LETTERS

Neurons in the orbitofrontal cortex encode economic value

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Economic choice is the behaviour observed when individuals select one among many available options. There is no intrinsically 'correct' answer: economic choice depends on subjective preferences. This behaviour is traditionally the object of economic analysis[1] and is also of primary interest in psychology[2]. However, the underlying mental processes and neuronal mechanisms are not well understood. Theories of human and animal choice[1–3] have a cornerstone in the concept of 'value'. Consider, for example, a monkey offered one raisin versus one piece of apple: behavioural evidence suggests that the animal chooses by assigning values to the two options[4]. But where and how values are represented in the brain is unclear. Here we show that, during economic choice, neurons in the orbitofrontal cortex[5–18] (OFC) encode the value of offered and chosen goods. Notably, OFC neurons encode value independently of visuospatial factors and motor responses. If a monkey chooses between A and B, neurons in the OFC encode the value of the two goods independently of whether A is presented on the right and B on the left, or vice versa. This trait distinguishes the OFC from other brain areas in which value modulates activity related to sensory or motor processes[19–25]. Our results have broad implications for possible psychological models, suggesting that economic choice is essentially choice between goods rather than choice between actions. In this framework, neurons in the OFC seem to be a good candidate network for value assignment underlying economic choice.

In our experiments, monkeys choose between two types of juice (A and B; where A is preferred) offered in different amounts. For example, in the session shown in Fig. 1, the monkey chooses between water (juice A) and unsweetened Kool-Aid (juice B). Offer types include 1B:2A, 1B:1A, 2B:1A, 3B:1A, 4B:1A, 6B:1A, and 10B:1A, and the 'forced choices' 0B:1A and 3B:0A. Behaviourally, we observe a trade-off between juice type and juice quantity. The monkey chooses A when 1B, 2B, or 3B are available as alternatives, it is roughly indifferent between the two juices when offered 4B:1A, and it chooses B when 6B or 10B are available.

We interpret this pattern of choice in terms of the 'relative value' of the two juices[4]: in this case, the value of 1A is roughly equal to the value of 4B. Fitting a sigmoid curve provides the better estimate $V(1\text{A}) = V(4.1\text{B})$, where $V(x)$ indicates the value of x. Assuming a linear value function, we obtain $V(\text{A}) = 4.1V(\text{B})$. This equation puts different quantities of juices A and B on the same value scale. On this basis, we can compute for each trial the value of the juice chosen by the monkey. Expressing values in units of $V(\text{B})$, the variable '*chosen value*' is about 4 when the monkey chooses 1A or 4B. When the monkey chooses 2A, the *chosen value* is about 8. When the monkey chooses 6B, 10B or 3B, the *chosen value* is respectively equal to 6, 10 or 3. Hence, we can make specific hypotheses regarding the neuronal representation of juice values. In different sessions and with different juices, we record different behavioural choice patterns. We then analyse each cell in relation to the choice pattern recorded in the same session.

Our recordings focused on area 13 in the OFC. Figure 2 illustrates the activity of one representative neuron. The cell's activity does not depend on whether juice A is offered on the left or on the right (Fig. 2b). It also does not depend on whether the monkey chooses the juice on the left or the juice on the right (that is, makes an eye movement to the left or to the right; Fig. 2c). However, the cell's activity varies with the offer type. This is consistent across the neuronal population. We recorded the activity of 931 cells and we analysed their neuronal responses in seven time windows (see Methods). We tested the activity of each cell in each time window with a three-way analysis of variance (ANOVA, with factors: [position of juice A] × [movement direction] × [offer type], $P < 0.001$). Rarely do responses depend on either the spatial configuration of the offers or the motor output (<5% neurons). In contrast, the activity of 505 (54%) neurons varies significantly depending on the offer type in at least one time window. Pooling time windows, a total of 1,379 responses are significantly modulated by the offer type (Supplementary Fig. S2).

The cell shown in Fig. 2d has a U-shaped response similar to that hypothesized for a neuron encoding the *chosen value*. For this session $V(\text{A}) = 1.9V(\text{B})$. Accordingly, the activity of the cell is

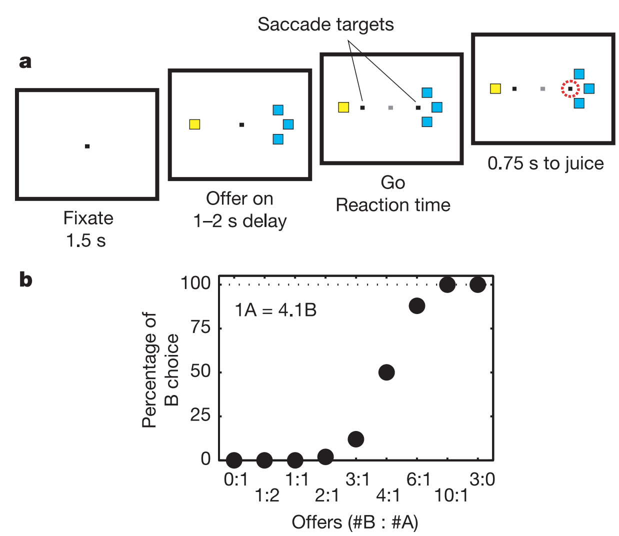

Figure 1 | Experimental design. a, Trial structure (see Methods). **b**, Example of behavioural choice pattern. The plot shows the percentage of trials in which the monkeys chose juice B (y axis) for various offer types (x axis). A sigmoid fit provides the measure of the relative value $n^* = 4.1$. The dotted red circle indicates the saccade target chosen by the monkey.

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low when the monkey chooses 1A or 2B (in units of V(B), *chosen value* ≈ 2), it is higher when the monkey chooses 2A or 4B (*chosen value* ≈ 4), and it is highest when the monkey chooses 3A or 6B (*chosen value* ≈ 6). A linear regression of this response on the variable *chosen value* provides $R^2 = 0.86$. Similar U-shaped responses are frequent in the OFC, and Fig. 3a–c illustrates three more examples. We also find other types of responses. For example, neuronal responses often reflect the value of one of the two juices alone. Figure 3d, e shows two cells in which activity covaries with the value of A offered and the value of B offered, respectively. We label these responses as related to the variable '*offer value*'. Other frequently observed responses vary in a binary fashion depending on the type of juice chosen by the monkey, independently of the amount (Fig. 3f). We interpret these responses as related to the variable juice '*taste*'.

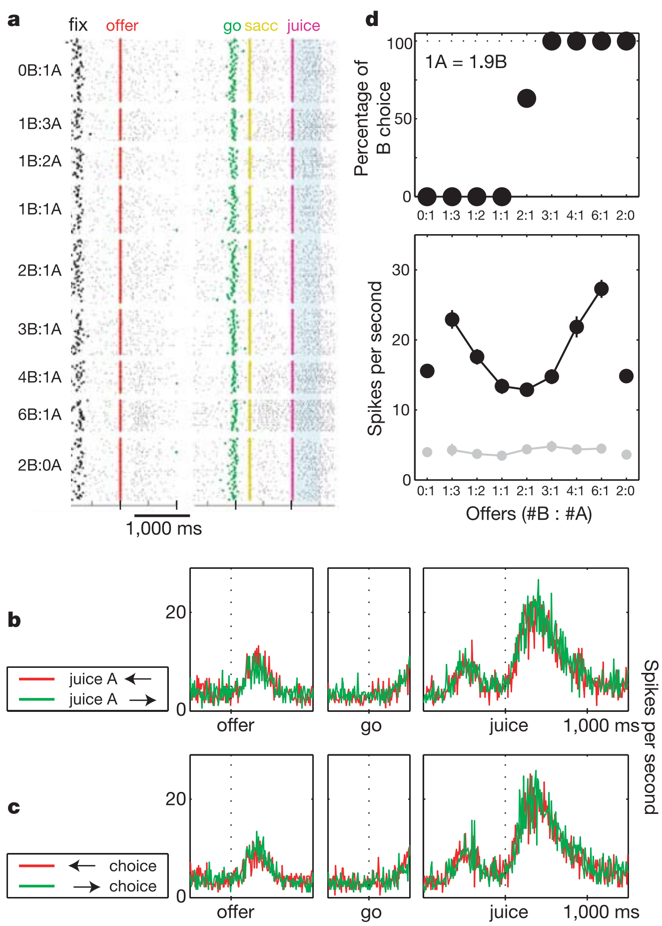

Figure 2 | Activity of one neuron. a, Rasters. Each line represents one trial and each small dot represents one spike. Trials, arranged by offer type, are aligned at the 'offer' (left) and at the 'juice' (right). The blue highlight marks the post-juice time window. 'Sacc' indicates the time of the saccade. **b**, Activity profiles shown separately for trials in which juice A is offered on the left (red) or on the right (green). The cell activity does not depend on the spatial configuration of the visual stimulus. **c**, Activity profiles shown separately for trials in which the monkey chooses the juice offered on the left (red) or on the right (green). The cell activity does not depend on the direction of the eye movement. **d**, The top panel shows the choice pattern recorded in this session ($n^* = 1.9$). The bottom panel shows the activity of the cell (±s.e.m.) recorded in the pre-offer (light grey, control) and post-juice (black) time windows. Note that the response does not reflect simple physical properties of the visual stimulus, such as the number of squares displayed on the monitor. For example, offer types 1B:3A and 3B:1A, which are visually identical except for the colour of the squares, elicit very different activation.

Although many neurons seem to encode *chosen value*, *offer value* or juice *taste*, the relation between their activity and these three variables could be subordinate to a correlation with other behavioural variables. For example, neurons in the OFC might encode the number of squares on the monitor (or variables proportional to number, such as juice quantity, or absolute luminance of the visual stimulus). To cast a wide net, we examine the linear dependence of neuronal data on 19 possible variables (Supplementary Fig. S1). For example, we analyse the variables '*chosen number*', '*total number*' and '*total value*'. We include in this analysis 1,379 responses significantly modulated by the offer type, and we regress each response separately on each variable. Collectively, the 19 variables explain 1,227 (89%) neuronal responses. However, the 19 variables are often highly correlated.

To identify a few variables that best describe the neuronal population, we adapt procedures for variable selection commonly used in multilinear regression in the presence of multi-collinearity. Both the stepwise and the best-subset methods identify the variables *offer value*, *chosen value* and *taste*, which explain well the large majority of responses (1,085/1,379 = 79% responses, with mean $R^2 = 0.63$). A post-hoc analysis indicates that the explanatory power of these three variables is significantly higher than that of challenging alternatives. Furthermore, data from the two monkeys analysed separately provide statistically indistinguishable results. Finally, a bilinear regression analysis indicates that in 890/1,085 (82%) cases, adding a second variable or a quadratic value term does not improve the regression significantly (Supplementary Results S5 to S10 and Supplementary Figs S4 to S11). We conclude that, as a population, OFC responses indeed encode the variables *offer value*, *chosen value* and *taste*.

We next turn to a specific analysis of U-shaped responses (Figs 2d, 3a–c). In our experiments, relative values were generally stable within any recording session. However, the relative value of any given pair of juices could vary from day to day. For example, the relative value of apple juice versus peppermint tea varied between 1.5 and 3. This variability provides a further opportunity to test the neuronal encoding of value; specifically, U-shaped responses should reflect this variability. For this analysis, we test the entire neuronal population with the regression function $a_0 + a_A(m_A) + a_B(m_B)$, where m_A and m_B represent the amounts of juices A and B chosen by the monkey. We define a response to be U-shaped if both a_A and a_B differ from zero ($P < 0.01$). If U-shaped responses indeed encode the value of the chosen juice, the slope ratio $k^* = a_A/a_B$ should be, for each U-shaped response, equal to the relative value (n^*) measured in that session. Most importantly, the slope ratio k^* obtained for different responses should covary with n^*. To test this prediction, we compute the regression $k^* = b_0 + b_1 n^*$ separately for every juice pair. Averaging across juice pairs, we obtain b_0 (±s.e.m.) = −0.13 (±0.15) and $b_1 = 1.05$ (±0.15), consistent with the identity $k^* = n^*$. This result demonstrates that U-shaped responses do not reflect the quantity of any particular juice ingredient (for example, sugar). Rather, they encode the value monkeys assign to the juice they choose to consume (Supplementary Results S10 to S12 and Supplementary Figs S12 to S14).

The timing of neuronal activation is as follows: the average neuronal activity peaks shortly after the offer, declines during the delay, is low before and during the eye movement, and has two secondary peaks at juice delivery (Supplementary Fig. S3). To appreciate how the variables *offer value*, *chosen value* and *taste* are represented in the OFC over time, we analyse the activity of each cell in 50-ms, non-overlapping time bins. Figure 4 shows the number of cells encoding each of the three variables at different times. Remarkably, the time profile of different variables seems to reflect the mental processes the monkey presumably undertakes during a trial. Shortly after the offer, when the monkey assigns values to the two juices, neurons encoding the *offer value* (that is, the value of one juice or the other) are most prevalent. Also during the delay, many neurons

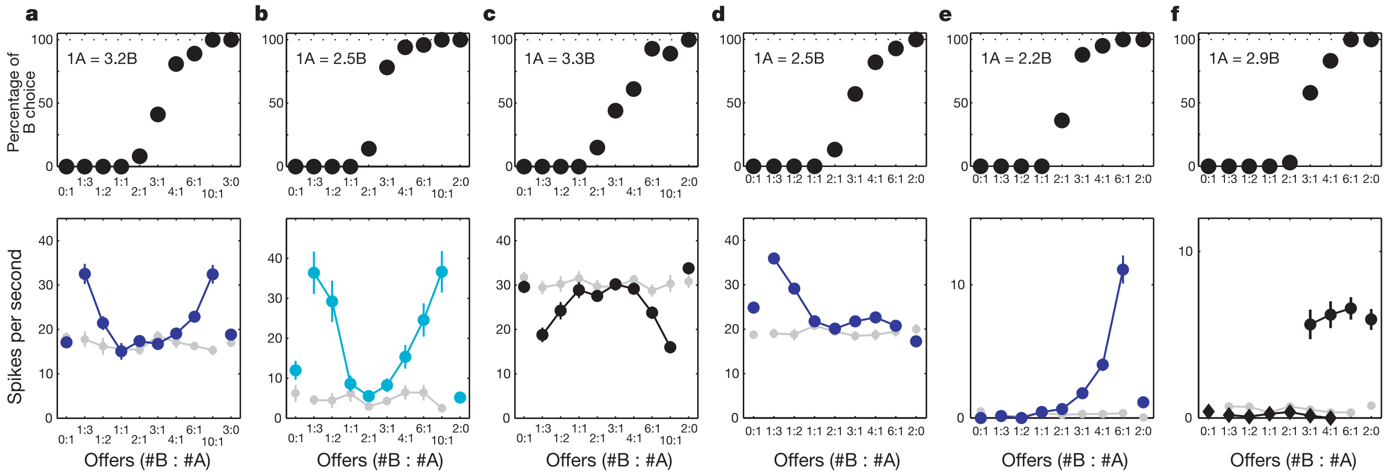

Figure 3 | **Activity of six neurons.** For each cell, the top panel shows the choice pattern, with the relative value indicated on the top left. The bottom panel shows the activity of the cell. **a–c**, Responses encoding the *chosen value*. The response in **c** is negatively correlated with the *chosen value* (high activity for low value). **d–e**, Responses encoding the value of juice A offered (**d**) and the value of juice B offered (**e**). We refer to these responses as related to the *offer value*. **f**, Response encoding the juice *taste*. Here we separate trials in which the monkey chose juice A (diamonds) or juice B (circles). The response reflects the chosen juice type independently of the amount. Responses were recorded in the post-offer (**a**, **d**, **e**, blue), pre-juice (**b**, cyan), and post-juice (**c**, **f**, black) time windows. For each cell, the curves in light grey show the activity in the pre-offer time window. Error bars represent s.e.m.

encode the *chosen value* (that is, the value of the juice the monkey will eventually consume), even though the choice is still covert (because the 'go' signal has not been given yet). Finally, after the monkey has indicated its choice, before and after juice delivery, many neurons encode the *taste* of the chosen juice.

Conceptually, responses encoding the *chosen value* are particularly interesting because, in addition to being independent of the visuomotor contingencies of the task, they are also independent of the specifics of the good, namely juice type and juice amount. These responses encode economic value in a non-specific way. Further research is necessary to establish whether this result generalizes to other kinds of goods, such as non-comestible goods[26]. The interpretation of *offer value* responses is made more cautiously because, assuming linear value functions, the value of a given amount of juice is proportional to the juice quantity.

'Value' is known to modulate the activity of neurons in several sensory and motor areas[19–25]. For example, neurons in the lateral intraparietal area activate when monkeys plan a saccade towards a particular location of the visual field; their response is enhanced when the eye movement is associated with higher value[20]. On this basis, it has been proposed that parietal neurons encoding the value of all possible courses of action form a common path for decision-making, and that their activity is actually the subject of economic theory[27]. According to this 'action-based' model, economic choice is fundamentally choice between actions. That neurons in the OFC encode the economic value of offered and chosen goods *per se*, as opposed to reflecting value as a modulation of visuomotor processes, suggests an alternative 'good-based' model, according to which economic choice is fundamentally choice between goods. In this view, choice is made between goods, and a suitable motor action is subsequently planned and executed.

Several arguments seem to favour the good-based model. From a computational perspective, a modular design separating the mental operations of 'choosing' and 'moving' is more parsimonious[28,29]. In addition, values processed in the OFC are logically sufficient for good-based choice. The action-based model would thus imply that, during economic choice, the nervous system operates in a computationally inefficient way, while undertaking all the processes needed to choose efficiently. Finally, a vast literature links choice in various domains to the OFC. For example, human patients and monkeys with OFC lesions can present eating disorders and hyperorality[6–8], abnormal risk-seeking and gambling behaviour[9,10], and impulsivity, altered personality and abnormal social behaviour[6,11]. In contrast, parietal lesions typically result in visuospatial deficits such as hemi-neglect or Balint's syndrome[30]. In conclusion, together with other lines of evidence, the present results support a good-based psychological model of economic choice behaviour.

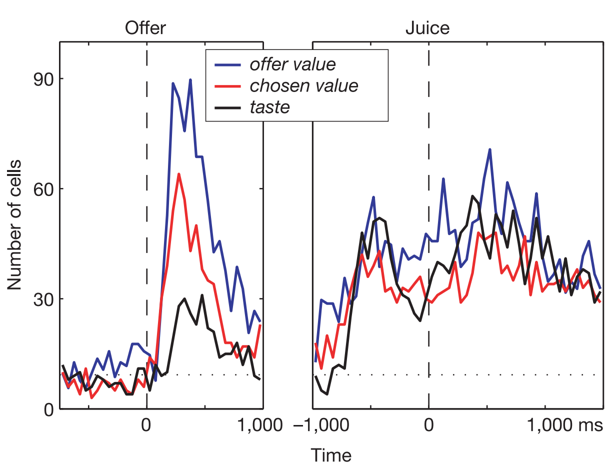

Figure 4 | **Time course.** We assign each neuron to one of the three variables only if the regression slope is significantly different from zero ($P < 0.01$), and we include all 931 neurons in the analysis. The dotted line indicates chance level (9.31).

METHODS

Each trial begins with the monkey fixating the centre of a computer monitor (Fig. 1a). After 1.5 s, two sets of squares appear on opposite sides of the fixation point ('offer'). The colour of the squares indicates the juice type and the number of squares indicates the juice amount. For example, a monkey offered three blue squares versus one yellow square chooses between three drops of peppermint tea and one drop of grape juice. After a randomly variable delay (1–2 s), two saccade targets appear near the offers ('go'). The monkey indicates its choice with an eye movement, and must maintain fixation on the target for an additional 0.75 s before juice delivery ('juice'). The trial is aborted if the monkey breaks fixation before the go signal. The amounts of the two offered juices (0–10 drops) vary pseudo-randomly. For a given offer type, left/right positions are counter-balanced (that is, the monkey may be offered 1A on the left and 3B on the right, or vice versa). A variety of different pairs of juices are used in different sessions (Supplementary Methods).

We analyse cell activity in the following time windows: 0.5 s pre-offer (a control time window); 0.5 s post-offer; late delay (0.5–1.0 s after the offer); 0.5 s pre-go; reaction time (from go to saccade); 0.5 s pre-juice; and 0.5 s post-juice. For the statistical analysis, we separate for each offer type trials in which the monkey chooses juices A and B (Supplementary Methods).

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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