



Brief article

Multi-stage mental process for economic choice in capuchins

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Abstract

We studied economic choice behavior in capuchin monkeys by offering them to choose between two different foods available in variable amounts. When monkeys selected between familiar foods, their choice patterns were well-described in terms of relative value of the two foods. A leading view in economics and biology is that such behavior results from stimulus-response associations acquired through experience. According to this view, values are not psychologically real; they can only be defined a posteriori. One prediction of this associative model is that animals faced for the first time with a new pair of foods learn to choose between them gradually. We tested this prediction. Surprisingly, we find that monkeys choose as effectively between new pairs of foods as they choose between familiar pairs of foods. We therefore, propose a cognitive model in which economic choice results from a two-stage mental process of value-assignment and decision-making. In a follow-up experiment, we find that the relative value assigned to three foods in sessions in which we tested them against each other combine according to transitivity.

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1. Introduction

In recent years, an increasing scientific interest has developed apropos the psychology of economic choice. A large body of evidence shows how humans engaged in various

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economic behaviors are subject to a variety of ‘fallacies’. Well-documented phenomena include hyperbolic discounting, loss aversion, framing effects, the Allais paradox, and fairness constraints (Ainslie, 1992; Camerer, 2003; Camerer, Loewenstein, & Rabin, 2003; Kagel & Roth, 1995; Kahneman & Tversky, 2000). The growing consensus is that a satisfactory account of economic behavior will entail a deeper understanding of the underlying mental processes. One area likely to contribute to this endeavor is the study of economic choices in other species, particularly in monkeys. Indeed, recent work has undertaken this approach (Brosnan & De Waal, 2003; de Waal & Davis, 2003; Hauser, Chen, Chen, & Chuang, 2003).

In general, behavioral economics has been most concerned with relatively complex choices. For example, a number of preference reversals and inconsistencies are observed in the presence of uncertainty, or in social contexts. But, arguably, a satisfactory psychological model is still lacking even for much simpler economic choices. For example, consider an animal choosing between two pieces of food, both equally and immediately available. Are its choices consistent across trials? And if so, what mental operations do they require?

Here, we present an experimental paradigm designed to help address these questions. In a first experiment, we offered monkeys two foods in variable amounts. We found that their choice patterns were well-described in terms of relative values of the two foods. In literature, animal food choices have been often described invoking theories of optimality, such as standard economics (Samuelson, 1947) or optimal foraging (Kamil, Krebs, & Pulliam, 1987). Our results were not inconsistent with these theories. However, these frameworks essentially imply an associative psychological model of choice (Skinner, 1953, 1981) (see Section 2.3). In a second experiment, we tested the major prediction of this model, namely that offer-choice associations develop through trial and error. To the contrary, we found that monkeys choose effectively even between foods that they have never encountered together before. As an alternative to the associative model, we propose a cognitive model according to which economic choice results from a two-stage process of value-assignment and decision-making.

Parts of these results have been previously presented in abstract form (Padoa-Schioppa, Jandolo, & Visalberghi, 2003)

2. Experiment 1: choice between familiar foods

2.1. Method

2.1.1. Subjects, apparatus and procedure

The experiments were conducted on capuchins (*Cebus apella*), a South American monkey species (Fragaszy, Visalberghi, & Fedigan, 2004). The subjects lived in three groups (3–12 subjects per group). Groups were housed in indoor–outdoor cages furnished with perches, slides, plastic toys, and wooden blocks. Group areas ranged from 90–135 m³ depending on group size. Every afternoon, monkeys received chow, fresh fruits and vegetables. Three times a week monkeys received a mixture of curd cheese, vitamins, egg, bran, oats and sugar. Experiments were carried daily before the afternoon meal.



Fig. 1. Apparatus. In this particular trial, the monkey chooses between two raisins and one piece of apple.

We tested 9 monkeys (4 males, 5 females), individually. The subject entered an indoor cage ($1.70 \times 1.90 \times 2.60$ m), outside of which the experimenters stood with the apparatus. The apparatus was a 40×27 cm horizontal tray divided by a 9-cm-high vertical barrier (Fig. 1). The entire apparatus could slide on its supporting cart, and was operated by hand by the experimenter. In each trial, two amounts of food were placed on the two sides of the tray, while the tray was in view but out of reach of the monkey. Shortly (1–2 s) thereafter, the experimenter pushed the tray towards the cage (*offer*), so that the monkey could choose one of the two amounts of food by reaching out of the cage. Response time (i.e. the time elapsed between the *offer* and when the monkey touched the chosen food) was recorded with a manual chronometer by a second experimenter during the session, and/or blindly off-line using a recorded video. For sessions in which both measures were available, on-line and off-line recordings provided similar results.

Foods were cut into pieces and each piece was weighed with a digital scale (an AND compact scale; 0.1 g accuracy). Each food was presented in pieces of approximately constant size and weight (for example, 1 g of apple). During familiarization sessions, monkeys chose in each trial between different amounts of one food. Within a couple of sessions, monkeys learned to correctly reach for only one side. They also learned to effectively choose the highest number of pieces of food available.

In test sessions, monkeys chose between two different foods. Before the session, we tested food preference by offering one piece of one food against one piece of the other food. Hereafter, we refer to the preferred food as food A and to the non-preferred as food B. During the session, monkeys chose between foods A and B offered in variable amounts. For instance on a given trial, the monkey might be offered one piece of food A against

three pieces of food B (offer type 1A:3B). We offered one piece of one food against 1–5 pieces of the other food (occasionally, we offered 10 pieces of food). The left/right arrangement of the two foods was counterbalanced within each session. The order of different offer types varied pseudo-randomly.

In experiment 1, we used the following familiar foods (weight range in parenthesis): apple (0.8–1.2 g); apricot (0.8–1.2 g); carrot (0.4–0.6 g); celery (0.4–0.6 g); pear (0.8–1.2 g); plum (0.8–1.2 g); small raisin (0.2–0.3 g) or big raisin (0.4–0.5 g). We tested 9 monkeys for a total of 65 sessions. Each subject was tested with multiple pairs of foods. Each session lasted 16–76 trials (typically 32–48 trials). Each offer type was tested 2–16 times (typically 4–8 times).

2.1.2. Data analysis

In each session, we analyzed the percentage of trials in which the monkey chose the least preferred food B as a function of the number of pieces of food B available (choice pattern). To assess whether the observed choice pattern was well fit by a step function, we used a bootstrap analysis. First, we fit the recorded choice pattern with the step function $\theta = \theta(x - n)$ such that $\theta = 0$ for $x < n$; $\theta = 0.5$ for $x = n$; and $\theta = 1$ for $x > n$. We found the number n^* that gave the best fit and the corresponding (minimal) square error r^2 . For each trial in the session, we then reassigned the choice randomly to the food placed on the left side or to the food placed on the right side of the plate. For the choice pattern so generated, we found n_b^* and r_b^2 . We repeated this operation $N = 10,000$ and we obtained a distribution of r_b^2 . We then compared the actually recorded r^2 with this distribution: We defined p as the ratio between the number of generated choice patterns for which $r_b^2 < r^2$ and the total number of generated choice patterns. Finally, we imposed the criterion of $P < 0.01$. Recorded choice patterns that satisfied this condition were identified as well fit by the step function. Note that this procedure also provided the number n^* corresponding to indifference. In general, n^* was an interval, not a unique number.

For the statistical analysis of response times (RT), we proceeded as follows. For each session, we fit the choice pattern with a sigmoid function and we obtained a single best estimate for the relative value. On that basis, we computed for each offer type the ratio between the value of the lesser food and the value of the better food. The value ratio varied between 0 and 1. We then normalized the RT data recorded in each session (we computed a $-n$ -score), and we pooled the RT data from all sessions (the normalization was necessary because mean RT varied considerably across monkeys). Finally, we performed a linear regression of the normalized RT on the value ratio.

2.2. Results

Fig. 2a illustrates the main result of the experiment, as recorded in a representative session. In this case, the monkey chose between raisin (food A, preferred) and apple (food B, non-preferred). In the figure, the x -axis indicates the offer type, and the y -axis indicates the percentage of time the monkey chose food B. The monkey always chose food A for offers 3A:1B, 2A:1B, and 1A:1B; he was roughly indifferent between 1A and 2B; and he always chose food B for offer 1A:nB with $n > 2$.

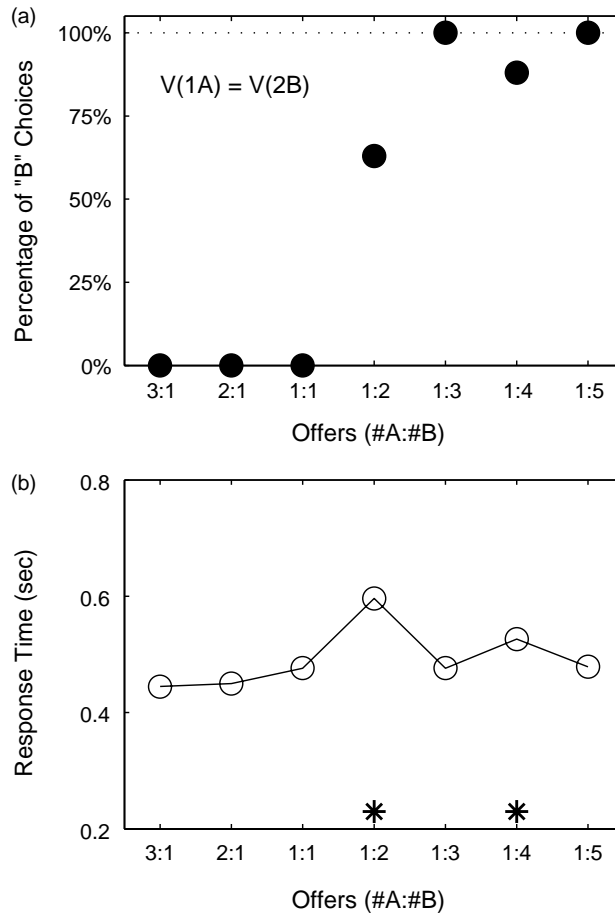


Fig. 2. (a) Pattern of choice recorded in one session. Here the monkey chooses between raisin (food A) and apple (food B). (b) Response times collected in the same session. The asterisks in the plot indicate offer types for which one 'error' was noted (see text for details).

This pattern of choice can be interpreted in terms of relative values of foods A and B. Using the notation $V(X)$ for the value of x , the pattern of choice of Fig. 2a reveals that $V(1A) \approx V(2B)$.

The bootstrap analysis indicated that in 61 of 65 (94%) sessions, the recorded choice pattern was well fit by a step function, so that the data could be explained in terms of relative values. In some cases, however, alternative explanations were also possible. For example, in a session in which the monkey was indifferent between 1A and 1B and always chose the most numerous offer otherwise, the choice pattern could also be described in terms of numerosity. In other cases choices could be explained in terms of food weight. Yet in other cases, although a step function formally fit the choice pattern, the monkeys always chose food A, no matter how many pieces of food B were available. Choice

patterns compatible with a value-based choice as well as with other simple choice criteria (numerosity, weight, always-food-A) were named ‘trivial,’ and accounted for 19 (29%) sessions. In the remaining 42 (65%) sessions, the results were non-trivial, in the sense that they could be explained in terms of relative value, but not in terms of numerosity or weight, or always-food-A.

Fig. 2b illustrates the response time (RT) recorded during the same session of Fig. 2a. Note that RT were longer for ‘difficult’ choices, when the two offers were close in value, and shorter for ‘easier’ choices. This trend suggested that choices between foods with similar value require more mental processing. Pooling data from the 9 monkeys, we found that the RT effect was highly significant (i.e. linear regression slope greater than zero, $P < 10^{-6}$, Fig. 3). Considering individuals separately, the effect was significant for 5 of the 9 monkeys ($P < 0.05$). For 2 other monkeys, the effect was significant when we analyzed data from experiment 2 (see below). We conclude that indeed, RT were longer when monkeys chose between foods of similar value.

During the experiments, monkeys’ interactions with the apparatus were generally very ‘proper,’ in the following senses: Within a couple of familiarization sessions preceding the experiments, monkeys learned to reach for and grab only one of the two foods. Monkeys also seemed generally confident of their choices. However, two kinds of ‘errors’ were sometimes observed. In some instances, monkeys tried to reach out of the cage with both hands and grab both foods. In other instances, monkeys grabbed one food, then released it, and took the other food instead. In all these cases, monkeys seemed particularly undecided between foods. We took note of these occurrences. Notably, ‘errors’ were most frequent

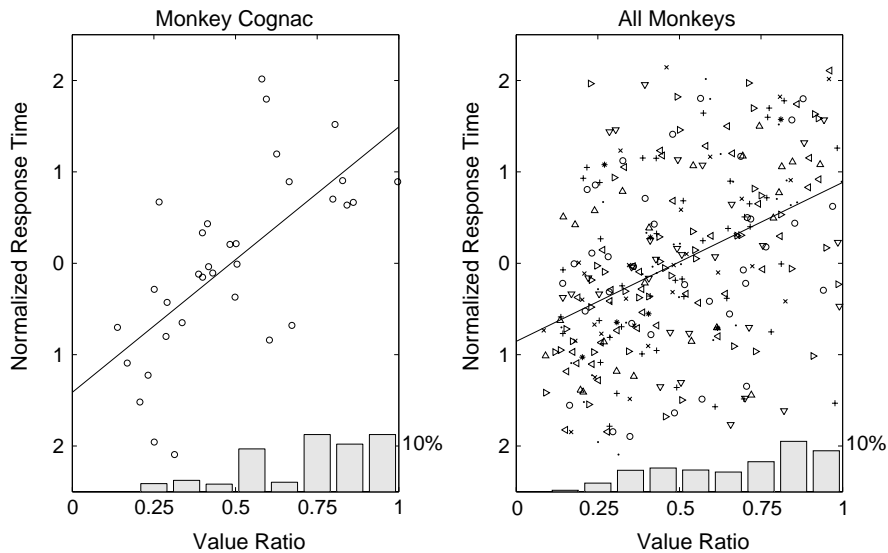


Fig. 3. Response times and ‘error’ frequency. The left panel shows data for one individual (monkey Cognac). The right panel shows cumulative data for the 9 monkeys (different symbols are used for different monkeys). Lines result from a linear regression. The histograms represent the average ‘error’ frequencies (scale shown on the right). See main text for details.

when the two offered foods were close in value (Fig. 3), consistently with the idea that when offers are close in value choice is more difficult.

2.3. Discussion

The choice pattern depicted in Fig. 2a is effectively described using the concept of *value*. Foods A and B are *qualitatively* different goods. The fact that monkeys switch their choices from A to B depending on relative *quantity* indicates that monkeys treat foods A and B as comparable in some sense. The two foods have a common currency. Monkeys' choices do not simply follow the physical attributes of foods, such as weight or numerosity. What makes foods A and B comparable is their *value*, a property that depends both on the physical attributes of the foods and on the individual preferences of the monkey.

With respect to the mental processes that generate the observed patterns of choice, we can entertain at least two alternative hypotheses. One possibility is that monkeys' choices are simple associations acquired through experience. In his first encounters with foods A and B, a monkey might choose randomly, and a feedback mechanism measures his 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. Eventually, choices become simple associations between a stimulus (e.g. the offer 1A:1B) and a response (e.g. the choice of 1A). In this view, choice patterns recorded in test sessions reflect a series of conditioned responses. This is the associative, or behaviorist, model of choice proposed by Skinner (1953, 1981). Importantly, according to the associative model, values are not real psychological quantities for the monkey, although they seem so to the observer. The alternative hypothesis is that economic choices require more elaborate mental processing than simple associations (see Section 5).

Interestingly, the associative model of choice is a sufficient assumption for much of standard economics (SE). In SE, agents 'maximize their utility'. Although this could imply two mental processes (utility assignment and maximization), the definition of utility is circular. In fact, SE denies in principle the possibility to measure utility independently of choices. Thus, according to SE, economic choices *might* result from multi-stage mental processes, but whether that is indeed the case *cannot* be addressed empirically. Taken together with a principle of epistemological parsimony, this stand is equivalent to asserting that economic choices are single-stage mental processes, akin to stimulus-response associations. Likewise, the associative model is a sufficient assumption for theories of optimal foraging (Kamil et al., 1987).

The problem with Skinner's associative model—at least for humans—is that people are perfectly capable of making effective choices in unfamiliar situations, an argument similar to that originally proposed by Chomsky (1959) for *verbal behavior* (Skinner, 1957). But while human choices seem too complex to result only from conditional responses, the associative model remains a reasonable hypothesis for other species, and cannot be dismissed lightheartedly. In experiment 2, we tested the associative model explicitly, by offering monkeys to choose between pairs of foods that they had never encountered together before.

3. Experiment 2: choice between new pairs of foods

3.1. Method

Subjects and apparatus were the same as those used for experiment 1. For this experiment, however, we used novel foods. In past years, we studied food preferences of the subjects participating in the current experiments, with particular interest for novel foods (Visalberghi, Sabbatini, Stammati, & Addessi, 2003; Visalberghi, Valente, & Frigaszy, 1998). Thus, we have a detailed record of the foods ever provided to these subjects, in most cases since birth. None of the foods here labeled as ‘novel’ was known to the monkeys prior to the current experiments.

In familiarization sessions, we used only one novel food, and monkeys chose between different amounts of it. (Although initially novel foods gradually became familiar, for sake of clarity, we will continue to label them ‘novel foods.’) Monkeys underwent 1–3 familiarization sessions (typically 2 sessions) with each of the novel foods. Familiarization sessions lasted 4–42 trials (typically 16–30 trials).

In test sessions, monkeys chose either between two novel foods, or between one novel food and one familiar food (in either case, monkeys faced a new *pair* of foods). Overall, we conducted a total of 54 sessions in which two foods were paired for the first time (‘first time’ sessions). Each ‘first time’ session lasted 10–76 trials (typically 16–48 trials). Each offer type was tested 1–12 times (typically 2–8 times).

Data were analyzed using the same procedure used in experiment 1. To analyze the correlation between first and last choice, we pooled data from different sessions and different monkeys.

We used the following novel foods: brazilian nut (0.2–0.3 g); dry apple (0.2–0.3 g); dry apricot (0.3–0.4 g); dry papaya (0.2–0.3 g); dry pineapple (0.2–0.3 g); marshmallow (0.2–0.3 g).

3.2. Results

In familiarization sessions, monkeys were initially cautious, and ate small amounts of novel foods. However, their consumption gradually increased as they became more familiar with them, a trend often observed with initially unfamiliar foods (Visalberghi et al., 1998).

The choice patterns recorded in experiment 2 with new pairs of foods were qualitatively similar to those obtained in experiment 1 with familiar pairs of foods. The choice pattern was well fit by a step function in 48 of 54 (89%) sessions. Choices were ‘non-trivial’ in 34 of the 54 (63%) sessions. These results are statistically indistinguishable from those obtained in experiment 1 with familiar pairs of foods ($P=0.6$; χ^2 analysis, factors [exp1, exp2] \times [non-step, trivial, non-trivial]).

Conceivably, choice patterns recorded in experiment 2 could reflect offer-choice associations established rapidly, ideally within two trials, at the beginning of the session. A specific analysis ruled out this possibility. For each session, we considered the first and the last trials in which a monkey faced a given offer type. According to the associative model, these two choices should be independent: the first choice should be random, while

the last choice should reflect the learned association. To the contrary, in 271 of 345 (79%) cases the first choice was identical to the last choice, a very significant departure from randomness ($P=0$, binomial test). This same analysis performed on data from experiment 1 provided very similar results: first and last choices were identical in 299 of 396 (76%) cases ($P=0$, binomial test). Thus, fast learning could not explain the observed choice patterns.

3.3. Discussion

Starting from the very first trial, monkeys are equally effective in choosing between new pairs of foods as they are in choosing between familiar pairs of foods. Thus, their choices cannot be simple associations between stimuli (i.e. offers) and responses learned by trial and error. This result clearly argues against the associative model of choice. It suggests that monkeys indeed assign values to foods A and B when making their choices. A congruent result was recently reported (de Waal & Davis, 2003) in the context of cooperation.

4. Experiment 3: transitivity

4.1. Method

Subjects and apparatus were the same used for experiments 1 and 2. In experiment 3, however, we used in each session three different foods (A, B and C, in decreasing order of preference). In each trial, monkeys chose between one pair of foods. Trials with the three possible pairs of foods (A:B, B:C, and A:C) were intermixed. We used the same foods as in experiments 1 and 2. Session lasted 25–64 trials (typically 48–60 trials). Each offer type was tested 2–6 times (typically 4 times). Data were analyzed using the same procedure used in experiments 1 and 2.

Since monkeys chose between three pairs of foods, we measured three relative equivalence values in each session. This design enabled us to test the transitivity of assigned values.

4.2. Results

Fig. 4 illustrates the results obtained in a representative session. The three choice patterns recorded for the three pairs of foods provide the following relative values: $V(1A) \in (V(1B), V(2B))$; $V(1B) \in (V(1C), V(2C))$; and $V(1A) \in (V(2C), V(3C))$. These value equations are consistent with transitivity in a weak sense, because A is preferred to B, B is preferred to C, and A is preferred to C. More interestingly, the value equations are also consistent with transitivity in a strong sense, because the relative value of A and C inferred from the choices of A versus B and from the choices of B versus C is consistent with the relative value obtained directly from the choices of A versus C. To illustrate this point, let us assume that $V(x)$ is roughly a linear function of x in the interval considered. We can re-write the three value equations as: $V(A) \in (1,2)V(B)$; $V(B) \in (1,2)V(C)$; and

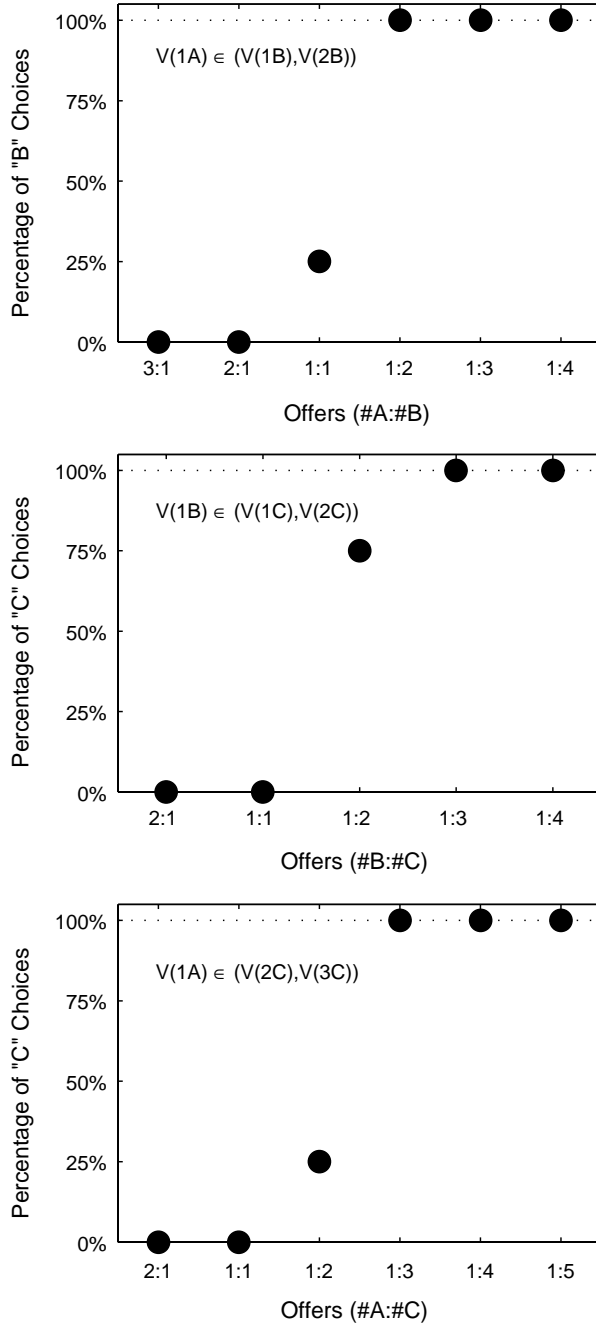


Fig. 4. Pattern of choice recorded in one session in experiment 3. Here, the monkey chooses between marshmallow (food A), raisin (food B) and apple (food C). Top, Choices of A:B; Center, Choices of B:C; Bottom, Choices of A:C.

$V(A) \in (2,3)V(C)$. Combining the first two equations, we infer that $V(A) \in (1,4)V(C)$. This result is consistent with the third equation because the intervals (1,4) and (2,3) overlap.

Monkeys were tested in a total of 29 sessions; in 20 sessions, all three choice patterns were well fit by a step function (valid sessions). In 18 of 20 sessions (90%), the recorded relative values were compatible with transitivity. However, compatibility could be more or less stringent depending on whether the three intervals were limited, or just defined by an inequality. For example, in one session, we obtained $V(A) \in (4,5)V(B)$; $V(B) \in (1,2)V(C)$; and $V(A) > 5V(C)$, a ‘non-stringent’ result. We obtained transitive but non-stringent intervals in 7 (35%) sessions. In the remaining 11 (55%) sessions, the choice pattern was compatible with transitivity and stringent.

4.3. Discussion

The results of experiment 3 indicate that the values assigned to foods A, B and C satisfy the condition of transitivity both in a weak sense (order of preference), and in a strong, quantitative sense.

During experiment 1, we had anecdotally observed that the relative value of two foods could vary across sessions for any individual, consistent with previous studies that manipulated the relative preference of two foods systematically (Baxter & Murray, 2002). The fact that at any given time the relative values of three foods combine transitively suggests that value fluctuations are not due to some sort of noise in the stimulus-response association (which would presumably be the associative account for value fluctuations), but rather reflect the internal state of the animal. Thus, this result consolidates the conclusion of experiments 1 and 2, namely that monkeys choose by assigning values to the different foods.

5. General discussion

You cannot compare apples and oranges, goes the saying. But, actually, people can and do so frequently. And, as we showed, monkeys do too. What makes different foods and, more generally, different goods comparable is their subjective value.

The idea that animals choose *as if* different foods had different values is broadly consistent with standard economics and with biological theories of economic choice (Kagel, Battalio, & Green, 1995; Kamil et al., 1987; Samuelson, 1947), including recent neurophysiological approaches (Izawa, Zachar, Yanagihara, & Matsushima, 2003; Platt & Glimcher, 1999; Shizgal, 1997; Sugrue, Corrado, & Newsome, 2004). As for the underlying mental processes, mainstream economics has historically abandoned a strong interpretation of value (Samuelson, 1947). As we have argued, the psychological model of choice implicitly assumed in standard economics is equivalent to the associative model originally proposed by Skinner (1953; 1981). According to that account, choices result from stimulus-response associations acquired through experience. Here, we tested the main prediction of that model, namely that monkeys faced with new pairs of foods learn to choose between them gradually. To the contrary, we found that monkeys choose as effectively in their first encounter with a new pair of foods as they choose between familiar pairs of foods.

Our data also provide three additional -though indirect -arguments against the associative model. If choices are indeed stimulus-response associations, they should all be equally difficult (or equally easy), independently of the offer. To the contrary, we observe that when offered foods are close in value, response times are longer and ‘errors’ are more frequent, two effects that cannot be simply due to the physical attributes of the foods. Moreover, although the value of any given food may vary over time, the relative values of three foods combine according to transitivity at any given time. We conclude that describing even the simple choice between two foods requires a more elaborate psychological model of choice.

The characteristic trait of the associative model is that economic choice entails a single-stage mental process, namely an association between the stimulus (the offer) and the response (the choice). The most parsimonious alternative hypothesis is that economic choice entails two distinct mental operations. In particular, we propose that choices result from the two-stage process of value-assignment and decision-making. One notable aspect of this cognitive model is that values are real psychological entities, computed by the monkeys to make their choice. Although this model may appear a minimal departure from the associative account, we shall notice that, from the point of view of economic theory, adding even a single degree of freedom has profound theoretical consequences.

Almost half a century has passed since the debate on verbal behavior (Chomsky, 1959; Skinner, 1957), and the ‘cognitive revolution’ has extended to most all areas of psychology. Yet, in the domain of economic choice, behaviorism seems to have gone largely unchallenged. One likely reason is that, in spite of evidence arguing against it, testing directly any alternative to the associative model remains difficult based on behavior alone. One approach that in principle can help disentangle different mental processes is to study the neurophysiological underpinnings of economic choice. An advantage of the behavioral paradigm presented here is that it provides an animal model of economic choice that can be used for neurophysiological recordings (Padoa-Schioppa & Assad, 2004). We hope that in the future, this neuroscience route will help testing cognitive models of economic choice.

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References

- Ainslie, G. (1992). *Picoeconomics: The strategic interaction of successive motivational states within the person*. New York, NY: Cambridge University Press.
- Baxter, M. G., & Murray, E. A. (2002). The amygdala and reward. *Nature Reviews Neuroscience*, 3(7), 563–573.

- Brosnan, S. F., & De Waal, F. B. (2003). Monkeys reject unequal pay. *Nature*, *425*(6955), 297–299.
- Camerer, C. (2003). *Behavioral game theory: Experiments in strategic interaction*. Princeton, NJ: Russell Sage Foundation–Princeton University Press.
- Camerer, C., Loewenstein, G., & Rabin, M. (2003). *Advances in behavioral economics*. Princeton, NJ: Russell Sage Foundation–Princeton University Press.
- Chomsky, N. (1959). A review of B.F. Skinner's. *Verbal Behavior. Language*, *35*(1), 26–58.
- de Waal, F. B., & Davis, J. M. (2003). Capuchin cognitive ecology: Cooperation based on projected returns. *Neuropsychologia*, *41*(2), 221–228.
- Fragaszy, D. M., Visalberghi, E., & Fedigan, L. M. (2004). *The complete capuchin: The biology of the genus Cebus*. New York, NY: Cambridge University Press.
- Hauser, M. D., Chen, M. K., Chen, F., & Chuang, E. (2003). Give unto others: Genetically unrelated cotton-top tamarin monkeys preferentially give food to those who altruistically give food back. *Proceedings of the Royal Society of London*, *270*(1531), 2363–2370.
- Izawa, E., Zachar, G., Yanagihara, S., & Matsushima, T. (2003). Localized lesion of caudal part of lobus parolfactorius caused impulsive choice in the domestic chick: Evolutionarily conserved function of ventral striatum. *Journal of Neuroscience*, *23*(5), 1894–1902.
- Kagel, J. H., Battalio, R. C., & Green, L. (1995). *Economic choice theory: An experimental analysis of animal behavior*. New York, NY: Cambridge University Press.
- Kagel, J. H., & Roth, A. E. (1995). *The handbook of experimental economics*. Princeton, NJ: Princeton University Press.
- Kahneman, D., & Tversky, A. (2000). *Choices, values and frames*. Cambridge, UK: Russell Sage Foundation–Cambridge University Press.
- Kamil, A. C., Krebs, J. R., & Pulliam, H. R. (1987). *Foraging behavior*. New York, NY: Plenum Press.
- Padoa-Schioppa, C., & Assad, J. A. (2004). Neuronal activity in orbitofrontal cortex during economic choice. *Society for Neuroscience Meeting Abstracts*, *30*, 7819.
- Padoa-Schioppa, C., Jandolo, L., & Visalberghi, E. (2003). A primate model for economic choice behavior. *Society for Neuroscience Meeting Abstracts*, *29*, 3857.
- Platt, M. L., & Glimcher, P. W. (1999). Neural correlates of decision variables in parietal cortex. *Nature*, *400*(6741), 233–238.
- Samuelson, P. A. (1947). *Foundations of economic analysis*. Cambridge, MA: Harvard University Press.
- Shizgal, P. (1997). Neural basis of utility estimation. *Current Opinion in Neurobiology*, *7*(2), 198–208.
- Skinner, B. F. (1953). *Science and human behavior*. New York, NY: Macmillan.
- Skinner, B. F. (1957). *Verbal behavior*. New York, NY: Appleton-Century-Crofts.
- Skinner, B. F. (1981). Selection by consequences. *Science*, *213*(4507), 501–504.
- Sugrue, L. P., Corrado, G. S., & Newsome, W. T. (2004). Matching behavior and the representation of value in the parietal cortex. *Science*, *304*(5678), 1782–1787.
- Visalberghi, E., Sabbatini, G., Stammati, M., & Addessi, E. (2003). Preferences towards novel foods in *Cebus apella*: The role of nutrients and social influences. *Physiology & Behavior*, *80*(2–3), 341–349.
- Visalberghi, E., Valente, M., & Fragaszy, D. (1998). Social context and consumption of unfamiliar foods by capuchin monkeys (*Cebus apella*) over repeated encounters. *American Journal of Primatology*, *45*(4), 367–380.