Orbitofrontal Cortex and the Computation of Economic Value

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ABSTRACT: Economic choice is the behavior observed when individuals select one of many available options solely based on subjective preferences. Behavioral evidence suggests that economic choice entails two mental processes: values are first assigned to the available options, and a decision is subsequently made between these values. Numerous reports show that lesions to the orbitofrontal cortex (OFC) lead to choice deficits in various domains, and imaging studies indicate that the OFC activates when people make choices. In this chapter, we review evidence from single cell recordings linking the OFC more specifically to valuation. Individual neurons in the OFC encode the value that monkeys assign to different beverages when they choose between them. These neurons encode economic value as a subjective quantity. Most importantly, neurons in the OFC encode economic value *per se*, not as a modulation of sensory or motor processes. This trait distinguishes the value representation in the OFC from that observed in other brain areas. That OFC neurons encode economic value independently of visuomotor contingencies suggests that economic choice is fundamentally a choice between goods (good-based model) rather than a choice between actions (action-based model).

KEYWORDS: neuroeconomics; economic choice; decision making; subjective value; monkey

INTRODUCTION

Economic choice is the behavior observed when choices are based on subjective preferences. It is a behavior we engage in frequently, for example, when we select an item from a restaurant menu, when we choose among different financial investments, or when we choose between a job that will pay better and one that we might enjoy more. It is called economic choice because this behavior has been traditionally the object of economic theory.[1,2] However, economic

choice has also been studied in psychology[3,4]; an extensive literature (behavioral economics) shows how human choices are often affected by "fallacies," such as hyperbolic discounting or loss aversion, that ultimately result in non-rational behavior.[5–7] Economic choice is also relevant from medical and clinical perspectives. Indeed, many disorders that affect the frontal lobe, such as frontotemporal dementia[8–11] and obsessive compulsive disorder,[12,13] can be characterized as patients making poor choices. Moreover, drug addiction can be thought of as an extreme case of dysfunctional choice behavior.[13,14] This review focuses on the cognitive and neuronal mechanisms of economic choice. As we will see, recent evidence indicates that the orbitofrontal cortex (OFC) participates in the computation of economic value, a process necessary for choice.[15,16]

ECONOMIC CHOICE, A DISTINCT MENTAL PROCESS

Consider a person sitting in a restaurant and choosing among different items on the menu. That choice can sometimes prove difficult—should she order the tuna tartare or the fried calamari? The Pinot Noir or the Nebbiolo? In these situations, the difficulty is not in comprehending what options are available, or in communicating our decision to the waiter. Sensory processing and motor control are both complex operations, but solving them successfully does not amount to choosing. The difficulty when choosing among different dishes or different wines on the menu is in introspecting, pondering options, and selecting the one that best satisfies our current desires. These mental processes and the resulting behavior are "economic choice."

In the following sections, we will describe recent results showing that when monkeys engage in economic choice, neurons in the OFC encode the value that animals assign to different goods. Before doing so, however, it is useful to distinguish the mental processes underlying economic choice from other mental processes examined in experiments that also encompass a "choice." Indeed, a number of papers in the past 10 years described neuronal activity related to values and decisions.

Ultimately, the mental processes of economic choice are distinct from the mental processes dissected by other behavioral tasks that can be construed as requiring a choice.[3] For example, some experiments present monkeys with perceptually ambiguous sensory stimuli and ask them to "choose" between two possible reports. In such cases, monkeys are not asked to introspect and decide what they *want*—no doubt they want the juice. Instead, monkeys are asked to report what they *perceive*. The mental process taking place in this kind of task has been referred to as a perceptual decision.[17,18] Conceptually, the demands of these tasks are very different from those we face, for example, when presented with a restaurant menu. Analogously, many experiments require monkeys to "choose" among multiple possible responses of which

one is intrinsically correct. For example, two perceptually unambiguous stimuli might be associated with two different quantities of the same juice.[19–26] Alternatively, two stimuli might be associated with a fixed amount of juice delivered with different probabilities.[22,27] In both cases, once monkeys have learned the association between the stimuli and the expected quantity of juice, "choices" reduce to trivial responses. It can thus be said that these tasks do not ask monkeys to decide what they want, but simply to demonstrate whether they remember the correct answer.

More recent experiments set monkeys in more complex situations in which there is no strictly correct answer in any particular trial, but there is an overall optimal strategy across trials. In the simplest of such cases, monkeys play the game "matching pennies," in which the ideal strategy for a subject playing against an infinitely intelligent opponent (reasonably approximated by a computer program) is to select one of two possible responses randomly and with equal probability in every trial.[28] In other games, the optimal strategy is to choose unpredictably but with unequal (and sometimes changing) probabilities.[29] Finally, other experiments (matching tasks) set monkeys in somewhat intermediate situations, in the sense that there is a locally (and statistically) correct answer, but the correct answer changes from trial to trial depending on previous choices and outcomes.[30] In all these tasks, however, the demand on the monkeys is always to *infer* the best possible response necessary to receive a given amount of juice, not to introspect and to decide what they want. In other words, these tasks tackle monkeys' intelligence, or ability to learn, not their will. In contrast, the experiments described here focus on mental processes that take place when monkeys choose among different goods with no correct answer or strategy, on the basis of only their subjective preferences.

ECONOMIC CHOICE, A MULTISTAGE MENTAL PROCESS

Behavioral studies on economic choice have often been concerned with complex choices and with choice "fallacies."[5–7] But in fact, relatively little is known about the cognitive and brain processes underlying even simple choices, such as choices between two foods. Consider, for example, the situation illustrated in FIGURE 1. In this experiment, capuchin monkeys (*Cebus apella*) chose between different foods offered in variable amounts.[15] In this particular session, a monkey chose between raisins (food A, preferred) and 1-g pieces of apple (food B). The *x* axis in the figure represents different offer types, and the *y* axis represents the percentage of times the monkey chose food B. When offered the choice between 1A and 1B, the monkey always chose 1A. However, when B was offered in sufficiently large amounts, the monkey chose it. For example, the monkey chose 4B over 1A and 3B over 1A. When offered 2B versus 1A, the monkey chose B roughly half of the time. In other words, the monkey was indifferent between 1A and 2B.
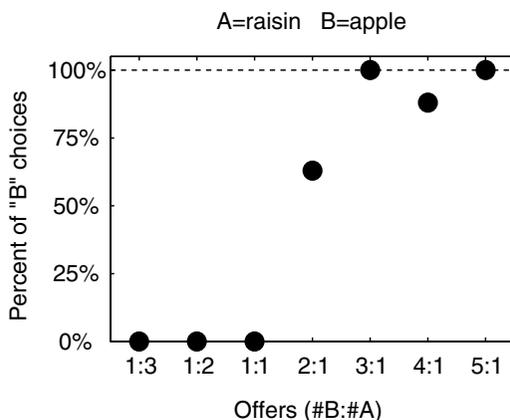
FIGURE 1. Food choice in capuchins. In this session, a capuchin monkey chose between raisins and 1-g pieces of apple. From Ref. 15.

The choice pattern illustrated in FIGURE 1 can be described in terms of relative values of the two foods. In this case, since the monkey was indifferent between 1A and 2B, the value of 1A is roughly equivalent to the value of 2B. But what psychological processes underlie this behavior?

One possibility is that monkeys' choices are simple associations between stimuli (for example, the offer 1A:3B) and responses (in this case, the choice 3B) acquired through experience. According to this view, in early encounters with foods A and B, a monkey chooses randomly, and feedback mechanisms measure its welfare after any given choice. Through multiple encounters with foods A and B, by trial and error, the monkey gradually learns to select 2A over 1B, 1A over 1B, 3B over 1A, etc. This associative model, originally proposed by Skinner,[31,32] represents the simplest possible psychological account of economic choice because it entails a single mental operation (an association). Interestingly, this model is a sufficient assumption from the point of view of standard economic theory.[33] The problem, however, is that human and animal choices often violate the main prediction of the associative model, namely that learning to choose takes time. For example, it was observed that monkeys choose between novel pairs of foods (i.e., pairs of foods that they never encountered together before) as effectively as they choose between familiar pairs of foods.[15] Remarkably, monkeys do so from the very first trial, a result inconsistent with choices being stimulus–response associations acquired by trial and error.[15] Hence, economic choice requires a more elaborate psychological account.

The next level of complexity is referred to as the cognitive model of choice. According to this hypothesis, economic choice results from a two-stage mental process: values are first assigned to the available options, and a decision is consequently made between these values.[15,34,35]

Notably, in spite of its intuitive appeal and relative simplicity, the cognitive model of choice cannot be tested directly based on behavior alone. The two mental operations of value assignment and decision making cannot be dissociated at the behavioral level because values cannot be measured behaviorally independently of choice. To appreciate this point, consider a simple example. Most people, given the choice between $1000 and a glass of water, will choose the money. Now suppose that one day you encounter Victoria, you offer her the choice between $1000 and a glass of water, and she chooses the water. One reason for her surprising behavior might be that her neurocognitive choice mechanisms malfunction, perhaps because she recently suffered a brain lesion. Another possibility is that Victoria's brain functions perfectly well, and she is so thirsty at that particular time that she would rather drink the water than take the money. The critical point is that it is impossible to distinguish between these two alternative hypotheses based on her choice alone.

That value cannot be measured behaviorally independently of choice implies that valuation and decision cannot be dissociated at the behavioral level. In fact, it can be argued that standard economic theory has historically resolved to such a rudimentary assumption as the associative model of choice precisely for this reason. On the other hand, value assignment and decision making could in principle be disentangled at the physiological level. For example, it is possible that the two mental operations are processed by distinct populations of neurons. In other words, in order to test whether values are actually assigned to the available options during economic choice, it is necessary to study the neuronal representation of economic value.

ECONOMIC CHOICE AND THE ORBITOFRONTAL CORTEX

Where in the brain does economic choice take place? Several lines of evidence point in particular to the OFC. For example, early clinical signs of frontotemporal dementia (a neurodegenerative disorder that initially affects the OFC)[8] include changes in eating habits, anorexia, and hyperorality.[9,10] When asked to exert simple preference judgments between foods, patients with OFC lesions make inconsistent or erratic choices significantly more often than either healthy subjects or patients with dorsolateral frontal lesions.[36] OFC patients also exhibit abnormal choice behavior in situations that involve uncertainty (enhanced risk-seeking)[11,37] and in social contexts (ultimatum game).[38] Damasio[39] refers to a deficit in "the ability to select an advantageous response among an array of available options." Interestingly, in multiattribute choice tasks, OFC patients present abnormal patterns of information acquisition.[40] Other deficits associated with OFC lesions include disrupted social behavior,[9,10] as exemplified by the famous case of Phineas Gage.[41] OFC patients also present perseveration in stimulus–reward association reversals.[42] In this case, subjects seemingly fail to reassign the proper value to a stimulus.

Lesion studies in monkeys provide consistent evidence, as OFC ablations result in abnormal eating patterns[43] and impairments in stimulus–reward association reversals.[44,45] Thus taken together, lesion studies in humans and monkeys suggest that the OFC may be a key neural substrate for choice behavior.

A second line of evidence linking the OFC to economic valuation and choice comes from imaging experiments in humans. Many studies found higher activation in the OFC when subjects were presented with affectively pleasant sensory stimuli compared to neutral stimuli (reviewed by O'Doherty).[46] Preference-dependent activation was consistently obtained with multiple sensory modalities including olfactory,[47,48] gustatory,[49] visual,[50,51] auditory,[52] and somatosensory,[53] suggesting that the OFC might represent behavioral valence as a common currency.[54] Supporting this view, the OFC was also activated when subjects earned money,[55,56] an intrinsically abstract stimulus. In all these studies, subjects were not asked to make choices. However, in the experiments of Arana and colleagues,[57] subjects did in fact make choices from a restaurant menu in a 2×2 design. Items in the menu had high or low incentive; in some cases, subjects were simply shown items on the menu, and in other cases they were asked to make a choice. Most interestingly, the medial OFC was significantly more activated in the choice condition compared to the no-choice condition. The same area was also more activated by high incentives compared to low incentives. In comparison, neural activation in the amygdala varied depending on the incentive level, but did not vary with task demands. A subsequent study found consistent results.[58]

With respect to the activity of individual OFC neurons, several studies used neurophysiological recordings in nonhuman primates to analyze neuronal responses associated with the expectation or the delivery of foods or beverages. While these experiments typically did not focus on choice behavior, several results are consistent with the hypothesis that OFC neurons might be a substrate for economic valuation. In an early study, Thorpe and colleagues[59] observed that neurons in the OFC responded to the presentation of visual stimuli in a way that was not purely sensory. For example, the response of one neuron to the visual presentation of a liquid-filled syringe depended on whether in previous trials the liquid was apple juice or salted water, even though the syringe was visually indistinguishable in the two conditions. Rolls and colleagues subsequently found that the activity of OFC neurons responding to a particular taste could be modulated by hunger and satiety, a modulation not observed in the primary taste area.[60] In summary, these results indicated that the activity of OFC neurons is modulated both by physical stimuli and by the motivational state of the animal.

In another study, Tremblay and Schultz (T&S) delivered to monkeys one of three types of juice (A, B, and C, in decreasing order of preference) in a fixed amount.[61] In their experiment, trials were blocked, with only one pair of juices employed in each block. T&S found OFC neurons that responded to juice A but not to juice B during A:B blocks, and to juice B but not to juice

C in B:C blocks. T&S interpreted this as neurons reflecting juice *preference* (i.e., ordinal ranking). However, subsequent work showed that OFC neurons encode juice *value* in a cardinal (i.e., numberlike) sense.[16,62] T&S's results thus suggest that the value representation may vary depending on the behavioral context.[63]

Other studies found that the activity of neurons in the OFC can be modulated by the amount of juice delivered to the monkey.[21,64,65] Roesch and Olson (R&O) also found that OFC neuronal activity varied depending on the duration of a time delay intervening before juice delivery.[64,65] Interestingly, there was an inverse correlation between the effects of juice amount and the effects of time delay. Under the assumption that the neurons recorded by R&O encode the subjective value at stake in any trial, one possible interpretation of this result is that the delay represents a cost to the monkey and that OFC neurons encode cost-affected values.

Taken together, the results reviewed above suggest that individual neurons in the OFC might represent the behavioral valence of goods. However, in the experiments with monkeys, the animals were never asked to choose based on their own preferences. Rather, monkeys were either simply delivered juice, or they were asked to select between two options, one of which was intrinsically correct. Consequently, these tasks could not distinguish value from the objective properties of the to-be-delivered juice (e.g., juice quantity, probability, and delivery time). In contrast, the behavioral paradigm described in FIGURE 1 does provide an operational measure for the subjective value monkeys assign to the food (or juice). In the experiments described in the following sections, this behavioral paradigm was employed to study the relationship between the activity of OFC neurons and economic value.

NEURONS IN ORBITOFRONTAL CORTEX ENCODE ECONOMIC VALUE

Electrophysiological experiments were conducted in rhesus macaques (*Macaca mulatta*).[16] The behavioral paradigm was similar to that illustrated in FIGURE 1, but in this case monkeys chose between different beverages. During the experiments, monkeys sat in front of a computer monitor in an electrically isolated enclosure with their heads restrained. Their eye positions were monitored through a scleral eye coil.[66] Every trial began with the monkey fixating on a small dot at the center of the monitor (FIG. 2A). After 1.5 s, two sets of squares appeared on opposite sides of the fixation point (*offer*). The colors of the squares indicated the juice type, and the number of squares indicated the juice amount. For example, a monkey offered 3 red squares versus 1 blue square chose between 3 drops of unsweetened Kool-Aid and 1 drop of water. After a randomly variable delay (1–2 s), two saccade targets appeared near the offers (*go* signal). The monkey indicated its choice with an eye move-
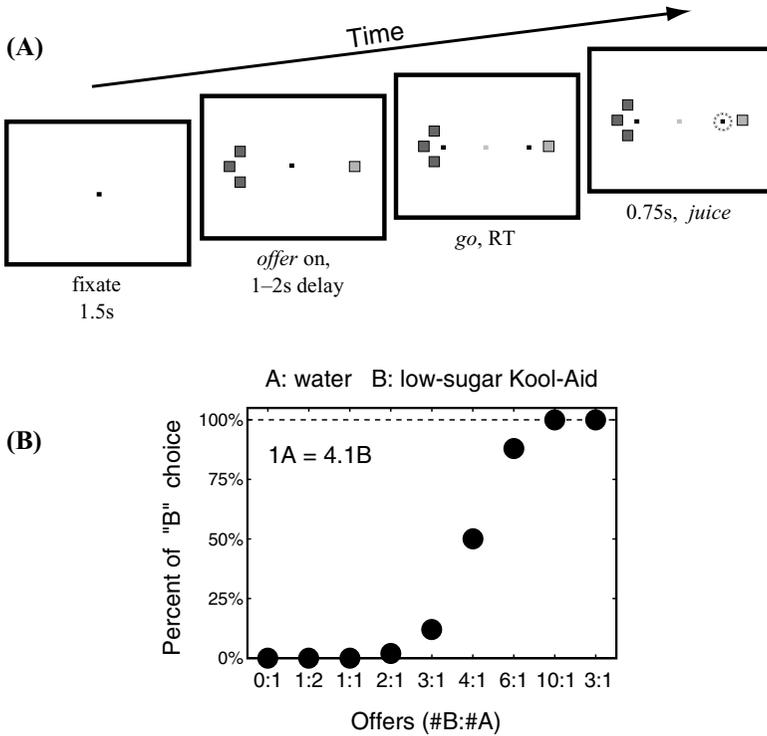
(A)

(B)

FIGURE 2. Experimental design (**A**) and choice pattern (**B**) in neurophysiology experiments. Adapted from Ref. 16.

ment and, after 0.75 s, the chosen juice was delivered (*juice*). In different sessions, we used a variety of different juices; in any given session, we referred to the preferred juice as juice A and to the less-preferred juice as juice B. The amounts of the two juices (0–10 drops) offered in any given trial varied pseudorandomly, and offer types included "forced choices" (such as 0B:1A or 2B:0A). For a given offer type, left/right positions were counterbalanced (e.g., the monkey could be offered 3B on the left and 1A on the right, or vice versa).

As shown in FIGURE 2B, the basic behavioral result obtained with solid foods was reproduced with beverages. To estimate the relative value of two juices in a given session, we fit the choice pattern with a sigmoid, and we determined the relative value from the flex point. Indicating with V(X) the value of X, for the session in FIGURE 2, we obtained $V(1A) = V(4.1B)$. In the analysis we assumed linear value functions, from which we obtained the equation $V(1A) = 4.1V(1B)$.

Like apples and oranges, A and B are different goods that in principle are not easy to compare. From the psychological point of view, value represents a
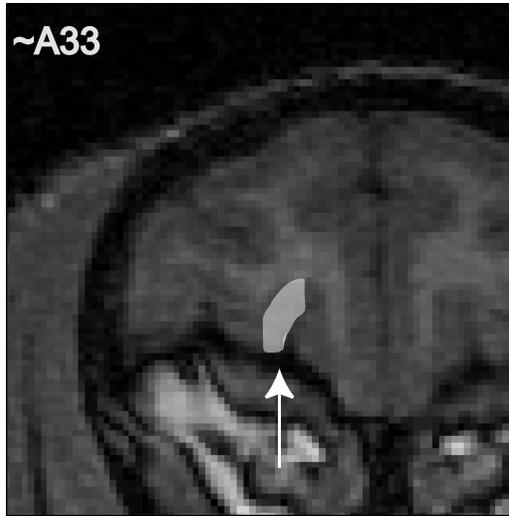
FIGURE 3. Recording sites were tentatively identified with area 13m.

common unit to make that comparison. For our analysis, the equation obtained from the choice pattern allowed us to measure quantities of A and B on a common value scale. We conventionally expressed values in units of V(B). We thus computed, for each trial, the value of the juice chosen by the monkey. For the session in FIGURE 2, the chosen value was ≈4 when the monkey chose 1A and when it chose 4B. When the monkey chose 2A, the chosen value was ≈8. When the monkey chose 6B, 10B, and 3B, the chosen value was respectively equal to 6, 10, and 3. In any session, we thus computed the variable chosen value. Similarly, we defined and computed other value-related variables.[16]

Neuronal recordings focused on the lateral bank of the medial orbital sulcus and the medial part of the posterior orbital gyrus (FIG. 3; presumably area 13m).[67,68] We recorded and analyzed the activity of 931 cells.[16]

As illustrated in FIGURE 4, OFC responses typically did not depend on the spatial configuration of the visual stimuli on the monitor (i.e., whether A was presented on the left and B on the right, or vice versa). Likewise, neuronal activity did not depend on the motor response used by the monkey to indicate its choice (i.e., a leftward or a rightward saccade). Overall, the activity of over 95% of OFC cells was independent of the spatial configuration and the motor response. However, the activity of neurons in OFC was often modulated by the offer type.

We defined seven 0.5-s time windows aligned with the *offer*, with the *go*, and with the *juice* delivery, and we analyzed the response of each neuron in each time window. In total, 1379 responses were significantly modulated by the offer type (ANOVA, $P < 0.001$), and 54% of cells were modulated in at least one time window. We analyzed further only responses modulated by the
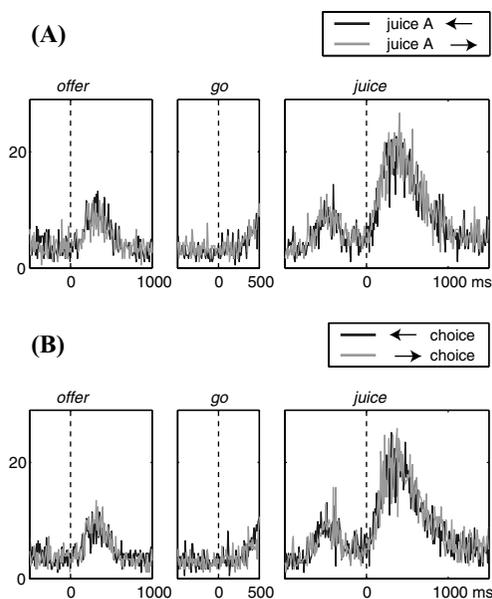
FIGURE 4. OFC responses are independent of visuomotor contingencies. **(A)** The two traces depict the activity of one representative neuron recorded when juice A was presented on the left and juice B on the right (dark trace) and with the reverse contingency (light trace). **(B)** In this case, the two traces depict the activity recorded when the monkey indicated its choice with a saccade to the left (dark trace) and with a saccade to the right (light trace). Adapted from Ref. 16.

offer type.

FIGURE 5 illustrates the activity of one representative neuron. In this session, the monkey chose between grape juice (A) and diluted cranberry juice (B). From the behavioral choice pattern (FIG. 5A, black symbols), we inferred V(A) = 3.0 V(B). The response of the cell (FIG. 5A, gray symbols) had a characteristic U shape, similar to what we would expect if the neuron encoded the value chosen by the monkey in any given trial. Indeed, the activity of the cells was low when the monkey chose 1A and when it chose 3B (in units of V(B), *chosen value* = 3); it was higher when the monkey chose 2A and when it chose 6B (*chosen value* = 6); and it was highest when the monkey chose 3A and when it chose 10B (*chosen value* ≈ 10). Plotted as a linear function of the numbers of A and B chosen (FIG. 5B), the U shape was asymmetrical. A linear regression of the response on the variable *chosen value* (FIG. 5C) provided $R^2 = 0.90$.

U-shaped responses seemingly encoding the *chosen value* were frequent in the OFC. In total, 54% of OFC neurons were modulated in the task, and about one-third of these (18% of the total) encoded the *chosen value* in at least one time window.
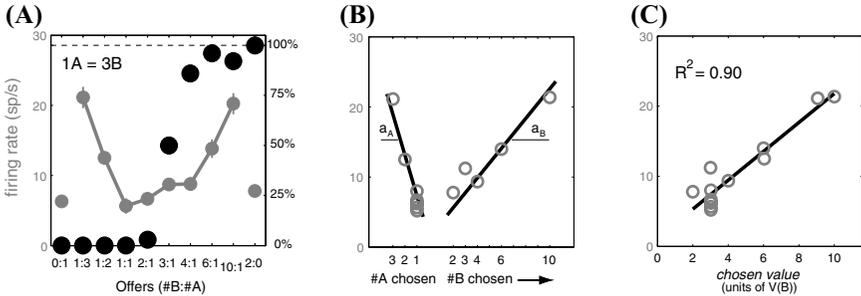
FIGURE 5. Activity of one OFC neuron encoding the *chosen value*. (**A**) Black symbols represent the behavioral choice pattern (with the *y* axis indicating the percent of B choices), and gray symbols indicate the firing rate. We conventionally express values in units of V(B). The cell activity is low when the monkey chooses 1 A and when it chooses 3B (offer types 1B:1A, 2B:1A, 3B:1A; *chosen value* = 3); it is higher when the monkey chooses 2A and when it chooses 6B (offer types 1B:2A, 6B:1A; *chosen value* = 6); and it is highest when the monkey chooses 3A and when it chooses 10B (offer types 1B:3A, 10B:1A; *chosen value* ≈ 10). (**B**) Same neuronal response plotted against the number of A and B chosen (linear scale). (**C**) Same neuronal responses plotted against the variable *chosen value* (expressed in units of V(B)). A linear regression provides $R^2 = 0.90$.

We also found other types of responses. For example, neuronal responses often encoded the *offer value*, that is, the value of one of the two juices alone. FIGURE 6A and B shows two neuronal responses encoding, respectively, *offer value A* and *offer value B*. Other frequently observed responses varied in a binary fashion depending on the type of juice chosen by the monkey, independently of the amount (FIG. 6C). We labeled these responses as encoding the juice *taste*.

Many OFC responses seemed to encode the variables *chosen value*, *offer value*, or *taste*. However, the relationship between the neuronal responses and these three variables could be subordinate to a correlation with other behavioral variables. For example, neurons in the OFC might encode the number of squares on the monitor (or variables proportional to the number, such as juice volume) or the variable *total value* (i.e., the value sum of the chosen juice and the other juice). In addition, OFC responses might encode other variables, such as the *value difference*. We examined quantitatively a total of 19 variables. Multiple procedures for variable selection all unequivocally identified *chosen value*, *offer value*, and *taste* as the three variables that best describe the population of responses. These three variables accounted for nearly 80% of OFC responses (mean $R^2 = 0.63$).[16]

Notably, the three types of responses are found in different proportions in different time windows. Comparing, in particular, the post-*offer* and post-*juice* time windows (corresponding, respectively, to the 0.5 s following the *offer* and the *juice*), we noted that *taste* responses were much more frequent at the time
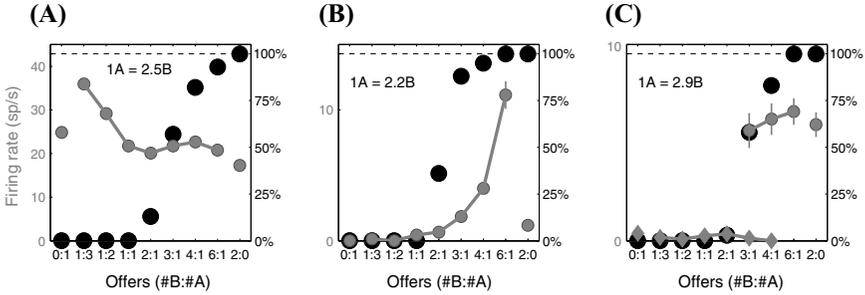
FIGURE 6. Activity of three neurons encoding the variables *offer value A* (**A**), *offer value B* (**B**), and *taste* (**C**). All conventions are as in FIGURE 5A. Adapted from Ref. 16.

of juice delivery than during the delay (FIG. 7). Also, *offer value* responses were most prevalent in the post-*offer* time window, consistent with the idea that, in order to choose, the monkey had to assign values to the two juices separately. This suggests the hypothesis that choices may be based upon the activity of *offer value* responses.

COMPARING BEHAVIORAL AND NEURONAL MEASURES OF ECONOMIC VALUE

Conceptually, responses encoding the *chosen value* are particularly interesting because, in addition to being independent of visuomotor contingencies, they are also independent of the specifics of the good (i.e., juice type and juice amount). A further analysis confirms that U-shaped responses encode the subjective value assigned by the monkeys as opposed to any physical property of the juices. Referring again to FIGURE 5B, we regress the activity of the neuron separately on the number of A chosen (#A) and on the number of B chosen (#B), and we obtain the two slopes a_A and a_B. The hypothesis that the response encodes the *chosen value* leads to a simple prediction regarding slopes a_A and a_B. Specifically, a_A should be proportional to the value of A, a_B should be proportional to the value of B, and the ratio $k^* \equiv a_A/a_B$ should be equal to the value ratio $V(A)/V(B)$. In other words, the slope ratio (k^*) provides a neuronal measure of the relative value of the two juices, independent of the behavioral measure of relative value (n^*), which represents the indifference point and which we obtain from the sigmoid fit. If U-shaped responses indeed encode the *chosen value*, we predict the identity $k^* = n^*$.

For the cell in FIGURE 5, this identity holds true. Indeed, from the two linear regressions, we obtain $k^* = 2.8$ (± 0.7), which is statistically indistinguishable from the behavioral measure $n^* = 3.0$. The following analysis shows that the identity $k^* = n^*$ holds true in general.

During the experiments, we used a large number of different juices and a total of 25 juice pairs.[16] Relative values were generally stable within any recording
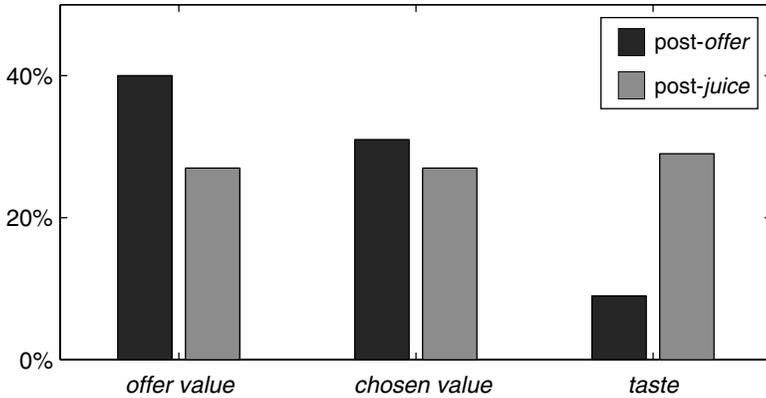
FIGURE 7. Class prevalence in different time windows. In the post-*offer* time window, a total of 284/931 (31%) of cells passed the ANOVA criterion. Of these, 40%, 31%, and 9% were classified as encoding, respectively, the *offer value*, *chosen value*, and *taste*. In the post-*juice* time window, a total of 332/931 (36%) of cells passed the ANOVA criterion. Of these, 27%, 27%, and 29% were classified as encoding, respectively, the *offer value*, *chosen value*, and *taste*.

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 can be exploited to test the prediction $k^* = n^*$, in the sense that the slope ratio k^* should covary with the behavioral measure of relative value n^*. We identify U-shaped responses as those for which both regression slopes a_A and a_B (FIG. 2B) are significantly nonzero ($P < 0.01$), and we analyze neuronal data from each juice pair separately. For example, FIGURE 8 illustrates all U-shaped responses recorded with apple juice and peppermint tea. In the figure, the x axis represents the behavioral measure of relative value (n^*), the y axis represents the neuronal measure (k^*), and each dot represents one U-shaped response. Different responses were recorded from different cells on different days. A linear relationship between the two variables can be observed in the figure. The linear regression $k^* = b_0 + b_1 n^*$ provides $b_0 = 0.08$ and $b_1 = 1.18$. Averaging the two coefficients across juice pairs, we obtain $\bar{b}_0 = -0.13$ (± 0.15) and $\bar{b}_1 = 1.05$ (± 0.15), a result consistent with the identity $k^* = n^*$.

The result illustrated in FIGURE 8 demonstrates that U-shaped responses indeed encode value as a subjective quantity, as opposed to any physical property of the juices. To appreciate this point, consider for example the hypothesis that U-shaped responses encode a physical property such as the quantity of one particular ingredient (e.g., sugar). If that were the case, for any given pair of juices, U shapes should not vary from session to session depending on the relative value the monkey assigns to the juices in that particular session. In other words, if U-shaped responses encoded a physical property of the juices,
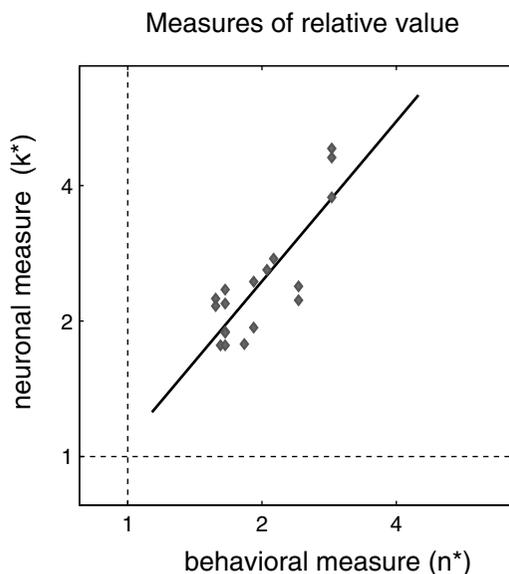
FIGURE 8. Measures of relative value. In the scatterplot, each data point represents one response, and all U-shaped responses recorded with apple juice and peppermint tea are shown. From the linear regression, we obtain $k^* = 0.08 + 1.18\, n^*$. Adapted from Ref. 16.

neuronal data should lie on a horizontal line in FIGURE 8, contrary to what we observe. We thus conclude that U-shaped responses indeed encode the value monkeys assign to the juice they choose to consume.[16]

REPRESENTATIONS OF VALUE IN ORBITOFRONTAL CORTEX AND OTHER BRAIN AREAS

A number of papers in recent years described how the activity of individual neurons in various brain areas can be modulated by value. Value-related activity has been documented in the lateral intraparietal area,[22,29,30] dorsolateral prefrontal cortex,[21,24,28] dorsal anterior cingulate,[69,70] ventral anterior cingulate,[71] posterior cingulate,[27] premotor cortex,[23] frontal eye fields,[23] supplementary eye fields,[23,72] superior colliculus,[19] basal ganglia,[20,25] amygdala,[73] and centromedian nucleus of the thalamus.[26] As a caveat, it should be noted that, at least in some cases, modulations described as related to value may also be explained in terms of visual attention, because most paradigms employed to study value-related phenomena fail to dissociate between these two alternative hypotheses.[74]

What distinguishes the representation of value found in the OFC is the fact that neurons in this area encode economic value *per se*, independently of

the visuomotor contingencies of choice (FIG. 4). In contrast, in many other brain areas, value modulates responses that are sensory or motor in nature. Notably, the phenomena observed in the OFC cannot be interpreted in terms of attention, because attention is usually thought of as modulating a sensory process, not as a quantity neurons would encode *per se*. As discussed next, the phenomena observed in the OFC might have important implications regarding possible psychological models of economic choice.

COGNITIVE MODELS OF ECONOMIC CHOICE: GOOD BASED VERSUS ACTION BASED

The fact that many brain areas where neuronal activity is modulated by value are indirectly or directly involved in the generation of movements led to the proposal that economic choices may ultimately be choices between actions.[35] Consider, for example, the lateral intraparietal area (LIP). Neurons in this area have a response field—they activate when a visual stimulus is placed in a particular region of the visual field and when monkeys plan the corresponding saccade. Several studies found that these neurons' activity is enhanced if the saccade is associated with higher value.[22,29,30] Different neurons in the LIP represent different saccades, and neurons in other areas of the parietal lobe represent other types of movements.[75] The LIP and other parietal areas can thus be thought of as forming maplike structures representing all possible courses of action.[35] Within this framework, one possible function of value-related modulations is that they may subserve action selection, which could unfold through a winner-take-all process.[35] Most relevant to our focus, it was proposed that these parietal areas provide a common pathway for decision making, and that they are the substrate upon which choice is actually generated.[35] In other words, according to this action-based model, economic choice is fundamentally choice between actions.

That neurons in the OFC encode economic value *per se*, and not as a modulation of sensorimotor processes, suggests an alternative good-based model, according to which economic choice is fundamentally choice between goods.[16] In this view, economic choice is first made between different goods, and a suitable motor action is subsequently planned and executed.

In principle, the good-based model and the action-based model of economic choice are both legitimate hypotheses, and their merits should be established on empirical ground. Here we present three arguments in favor of the good-based model.

The first argument is that the action-based model violates a simple principle of modularity.[76–78] According to the action-based model, the physiological substrate of economic choice depends on the modality of the motor act employed to reveal the choice. For example, suppose that you are having lunch in a restaurant and that you have to choose, from the menu, between pizza

and salad. According to the action-based model, the way you choose between pizza and salad depends on whether you indicate your choice with a left arm movement or with a right arm movement. If you indicate your choice verbally, the way you choose what to have for lunch depends on precisely what words you use to communicate with the waiter, because different sequences of words, which represent distinct courses of action, are processed and evaluated separately by the nervous system. In fact, according to the action-based model, as you choose between pizza and salad, many possible motor acts (different arm movements, different sequences of words, etc.) all representing the same food choice (e.g., salad) compete with each other.

The action-based hypothesis violates a principle of modularity because the nervous system could certainly break down the complex operation [choosing & moving] into two separate and simpler operations, [choosing] and [moving]. From a computational point of view, a modular organization offers tremendous advantages.[76] Controlling even a simple voluntary motor act, such as an arm reaching, is a challenging operation that involves many degrees of freedom and requires resolving multiple problems with infinite solutions.[79,80] If convolving the control of any motor act with economic choice requires even a minimal extra computational power, the great redundancy of the motor systems would make a nonmodular design ([choosing & moving]) enormously more expensive than a modular design ([choosing] and [moving]). For this reason, the good-based hypothesis is in principle more parsimonious.

Of course, natural selection does not always find optimal solutions. It is possible that primates may have evolved to make action-based economic choices, even though it is a costly way to function. After all, neurons in the parietal lobe and other premotor areas *are* modulated by value. If neurons encoding the value of goods independently of motor acts were not found in any brain area, the action-based model should certainly remain a leading hypothesis. In this sense, the results reviewed in previous sections provide an existence proof that directly supports the good-based model. Indeed, neurons in the OFC encode the value of offered and chosen goods *per se*, independently of visuo-motor contingencies. In other words, they encode the variables necessary for efficient, good-based economic choices.

Another argument against the action-based model—and specifically against the idea that areas in the parietal lobe are the substrate upon which choice is generated—comes from common observations in neuropsychology. Typically, lesions of the parietal cortex result in visuospatial deficits, such as hemi-neglect and Balint's syndrome.[81,82] In contrast, economic choices are typically affected by orbitofrontal lesions.[9–11,36–38,40] Hence, unlike the OFC, parietal areas are not strictly necessary for economic choice behavior.

The results reviewed here, together with other lines of evidence, thus support the good-based model of economic choice. What, then, might be the functional significance of value-related modulations observed in sensory and motor areas? Two hypotheses (mutually nonexclusive) can be considered. First,

value modulations in motor areas might indeed subserve action selection—as a distinct process, computationally downstream of economic choice. In other words, while economic choice is likely good based, action selection is likely action based. Second, it is certainly possible that information about the value assigned to objects flows from the frontal lobe to other sensory and motor areas, perhaps to increase the accuracy of the neuronal processes taking place in these areas. In the sensory domain, value modulations could serve perceptual attention. In the motor domain, value modulations could similarly serve a function of motor attention to increase motor accuracy. Verifying the merits of these hypotheses is an important goal for future research.

COMPARISON WITH OTHER SPECIES

From an evolutionary perspective, it is interesting to notice that there is a qualitative difference between OFC responses observed in monkeys and those observed in rodents. Two recent studies found that the activity of OFC neurons in rats actually does depend on spatial or motor contingencies.[83,84] Moreover, using behavioral paradigms that involve time discounting, researchers observed that value and time are represented separately in the rat OFC.[84] In contrast, in monkeys, OFC neurons reflect time-discounted values.[65]

Although it is possible that the recording region in rats was not exactly homologous to that in monkeys, these studies suggest that the representation of economic value in primates may be substantially more abstract than the representation in rodents.[85] With respect to the preceding discussion, this observation suggests that good-based choices may have emerged relatively late in the course of evolution. Importantly, this hypothesis is contingent upon future research, necessary to establish whether any abstract representation of value actually exists in the rat brain. Conversely, it remains to be determined whether OFC responses in rodents actually encode economic value in the sense defined in this chapter, as opposed to physical properties of appetitive stimuli (e.g., food volume or weight).

CONCLUSION

In summary, we defined economic choice and we described an experimental paradigm to study this behavior in nonhuman primates. Behavioral evidence indicates that choices cannot be explained as simple stimulus–response associations. According to a cognitive model, economic choice entails assigning values to the available options and deciding consequently. A rich literature from lesion studies, functional imaging, and primate neurophysiology suggests that critical mechanisms for economic choice might take place in the OFC. More specifically, recent results from single cell recordings in monkeys

link the OFC to the computation of economic value. We showed that the value representation in the OFC reflects the subjective nature of economic value, and that neurons in this area encode value *per se*, independently of the visuomotor contingencies of choice. Finally, we discussed the implications of this result for possible cognitive models of choice, and we advocated the hypothesis that economic choices are fundamentally choices between goods rather than choices between actions.

A number of important issues remain open. For example, it is not clear whether the same neuronal population described here encodes the value of other types of commodities (e.g., socially valuable commodities).[86] The neuronal mechanisms by which values are compared (i.e., by which decisions are made) are also currently unknown. Research in the coming years will hopefully shed light on these fundamental questions.

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