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ORIGINAL PAPER

Evolutionary origins of money categorization and exchange: an experimental investigation in tufted capuchin monkeys (*Sapajus* spp.)

Francesca De Petrillo[1,2,3] · Martina Caroli[2] · Emanuele Gori[2] · Antonia Micucci[2,4] · Serena Gastaldi[2] · Sacha Bourgeois-Gironde[5,6] · Elsa Addessi[2]

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Abstract

Money is a cultural artefact with a central role in human society. Here, we investigated whether some features of money may be traced back to the exchange habits of nonhuman animals, capitalizing on their ability to flexibly use tokens in different domains. In Experiment 1, we evaluated whether capuchins can recognize token validity. Six subjects were required to exchange with the experimenter valid/familiar tokens, valid/unfamiliar tokens, invalid tokens, and no-value items. They first exchanged a similar number of valid/familiar and valid/unfamiliar tokens, followed by exchanges of invalid tokens and no-value items. Thus, as humans, capuchins readily recognized token validity, regardless of familiarity. In Experiment 2, we further evaluated the flexibility of the token–food association by assessing whether capuchins could engage in reverse food–token exchanges. Subjects spontaneously performed chains of exchanges, in which a food item was exchanged for a token, and then the token was exchanged for another food. However, performance was better as the advantage gained from the exchange increased. Overall, capuchins recognized token validity and successfully engaged in chains of reverse and direct exchanges. This suggests that—although nonhuman animals are far from having fully-fledged monetary systems—for capuchins tokens share at least some features with human money.

Keywords Money · Token · Primate · Validity · Categorization · Exchange

Introduction

Money is universally recognized as the most efficient medium to acquire goods and services and, at the same time, as an effective incentive that activates the same brain areas involved in reward processing. Although money is a cultural artefact without any apparent biological meaning, its power is so pervasive in human societies that it becomes crucial to understand what are the biological underpinnings of human attraction to money (Lea and Webley 2006).

In this respect, a prominent basic question is how and when the brain identifies monetary validity, defined as the ability of money to be efficiently exchanged for a consumable good. To this purpose, money is considered only as a disc of metal that, upon social agreement, can be exchanged for goods and services—i.e., in terms of its purchasing power and means for exchange, not evaluating other possible money properties such as unit of account and storage of value. In a study addressing the above question in adult humans, participants were tested in a one-back task, in which

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✉ Elsa Addessi
elsa.addessi@istc.cnr.it

1 Institute for Advanced Study of Toulouse, Toulouse, France

2 Istituto di Scienze e Tecnologie della Cognizione, CNR, Rome, Italy

3 Department of Psychology, University of Michigan, Ann Arbor, USA

4 Department of Psychology, University of Bologna, Bologna, Italy

5 Université Paris II, Lemma, France

6 Institut Jean Nicod, Ecole Normale Supérieure, CNRS, Paris, France

they were required to respond whenever two identical images of coins were presented in a row. Magneto-encephalographic recordings obtained during this task showed that the ventral visual system rapidly distinguishes between valid and invalid coins, regardless of familiarity, in a time window comprised between 150 and 175 ms from stimulus presentation (Tallon-Baudry et al. 2011). Since money is a very recent human invention, dating back to a few thousand years ago, it is unlikely that, within this evolutionarily short time frame, a brain mechanism specifically devoted to money processing evolved (Burgoyne and Lea 2006). Thus, according to Tallon-Baudry et al. (2011), the ability to categorize money is likely rooted in evolutionarily ancient abilities of the ventral visual system to process symbolic stimuli (though other brain areas underlie the reward properties of money; e.g., Knutson et al. 2001; McClure et al. 2004; Zink et al. 2004), and, therefore, may be traced back to other animal species.

Although no species other than humans has developed a monetary system, plenty of studies have shown that nonhuman animals can flexibly use tokens, i.e. inherently non-valuable exchangeable objects. Tokens are generally considered as conditioned reinforcers, whose function is established through the relation to other reinforcer(s) and, in an economic framework, as a type of currency that is earned and exchanged for other commodities (Hackenberg 2009). The exchange of tokens between nonhuman subjects and human experimenters has attracted the interest of various scholars because the intentional giving of objects is an aspect of complex human socio-cognitive abilities. As such, it made it possible for exchanges based on reciprocity to emerge (Mauss 1950).

The first experimental work on token use in nonhuman primates was carried out on chimpanzees (*Pan troglodytes*) and capuchin monkeys (*Sapajus* spp.) in the '30 s of the past century (Carpenter and Locke 1937; Cowles 1937; Wolfe 1936). Relevant for the present study, this early research addressed (1) the discrimination between tokens with and without exchange value, (2) the preference for tokens associated with qualitatively different reinforcers, and (3) a comparison of the effectiveness of token and food reinforcers in the acquisition and maintenance of behaviour. In the Wolfe's (1936) study, chimpanzees were trained to deposit manipulable tokens into a vending machine to obtain food as reward and learned to prefer tokens with exchange value (white tokens, exchangeable for food), while extinguishing their response towards tokens without exchange value (brass tokens, whose exchange did not produce any food reward). Accordingly, when the two types of tokens were scattered on the floor, the chimpanzees collected and deposited in the vending machine only the tokens with exchange value. The single capuchin monkey tested by Carpenter and Locke (1937) was much less proficient than chimpanzees when presented with multiple tokens, each associated with a differently preferred food item. The order in which the capuchin exchanged the tokens did not show a clear pattern of token-mediated food preference; moreover, he kept exchanging also tokens associated with a low-preferred food (that was not eaten) and tokens whose exchange was not rewarded.

In multiple studies, tokens proved to be functionally equivalent to unconditioned reinforcers in cognitive tasks, although subjects were slightly less proficient with tokens than with food. In the Wolfe's (1936) study, three chimpanzees, trained to operate a weight-lifting apparatus to obtain a reward, showed a similar performance when reinforced with either food or tokens, whereas a fourth individual showed a better performance with food than with tokens. In the Cowles' (1937) study, two chimpanzees rapidly learned a discrimination task both when food and tokens were provided as reward, but one of the two subjects showed an overall better performance with food than with tokens. These findings extended also to non-primate species, namely rats and pigeons, and to non-manipulable tokens (Hackenberg 2009). Moreover, in chimpanzees, matching-to-sample performance initially acquired by receiving food as reward was maintained when token reinforcers were introduced and, most notably, chimpanzees learned a novel matching-to-sample task when only tokens were provided as reward (Sousa and Matsuzawa 2001). Along these lines, in numerical discrimination tasks capuchin monkeys used similar cognitive mechanisms when choosing between either food or token options (Addessi et al. 2008a) and in economic choice tasks they combined the relative values assigned to three foods or to three tokens according to value transitivity (that holds when the relationship $n\ A{:}B \times n\ B{:}C = n\ A{:}C$ is statistically significant, Addessi et al. 2008b).

Capuchin monkeys and chimpanzees can also perform flexible computations to maximize their payoff when presented with binary choices between various amounts and combinations of different types of tokens (Addessi et al. 2007, 2008a; Beran et al. 2011; Beran and Evans 2012; Evans et al. 2010) or between mixed food–tokens comparisons (Beran et al. 2011; Beran and Evans 2012; Judge and Essler 2013; for similar results in parrots see also; Krasheninnikova et al. 2018). Furthermore, paradigms based on token exchange have been widely employed to investigate nonhuman primate responses to social inequity (Brosnan and de Waal 2014), decision-making biases (Santos and Chen 2009), and self-control (Addessi and Rossi 2011; Addessi et al. 2014). Nonetheless, there is still limited knowledge about which features tokens share with human money. To shed light on the above issue, we presented capuchin monkeys with two token-trading experiments to examine the occurrence of some proto-monetary behaviours, which could provide insights into the origins of human economy.

The first aim of the present study was to assess how token exchange is affected by token validity and familiarity in capuchin monkeys, a South-American primate species that, despite more than 35 million years of independent evolution, shows many behavioural and cognitive convergences with hominids (Fragaszy et al. 2004). In Experiment 1, capuchins were simultaneously presented with four types of items and required to exchange them in their preferred order. Specifically, they could choose among: (1) valid/familiar tokens: used in previous experiments, leading to a food reward, (2) valid/unfamiliar tokens: introduced in the present study, leading to a food reward, (3) invalid tokens: used in previous experiments, but here lost exchange value, and (4) no-value items: introduced in the present study, with no exchange value. We scored multiple measures of token preference: the latency to exchange each item, the order in which each item was exchanged within each session and the total number of exchanged items. According to the principles of reinforcement learning theory (Skinner 1938) and to the early findings in chimpanzees reported above (Wolfe 1936), we expected capuchins to prefer valid tokens, which were associated with a food item, to invalid tokens and no-value items, whose exchange was not rewarded. We also expected invalid tokens, which were explicitly not reinforced during an extinction training procedure, to acquire a lower value than no-value, neutral items. Moreover, on the basis of the results reported in Tallon-Baudry et al. (2011) with humans, we expected capuchins to rapidly engage in token exchanges with valid/unfamiliar tokens to a similar extent as well-known valid/familiar tokens.

In Experiment 2, we took further steps to assess the flexibility of the token–food association by investigating whether capuchins could engage in reverse food–token exchanges in several phases, in which we varied the difference in value between the token and the food. Moreover, to assess whether capuchins actually understand that tokens should be valuable to be worthwhile to engage in reverse food–token exchanges, in a control phase they were presented with chains of exchanges involving a no-value item (i.e., a token-like object with no conditioned value). In this paradigm, to perform a successful chain of exchanges, the first food item must be treated as a signal (indicating later access to a more preferred food through token exchange) rather than as a reward, by inhibiting the drive to immediately consume it. Whereas a few nonhuman animal species successfully performed simple and multiple food–food exchanges (western lowland gorillas, *Gorilla gorilla gorilla*, Chalmeau and Peignot 1998; capuchin monkeys; Drapier et al. 2005; Ramseyer et al. 2006; Westergaard et al. 2004; common ravens, *Corvus corax*, and carrion crows, *Corvus corone*; Hillemann et al. 2014; chimpanzees; Beran et al. 2016), to date no work has explored whether nonhuman animals can exchange an edible food item for an inedible token, that can be subsequently exchanged for another food item. On the basis of a reward-based account that conceptualizes tokens as conditioned reinforcers and on the above-reported literature on food–food exchanges, capuchins should engage in reverse food–token exchanges only when there is a substantial difference in value between food and token.

Overall, we expected our findings to go beyond what we already know about the abilities of nonhuman animals to use tokens as secondary reinforcers in two ways. First, by evidencing whether capuchins exhibit human-like abilities to recognize which features a medium of exchange—here tokens—must have to function effectively (Tallon-Baudry et al. 2011). Second, by examining whether capuchins spontaneously engage in food–token exchanges, which would represent a first evidence of the emergence of commodity money in a nonhuman primate species.

Experiment 1

Methods

Subjects

We individually tested six adult capuchins (three females) hosted at the Primate Center of the ISTC-CNR, Rome, Italy. All subjects had similar previous token exchange experience (Addessi et al. 2007, 2008a, 2010, 2011). They belonged to three social groups, each housed in enriched indoor–outdoor enclosures (indoor: 25.4 m^3; outdoor: 53.2–127.4 m^3, depending on group size), and were tested in their indoor enclosure between 10:00 AM and 3:00 PM, 5 days a week. They received one testing session a day. Separation for individual testing was achieved by first splitting the group into smaller units by means of sliding doors and then allowing one individual to enter the indoor compartment. Fresh fruit, vegetables and monkey chow were provided in the afternoon after testing. Water was available *ad libitum*. This study complied with protocols approved by the Italian Health Ministry (DM 123/214-C to E. Addessi) and was performed in full accordance with the Directive 2010/63/EU on the protection of animals used for scientific purposes.

Procedure

The study involved four training phases, in which capuchins learned (or refreshed) the features of four different types of items (Table 1; Fig. 1, see below), followed by an experimental phase.

Table 1 Experiment 1

Subject	Valid and familiar	Valid and unfamiliar	No-value	Invalid
Carlotta	Brass plug[a]	Metal T	Wooden cross	Metal nut[a]
Gal	Grey cylinder[a]	Screwdriver bit	Metal T	Yellow chip[a]
Paprica	Grey cylinder[a]	Metal screw	Metal T	Wooden knob[a]
Robinia	Grey cylinder[a]	Wooden cross	Screwdriver bit	Wooden knob[a]
Robot	Blue chip[a]	Metal T	Wooden cross	Metal nut[a]
Sandokan	Yellow chip[a]	Screwdriver bit	Metal T	Brass plug[a]

The table reports the different types of items used for each subject
[a]Previously used in Addessi et al. (2007, 2008a, 2010, 2011)

Fig. 1 The left panel depicts the items among which a unique combination of three tokens and one no-value item was selected for each subject in Experiment 1 (**a**), the middle panel depicts the tokens used in both experiments (**b**), and the right panel depicts the tokens used only in Experiment 2 (**c**). The euro coin serves as a size reference

Training phases

For each subject, we selected a unique combination of four different items of similar dimensions but differing in shape, material and colour (Table 1; Fig. 1). We carried out three separate training phases for the valid/familiar tokens, valid/unfamiliar tokens and invalid tokens, and one familiarization phase for the no-value items (see below for a description of the features of each item). The order of presentation of the four phases was counterbalanced across subjects.

The general procedure employed in the training phases was the same for valid/familiar tokens, valid/unfamiliar tokens, and invalid tokens. Tokens were scattered on the floor of the testing enclosure. The experimenter sat in front of the enclosure hosting the subject and requested a token every 15 s by saying ‘give me’ while showing her right hand outstretched with palm up. While performing this request, the experimenter did not look at or point to any specific item but just prompted the subject to return any one of the tokens on the floor. If a token was not exchanged within 60 s, the experimenter made a new token request after 10 s.

The valid/familiar token has already been employed in previous studies (Addessi et al. 2007, 2008a, 2010, 2011; Table 1). To refresh the association between this type of token and the corresponding reward (one high-preferred food item, i.e., 1/8 of peanut seed), we carried out three daily sessions in which each subject was presented with a budget of 20 identical valid/familiar tokens. Token exchanges were always immediately rewarded. Each session lasted about 5 min, until all tokens were transferred to the experimenter.

The valid/unfamiliar token was a novel item (Table 1). To introduce this type of token to capuchins, we carried out a training phase with the same procedure and food reward as described above for the valid/familiar token.

The invalid token was a previously valid/familiar token (employed in past studies and corresponding to one high-preferred food item; Addessi et al. 2007, 2008a, 2010; Table 1), which in the present study lost its exchange value during an extinction training. Each subject was presented with a budget of 20 identical tokens and the experimenter requested a token every 15 s, as in the training with valid/familiar and valid/unfamiliar tokens. However, token exchanges were not rewarded, and the experimenter remained still with a neutral face for 15 s; at the end of this time interval, the experimenter made a new token request. If a token was not exchanged within 60 s, the experimenter made a new token request after 10 s. In each session, capuchins were tested up until no exchanging attempts were done for three consecutive trials. Extinction training was considered complete after at least three consecutive sessions in which capuchins did not exchange a token within 60 s in three consecutive trials.

Finally, to familiarize capuchins with no-value items (Table 1), which are novel token-like items with no exchange value, we carried out three daily sessions in which each subject was provided with a budget of 20 identical items, not corresponding to any reward. In each session subjects could manipulate the no-value items for 5 min (a period of time equivalent to the duration of each training session carried out with valid tokens). The experimenter was present during the whole session but never requested the subject to exchange.

Experimental phase

The experimental phase started after the end of the training phase and consisted of ten sessions. In each session, subjects were provided with ten units of each of the four different types of item, for a total of 40 items. Items were scattered on the floor of the testing enclosure taking care that items of the same type were not close to each other, and every 15 s the subjects were requested to exchange an item with the experimenter, within a 10-min time limit. As dependent variables, for each item we recorded the order in which it was exchanged (hereafter "order of exchange", i.e., whether it was exchanged as first, second, third, and so on, up to a maximum of thirty-first, depending on the pace of each individual's exchanges within the 10-min session) and the latency to exchange (i.e., the time elapsing from the experimenter's request to the delivery of an item). Moreover, we computed the total number of exchanged items. FDP, EG and AM alternated in performing the exchanges in both the training and experimental phases.

Statistical analyses

We applied regression methods for longitudinal data analysis (van de Pol and Wright 2009; Snijders and; Bosker 1999) using the software Stata 14 (StataCorp. 2015. College Station, TX: StataCorp LP). For all regressions, the identity of the subject was included as a random effect and the significance of interaction effects was tested using the Wald test. Non-significant interactions were dropped from the model and the analysis was run again. We also compared the number of the different types of tokens exchanged by means of a within-subject ANOVA with Bonferroni post-hoc comparisons. Significance level was set at $P < 0.05$.

Results

Training phase

Valid tokens. We fit a fixed-effects within-subject regression model with latency to exchange as dependent variable, and type of token (valid/familiar, valid/unfamiliar), session number, and trial number (within the same session) as independent variables. Non-significant interactions between type of item and session ($F_{1,704} = 1.58$, $p = 0.21$) and type of item and trial ($F_{1,704} = 0.97$, $p = 0.33$) were dropped from the initial model and the last step examined the main effects. Latency to exchange did not significantly differ between valid/unfamiliar and valid/familiar tokens (coeff. = 0.67, $t = 1.39$, $p = 0.16$; Table 2) and did not significantly vary across sessions (coeff. = −0.46, $t = -1.54$, $p = 0.12$), whereas it significantly decreased over trials (coeff. = −0.13, $t = -3.07$, $p = 0.002$).

Invalid tokens. During the extinction training, capuchins took a variable number of sessions to stop exchanging invalid tokens (Table 2). We fit a fixed-effects within-subject regression model with latency to exchange as dependent variable, and session number and trial number as independent variables. Latency to exchange increased across sessions (coeff. = 1.11, $t = 10.83$, $p < 0.001$), whereas it decreased over trials (coeff. = −0.93, $t = -10.42$, $p < 0.001$).

Experimental phase

Capuchins exchanged a significantly higher number of valid tokens than no-value items or invalid tokens (Within-subject ANOVA: $F_{3,15} = 46.47$, $p < 0.001$; Bonferroni post-hoc tests: valid/familiar vs. no-value: $p < 0.001$; valid/familiar vs. invalid: $p < 0.001$; valid/unfamiliar vs. no-value: $p < 0.001$; valid/unfamiliar vs. invalid: $p < 0.001$; Fig. 2). They exchanged a similar number of valid/familiar and valid/unfamiliar tokens ($p = 1.0$) and of invalid tokens and no-value items ($p = 0.063$).

We fit two fixed-effects within-subject regression models with, respectively, the order of exchange and the latency to exchange as dependent variables, and type of item (valid/familiar, valid/unfamiliar, invalid, no-value) and session

Table 2 Experiment 1

	Latency to exchange (mean ± SEM)		Invalid tokens	
	Valid/familiar	Valid/unfamiliar	Sessions to criterion	Exchanged tokens
Carlotta	4.10 ± 0.46	15.34 ± 4.43	7	78
Gal	2.76 ± 0.26	2.48 ± 0.56	12	147
Paprica	4.56 ± 0.61	3.06 ± 0.37	26	347
Robinia	5.68 ± 0.75	5.08 ± 1.35	4	36
Robot	6.27 ± 1.06	4.63 ± 1.56	15	187
Sandokan	5.44 ± 1.69	2.24 ± 0.32	21	285

Training phase. For each subject, the table reports the latency to exchange (s) for the valid tokens, the number of sessions to reach criterion for the invalid tokens and the number of invalid tokens exchanged before reaching the criterion

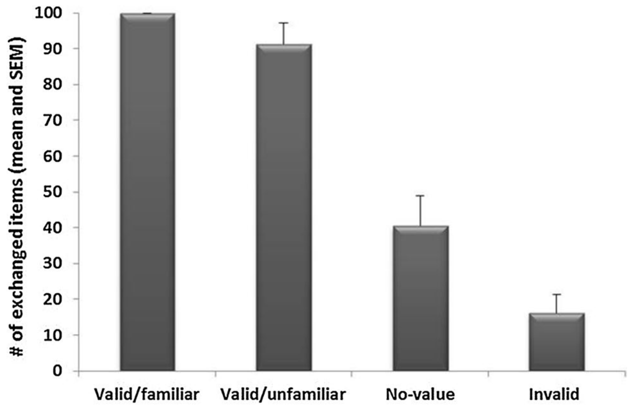

Fig. 2 Experiment 1, experimental phase. For each type of item, the graph depicts the total number of correct exchanges (mean and SEM)

number as independent variables. As for the order of exchange, there was a significant interaction between type of item and session ($F_{3,2383} = 9.33$, $p < 0.001$). As shown in Fig. 3 and Table 3, in all sessions valid/familiar tokens were exchanged significantly earlier than valid/unfamiliar tokens, which were always exchanged earlier than no-value items and invalid tokens. In all sessions but one, the order in which no-value items and invalid tokens were exchanged did not significantly differ. Across sessions, no-value items were exchanged increasingly later (coeff. = 0.13, $t = 2.11$, $p = 0.035$), whereas valid/unfamiliar tokens were exchanged increasingly earlier (coeff. = −0.38, $t = -5.45$, $p < 0.001$); the order of exchange of valid/familiar and invalid tokens did not significantly change across sessions (valid/familiar: coeff. = 0.079, $t = 1.25$, $p = 0.21$; invalid: coeff. = −0.07, $t = -1.40$, $p = 0.16$).

Similarly, for the latency to exchange there was a significant interaction between type of item and session ($F_{3,2383} = 7.08$, $p < 0.001$). As shown in Fig. 4 and Table 4, in

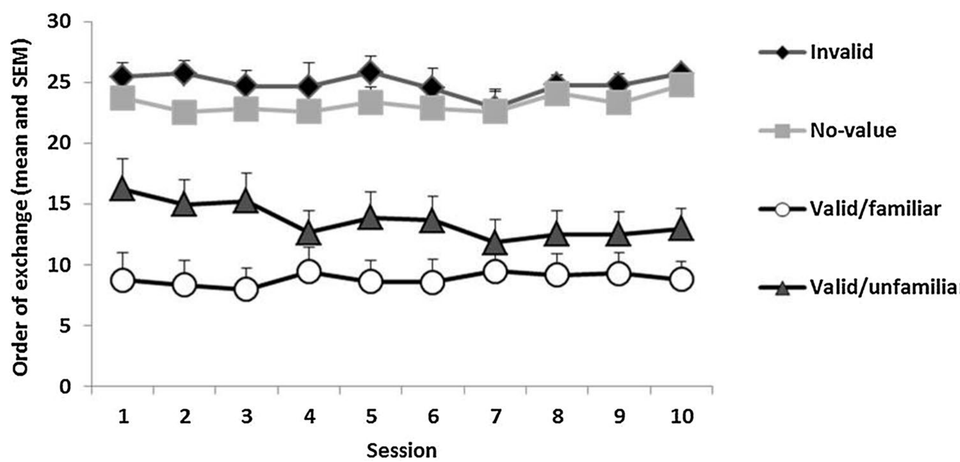

Fig. 3 Experiment 1, experimental phase. For each type of item, the graph depicts the average order in which it was exchanged, per subject, across experimental sessions (mean and SEM)

Table 3 Experiment 1

Sessions	Valid/familiar vs. valid/unfamiliar	Valid/familiar vs. no-value	Valid/familiar vs. invalid	Valid/unfamiliar vs. no-value	Valid/unfamiliar vs. invalid	No-value vs. invalid
1	**$t = -6.27$****	**$t = -12.57$****	**$t = -13.99$****	**$t = -6.30$****	**$t = -7.73$****	$t = -1.43$
2	**$t = -6.79$****	**$t = -14.54$****	**$t = -17.80$****	**$t = -7.75$****	**$t = -11.01$****	**$t = -3.26$***
3	**$t = -7.28$****	**$t = -14.89$****	**$t = -16.79$****	**$t = -7.61$****	**$t = -9.51$****	$t = -1.89$
4	**$t = -3.38$***	**$t = -13.78$****	**$t = -16.03$****	**$t = -10.41$****	**$t = -12.70$****	$t = -2.43$
5	**$t = -5.49$****	**$t = -15.37$****	**$t = -17.94$****	**$t = -9.88$****	**$t = -12.45$****	$t = -2.57$
6	**$t = -5.38$****	**$t = -15.17$****	**$t = -16.91$****	**$t = -9.80$****	**$t = -11.53$****	$t = -1.73$
7	**$t = -2.73$***	**$t = -15.64$****	**$t = -15.61$****	**$t = -12.51$****	**$t = -12.88$****	$t = -0.37$
8	**$t = -3.82$****	**$t = -17.00$****	**$t = -17.91$****	**$t = -13.20$****	**$t = -14.09$****	$t = -0.83$
9	**$t = -3.63$****	**$t = -15.75$****	**$t = -17.34$****	**$t = -12.12$****	**$t = -13.71$****	$t = -1.59$
10	**$t = -4.76$****	**$t = -18.25$****	**$t = -19.33$****	**$t = -13.49$****	**$t = -14.58$****	$t = -1.08$

Experimental phase. Order in which each item was exchanged. The table reports, for each session, the results of the pairwise comparisons between the four type of items (fixed-effects within-subject regression, see main text). Bonferroni-corrected significant results are highlighted in bold

*$p < 0.0083$, **$p < 0.001$

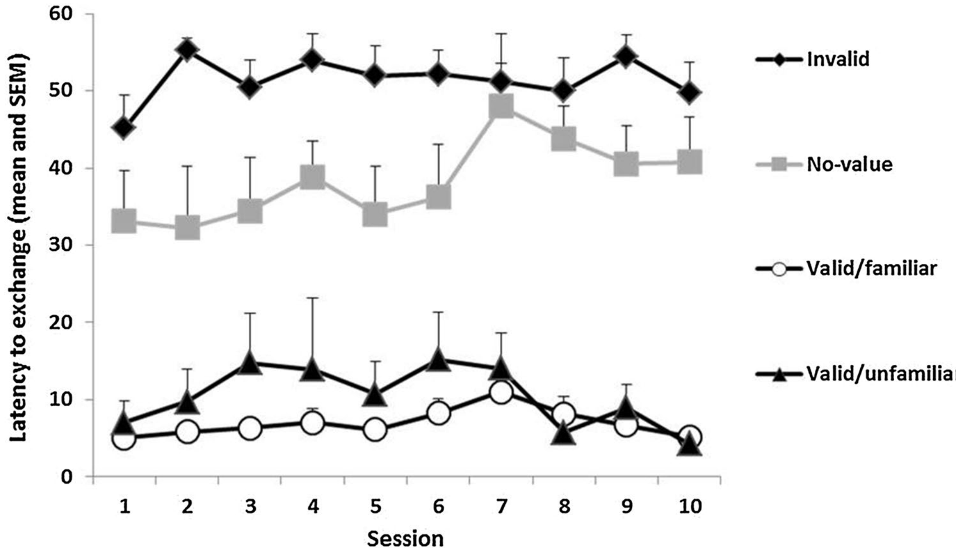

Fig. 4 Experiment 1, experimental phase. For each type of item, the graph depicts the average latency to exchange, per subject, across experimental sessions (mean and SEM)

Table 4 Experiment 1

Sessions	Valid/familiar vs. valid/unfamiliar	Valid/familiar vs. no-value	Valid/familiar vs. invalid	Valid/unfamiliar vs. no-value	Valid/unfamiliar vs. invalid	No-value vs. invalid
1	$t = -0.56$	$\mathbf{t = -7.83}$**	$\mathbf{t = -11.18}$**	$\mathbf{t = -7.27}$**	$\mathbf{t = -10.62}$**	$\mathbf{t = -3.35}$*
2	$t = -1.21$	$\mathbf{t = -8.19}$**	$\mathbf{t = -15.32}$**	$\mathbf{t = -6.98}$**	$\mathbf{t = -14.11}$**	$\mathbf{t = -7.13}$**
3	$t = -2.41$	$\mathbf{t = -8.03}$**	$\mathbf{t = -12.62}$**	$\mathbf{t = -5.62}$**	$\mathbf{t = -10.20}$**	$\mathbf{t = -4.59}$**
4	$t = -2.18$	$\mathbf{t = -10.14}$**	$\mathbf{t = -14.98}$**	$\mathbf{t = -7.96}$**	$\mathbf{t = -12.83}$**	$\mathbf{t = -4.98}$**
5	$t = -1.43$	$\mathbf{t = -8.55}$**	$\mathbf{t = -14.08}$**	$\mathbf{t = -7.12}$**	$\mathbf{t = -12.64}$**	$\mathbf{t = -5.52}$**
6	$t = -2.05$	$\mathbf{t = -8.26}$**	$\mathbf{t = -12.96}$**	$\mathbf{t = -6.21}$**	$\mathbf{t = -10.91}$**	$\mathbf{t = -4.70}$**
7	$t = -0.96$	$\mathbf{t = -11.69}$**	$\mathbf{t = -12.71}$**	$\mathbf{t = -10.73}$**	$\mathbf{t = -11.75}$**	$t = -1.02$
8	$t = 0.75$	$\mathbf{t = -11.35}$**	$\mathbf{t = -13.38}$**	$\mathbf{t = -12.10}$**	$\mathbf{t = -14.13}$**	$t = -1.98$
9	$t = -0.75$	$\mathbf{t = -11.19}$**	$\mathbf{t = -15.79}$**	$\mathbf{t = -10.44}$**	$\mathbf{t = -15.03}$**	$\mathbf{t = -4.59}$**
10	$t = 0.30$	$\mathbf{t = -11.36}$**	$\mathbf{t = -14.23}$**	$\mathbf{t = -11.65}$**	$\mathbf{t = -14.53}$**	$\mathbf{t = -2.88}$*

Experimental phase. Latency to exchange. The table reports, for each session, the results of the pairwise comparisons between the four type of items (fixed-effects within-subject regression, see main text). Bonferroni-corrected significant results are highlighted in bold

*$p < 0.0083$, **$p < 0.001$

all sessions latencies to exchange valid/familiar tokens and valid/unfamiliar tokens did not significantly differ and both types of valid tokens were exchanged with a significantly shorter latency than no-value items and invalid tokens. In eight out of ten sessions, no-value items were exchanged with a significantly shorter latency than invalid tokens. Across sessions, no-value items were exchanged with an increasingly longer latency (coeff. = 1.24, $t = 3.57$, $p < 0.001$), whereas valid/unfamiliar tokens were exchanged with an increasingly shorter latency (coeff. = -0.43, $t = -2.11$, $p = 0.035$); the latency to exchange valid/familiar and invalid tokens did not significantly vary across sessions (valid/familiar: coeff. = 0.18, $t = 1.90$, $p = 0.057$; invalid: coeff. = 0.16, $t = 0.60$, $p = 0.55$).

Experiment 2

Methods

Subjects

We individually tested the same six adult capuchins that participated in Experiment 1, except that in part of testing phase 3 and in testing phase 4, in which we tested five individuals (one female died before the completion of Experiment 2).

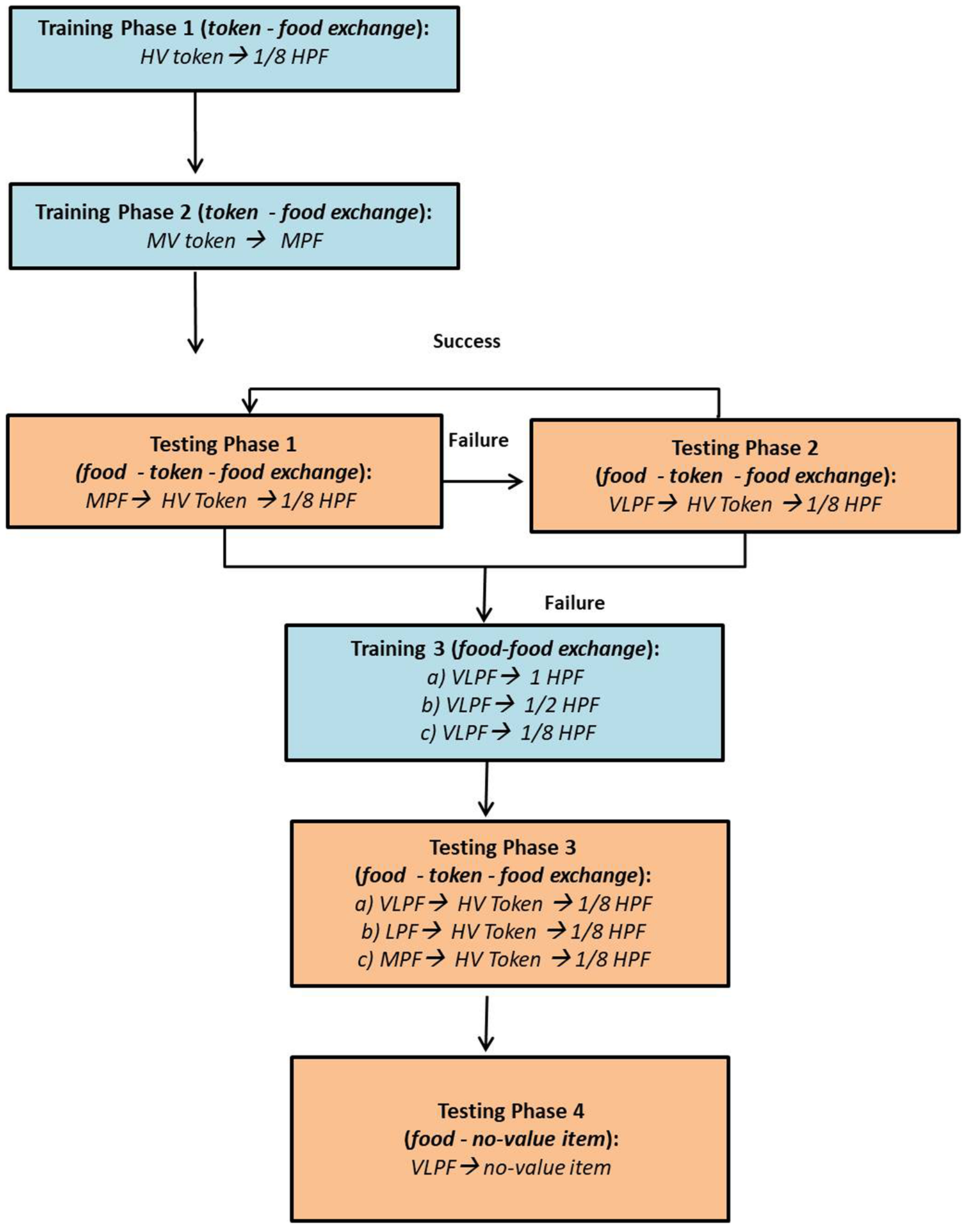

Fig. 5 Experiment 2. Schematic representation of the training and testing phases (*HV token* high-value token, *HPF* high-preferred food, *MV token* medium-value token, *MPF* moderately-preferred food, *LPF* low-preferred food, *VLPF* very low preferred food)

Procedure

The study involved seven consecutive phases (Fig. 5). In all phases, the experimenter sat in front of the subject's compartment, showing the monkey one of two different items (food or token, according to condition) in each hand for 3 s. After this time expired, the experimenter offered one of the two items to the subject while the other remained visible in the experimenter's other hand for 3 s. Then, the experimenter requested the subject to return the item in its possession, repeatedly saying 'give me' while showing the empty hand outstretched with palm up. If the subject gave back the item to the experimenter, it could receive the other item (with the only exception of testing phase 4, in which food exchanges were not rewarded). If the subject did not take the item from experimenter's hand, ate the item in its possession before 3 s, did not return the item within 60 s, or throw the item rather than correctly placing it into the experimenter' hand, s/he received nothing, and the trial ended. There was a 30-s intertrial interval. MC and SG alternated in performing the exchanges in all phases.

Training phases 1 (high-value token for high-preferred food) and 2 (medium-value token for moderately-preferred food)

The aim of these phases was both refreshing the token–food associations that have been previously established and

Table 5 Experiment 2

Subjects	HPF	MPF	LPF	VLPF
Carlotta	Raisin	Sunflower seed	Raw asparagus	Monkey chow
Gal	Peanut	Rice-krispies	Cooked radish	Monkey chow
Paprica	Peanut	Sunflower seed	Raw lettuce	Monkey chow
Robinia	Peanut	Sunflower seed	Raw celery	Monkey chow
Robot	Peanut	Dry apricot	Raw celery	Monkey chow
Sandokan	Peanut	Sunflower seed	Monkey chow	Fresh ginger

The table reports, for each subject, the four food items used during the study

HPF high-preferred food, *MPF* moderately-preferred food, *LPF* low-preferred food, *VLPF* very low preferred food

Table 6 Experiment 2

Subjects	Token associated with HPF	Token associated with MPF
Carlotta	Brass plug[a]	Brass hook[b]
Gal	Grey cylinder[a]	Black tube[b]
Paprica	Grey cylinder[a]	Green chip[b]
Robinia	Grey cylinder[a]	Green chip[b]
Robot	Blue chip[a]	Black tube[b]
Sandokan	Brass plug[a]	Brass hook[b]

The table reports, for each subject, the tokens associated with the high-preferred food (HPF) and with the moderately-preferred food (MPF)

[a]Previously used in Addessi et al. (2007, 2008a, 2011) and as valid/familiar token in Experiment 1 (except that for Sandokan, for which the token associated with HPF was the invalid token used in Experiment 1; however, Sandokan was re-trained to exchange this token for the high-preferred food and quickly resumed the exchange behaviour by reaching the criterion by session 6)

[b]Previously used in Addessi et al. (2008b)

training capuchins to exchange tokens for food with a novel procedure not used before (see above, Procedure). We required each subject to return one high-value token for one high-preferred food item (Training phase 1; please see Table 5), and one medium-value token for one moderately-preferred food item (Training phase 2; please see Table 5). We chose token–food pairs that had been used in previous token studies (Addessi et al. 2007, 2008a, b; Tables 5, 6; Fig. 1).

Each session included 12 trials. Criterion was set at 80% of correct responses within two consecutive sessions. For all subjects but one (Sandokan), the high-value token was the valid/familiar token used in Experiment 1. For the subject Sandokan, the high-value token was the invalid token used in Experiment 1; however, Sandokan was re-trained to exchange this token for the high-preferred food and quickly resumed the exchange behaviour by reaching the criterion by session 6.

Testing phases 1A (moderately-preferred food for high-value token), 2 (very low preferred food for high-value token) and 1B (moderately-preferred food for high-value token)

The aim of these phases was to evaluate whether capuchins could sustain a chain of advantageous food–token–food exchanges. In testing phase 1A, we required each subject to return one moderately-preferred food item for one high-value token that could be then exchanged for the corresponding high-preferred food. We presented five 12-trial sessions. The dependent measure was the number of successful exchanges. Additionally, we scored all the episodes in which subjects refused to take the food from the experimenter's hand, did not exchange the food item or performed incorrect exchanges (please see Procedure above).

Since virtually no subject succeeded in testing phase 1A (please see "Results" section), we carried out testing phase 2 with the same procedure as testing phase 1A, but with the only exception that we used a very low preferred food. As very low preferred food, we chose monkey chow on the basis of a previous study on capuchins' food preferences (Addessi et al. 2005). In testing phase 2, we required each subject to return one very low preferred food item for one high-value token, which could be then exchanged for the corresponding high-preferred food. Also in this phase, we presented five 12-trial sessions.

As shown in Fig. 5, the subjects who succeeded in more than 50% of the trials of testing phase 2 were tested in testing phase 1B (with exactly the same procedure used in testing phase 1A) and then in Training phase 3; the other subjects moved directly to Training phase 3.

Training phase 3 (food–food exchanges)

The aim of this phase was to train capuchins to perform food–food exchanges. Training phase 3 involved three consecutive conditions, in which each subject had to return one unit of very low preferred food to obtain as a reward: (1) Training phase 3A—one high-preferred food item (one peanut seed or one raisin, according to food preferences, as reported in Table 5), (2) Training phase 3B—½ high-preferred food item, (3) Training phase 3C—1/8 high-preferred food item. We expected these conditions to present an increasing level of difficulty. In each condition, criterion was set at 80% of correct responses within two consecutive 12-trial sessions. After reaching criterion in Training phase 3, capuchins were presented with food preference tests and then tested in testing phase 3.

Food preference tests

Since during testing phase 2, one of the subjects (Sandokan) showed a higher preference for the monkey chow compared to the other subjects (please see "Results" section below), before proceeding with the phase 3 (see below), we carried out a series of food preference tests aiming to select one low-preferred food and one very low preferred food. In every trial, each subject faced a binary choice between one unit of high-preferred food and one unit of another food (pieces were equally sized and weighed on average 0.2 g). The left/right combination of the offers was counterbalanced within each session. We tested one high-preferred/less-preferred food comparison at a time for a total of ten trials each. We selected as less-preferred food the one that the subject chose in 10% (or less) of the trials. If this was not the case, we tested another food against the high-preferred food. After obtaining two food types less preferred than the high-preferred food, we tested them against each other with the same binary choice procedure reported above, to identify the low-preferred food and the very low preferred food. Specifically, the food chosen in at least 70% of the trials was labelled as the low-preferred food and the other food as the very low preferred food. The low-preferred food assigned to each capuchin is reported in Table 5. For all subjects but Sandokan, the food preference tests confirmed monkey chow as the very low preferred food, whereas Sandokan had fresh ginger as very low preferred food and monkey chow as low-preferred food.

Testing phase 3 (very low preferred food, low-preferred food or moderately-preferred food for high-value token)

As the previous testing phases, the aim of testing phase 3 was to evaluate whether capuchins could sustain a chain of food–token–food exchanges. Testing phase 3 involved three consecutive conditions. As in testing phase 2, in the first condition of testing phase 3 (testing phase 3A), subjects were required to return one very low preferred food item for one high-value token, which could be then exchanged for one high-preferred food item (e.g., 1/8 peanut seed or raisin). In the second condition (testing phase 3B), subjects were required to return one low-preferred food item for one high-value token, which could be then exchanged for one high-preferred food item. In testing phase 3C, subjects were required to return one moderately-preferred food item for one high-value token, which could be then exchanged for one high-preferred food item. There were five 12-trial sessions for each condition. The dependent measure was the number of successful exchanges. Additionally, we scored all the episodes in which subjects refused to take the food from the experimenter's hand, did not exchange the food item or performed incorrect exchanges (please see Procedure above).

Testing phase 4 (very low preferred food for no-value item)

The aim of testing phase 4 was to evaluate whether capuchins would engage in reverse food–token exchanges when a no-value item (i.e., a token-like object with no exchange value) was involved (Fig. 1). We required each subject to return one very low preferred food item for a no-value item, whose exchange did not yield to any reward. For all subjects, the no-value item was the same used in Experiment 1 (Table 1). As in the previous testing phases, we presented five 12-trial sessions. The dependent measure was the number of exchanges. Additionally, we scored all the episodes in which subjects refused to take the food from the experimenter's hand, did not exchange the food item or performed incorrect exchanges (please see Procedure above).

Statistical analyses

As in Experiment 1, we applied regression methods for longitudinal data analysis.

Results

Training phases 1 (high-value token for high-preferred food) and 2 (medium-value token for moderately-preferred food)

In training phase 1, capuchins took from 2 to 11 sessions to reach criterion (mean ± SEM: 5.17 ± 1.38). We fit a conditional fixed-effects logistic regression model with correct exchange as dependent variable, and session number and trial number (within the same session) as independent variables. Performance significantly improved across sessions ($z = 4.37$, $p < 0.001$) but not over trials within the same session ($z = 1.70$, $p = 0.089$). In training phase 2, capuchins took from 2 to 7 sessions to reach criterion (mean ± SEM: 3.17 ± 0.79). We analyzed the data as in training phase 1; performance significantly improved across sessions ($z = 3.06$, $p = 0.002$) and over trials within the same session ($z = 2.37$, $p = 0.018$). Please see Fig. 6 for a detailed representation of individual performance across the five sessions of training phases 1 and 2.

Testing phases 1A (moderately-preferred food for high-value token), 2 (very low preferred food for high-value token) and 1B (moderately-preferred food for high-value token)

In testing phase 1A, only one subject (Robot) succeeded in six trials (session 1, trials 11 and 12; session 5, trials 4, 8,

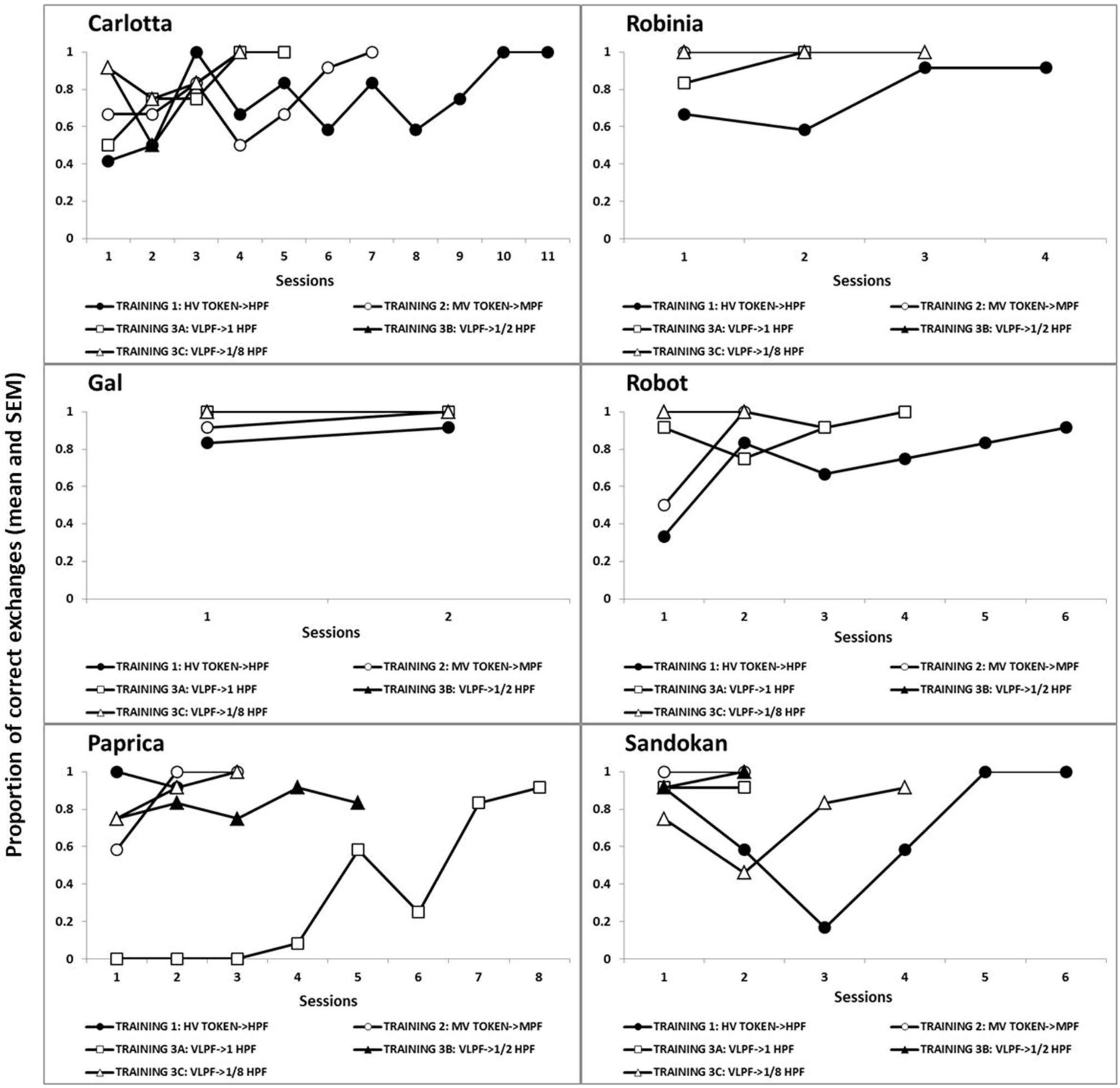

Fig. 6 Experiment 2. The figure depicts the mean proportion of correct exchanges (and SEM) in each session of the training phases (*HV token* high-value token, *HPF* high-preferred food, *MV token* medium-value token, *MPF* moderately-preferred food, *VLPF* very low preferred food)

10, and 12). After testing phase 1A, all subjects were tested in testing phase 2, in which all subjects but one (Sandokan) succeeded in at least some trials. Three subjects were successful since the first session (Carlotta 8.3%, Gal 83.3%, and Robinia 66.7%). Please see Fig. 7 for a detailed representation of individual performance across the five sessions of each testing phase.

The two subjects who succeeded in more than 50% of the trials of testing phase 2 (Gal and Robinia) were tested in testing phase 1B with the same procedure as testing phase 1A. However, both of them did not perform any correct exchange.

Training phase 3 (food–food exchanges)

In training phase 3, capuchins took from 2 to 8 sessions to reach criterion (mean ± SEM: training phase 3A—one high-preferred food item: 3.67 ± 0.95; training phase 3B—½ high-preferred food item: 2.83 ± 0.54; training phase 3C—1/8 high-preferred food item: 3.0 ± 0.36). We fit a conditional

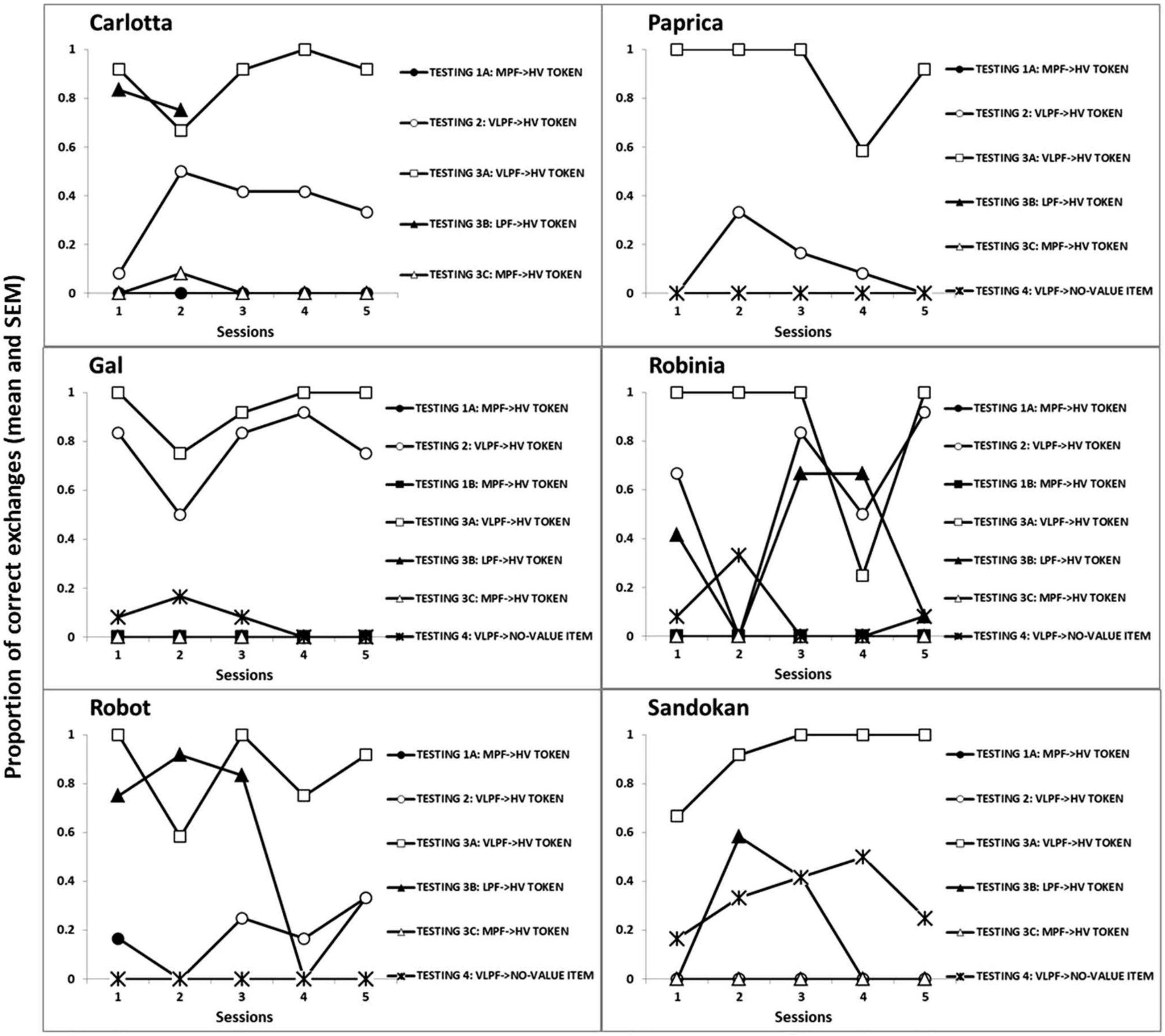

Fig. 7 Experiment 2. The figure depicts, for each individual, the mean proportion of correct exchanges (and SEM) in each session of the testing phases (*HV token* high-value token, *MPF* moderately-preferred food, *LPF* low-preferred food, *VLPF* very low preferred food; for details please see main text)

fixed-effects logistic regression model with correct exchange as dependent variable, and condition (training phase 3A—one high-preferred food item, training phase 3B—½ high-preferred food item, training phase 3C—1/8 high-preferred food item), session number and trial number (within the same session) as independent variables. Performance significantly improved across sessions ($z = 5.07$, $p < 0.001$) and there was a significant interaction between condition and trial ($\chi^2_2 = 11.12$, $p = 0.004$). Specifically, only in the training phase 3C—1/8 high-preferred food item condition, performance improved over trials within the same session ($z = 3.65$, $p < 0.001$), whereas in the other two conditions it did not significantly vary (training phase 3A—one high-preferred food item: $z = 0.03$, $p = 0.98$; training phase 3B—½ high-preferred food item: $z = 0.58$, $p = 0.56$). Please see Fig. 6 for a detailed representation of individual performance across the five sessions of training phase 3.

Testing phase 3 (very low preferred food, low-preferred food or moderately-preferred food for high-value token)

In testing phase 3, capuchins succeeded to a different extent, depending on the preference for the food to be exchanged for the token. In testing phase 3A (with VLPF food), all subjects succeeded in over 80% of the trials. In testing phase 3B (with LPF food), two subjects (Gal and Paprica) never succeeded;

the remaining four subjects succeeded to a variable extent. Finally, in testing phase 3C (with MPF food), only one subject (Carlotta) succeeded in one trial (session 2, trial 7). Please see Fig. 7 for a detailed representation of individual performance across the five sessions of each testing phase.

Testing phase 4 (very low preferred food for no-value item)

In testing phase 4, only one subject (Sandokan) exchanged a very low preferred food for a no-value item in one-third of the trials. Two subjects (Gal and Robinia) did so in four and six trials out of 60, respectively (Gal: session 1, trial 11; session 2, trials 6 and 11; session 3, trial 1; Robinia: session 1, trial 11; session 2, trials 8, 10, 11, and 12; session 5, trial 12) and two subjects (Paprica and Robot) never performed correct exchanges. Please see Fig. 7 for a detailed representation of individual performance across the five sessions of testing phase 4.

Analyses of testing phases 2, 3A, 3B and 4

We performed a group level analysis including all the testing phases with at least three successful subjects (testing phases 2, 3A, 3B and 4). Although Carlotta was successful in testing phase 3B, her data were dropped from this analysis since she was able to perform only two sessions (out of five) before dying.

We fit a conditional fixed-effects logistic regression model with correct exchange as dependent variable, testing phase, session number and trial number (within the same session) as independent variables. There was a significant interaction between testing phase and session ($\chi^2_3 = 18.27$, $p < 0.001$). As shown in Fig. 8, performance significantly improved across sessions in testing phase 2 ($z = 2.70$, $p = 0.007$), significantly decreased across sessions in testing phases 3B ($z = -4.06$, $p < 0.001$), and did not vary significantly in testing phases 3A ($z = 0$, $p = 1$) and 4 ($z = -0.61$, $p = 0.54$). Additionally, performance improved over trials in all testing phases (testing phase 2: $z = 4.79$, $p < 0.001$; testing phase 3A: $z = 2.15$, $p = 0.031$; testing phase 3B: $z = 3.79$, $p < 0.001$; testing phase 4: $z = 3.08$, $p = 0.002$).

Pattern of errors

As reported in Table 7, in all testing phases the chain of exchanges usually interrupted at the very beginning: in 93.7% of errors, capuchins did not exchange the food for the token ("no exchange errors"), either because they ate it ("eats"; this occurred in 98.2% of the no exchange errors) or because, very rarely, they did not return the food back to the experimenter within 1 min ("no food back"; this occurred in 1.8% of the no exchange errors). In 5.2% of errors, capuchins performed an incorrect exchange, either because they throw the food rather than correctly placing into the experimenter's hand ("throw food"; this occurred in 97.9% of the incorrect exchange errors) or because, very rarely and only in the testing phase 4, they throw the token ("throw token"; this occurred in 2.1% of the incorrect exchange errors). Finally, in 1.1% of errors, capuchins refused to take the food from the experimenter.

Discussion

The present work included two experiments aiming to assess whether some features of human money may be traced back to the exchange habits of nonhuman animals. We investigated this issue in capuchin monkeys, which have repeatedly demonstrated to flexibly use tokens in different domains (e.g., Addessi et al. 2007, 2008a, b, 2014; Addessi and Rossi 2011; Judge and Essler 2013; Santos and Chen 2009).

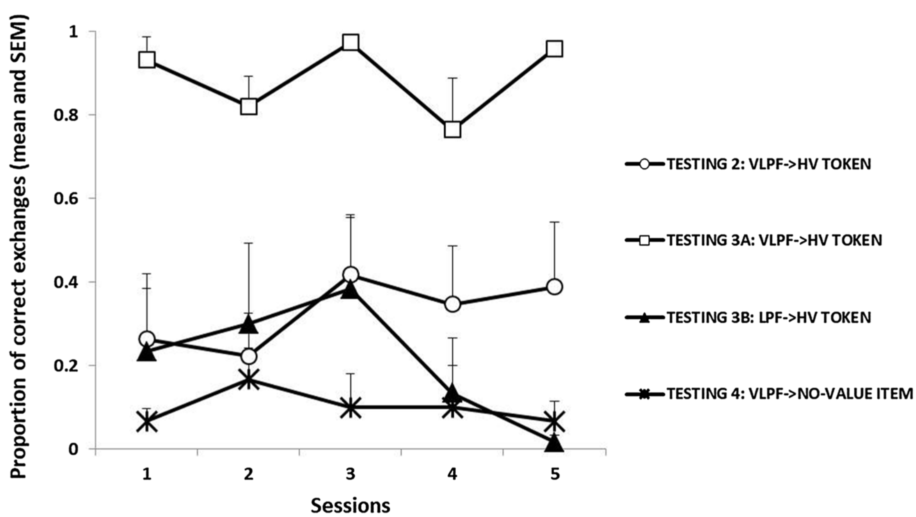

Fig. 8 Experiment 2. The figure depicts the mean proportion of correct exchanges (and SEM) in testing phases 2, 3A, 3B and 4 (*HV token* high-value token, *LPF* low-preferred food, *VLPF* very low preferred food)

Table 7 Experiment 2

	Errors/trials (%)	No exchange	Eats food No food back	Incorrect exchange	Throw food Throw token	Refusals to take food
TESTING 1A MPF->HV TOKEN	354/360 (98.3%)	354 (100%)	352 (99.4%) 2 (0.6%)	0	0 0	0
TESTING 2 VLPF->HV TOKEN	242/360 (67.2%)	232 (95.9%)	224 (96.6%) 8 (3.4%)	10 (4.1%)	10 (100%) 0	0
TESTING 1B MPF->HV TOKEN	120/120 (100%)	120 (100%)	120 (100%) 0	0	0 0	0
TESTING 3A VLPF->HV TOKEN	40/360 (11.1%)	32 (80%)	30 (93.7%) 2 (6.3%)	7 (17.5%)	7 (100%) 0	1 (2.5%)
TESTING 3B LPF->HV TOKEN	236/300 (78.7%)	233 (98.7%)	233 (100%) 0	3 (1.3%)	3 (100%) 0	0
TESTING 3C MPF->HV TOKEN	359/360 (99.7%)	359 (100%)	359 (100%) 0	0	0 0	0
TESTING 4 VLPF->NO-VALUE TOKEN	270/300 (90%)	220 (81.5%)	215 (97.7%) 5 (2.3%)	36 (13.3%)	33 (91.7%) 3 (8.3%)	14 (5.2%)

For each testing phase, the table reports the number of errors on the total number of trials (and relative %), the number (and relative %) of "no exchange" errors and of their subtypes ("eats food" and "no food back"), the number (and relative %) of "incorrect exchange" errors and of their subtypes ("throw food" and "throw token"), and the number (and relative %) of refusals to take food from the experimenter

In Experiment 1, we evaluated whether capuchins can recognize token validity, regardless of familiarity, as it has been previously shown in human subjects tested in a different paradigm with coins (Tallon-Baudry et al. 2011). Overall, capuchin monkeys presented with the opportunity of freely exchanging four types of items differing in their validity and/or novelty, readily appreciated the features of each type of item and behaved accordingly.

After a very short refresh exposure, capuchins were eager to exchange valid/familiar tokens, although more than 5 years have passed since the last study in which they encountered this type of token (Addessi et al. 2007, 2008a, 2011). Notably, a short training was sufficient to introduce valid/unfamiliar tokens: latency to exchange was similar for valid/familiar and valid/unfamiliar tokens, and remained stable across training sessions. Likewise, in the experimental phase, capuchins behaved similarly towards both types of valid tokens, by exchanging a similar number of valid/familiar and valid/unfamiliar tokens with a similar latency. Token familiarity did affect only the order in which each type of item was exchanged: in the course of each experimental session capuchins consistently exchanged valid/familiar tokens before valid/unfamiliar tokens, likely because of some cautiousness towards novel items (Visalberghi et al. 2003).

After a relatively short extinction training, all capuchins learned that tokens employed in previous studies and associated with a high-preferred food reward (Addessi et al. 2007, 2008a, 2010) were no longer valid. As expected, latency to exchange invalid tokens increased across sessions (since exchanging attempts were never rewarded). Although there were interindividual differences in the number of sessions required to stop exchanging attempts during the extinction training, these differences cannot be accounted for by the shape and/or colour of the tokens employed with different subjects. In fact, subjects assigned to the same type of token (as Robinia and Paprica) showed a very different learning speed. In the experimental phase, invalid tokens were treated similarly to no-value items, i.e., objects of token-like appearance but without any conditioned value, since capuchins exchanged a similar number of both invalid tokens and no-value items. Actually, in most sessions latency to exchange was shorter for no-value items than for invalid tokens, likely because, as a result of the extinction training, the value of invalid tokens dropped below that of neutral items.

Importantly, capuchins readily recognized the validity of the medium of exchange regardless of its familiarity, as did human subjects (Tallon-Baudry et al. 2011), by consistently exchanging a higher number of valid tokens than invalid tokens or no-value items. Moreover, from the very first session they exchanged valid tokens earlier and faster than both types of no-value items. Capuchins' behaviour towards tokens is consistent with the principles of reinforcement learning theory (Skinner 1938). Interestingly, they behaved more similarly to the chimpanzees tested by Wolfe (1936), which learned to preferentially exchange valuable tokens and to refrain returning tokens devoid of exchange value, rather than to the single capuchin monkey tested by Carpenter and Locke (1937), which kept repeatedly exchanging also no-value tokens, whose exchange was not rewarded. These findings add to the growing evidence of convergence in many cognitive skills between capuchin monkeys and chimpanzees (Visalberghi et al. 2015) and, at the same time, underline the crucial role played by individual differences in cognitive performance and the importance to test multiple individuals of the same species before drawing any conclusion about a species' cognitive abilities.

In Experiment 2, we evaluated the flexibility of the token–food association by assessing whether capuchins could engage in reverse food–token exchanges in several phases, varying for the difference in value between the food and the token.

In training phases 1 and 2, capuchins quickly mastered the novel exchange procedure (consisting of receiving a token from the experimenter and exchanging it back for the corresponding reward after a brief delay), although it differed from the usual exchange procedures to which they were accustomed (e.g., Addessi et al. 2007, 2008a, b, 2010, 2011). This was expected on the basis of a previous study in which individuals belonging to another capuchin group successfully retained a food item for a certain time interval before returning it to the experimenter for a more preferred food item (Ramseyer et al. 2006).

In testing phase 2 (in which a very low preferred food had to be exchanged for a high-value token), virtually all capuchins spontaneously engaged in a simple chain of food–token–food exchanges, although with some interindividual differences in the rate of success. Thus, capuchins were able to reverse the previously acquired rule of exchanging a token for a food item. In doing so, they treated the first food item as a signal (indicating later access to a more preferred food through token exchange) rather than as a reward, showing both the ability of inhibiting the drive to immediately consume the food (as shown, although with some limitations, also in Addessi et al. 2013) and a high-degree of behavioural flexibility (as they did in other contexts, as for instance in token choices; e.g., Addessi et al. 2007). Only one subject (Sandokan) consistently failed in testing phase 2, since he always ate the supposed very low preferred food. Although we carefully chose monkey chow as the very low preferred food on the basis of the preferences shown by the same capuchin colony in a previous study (Addessi et al. 2005), after further preference tests we verified that Sandokan preferred the monkey chow to a higher extent than the other capuchins. When we replaced the very low preferred food with a different food item (fresh ginger), in testing phase 3A Sandokan performed food–token–food exchanges at a comparable level with the other individuals.

Whilst all capuchins were successful when facing highly advantageous exchanges—that is when the food to return to the experimenter was very low preferred compared to the food corresponding to the high-value token—they succeeded to a lower extent and with broader differences among individuals when the food item to be exchanged for the high-value token was of slightly better quality than the very low preferred food (testing phase 3B) and, only occasionally, when the food was judged as mid preferred (testing phases 1A and 3C). Virtually all errors in performing food–token exchanges were failures in self-control (Beran et al. 2016), in which capuchins ate the food before exchanging it, rather than incorrect food or token exchanges (which occurred much more rarely). The above findings were expected on the basis of a reward-based account that conceptualizes tokens as conditioned reinforcers and mirrors the results obtained in the context of food–food exchanges in other capuchin groups, crows and ravens, which were generally less likely to exchange with the experimenter their initial food item when it was of a similar or lower quality than the expected reward (Drapier et al. 2005; Hillemann et al. 2014; Westergaard et al. 2004). Likewise, in a study in which capuchins, after exchanging a token, could choose between the corresponding food reward and a higher-value token, subjects succeeded most when the difference in value between the food reward and the token was more pronounced (Judge and Essler 2013; for similar results in parrots see also Krasheninnikova et al. 2018).

Although capuchins could engage in spontaneous food–token exchanges even in the absence of a specific training, their performance greatly improved from testing phase 2 to testing phase 3A (i.e., the two phases in which a very low preferred food had to be exchanged for a high-value token), likely as a result of training in performing food–food exchanges during training phase 3. This finding suggests that tokens are virtually equivalent to food stimuli (Addessi et al. 2008a, b; Beran et al. 2011; Cowles 1937; Hackenberg 2009; Sousa and Matsuzawa 2001). However, further experiments involving food–food and token–food exchanges between several qualitatively different items are needed to confirm this hypothesis.

In a control phase (testing phase 4), capuchins were required to return a very low preferred food item for a no-value item, whose exchange did not yield to any reward. Theoretically, in this phase capuchins should have refrained from exchanging the food item in their possession for the valueless tokens. Indeed, two subjects did so, and two other subjects performed food–token exchanges only occasionally. Only one subject (Sandokan) exchanged the very low preferred food for the valueless token in about one-third of the trials. Again, food preference level possibly explains Sandokan's behaviour. He may have liked his very low preferred food (fresh ginger) to a lower extent than the other capuchins liked their low-preferred food (monkey chow), thus being more prone to exchange the food, even for a valueless token, rather than eating it. The apparently irrational Sandokan's exchange behaviour may have been prompted also by his extraordinary motivation to exchange tokens, that he has repeatedly shown across different studies and that led him to be the best performing capuchin of this colony (e.g., Addessi et al. 2007, 2008a). However, it should be noted that in testing phase 4, Sandokan performed food–token exchanges to a much lower extent than in testing phase 3A (in which the very low preferred food was exchanged for the high-value token and he succeeded in more than 90% of the trials).

In all the testing phases that were analyzable (2, 3A, 3B, and 4), food–token exchanges increased over trials (within the same session), possibly due to a progressive increase in satiety that reduced the propensity to eat the food before exchanging it with the experimenter. Across sessions, food–token exchanges increased in testing phase 2 (as an effect of the repeated experience of exchanging a very low preferred food for a high-value token), remained stable in testing phase 3A (where all subjects showed a highly accurate performance from the first session) and in testing phase 4 (where a very few exchanges were performed), and worsened in testing phase 3B (possibly because the positive effect of training phase 3 was not long lasting when a food of acceptable quality, as the low-preferred food, was involved).

Overall, from the findings of Experiment 2 it emerged that at least five factors influence the individual's decision-making process when provided with the opportunity of performing reverse food–token exchanges: food quality, satiety, token value, level of experience, and motivation to exchange. It seems that the first three factors, and especially food quality (which affects self-control), are the most important determinants of capuchins' willingness to perform reverse food–token exchanges. Further research will be needed to systematically explore the relative role and the interplay of these variables.

In conclusion, the present study reported empirical evidence of at least some analogies between capuchin tokens and human money. In Experiment 1, capuchin monkeys used tokens as a medium of exchange and readily understood which features tokens must have to function effectively, as shown in humans with coins (Tallon-Baudry et al. 2011). In Experiment 2, capuchins were able to reverse the token–food exchange sequence, previously learned in several studies (Addessi et al. 2007, 2008a, b, 2010, 2011) and further trained in the present work, by spontaneously engaging in food–token exchanges. To that extent, our work expands what is already known in the nonhuman primate token literature and opens the possibility that some precursors of a proto-monetary behaviour, according to which an exchange is mediated through an item that is in principle a primary reinforcer and temporarily becomes a secondary reinforcer, may be found in at least some primate species. The transition from primary to secondary reinforcers is essential for the emergence of commodity money and here capuchin monkeys showed a similar ability to use "commodity money" (very low preferred food items) and "fiat money" (tokens).

Nonetheless, nonhuman primates are still far from having a fully-fledged monetary system. In fact, although in capuchin monkeys tokens can function as generalized reinforcers (Addessi et al. 2011; Santos and Chen 2009; see also Andrade and Hackenberg 2017; DeFulio et al. 2014; Tan and Hackenberg 2015, for evidence in pigeons), and some individual chimpanzees showed spontaneous instances of token savings (Sousa and Matsuzawa 2001)—which are among the most prominent features of money—other crucial money characteristics, such as spontaneous interspecific exchange, are lacking (Brosnan and Beran 2009).

Notwithstanding the above limitation, future studies should assess whether the similarity between tokens and money extends to other contexts and species, as capuchin monkeys have been identified as one of the taxa that have evolved more sophisticated cognitive skills among nonhuman primates (e.g., Reader et al. 2011). In addition, investigating whether the same neural correlates are recruited during trading in both humans and nonhuman primates could shed further light into the evolutionary origins of our complex monetary system.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical statements All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This study complied with protocols approved by the Italian Health Ministry (DM 123/214-C to E. Addessi) and was performed in full accordance with the Directive 2010/63/EU on the protection of animals used for scientific purposes.

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