistent across choice tasks. **(A)** Contingency table ($N = 645$ cells). Numbers and gray scale indicate cell counts. **(B)** Table of odds ratios. For each entry in panel A we computed the odds ratio (*OR*; see **Methods, Eq.4**). *OR*s are indicated here by numbers and gray scale colors. Chance level corresponds to $OR = 1$; conversely, $OR > 1$ ($OR < 1$) indicate that the cell count was higher (lower) than expected by chance. Red asterisks (*) indicate that the *OR*s was significantly > 1 ($p < 0.01$, Fisher's exact test). For all entries on the main diagonal, *OR* was significantly > 1 , indicating that the two choice tasks yielded the same classification results. Of note, cell counts on the first column (untuned in Task 1) and cell counts on the first row (untuned in Task 2) were all at chance level. **(C)** Fisher's exact test, *p* values. Red/blue asterisks (*) indicate that the *OR* was significantly higher/lower than 1 ($p < 0.01$).

Figure 5. Significant departures from chance level in *OR* table reflect correlations between the encoded variables. **(A)** Correlation matrix between encoded variables (*Z* table). Correlations between the encoded variables were first calculated separately for both Task 1 and Task 2. The results were then averaged across tasks and shown here. Green circles highlight entries where correlation was > 0.5 . **(B)** Correlation between *OR* table and *Z* table. Corresponding entries were plotted against each other. The gray line is from a linear regression, and *p* values are indicated in the panel. Red data points highlight entries in the *OR* table that were significantly > 1 . The large correlation measured here ($r = 0.75$) indicates that significant departures from chance in the *OR* table were likely due to mis-classifications induced by the correlation between encoded variables.

Figure 6. Comparing neuronal classification within and across choice tasks. **(A)** Odds ratios obtained for Task 1. For each neuron, we divided trials randomly in two sets (set 1 and set 2; see **Methods**). We analyzed the two sets of trials separately and thus obtained two independent classifications. We repeated this operation for each cell in the population, and generated a contingency table (not shown) and a table of *OR*s, shown here, where rows and columns corresponded to set 1 trials and set 2 trials, respectively. Conventions here are as for **Fig.4B**. Since the two sets of trials were interleaved and the criterion used to separate them was arbitrary, the tables of *OR*s were expected to be concentrated on the diagonal. Indeed, all diagonal entries were significantly above chance ($p < 0.01$, Fisher's exact test). Conversely, off-diagonal entries captured the noise in classification procedures. **(B)** Odds ratios obtained for

Task 2. We repeated this analysis for Task 2 trials and obtained an equivalent table of *ORs*. Again, all diagonal entries were significantly above chance ($p < 0.01$, Fisher's exact test). **(C)** Comparing the classification consistency obtained within and across tasks. Each entry in this panel indicates the p value obtained from a Breslow-Day test, and $p < 0.01$ would indicate significant differences across *OR* tables. In practice, we obtained $p > 0.01$ for all 81 entries. In other words, the neuronal classification was as consistent across tasks as it was within tasks.

Figure 7. Maximum selectivity windows (*MSWs*) are matched across choice tasks. **(A)** Contingency table of *MSWs* ($N = 776$ pairs of time windows from 645 cells). Rows and columns indicate time windows in Task1 and Task2, respectively. Numbers and gray scale indicate cell counts. Cells for which $SAR=0$ were classified as "no *MSW*". **(B)** Table of odds ratios (*ORs*). Magenta asterisks (*) indicate that *OR* was significantly > 1 ($p < 0.05$, Fisher's exact test). **(C)** Fisher's exact test, exact p values. Magenta/blue asterisks (*) indicate that *OR* was significantly higher/lower than 1 ($p < 0.05$).

686

Task 1		
	Variable	Definition
1	<i>offer value A</i>	ρq_A
2	<i>offer value B</i>	q_B
3	<i>chosen value</i>	value of chosen offer
4	<i>chosen juice</i>	binary; 1 if A chosen; 0 if B chosen
Task 2		
	Variable	Definition
1	<i>AB BA</i>	binary; 1 in AB trials; 0 in BA trials
2	<i>offer value A AB</i>	ρq_A in AB trials, 0 in BA trials
3	<i>offer value A BA</i>	ρq_A in BA trials, 0 in AB trials
4	<i>offer value B AB</i>	q_B in AB trials, 0 in BA trials
5	<i>offer value B BA</i>	q_B in BA trials, 0 in AB trials
6	<i>offer value 1</i>	value of offer1
7	<i>offer value 2</i>	value of offer2
8	<i>chosen value</i>	value of chosen offer
9	<i>chosen value A</i>	<i>chosen value</i> if A chosen, 0 otherwise
10	<i>chosen value B</i>	<i>chosen value</i> if B chosen, 0 otherwise
11	<i>chosen juice A</i>	binary; 1 if A chosen; 0 if B chosen
12	<i>chosen juice B</i>	binary; 0 if A chosen; 1 if B chosen

687 **Table 1.** Definition of variables in Task 1 and Task 2. Values were always defined in units of
688 juice B (uB) based on relative values derived from the probit regressions (**Eqs.1-2**). Thus, the
689 value of q_B drops of juice B was equal to q_B ; the value of q_A drops of juice A was equal to ρq_A .
690 Each variable could be encoded with a positive or negative sign. For Task 2, variables *chosen*
691 *juice A* and *chosen juice B* coincided except for the sign (we use this notation for clarity).

692

Seq #	Time windows		
	post-offer1	post-offer2	post-juice
#1	offer value A AB +	offer value A BA +	chosen value A +
#2	offer value A AB -	offer value A BA -	chosen value A -
#3	offer value B BA +	offer value B AB +	chosen value B +
#4	offer value B BA -	offer value B AB -	chosen value B -
#5	AB BA +	AB BA -	chosen juice A
#6	AB BA -	AB BA +	chosen juice B
#7	offer value1 +	offer value2 +	chosen value +
#8	offer value1 -	offer value2 -	chosen value -

Table 2. Neuronal classification in Task 2. Ballesta and Padoa-Schioppa (2019) found that under sequential offers neurons in OFC encoded different variables in different time windows. However, focusing on three primary time windows, the vast majority of neurons presented one of 8 specific patterns of variables, referred to as variable “sequences”. The 8 sequences identified in that study are defined in this table, where + and - indicate the sign of the encoding. These sequences seem roughly analogous to the variables identified under simultaneous offers. For example, *seq #1* encodes the value of juice A when the animal is offered that juice (post-offer1 in AB trials; post-offer2 in BA trials). Upon juice delivery, *seq #1* encodes the value of juice A conditioned on juice A being chosen. Thus neurons classified as *seq #1* seem analogous to *offer value A+* neurons found under simultaneous offers. Similarly, cells classified as *seq #2*, *seq #3* and *seq #4* seem analogous to *offer value A-*, *offer value B+* and *offer value B-* cells found under simultaneous offers, respectively. Cells classified as *seq #5* or *seq #6* encode in a binary way the identity of the juice (A or B) offered to the animal or chosen by the animal. These neurons appear tentatively analogous to *chosen juice* cells identified under simultaneous offers. Finally, cells classified as *seq #7* or *seq #8* encode the value of either juice, provided that the animal focuses on it. They appear tentatively analogous to *chosen value+* and *chosen value-* cells identified under simultaneous offers, with the understanding that the value encoded by these neurons is that upon which the animal places its mental focus and not necessarily the chosen one.

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784

Task 1

Task 1

A

offer value A +	1.00	-1.00	-0.24	0.24	0.69	-0.69	0.50	-0.50
offer value A -	-1.00	1.00	0.24	-0.24	-0.69	0.69	-0.50	0.50
offer value B +	-0.24	0.24	1.00	-1.00	-0.63	0.63	0.53	-0.53
offer value B -	0.24	-0.24	-1.00	1.00	0.63	-0.63	-0.53	0.53
chosen juice A	0.69	-0.69	-0.63	0.63	1.00	-1.00	0.02	-0.02
chosen juice B	-0.69	0.69	0.63	-0.63	-1.00	1.00	-0.02	0.02
chosen value +	0.50	-0.50	0.53	-0.53	0.02	-0.02	1.00	-1.00
chosen value -	-0.50	0.50	-0.53	0.53	-0.02	0.02	-1.00	1.00
offer value A +								
offer value A -								
offer value B +								
offer value B -								
chosen juice A								
chosen juice B								
chosen value +								
chosen value -								

B

Task 1