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How Social Context, Token Value, and Time Course Affect Token Exchange in Capuchin Monkeys (*Cebus apella*)

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Abstract Although numerous studies have examined token-directed behaviors in primates, few have done so in a social context despite the fact that most primate species live in complex groups. Here, we provided capuchin monkeys with a relatively limited budget of tokens, likely to elicit intragroup competition, and, after an overnight delay, we allowed them to exchange tokens while in a group setting. We aimed to 1) evaluate whether social context affects token-directed behaviors of knowledgeable subjects, i.e., subjects already proficient in token exchange before the present study, as well as of naïve subjects, i.e., subjects that never showed exchange behavior before this study; 2) appraise whether capuchins indeed value tokens; and 3) assess whether capuchins can refrain from throwing tokens outside their enclosure when the experimenter is not present. Overall, the social context positively affected high-ranking individuals and negatively affected low-ranking ones. All 6 high-ranking naïve subjects, but none of the 4 low-ranking ones, quickly acquired token exchange behavior, whereas 9 of 12 low-ranking knowledgeable subjects, but only 1 high-ranking knowledgeable subject, never displayed token exchange in social contexts. Thus, competition constrained token exchange in low-ranking subjects and prompted exchange behavior in high-ranking naïve subjects. Capuchins were unable to inhibit the exchange of valueless items when the experimenter was soliciting them and, at the group level, knowledgeable subjects did not exchange more valuable tokens than less valuable (or valueless) ones. However, the 3 high-ranking knowledgeable subjects that exchanged most of the tokens first preferentially exchanged more valuable tokens over less valuable or valueless ones. Finally, capuchins inhibited exchange behavior in the absence of the experimenter, thus recognizing the appropriate conditions in which a successful exchange could occur.

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Introduction

In many animal species, acting together with group members facilitates the acquisition of novel behaviors (Fragaszy and Perry 2003; Fragaszy and Visalberghi 2004; Heyes and Galef 1996; Tomasello and Call 1997). For instance, animals learn to solve a new task more readily when they can act together with a proficient partner because the individual's attention is drawn to where other group members are or to the activity they are performing, thus making it more likely for the individual to learn a novel behavior by local/stimulus enhancement (Fragaszy and Visalberghi 2004; Spence 1937; Thorpe 1956). However, group living also increases intragroup feeding competition (van Schaik 1989), and dominant individuals tend to monopolize access to food when resources are clumped (Janson 1985; Koenig *et al.* 1998; van Schaik and van Noordwijk 1988). As a result, the social factors associated with this competition may inhibit performance: low-ranking individuals may avoid the expression of acquired behaviors when in the presence of high-ranking group members but readily perform them when individually tested (Drea and Wallen 1999; Fragaszy and Visalberghi 1990). Recently, Bonnie *et al.* (2007) studied the transfer of an arbitrary convention involving the use of tokens in 2 groups of chimpanzees. After observing a model being rewarded when inserting tokens in a receptacle, the most dominant individuals monopolized both tokens and the receptacle, but only about half of the subjects performed the correct behavior. Thus, social factors inhibited some chimpanzees from trying to employ a sequence of initially arbitrary actions involving tokens.

Still, competition may improve performance in cognitive tasks. According to Hare's (2001) competitive cognition hypothesis, the competitive nature of chimpanzee social life leads them to perform better in competitive than in cooperative tasks because a competitive environment enhances subjects' motivation, thus increasing attention to the features of the task. The ability of chimpanzees both to take the perspective of others into account (Hare *et al.* 2000) and to use human communicative cues to retrieve hidden food (Hare and Tomasello 2004) emerged when employing competitive paradigms instead of cooperative ones, and this was more evident when the competitor was another chimpanzee rather than a human.

Tokens are inherently nonvaluable objects that acquire an arbitrary value upon exchange with the experimenter (Brosnan and de Waal 2004). Many studies have employed the paradigm of token exchange to assess a variety of cognitive skills in monkeys and apes, such as the effectiveness of tokens as secondary reinforcements (Cowles 1937; Kelleher 1956, 1957a, b; Sousa and Matsuzawa 2001; Wolfe 1936), the use of tokens to request a specific food (Brosnan and de Waal 2004, 2005) or a tool (Westergaard *et al.* 1998), cognitive biases in economic behavior (Chen *et al.* 2006; Lakshminaryanan *et al.* 2008), numerical competence (Addessi *et al.* 2007, 2008a), preference transitivity (Addessi *et al.* 2008b), delay of gratification (Dufour *et al.* 2007; Ramseyer *et al.* 2006), and calculated reciprocity (Dufour *et al.* 2009). Nonhuman primates can be trained to associate tokens with specific amounts or types of reward (Addessi *et al.* 2007, 2008a, b; Brosnan and de Waal 2004).

Capuchins offered binary choices between arrays of different tokens consistently choose the array corresponding to the higher amount of food (Addessi *et al.* 2007, 2008a) and employ similar cognitive mechanisms to choose between tokens and between real foods (Addessi *et al.* 2008b). Moreover, capuchins seem to determine an item's value on the basis of its perceived utility because they exchange only low-preferred foods for a tool necessary to reach a more preferred reward (Westergaard *et al.* 2004). Further, individually tested capuchins were able to recognize the appropriate conditions in which a successful exchange could occur, e.g., presence of the experimenter and request to exchange tokens, from inappropriate ones, e.g., absence of the experimenter (Westergaard *et al.* 2004).

Besides being a useful tool to explore many different cognitive skills, tokens can allow for assessment of how nonhuman primates process meaningful sign-object associations and, thus, to trace the evolutionary roots of human symbolic competence. Though capuchins can easily learn to associate different types of tokens with different amounts or types of food (Addessi *et al.* 2007, 2008a, b; Brosnan and de Waal 2004), tokens are not dealt with in exactly the same manner as the food for which they are exchanged. In particular, in our previous study on preference transitivity, for any pair of items the relative value of the preferred food increased when capuchins chose between the corresponding tokens, probably because the dual nature of tokens is difficult to grasp (Addessi *et al.* 2008b).

Although the great majority of primate species live in complex social groups, researchers have rarely addressed token-directed behavior in a social context (Bonnie *et al.* 2007; Brosnan and de Waal 2004; Dufour and Sterck 2008). Thus, in the present study we provided 4 groups of capuchins with a relatively limited budget of tokens, likely to elicit intragroup competition, and after an overnight delay we allowed them to exchange tokens for food while in a group setting. Our first aim was to evaluate whether social context affects the token-directed behavior of knowledgeable subjects, i.e., subjects already proficient in token exchange before the onset of the present study (Addessi *et al.* 2007, 2008a, b) as well as of naïve subjects, i.e., subjects that never showed exchange behavior before this study. We expected social context to affect the capuchins' behavior in multiple ways. First, given that social influences facilitate the acquisition of novel behaviors (Fragaszy and Visalberghi 2004), that capuchins can be quite competitive (Ferreira *et al.* 2008; Fragaszy *et al.* 2004; Janson 1985) and that competition may enhance an individual's motivation to perform a task (Hare 2001), we expected naïve subjects to acquire token exchange behavior during the present study. However, on the basis of previous findings in chimpanzees (Bonnie *et al.* 2007), we expected only high-ranking naïve subjects to display token exchange behavior in the social context. Second, we expected capuchins to compete for tokens as they do for food, with high-ranking subjects monopolizing access to this valuable resource and low-ranking ones abstaining from displaying token exchange behavior in the social context. To assess whether the social context constrained the low-ranking individuals either by limiting the display of token exchange behavior or by preventing token exchange acquisition, after we completed testing, we ran a control phase in which each subject was required to exchange tokens when tested alone.

Our second aim was to appraise whether capuchins indeed value tokens. If this was the case, we predicted that 1) they would exchange a higher number of tokens

than other objects available in their enclosure and that 2) knowledgeable subjects would exchange a higher number of valuable tokens than less valuable or valueless ones. Our third aim was to assess how the time lag between receiving tokens and being allowed to exchange them for a reward affects token-directed behavior of capuchins. In particular, we assessed whether the subjects could refrain from throwing tokens outside the enclosure during an overnight delay when the experimenter was not present. We predicted that, even over a much longer time lag than in the study of Westergaard *et al.* (2004), in which a time lag of 15 min was employed, capuchins would refrain from throwing tokens out of the cage in the absence of the experimenter. To assess whether capuchins kept the tokens inside their enclosure more than valueless items, after the completion of testing we conducted a control condition in which we provided each group with familiar objects to which no value was assigned and we compared the rate in which valueless items and tokens were thrown out of their enclosure.

Materials and Methods

Subjects

Twenty-eight captive-born capuchin monkeys (11 males, 17 females, age: mean = 14 yr, range = 5–29; 12 high-ranking and 16 low-ranking individuals) participated in the study. We divided our subjects into 2 rank classes (Drea and Wallen 1999; Schino 2004) on the basis of aggressive interactions, submissive behaviors, and access to food at feeding time (Verbeek and de Waal 1997). For each group, we performed rank assignment before starting data collection; rank remained stable for all individuals through the study period (10 d for each group).

The focal subjects lived in 4 groups at the Primate Center of the Institute of Cognitive Sciences and Technologies of the CNR, in Rome (Table I). Each group was housed in indoor–outdoor compartments. The size of the outdoor compartment depends on group size (Patè's: 53.2 m^3; Gal's: 106.5 m^3; Pepe's: 127.4 m^3; Cognac's: 374.0 m^3). The indoor compartment measured 25.4 m^3 for all groups. All compartments were furnished with wooden perches, tree trunks, and branches. Monkeys were not food deprived for testing. The main meal took place at 1530 h, when fresh fruits, vegetables, and monkey chow were provided. Water was constantly available.

We tested 18 knowledgeable subjects and 10 naïve subjects. Of the 18 knowledgeable subjects, 11 (4 high-ranking and 7 low-ranking) had previously learned to exchange the 2 types of tokens used in the present study, i.e., high- and low-value tokens (Addessi *et al.* 2007). The remaining seven knowledgeable subjects (2 high-ranking and 5 low-ranking) were also previously trained to exchange tokens (Silberberg *et al.* 2009), and learned to exchange the low-value tokens and the high-value tokens during the training phase of the present study. The 10 naïve subjects had never been observed to exchange any object spontaneously nor had they witnessed their group members exchanging tokens before this study. A few months before the onset of the present study, we attempted, without success, to train 6 of them to exchange tokens by using a shaping procedure.

Table I Sex, age, group, rank, and experience (knowledgeable or naïve) of each subject, and mean number (SE) of tokens and other items exchanged with the experimenter. For naïve subjects, we reported the session in which they first exchanged a token

Subject	Sex	Age	Group	Rank	Experience	First token	Tokens	Other items
Gal	M	17	Gal	D	Knowledgeable	–	37.5 (2.0)	6.1 (2.8)
Rame[a]	F	20	Gal	D	Naïve	1	8.0 (1.2)	24.5 (5.2)
Paprica	F	18	Gal	S	Knowledgeable	–	–	0.5 (0.2)
Carlotta	F	23	Gal	S	Knowledgeable	–	–	0.3 (0.2)
Cammello	M	29	Gal	S	Knowledgeable	–	–	–
Robinia	F	13	Patè	D	Knowledgeable	–	26.0 (1.0)	2.1 (0.9)
Patè[a]	M	16	Patè	D	Naïve	4	1.3 (1.0)	–
Robot	M	12	Patè	S	Knowledgeable	–	–	3.5 (2.8)
Saroma[a]	F	6	Patè	S	Naïve	Never	–	–
Bramhs[a]	F	25	Patè	S	Naïve	Never	–	–
Pepe	M	20	Pepe	D	Knowledgeable	–	5.9 (1.8)	0.3 (0.3)
Vispo[a]	M	7	Pepe	D	Naïve	2	1.6 (0.6)	0.5 (0.5)
Roberta	F	21	Pepe	D	Knowledgeable	–	–	–
Virginia	F	8	Pepe	S	Knowledgeable	–	0.4 (0.3)	0.7 (1.8)
Sandokan	M	7	Pepe	S	Knowledgeable	–	–	4.1 (0.5)
Pippi	F	26	Pepe	S	Knowledgeable	–	–	–
Cognac	M	20	Cognac	D	Naïve	2	53.4 (6.3)	47.0 (9.4)
Paquita	F	17	Cognac	D	Knowledgeable	–	1.9 (0.9)	12.4 (9.8)
Penelope	F	8	Cognac	D	Knowledgeable	–	0.9 (0.3)	6.5 (2.6)
Peonia	F	3	Cognac	D	Naïve	1	0.1 (0.1)	0.9 (0.5)
Robin hood[a]	M	10	Cognac	D	Naïve	4	0.3 (0.2)	2.6 (1.0)
Rucola	F	7	Cognac	S	Knowledgeable	–	–	2.8 (1.6)
Pacchia	F	11	Cognac	S	Knowledgeable	–	–	
Pacajà	F	10	Cognac	S	Knowledgeable	–	–	0.1 (0.1)
Rubens	M	6	Cognac	S	Knowledgeable	–	0.7 (0.4)	4.6 (2.2)
Pedro	M	6	Cognac	S	Knowledgeable	–	0.7 (0.6)	1.8 (0.7)
Quincy	F	4	Cognac	S	Naïve	Never	–	0.1 (0.1)
Robiola	F	10	Cognac	S	Naïve	Never	–	–

[a] Subjects that failed a token exchange training before this study

Tokens

Tokens were inherently nonvaluable objects of similar dimensions, differing in shape, material, and color. Specifically, we used colored plastic poker chips (diameter: 3.7 cm), a gray PVC cylinder (diameter: 3 cm; height: 0.7 cm), a brass plug (diameter: 2 cm), a metal nut (diameter: 2 cm), and a brass hook (length: 4.3 cm). These objects were familiar to all subjects.

We assigned to each knowledgeable subject 3 different objects as low-value, high-value, and no-value tokens. The low-value tokens corresponded to 1 reward, while the high-value tokens corresponded to 3 rewards; a reward consisted of 1/8 of

a peanut, weighing on average 0.11±0.004 g. For the no-value token, for which we did not reward exchange, no training was performed.

Procedure

Training Phase Seven subjects participated in an initial training phase, and trained each one individually. The training procedure consisted of placing 12 tokens of the same type into the indoor compartment, and repeatedly saying "give me" to the subject while requesting a token, with left hand outstretched and palm up. The reward was given upon the placement of 1 token into the experimenter's left hand. There was a 10-s interval between each trial. We did not reward incorrect exchanges, in which the subject threw tokens out of the cage or did not place tokens into the experimenter's hand. If the subject did not exchange a token within 30 s, then we considered the trial incorrect and we started a new trial after 10 s. Subjects received 1 training session per day. Each session consisted of 2 blocks of 12 trials each, for a total of 24 trials. We set criterion at 90% correct responses within 2 consecutive sessions. Subjects first learned to exchange the low-value token and then the high-value token. When criterion was reached for both types of tokens, each subject received 6 sessions of consolidation, with the low-value token and the high-value token alternated across days. Subjects completed training, excluding the 6 sessions of consolidation, in a mean of 2.29±0.18 sessions for the low-value token, and in a mean of 3.29±0.52 sessions for the high-value token. These values did not significantly differ (Wilcoxon signed-ranks test: $T=2$, $N=7$, $p=0.14$).

Experimental Phase During the experimental phase, each group received 15 tokens (5 high-value, 5 low-value, and 5 no-value) for each knowledgeable subject. To make the level of competition among knowledgeable subjects as similar as possible in all groups, the number of tokens supplied to each group was proportional to the number of knowledgeable subjects present. Specifically, we provided 30 tokens to Patè's group, 60 tokens to Gal's group, 75 tokens to Pepe's group, and 105 tokens to Cognac's group (Table II). We placed tokens inside the indoor compartment together with the daily meal at 1530 h; after this time, no other test occurred. Both overnight and during the following experimental phase, capuchins had continuous access to the indoor–outdoor compartments. The experimental phase started about 16 h later (at *ca.* 0700 h on the following day). Immediately before starting a session, we counted the number of tokens outside the indoor–outdoor compartments, which had been

Table II Total number of subjects, knowledgeable subjects, and experimenters trading tokens for each group

Group	Total no. of subjects	Knowledgeable subjects	Experimenters	No. of tokens assigned
Patè	5	2	1	30
Gal	5	4	2	60
Pepe	6	5	2	75
Cognac	12	7	3	105

The number of experimenters and tokens assigned to each group was proportional to the number of knowledgeable subjects in each group

thrown out of the enclosure, and the number of tokens still present inside the indoor compartment.

We group tested capuchins in the outdoor compartment. In each session, we required capuchins to exchange the tokens available in the indoor–outdoor compartments with ≥1 experimenters. The number of experimenters varied from 1 to 3 and was proportional to the number of knowledgeable subjects in each group (Table II). To make the level of competition as similar as possible in groups with >2 knowledgeable subjects, experimenters stood in different places around the outdoor compartment, at *ca.* 20 cm from the wire-mesh wall. All experimenters simultaneously performed a request every 10 s, by saying the words "give me" while requesting a token, with left hand outstretched and palm up.

We rewarded knowledgeable subjects according to the value of each token assigned during the training phase. When a naïve subject correctly exchanged a token, she was always rewarded with 1 piece of peanut seed, regardless of the type of token returned. If a knowledgeable subject or a naïve subject performed an incorrect exchange, i.e., exchanging 2 tokens simultaneously or incorrectly placing a token into the experimenter's hand, or if they exchanged a no-value token or any different object, e.g., stones, wooden chips, twigs (hereafter, other items), the experimenter did not reward them and waited 10 s before making a new request.

We collected data by paper and pencil and, for each subject, we scored the order and type of tokens returned. Each session ended when all the tokens provided to the group were exchanged or after 1 h, whichever occurred first. All groups received 10 sessions (1 session per day for 10 consecutive days). We tested 3 groups between July and September 2007, and the fourth group (Cognac's) in August–September 2008.

Control Phase 1 To evaluate whether naïve subjects learned to exchange tokens during the experimental phase and to what extent their performance differed from that of knowledgeable subjects, after the experimental phase we required each subject exchange tokens to individually in a single session of 24 trials. We tested subjects in the indoor compartment by employing the same procedure used in the training phase.

Control Phase 2 To assess the rate in which capuchins kept no-value items within the indoor compartment or threw them out of the enclosure, after the completion of the experimental phase we provided each group with familiar objects to which no value was assigned (crown caps; Maranesi and Addessi *unpubl. data*) in the same number as the tokens provided in the experimental phase, i.e., 30 for Patè's group, 60 for Gal's group, 75 for Pepe's group, and 105 for Cognac's group.

We employed the same procedure used in the experimental phase, with the only exception being that, after the overnight delay, we did not require capuchins to exchange the no-value items present in the enclosure. Instead, we first removed and counted the items thrown out of the enclosure; then we restricted the capuchins to the outdoor portion of the enclosures and removed and counted the no-value items indoors. We then restricted the capuchins to the indoor portion of the enclosures and removed and counted the no-value items outdoors.

Data Analysis

We employed the Fisher's exact test 1) to assess whether previous participation in a token exchange shaping procedure affected the likelihood of naïve subjects to exhibit token exchange in the present study, and 2) to evaluate how rank affected token exchange behavior in naïve individuals.

We used the Mann–Whitney *U* test to assess whether 1) the number of tokens exchanged differed between knowledgeable and naïve subjects, and whether 2) the number of tokens and other items exchanged differed between high-ranking and low-ranking individuals. We used the Friedman ANOVA to evaluate whether there was a difference in the percentage of high-value, low-value, and no-value tokens exchanged by knowledgeable subjects, and the Wilcoxon signed-ranks test to assess whether 1) capuchins exchanged more tokens than other items, and whether 2) they exchanged tokens and other items more frequently in the first half or in the second half of the exchange episodes.

We performed a χ^2 test and standardized residual analysis on the number of high-, low- and no-value tokens exchanged by the 3 knowledgeable subjects that returned the highest number of tokens (Gal, Pepe, and Robinia) to assess whether they exchanged significantly more high-value tokens in the first half of the episodes and less low-value (or valueless) tokens in the second half of the episodes than expected by chance. We employed the χ^2 test also to evaluate whether 1) the percentages of tokens (experimental phase) and no-value items (control phase 2) outside the enclosure and inside the indoor compartment at the beginning of the session differed among groups, and whether 2) the number of tokens and no-value control items found outside the enclosure and inside the indoor compartment differed between the experimental phase and control phase 2.

Finally, for each group we ran Spearman correlations to evaluate whether the percentage of tokens (experimental phase) and no-value items (control phase 2) outside the enclosure and in the indoor compartment at the beginning of the session varied over time.

Results

Exchange Behavior

Knowledgeable Subjects and Naïve Subjects In the experimental phase, of the 18 knowledgeable subjects, 10 never exchanged tokens (6 of them exchanged only other items, and 4 never exchanged any item). All knowledgeable subjects that discontinued token exchange were, with 1 exception, low-ranking individuals. Of the 10 naïve subjects, 6 exhibited exchange, of both tokens and other items (Table I), and 1 subject (Quincy) exchanged 1 other item during only on 1 occasion. All naïve subjects that exchanged tokens were high-ranking individuals. Previous participation in a token exchange shaping procedure did not affect the likelihood that naïve subjects would exhibit token exchange in the present study (Fisher's exact, $p=0.55$).

In control phase 1, all 18 knowledgeable subjects correctly exchanged tokens in virtually all trials (high-ranking individuals: 96.6%, low-ranking individuals:

96.2%). Of the 6 naïve high-ranking individuals that exchanged tokens in the experimental phase, 3 exchanged tokens in 84.7% of trials when individually tested (Vispo: 91.7%, Robin Hood: 75%, Rame: 87.5%), and 3 subjects did not. None of the 4 naïve low-ranking individuals, which never exchanged tokens in the experimental phase, exchanged tokens when individually tested.

In the experimental phase, for both tokens and other items, there were no differences between the 18 knowledgeable subjects and the 10 naïve subjects (Mann–Whitney U test: tokens, Z=–0.57, n_1=10, n_2=18, p=0.56; other items, Z=0.60, n_1=10, n_2=18, p=0.55). We therefore performed all analyses on their pooled data (N=28), except those on token value, which we performed on knowledgeable subjects only (N=18).

Social status affected exchange behavior. All 6 naïve subjects that exhibited token exchange during this study were high-ranking individuals, whereas all 4 that did not were low-ranking individuals (Fisher's exact, p<0.01). High-ranking individuals exchanged significantly more tokens and other items than low-ranking ones (Mann–Whitney U test: Z=3.74, n_1=10, n_2=18, p<0.001; Z=2.07, n_1=10, n_2=18, p=0.04; Fig. 1). However, token availability did not seem to affect the behavior of low-ranking individuals. Although in Gal's and Robinia's groups the average number of tokens per individual was 6 and 12, respectively, the 2 high-ranking individuals of each group (Gal and Rame in Gal's group and Robinia and Patè in Robinia's group) monopolized token exchange; in both groups the 3 low-ranking individuals never exchanged tokens. Moreover, although in Cognac's group there were fewer tokens available per individual than in Pepe's group (8.75 and 12.5, respectively), in Cognac's group 7 individuals exchanged tokens, whereas in Pepe's group only 3 individuals did so.

Capuchins did not preferentially exchange tokens vs. other items (Wilcoxon signed-ranks test: Z=0.94, N=28, p=0.35). To determine whether the capuchins' behavior changed during the session, we divided the number of exchange episodes performed by each subject into 2 halves and compared what individuals exchanged in the first and second halves of the episodes. Token exchanges occurred more frequently in the first half than in the second half of the episodes (Wilcoxon signed-ranks test: Z=3.0, N=28, p<0.01), whereas individuals tended to exchange other items in the second half more often than in the first half of the episodes (Wilcoxon signed-ranks test: Z=1.94, N=28, p=0.052; Fig. 2). However, in the second half of exchanging episodes, an average of 25.3% of the initial token budget was still available for capuchins to exchange (Patè's group: 40.3%; Gal's group: 18.6%; Pepe's group: 28.6%; Cognac's group: 13.8%).

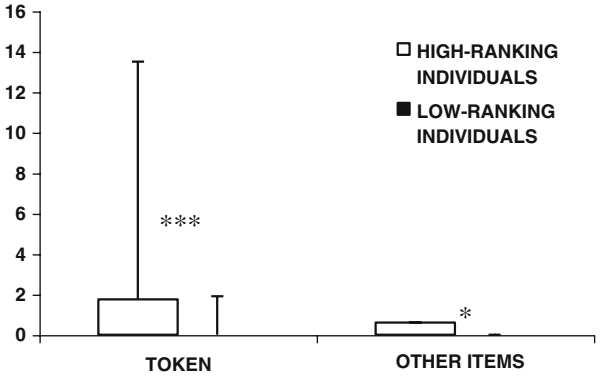

Fig. 1 Median and IQR for tokens and other items exchanged by high-ranking and low-ranking individuals (white and black bars, respectively). ***p<0.001; *p<0.05.

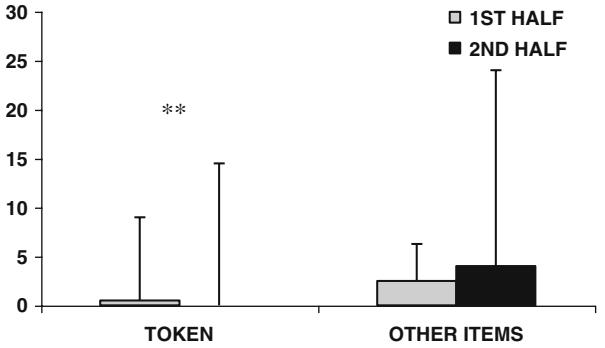

Fig. 2 Median and IQR for tokens and other items exchanged in the first and second half of exchange episodes (gray and black bars, respectively). **$p<0.01$.

Knowledgeable Subjects The percentage of high-value, low-value, and no-value tokens exchanged by knowledgeable subjects did not significantly differ (Friedman ANOVA, $\chi_2{}^2=2.0$, $N=18$, $p=0.37$). Moreover, knowledgeable subjects exchanged a similar number of high-value and no-value tokens in the 2 halves of the episodes (Wilcoxon signed-ranks test: $Z=1.36$, $N=18$, $p=0.17$; $Z=0.73$, $N=18$, $p=0.46$, respectively), and more low-value tokens in the first half than in the second half of the episodes (Wilcoxon signed-ranks test: $Z=2.20$, $N=18$, $p=0.03$). Further, high-ranking knowledgeable subjects exchanged significantly more high-, low-, and no-value tokens than did low-ranking knowledgeable subjects (Mann-Whitney U test: high-value: $Z=2.06$, $n_1=6$, $n_2=12$, $p=0.04$; low-value: $Z=1.97$, $n_1=6$, $n_2=12$, $p=0.05$; no-value: $Z=2.67$, $n_1=6$, $n_2=12$, $p=0.01$).

The 3 knowledgeable subjects that returned the highest number of tokens (Gal, Pepe, and Robinia; Table I) exchanged significantly more high-value tokens in the first half of the episodes and less low-value or valueless tokens in the second half of the episodes than expected by chance (χ^2 test: Gal: $\chi_2{}^2=136.08$, $p<0.001$; Pepe: $\chi_2{}^2=7.86$, $p<0.05$; Robinia: $\chi_2{}^2=21.85$, $p<0.001$). Specifically, Gal exchanged 1) more high-value tokens and fewer low-value tokens in the first half of the episodes (standardized residual analysis: high-value: 6.24, $p<0.01$; low-value: –6.24, $p<0.01$) and 2) less high-value tokens and more low-value tokens in the second half of the episodes (standardized residual analysis: high-value: –5.40, $p<0.01$; low-value: 5.71, $p<0.01$), Pepe exchanged fewer high-value tokens and more low-value tokens in the second half of the episodes (standardized residual analysis: high-value: –2.12, $p<0.01$; low-value: 2.24, $p<0.01$), and Robinia exchanged fewer high-value tokens in the second half of the episodes (standardized residual analysis: high-value: –1.96, $p<0.05$). Robinia exchanged less no-value tokens in the first half of the episodes and more no-value tokens in the second half of the episodes (standardized residual analysis: first half: –2.67, $p<0.01$; second half: 2.69, $p<0.01$), whereas for Gal and Pepe the number of the no-value tokens exchanged in the 2 halves of the episodes did not differ from that expected by chance.

Group Behavior over Time and Comparisons Among Groups

In the experimental phase, for all groups the percentage of tokens outside the enclosure at the beginning of the session did not vary over time (Spearman

correlations: Patè's group, r_s=–0.36, N=10, p=0.31; Gal's group, r_s=–0.20, N=10, p=0.58; Pepe's group, r_s=–0.29, N=10, p=0.42; Cognac's group, r_s=–0.43, N=10, p=0.21), whereas the percentage of tokens in the indoor compartment significantly increased across sessions for all groups but one (Spearman correlations: Patè's group, r_s=0.42, N=10, p=0.23; Gal's group, r_s=0.85, N=10, p<0.01; Pepe's group, r_s=0.88, N=10, p<0.001; Cognac's group, r_s=0.89, N=10, p<0.001). Moreover, the percentages of tokens outside the enclosure and inside the indoor compartment at the beginning of the session were similar among groups (tokens outside the enclosure: Patè's group: 2.9%, Gal's group: 5.4%, Pepe's group: 6.0%, Cognac's group: 8.5%; χ^2 test: χ_3^2=2.83, p=0.42; tokens inside the indoor compartment: Patè's group: 74.3%, Gal's group: 68.2%, Pepe's group: 60.1%, Cognac's group: 51.1%; χ^2 test: χ_3^2=4.78, p=0.19).

In control phase 2, when we provided only no-value items to each group, the percentages of no-value items outside the enclosure and inside the indoor compartment at the beginning of the session were similar among groups (no-value items outside the enclosure: Patè's group: 2.3%, Gal's group: 1.0%, Pepe's group: 0.7%, Cognac's group: 0.5%; χ^2 test: χ_3^2=1.88, p=0.60; no-value items inside the indoor compartment: Patè's group: 89.3%, Gal's group: 96.0%, Pepe's group: 97.7%, Cognac's group: 97.9%; χ^2 test: χ_3^2=0.51, p=0.92). The percentages of the no-value items both outside the enclosure and inside the indoor compartment at the beginning of the session did not vary over time (no-value items outside the enclosure, Spearman correlations: Patè's group, r_s=0.56, N=10, p=0.09; Gal's group, r_s=0.27, N=10, p=0.45; Pepe's group, r_s=0.34, N=10, p=0.34; Cognac's group, r_s=0.28, N=10, p=0.44; no-value items inside the indoor compartment, Spearman correlations: Patè's group, r_s=0.18, N=10, p=0.62; Gal's group, r_s=0.04, N=10, p=0.90; Pepe's group, r_s=–0.56, N=10, p=0.09; Cognac's group, r_s=0.15, N=10, p=0.68).

The number of tokens and of no-value control items found outside the enclosure and inside the indoor compartment did not differ significantly between the experimental phase and control phase 2 (no-value items outside the enclosure: χ^2 test: χ_3^2=3.87, p>0.20; no-value items inside the indoor compartment: χ^2 test: χ_3^2= 4.42, p>0.20).

Discussion

Effect of Social Context on Token-Directed Behavior

Social context had both positive and negative effects on individual behavior (Fragaszy and Visalberghi 1990). Six of 10 naïve subjects exchanged tokens in the initial sessions, and across sessions they behaved similarly to knowledgeable subjects. Social influences seemed more effective in eliciting token exchange by naïve subjects than a shaping procedure that some of them underwent earlier without ever being successful, although the small number of subjects tested in this shaping procedure does not allow firm conclusions to be drawn in this respect. Although naïve subjects valued all types of tokens the same and knowledgeable subjects knew the relative value of the different tokens, (Addessi *et al.* 2007, 2008a, b), the

different reinforcement they experienced during the study did not affect the number of tokens exchanged by knowledgeable and naïve subjects.

Local/stimulus enhancement (Fragaszy and Visalberghi 2004; Spence 1937; Thorpe 1956) and competition (Hare 2001) may have fostered the acquisition of token exchange by naïve capuchins. Clear evidence of the influence of competition on cognitive performance and learning comes from the high degree of effectiveness of the model/rival approach used to train Alex, an African gray parrot (*Psittacus erithacus*), to label different objects vocally (Bandura 1971, 1977; Mowrer 1950; Pepperberg 1990; Todt 1975). In this approach, one experimenter acts as trainer and the other as trainee, the latter being both a model and a potential competitor for Alex. For any incorrect response, Alex's trainer repeats the question to the trainee who answers correctly and is rewarded in Alex's presence. Similarly, in a study where students participating in a Chinese typewriting course experienced a high or a low level of competition, those belonging to the high-competition group had a better performance in an easy version of the final test (Lam *et al.* 2004).

In the present study, the effect of the social context on the acquisition of token exchange by naïve individuals depended on their hierarchical rank: Whereas the presence of group members was effective in prompting the acquisition of token exchange behavior by high-ranking naïve subjects, it impaired learning by low-ranking naïve subjects. None of the 4 low-ranking naïve subjects displayed token exchange behavior either when socially tested (experimental phase) or when individually tested (control phase 1), whereas 3 of the 6 high-ranking naïve subjects that exchanged tokens in a social context continued to do so. In knowledgeable capuchins, competition impaired low-ranking individuals from displaying token exchange, as previously shown by Drea and Wallen (1999) and by Fragaszy and Visalberghi (1990): Although all 18 knowledgeable capuchins proved to be highly motivated and skillful token exchangers when individually tested (Addessi *et al.* 2007, 2008a, b), 10 of them, all low-ranking individuals, never displayed token exchange in the social context. In addition, high-ranking individuals, regardless of whether they were knowledgeable or naïve, monopolized the experimenters and exchanged more tokens, regardless of their value, and other items than low-ranking individuals. They often brought multiple tokens from the indoor compartment to the outdoor compartment, accumulated them in front of the experimenter, and then exchanged them 1 at a time.

Do Capuchins Value Tokens?

Capuchins exploited their token budget as soon as the opportunity arose. They exchanged a higher percentage of tokens in the first half of the exchange episodes of each session than in the second half. Token availability partly affected the capuchins' behavior toward other items that were exchanged more in the second half of the exchange episodes, when the available tokens decreased to *ca.* 25% of the initial token budget, than in the first half.

In contrast to our expectations, capuchins did not exchange tokens more than other items, possibly because wooden chips, twigs, and stones were dramatically more abundant and ubiquitous than tokens, being enrichment devices entirely covering the ground of the outdoor compartments. Moreover, "trading *per se* might

be sufficient motivation for the animals to continue exchanging" (Carpenter and Locke 1937, p. 273). In fact, although exchanging no-value tokens or other items does not lead to a food reward, this is probably an intrinsically motivating behavior, i.e., an activity that is performed for its own sake (Deci and Ryan 1985), especially for high-ranking individuals that monopolized access to the experimenters. At the group level, knowledgeable subjects neither exchanged more valuable tokens than less valuable or valueless ones, nor did the percentages of high- and no-value tokens exchanged consistently differ between the first and second halves of the episodes, with the exception of low-value tokens. Nevertheless, the 3 high-ranking knowledgeable subjects that returned most of the tokens (Gal, Pepe, and Robinia) exchanged the most valuable tokens before the less valuable or valueless ones. This suggests that, when social factors do not limit token availability and access to tokens, capuchins are able to exploit tokens according to their value.

Effect of Time Lag on Token-Directed Behavior

Capuchins are well known for their spontaneous tendency to insert objects into holes, and in captivity they often toss objects through wire-mesh barriers (Fragaszy *et al.* 2004). Overall, our subjects inhibited this behavior when tokens were involved. In fact, the percentage of tokens outside the enclosure was <10% for all groups, did not differ from the percentage of no-value items found in the control condition, and did not vary over time. This suggests that capuchins recognized since the first sessions of testing a key feature of token exchange, i.e., that the presence of the experimenter is necessary for trading valuable tokens, as do individually tested capuchins (Westergaard *et al.* 2004).

Interestingly, capuchins learned over time to leave tokens in the indoor compartment, where the experimenters originally placed them, until it was time for exchanging, instead of carrying and spreading tokens outdoors, where the probability to lose them is high. In fact, the percentage of tokens found indoors at the beginning of the session was >50% for all groups and increased over time for all groups but 1. In contrast, when we provided the subjects with an equivalent number of no-value control items, we did not observe a significant decrease across sessions of the number of items left in the indoor compartment. These findings might suggest the development of very basic token saving strategies, though certainly less sophisticated than reported by Sousa and Matsuzawa (2001) for chimpanzees. In the latter study, in which tokens were used as rewards in cognitive tasks, all chimpanzees spontaneously saved tokens, thus showing that, at least in a brief time interval, they can plan a future action and delay gratification. However, contrasting evidence is provided by the study of Dufour and Sterck (2008), in which no chimpanzees systematically selected the specific object required to later perform a series of exchanges with the experimenter. Because our study was not specifically designed to investigate token saving strategies, future studies should address this issue by giving capuchins access to tokens for a limited period of time or by video-recording their behavior overnight, to follow every single token manipulation and to track the identity of the individuals manipulating the tokens.

In conclusion, social influences had both positive and negative effects on token exchange behavior. All high-ranking naïve subjects and none of the low-ranking

ones acquired token exchange behavior, and did so in the initial experimental sessions, whereas most low-ranking knowledgeable subjects and only one high-ranking knowledgeable subject never displayed token exchange in social contexts. Overall, knowledgeable subjects did not exchange more high-value tokens than low-value or valueless ones, although at the individual level the 3 high-ranking knowledgeable subjects that exchanged most of the tokens took into account their value and exchanged the more valuable tokens first. Finally, capuchins recognized that the experimenter's presence was a *condicio sine qua non* for token exchange to be successful, although they could not restrain from exchanging whatever object was available, regardless of its value.

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References

Addessi, E., Crescimbene, L., & Visalberghi, E. (2007). Do capuchin monkeys (*Cebus apella*) use tokens as symbols? *Proceedings of the Royal Society of London B – Biological Sciences, 274*, 2579–2585.

Addessi, E., Crescimbene, L., & Visalberghi, E. (2008a). Food and token quantity discrimination in capuchin monkeys (*Cebus apella*). *Animal Cognition, 11*, 275–282.

Addessi, E., Mancini, A., Crescimbene, L., Padoa-Schioppa, C., & Visalberghi, E. (2008b). Preference transitivity and symbolic representation in capuchin monkeys (*Cebus apella*). *PloS ONE, 3*, e2414. doi:10.1371/journal.pone.0002414.

Bandura, A. (1971). Analysis of social modeling processes. In A. Bandura (Ed.), *Psychological modeling*. Chicago: Aldine-Atherton.

Bandura, A. (1977). *Social modeling theory.* Chicago: Aldine-Atherton.

Bonnie, K. E., Horner, V., Whiten, A., & de Waal, F. B. M. (2007). Spread of arbitrary conventions among chimpanzees: a controlled experiment. *Proceedings of the Royal Society of London B – Biological Sciences, 274*, 367–372.

Brosnan, S., & de Waal, F. B. M. (2004). A concept of value during experimental exchange in brown capuchin monkeys, *Cebus apella*. *Folia Primatologica, 75*, 317–330.

Brosnan, S. F., & de Waal, F. B. M. (2005). Responses to a simple barter task in chimpanzees, *Pan troglodytes*. *Primates, 46*, 173–182.

Carpenter, C., & Locke, N. (1937). Notes on symbolic behavior in a cebus monkey (*Capucinus appella*). *Journal of Genetic Psychology, 51*, 267–278.

Chen, M. K., Lakshminarayanan, V., & Santos, R. (2006). How basic are behavioural biases? Evidence from capuchin monkeys trading behavior. *Journal of Political Economy, 114*, 517–537.

Cowles, J. (1937). Food-tokens as incentive for learning by chimpanzees. *Comparative Psychology Monographs, 14*, 1–96.

Deci, E. L., & Ryan, R. M. (1985). *Intrinsic motivation and self-determination in human behavior.* New York: Plenum.

Drea, C. M., & Wallen, K. (1999). Low-status monkeys "play dumb" when learning in mixed social groups. *Proceedings of the National Academy of Sciences of the USA, 96*, 12965–12969.

Dufour, V., & Sterck, E. H. M. (2008). Chimpanzees fail to plan in an exchange task but succeed in a tool-using procedure. *Behavioural Processes, 79*, 1927.

Dufour, V., Pelé, M., Sterck, E. H. M., & Thierry, B. (2007). Chimpanzee (*Pan troglodytes*) anticipation of food return: Coping with waiting time in an exchange task. *Journal of Comparative Psychology, 121*, 145–155.

Dufour, V., Pelé, M., Neumann, M., Thierry, B., & Call, J. (2009). Calculated reciprocity after all: computation behind token transfers in orang-utans. *Biology Letters, 5*, 172–175.

Ferreira, R. G., Lee, P., & Izar, P. (2008). Food competition in a semi-free-ranging *Cebus apella* group. *Folia Primatologica, 79*, 463–475.

Fragaszy, D., & Perry, S. (2003). *The biology of traditions. Models and evidence*. Cambridge: Cambridge University Press.

Fragaszy, D., & Visalberghi, E. (1990). Social processes affecting the appearance of innovative behaviors in capuchin monkeys. *Folia Primatologica, 54*, 155–165.

Fragaszy, D., & Visalberghi, E. (2004). Socially biased learning in monkeys. *Learning & Behavior, 32*, 24–35.

Fragaszy, D. M., Fedigan, L. M., & Visalberghi, E. (2004). *The complete capuchin. The biology of the genus Cebus*. Cambridge: Cambridge University Press.

Hare, B. (2001). Can competitive paradigms increase the validity of experiments on primate social cognition? *Animal Cognition, 4*, 269–280.

Hare, B., & Tomasello, M. (2004). Chimpanzees are more skilful in competitive rather than in cooperative tasks. *Animal Behaviour, 68*, 571–581.

Hare, B., Call, J., Agnetta, B., & Tomasello, M. (2000). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour, 59*, 771–785.

Heyes, C. M., & Galef, B. G., Jr. (1996). *Social learning in animals. The roots of culture*. San Diego: Academic.

Janson, C. H. (1985). Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology and Sociobiology, 18*, 125–138.

Kelleher, R. T. (1956). *Intermittent conditioned reinforcement in chimpanzees. Science, 124*, 679680.

Kelleher, R. (1957a). A multiple schedule of conditioned reinforcement with chimpanzees. *Psychological Reports, 3*, 485–491.

Kelleher, R. (1957b). A comparison of conditioned and food reinforcement on a fixed-ratio schedule in chimpanzees. *Psychology Newsletter, 8*, 88–93.

Koenig, A., Beise, J., Chalise, M. K., & Ganzhorn, J. U. (1998). When females should contest for food: testing hypotheses about resource density, distribution, size, and quality with Hanuman langurs (*Presbytis entellus*). *Behavioral Ecology and Sociobiology, 42*, 225–237.

Lakshminaryanan, V., Chen, M. K., & Santos, L. R. (2008). Endowment effect in capuchin monkeys. *Philosophical Transactions of the Royal Society B, 363*, 3837–3844.

Lam, S., Yim, P., Law, J. S. F., & Cheung, R. W. Y. (2004). The effects of competition on achievement motivation in Chinese classrooms. *British Journal of Educational Psychology, 74*, 281–296.

Mowrer, O. H. (1950). *Learning theory and personality dynamics*. New York: Ronald.

Pepperberg, I. M. (1990). Conceptual abilities of some nonprimate species, with an emphasis on African Gray Parrot. In S. T. G. Parker & K. R. Gibson (Eds.), *"Language" and intelligence in monkeys and apes* (pp. 476–477). Cambridge: Cambridge University Press.

Ramseyer, A., Pelè, M., Dufour, V., Chauvin, C., & Thierry, B. (2006). Accepting loss: the temporal limits of reciprocity in brown capuchin monkeys. *Proceedings of the Royal Society of London B – Biological Sciences, 273*, 179184.

Schino, G. (2004). Birth sex ratio and social rank: consistency and variability within and between primate groups. *Behavioral Ecology, 15*, 850–856.

Silberberg, A., Crescimbene, L., Addessi, E., Anderson, J., & Visalberghi, E. (2009). Does inequity aversion depend on a frustration effect? A test with capuchin monkeys (*Cebus apella*). *Animal Cognition, 12*, 505–509.

Sousa, C., & Matsuzawa, T. (2001). The use of tokens as rewards and tools by chimpanzees (*Pan troglodytes*). *Animal Cognition, 4*, 213–221.

Spence, K. W. (1937). Experimental studies of learning and the mental processes in infra-human primates. *Psychological Bulletin, 34*, 806–850.

Thorpe, W. H. (1956). *Learning and instinct in animals*. London: Methuen.

Todt, D. (1975). Social learning of vocal patterns and models of their application in Gray parrots. *Zeitschrift für Tierpsychologie, 39*, 178–188.

Tomasello, M., & Call, J. (1997). *Primate cognition*. Oxford: Oxford University Press.

van Schaik, C. (1989). The ecology of social relationships amongst female primates. In V. Standen & R. Foley (Eds.), *Comparative socioecology: The behavioural ecology of humans and other mammals* (pp. 95–218). Oxford: Blackwell.

van Schaik, C. P., & van Noordwijk, M. A. (1988). Scramble and contest in feeding competition among female long-tailed macaques (*Macaca fascicularis*). *Behaviour, 105*, 77–98.

Verbeek, P., & de Waal, F. B. M. (1997). Postconflict behavior of captive brown capuchins in the presence and absence of attractive food. *International Journal of Primatology, 18*, 703–725.

Westergaard, G., Liv, C., Chavanne, T. J., & Suomi, S. (1998). Token-mediated tool-use by a tufted capuchin monkey (*Cebus apella*). *Animal Cognition, 1*, 101–106.

Westergaard, G., Liv, C., Rocca, A. M., Cleveland, A., & Suomi, S. (2004). Tufted capuchins (*Cebus apella*) attribute value to foods and tools during voluntary exchanges with humans. *Animal Cognition, 7*, 1924.

Wolfe, J. (1936). Effectiveness of token-rewards for chimpanzees. *Comparative Psychology Monographs, 12*, 1–72.