

# Bonobos and orangutans, but not chimpanzees, flexibly plan for the future in a token-exchange task

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Received: 18 December 2013 / Revised: 28 May 2014 / Accepted: 30 May 2014 / Published online: 19 June 2014  
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**Abstract** Non-human animals, including great apes, have been suggested to share some of the skills for planning that humans commonly exhibit. A crucial difference between human and non-human planning may relate to the diversity of domains and needs in which this skill is expressed. Although great apes can save tools for future use, there is little evidence yet that they can also do so in other contexts. To investigate this question further, we presented the apes with a planning token-exchange task that differed from standard tool-use tasks. Additionally, we manipulated the future outcome of the task to investigate planning flexibility. In the *Exchange* condition, subjects had to collect, save and transport tokens because they would need them 30 min later to exchange them for food with a human, i.e., “bring-back” response. In the *Release* condition, the collection and transport of tokens were not needed as no exchange took place after 30 min. Out of 13 subjects, eight

solved the task at least once in the *Exchange* condition, with chimpanzees appearing less successful than the other species. Importantly, three individuals showed a clear differential response between conditions by producing more “bring-back” responses in the *Exchange* than in the *Release* conditions. Those bonobo and orangutan individuals hence adapted their planning behavior according to changing needs (i.e., they brought tokens back significantly more often when they would need them). Bonobos and orangutans, unlike chimpanzees, planned outside the context of tool-use, thus challenging the idea that planning in these species is purely domain-specific.

**Keywords** Future planning · Anticipation · Foresight · Non-human primate · Token exchange

## Introduction

Planning ahead is a crucial competence in several domains of human life, including problem solving, social interaction,

**Electronic supplementary material** The online version of this article (doi:10.1007/s10071-014-0768-6) contains supplementary material, which is available to authorized users.

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and economic welfare. Additionally, human planning is characterized by its flexibility. In considering future retirement, for example, individuals can either save money or trust the governmental pension, but they can easily reassess their choice and shift strategy if their knowledge of the future changes. Cognitively speaking, planning is highly demanding. It occurs when an individual achieves a future goal through a series of intermediate actions (Owen 1997; Szpunar 2010), which are generated by internal simulations reconstructed from personal past memories (i.e., episodic memory, Tulving 1983) (Bar 2007; Schacter et al. 2008). Other animal species, including great apes, have been suggested to share some of the skills for planning that human exhibit (Raby and Clayton 2009). They can generate future action plans based on personal past experience (e.g., Mulcahy and Call 2006; Feeney et al. 2011; Cheke and Clayton 2012). However, experimental evidence of planning is generally demonstrated in domains in which the individuals are known to be already naturally competent, i.e., planning for food availability in food-caching birds, or planning for tool use in great apes (see Raby and Clayton 2009 for a review). A crucial difference between human and non-human planning may relate to the diversity of domains and needs in which this skill is expressed (Roberts 2002; Suddendorf and Corballis 2007, 2010; Gilbert and Wilson 2007).

The question of domain-specificity is probably best illustrated by bird research. When they are foraging (i.e., experimentally assessed by offering food choice) some food-caching birds can give priority to future states over present preferences (e.g., scrub jays: Correia et al. 2007; black-capped chickadees: Feeney et al. 2011). Scrub jays anticipate their future feeding needs by caching pine seeds the night before they would need to eat them (Raby et al. 2007). Eurasian jays can plan for two temporally distinct future feeding needs by preferentially caching the food that they will desire most at specific retrieval times (either a few hours later or the next day, Cheke and Clayton 2012). Evidence of similar feats in other domains is largely missing. Great ape planning may also appear domain-specific at first sight since it has only been experimentally demonstrated in the context of tool-use. Indeed, great apes can collect tools not currently needed and save them for a future opportunity to use them up to 14 h later (Mulcahy and Call 2006; Dufour and Sterck 2008; Osvath and Osvath 2008). When they were tested in a similar paradigm, but adapted to a token-exchange task, chimpanzees (but also Tonkean macaques and capuchin monkeys) failed to demonstrate planning skills (Dufour and Sterck 2008; Bourjade et al. 2012), whereas they succeeded in deferring exchanges after short delays (Osvath and Persson 2013). Interestingly, a recent study in wild orangutans showed that sexually mature males may announce their intended travel direction to conspecifics (van Schaik et al. 2013). This may be the best indication yet of domain-

generality of planning in a non-human species. To investigate this question further, we need to experimentally compare planning skills of several great ape species in a task that differs from standard tool-use tasks. Additionally, detecting whether animals can adapt their planning behavior according to changing needs remains to be evaluated in great apes.

To experimentally assess future planning in animals, it must be shown that future-oriented behaviors exclusively rely on the recollection of individual information, in contrast to available environmental cues. This recollection serves to simulate future goals and actions that are not driven by current motivational states (Tulving 2005; Suddendorf and Busby 2005; Roberts and Feeney 2009, 2010). In that respect, the “room task” (Suddendorf and Busby 2005) and the “spoon test” (Tulving 2005) developed by psychologists to test nonverbal beings have become standard procedure to investigate planning. The rationale is to provide subjects with an opportunity to revisit past experience (i.e., generally an initial failure to pass the test), anticipate future scenarios, and organize their own behavior into several key actions that must be performed before the problem appears, to secure future needs not currently experienced.

In the current study, we presented bonobos, chimpanzees, and orangutans with a token-exchange task rather than a tool-use task to investigate a context that differs from the task already applied on the same species (Mulcahy and Call 2006; Dufour and Sterck 2008). Additionally, we manipulated the future needs to detect if individuals modified their planning accordingly. More specifically, the task required subjects to collect and transport tokens (in a serial order and at specific times) to exchange them for food with a human 30 min later. Individuals had to perform a selective collection of tokens (among distracters) at a time where they had no access to either the human or the food, owing to the fact that both were out of the testing area. Token collection could therefore not be prompted by the presence of the human or the food that remained out of sight throughout the testing. Tokens had then to be saved in a different room for a fixed delay, prior to being transported back later on, at the time of exchange. The need for planning was manipulated by offering two conditions. In the *Exchange* condition, collecting and transporting tokens was useful as they could later exchange them for food, while in the *Release* condition, the collection and transport of tokens were not needed as no exchange was offered at the end of the delay.

## Methods

### Subjects

Four orangutans (*Pongo abelii*), four chimpanzees (*Pan troglodytes*) and five bonobos (*Pan paniscus*) participated

**Table 1** Characteristics of the subjects that participated in the study

Name	Species	Sex	Age	Rearing history	Valuable tokens (this study)	Nb of training sessions to criterion	Order of presentation to conditions	Previous experience with token exchange	Previous experience with planning for tool use
Joey	Bonobo	Male	27	Human reared	Green PVC tube	3	Exchange/Release	Pelé et al. (2009)	Mulcahy and Call (2006)
Limbuko	Bonobo	Male	15	Human reared	Green PVC tube	9	Exchange/Release	Pelé et al. (2009)	Mulcahy and Call (2006)
kuno	Bonobo	Male	14	Human reared	Gray PVC cube	3	Release/Exchange	Pelé et al. (2009)	Mulcahy and Call (2006)
Ulindi	Bonobo	Female	17	Mother reared	Green PVC tube	9	Release/Exchange	Pelé et al. (2009)	–
Yasa	Bonobo	Female	13	Mother reared	Gray PVC cube	3	Exchange/Release	Pelé et al. (2009)	–
Jahaga	Chimpanzee	Female	17	Mother reared	Gray PVC cube	4	Exchange/Release	Pelé et al. (2009)	–
Gertrudia	Chimpanzee	Female	17	Mother reared	Green PVC tube	4	Release/Exchange	Pelé et al. (2009)	–
Alex	Chimpanzee	Male	9	Human reared	Gray PVC cube	5	Release/Exchange	–	–
Alexandra	Chimpanzee	Female	11	Human reared	Green PVC tube	4	Exchange/Release	–	–
Bimbo	Orangutan	Male	30	Unknown	Gray PVC cube	3	Release/Exchange	Pelé et al. (2009) Dufour et al. (2009)	–
Dokana	Orangutan	Female	21	Mother reared	Green PVC tube	3	Release/Exchange	Pelé et al. (2009) Dufour et al. (2009)	Mulcahy and Call (2006)
Pini	Orangutan	Female	22	Mother reared	Green PVC tube	3	Exchange/Release	Pelé et al. (2009)	–
Padana	Orangutan	Female	13	Mother reared	Gray PVC cube	5	Exchange/Release	Pelé et al. (2009)	–

in this study. There were seven females and five males ranging in age from 9 to 30 years. All apes were housed at the Wolfgang Köhler Primate Research Center at Leipzig Zoo (Germany), where they lived in social groups of 6–18 individuals. Each group had access to an indoor (175–430 m<sup>2</sup>) or outdoor (1,400–4,000 m<sup>2</sup>) areas according to the season, both furnished with various climbing structures, shelters, natural vegetation and enrichment devices such as foraging containers. During testing, water was available ad libitum and apes were fed according to daily routine. They were provided with fresh fruits, vegetables, cereals and leaves three times a day, with regular addition of eggs and meat. Subjects were individually tested in special test cages (5.1–7.3 m<sup>2</sup>) interconnected by lockable doors. Prior to the study, they have been involved in various cognitive tasks and have been already tested in exchange tasks (Dufour et al. 2009; Pelé et al. 2009).

Table 1 presents subjects' age, sex, rearing history, together with the type of token rewarded in this study, the timing of presentation of the conditions and the previous experience with token-exchange and planning tasks. The study complied with the German law on animal use in research and the European directive 86/609/CEE.

#### Tokens

We used three types of tokens differing in shape and color; green PVC tubes 5 cm long, gray PVC cubes 5 cm wide and metallic chains 5 cm long. All types had been used in a former study on intraspecific token transfers (Pelé et al. 2009) and were therefore known to all subjects except two chimpanzees (Alex, Alexandra). Each subject could exchange only one type of token for food, designed as *valuable*, the others being *non-valuable*.

## Training procedure

Subjects were individually trained to exchange one of the three types of tokens for food in a testing area of 25 m<sup>2</sup> divided in two compartments, room A and room B. Prior to each training session the experimenter lined up 12 exemplars of each type of tokens (i.e., 36 alternating tubes, cubes and chains) on the lower ledge of the exchange panel, i.e., a mesh panel of 68 × 48 cm, inside room A. Two cameras were positioned to record both rooms. Then, the subject entered the testing area, was placed in room A, and the sliding door between rooms A and B was closed. The subject was kept waiting alone for 10 min before the experimenter entered the testing area with the food rewards (pieces of banana), a bowl and a bucket. The experimenter sat down in front of the exchange panel and began requesting tokens holding an open palm out in front of the subject. Each time the subject returned a valuable token, the experimenter gave the subject a food reward. Valuable tokens were placed inside a bowl, whereas non-valuable tokens were thrown away in a bucket without being rewarded. Once the subject had returned all his/her valuable tokens, the experimenter left the testing area and the subject was released. The training ended when subjects selectively exchanged 90 % of their valuable tokens first over three consecutive training sessions. To make subjects well accustomed with the exchange activity, we ran three additional sessions with the same procedure after reaching the training criterion. Six to 12 training sessions were necessary (3 additional routine sessions included) depending on the subjects (mean ± SEM = 7.46 ± 0.59; Table 1).

## Testing procedure

Testing sessions took place in the same testing area following the last training session.

In the *Exchange* condition, the procedure was as follows. Prior to each testing session and out of subjects' view, the experimenter placed the same set of 36 tokens in the room A and turned on the two cameras to record both rooms. The experimenter left the testing area and remained out of the sight of the subject until the end of the test. Then, the subject entered the testing area and got free access to both rooms A and B for 10 min. This 10 min time-window represented the *collection period* during which the subject could collect, save or keep tokens with him/her. The tokens were easily transportable in the hand or in the mouth, and subjects had plenty of time to make multiple trips between the two rooms if they desired to do so. Note, however, that the apes did not have any experience with transporting tokens between two rooms and that this behavior had not been trained. Once the collection period was over, a caretaker ushered the subject into room B and closed the sliding

door between rooms A and B. The caretaker removed all the remaining tokens left in room A in full sight of the subject before leaving the testing area. The number of collected tokens of each type was determined and recorded by the experimenter by subtracting the number of remaining tokens from the total number of tokens deposited in room A. The subject was kept waiting for 20 min more in room B before the caretaker came back, opened the sliding door and ushered him/her in room A. Once the subject was in room A, with or without tokens, the caretaker closed the sliding door between rooms A and B and left the testing area. This 20-min time-window was considered as the *waiting period* preceding the crucial time of bringing tokens back to the room A where the exchange activity usually occurred.

At the end of the waiting period, the experimenter entered the testing area with the food rewards, a bowl and a bucket and sat in front of the exchange panel. The experimenter began requesting tokens holding an open palm out in front of the subject for a minimum duration of 3 min and up to the duration needed to exchange all valuable tokens brought back by the subject. The experimenter gave the subject the food reward each time s/he returned the correct type of tokens. Once the subject had returned all his/her valuable tokens, the experimenter left the testing area and the subject was released.

The *Release* condition was similar to the *Exchange* condition, except that the subject was released at the end of the waiting period without having the possibility to exchange his/her tokens with the experimenter. In fact the experimenter never even came into view of the subject. Note that the caretakers were blind to the condition until they transferred the ape from room B to room A, where the caretaker either made the subject wait in room A (*Exchange* condition) or released her from room A (*Release* condition). Video footage was used to keep track of the number of tokens of each type that had been collected, transported and when possible exchanged.

We presented the apes with the two conditions in a balanced design (see Table 1) with half of the subjects (i.e., six individuals) randomly assigned first to the *Release* condition and then presented with the *Exchange* condition (RE group). The seven remaining individuals were presented first with the *Exchange* condition and then switched to the *Release* condition (ER group). Each condition was presented 16 times (trials), but only once per day. The first trial was considered as a pretest that acted as an event to remember (i.e., an initial failure for example) and was therefore not considered in the analysis.

## Statistical analyses

A “bring-back” response was scored whenever the subject brought back at least one valuable token from room B to

room A at the end of the waiting period. In the *Exchange* condition, it meant that the subject received a reward for each valuable token brought back, whereas in the *Release* condition bringing back valuable tokens was not rewarding owing to the absence of the experimenter at the end of the delay. We fitted generalized linear mixed models on this binary variable (1 for “bring-back” responses/0 for “does not bring back any valuable token”) with a Binomial family and a Logit link function (Brown and Prescott 2006). Pseudoreplication due to repeated observations of the same individual was taken into consideration by adding the individual or the interaction between *individual* and *condition* as random effects (model fitting procedure is given in Online Resources 1 and 2). Best fitting models were selected on the basis of the lowest AIC, i.e., Akaike Information Criterion.

We used nonparametric statistical tests to assess subjects’ preference and selectivity for collecting/transporting valuable *versus* non-valuable tokens. *Collecting tokens* referred to collecting tokens in room A, transporting tokens from room A to room B, and keeping tokens in room B during the waiting period. *Transporting tokens* referred to picking up tokens in room B at the end of the waiting period and transporting them in room A before the sliding door was closed. Subjects’ preference for collecting/transporting valuable tokens was assessed by dividing the total number of valuable tokens collected/transported by the total number of tokens collected/transported in each condition. Subjects’ selectivity for collecting/transporting valuable tokens in the *Exchange* rather than the *Release* condition was assessed as follows: for each condition, we calculated (1) the mean proportion of tokens collected over the total amount of tokens available of each type (i.e., 12 valuable and 24 non-valuable tokens) in room A and (2) the mean proportion of transported tokens over the total amount of tokens of each type available in room B (i.e., tokens initially collected from room A to room B). All tests were two-tailed and performed with R 2.10.1 software (<http://cran.r-project.org>). The level of significance was set at 0.05.

## Results

### Rates of “bring-back” response according to the condition

Two bonobos (Kuno, Yasa), two chimpanzees (Jahaga, Alex), and one orangutan (Bimbo) did not show any interest in the task and never collected tokens. Of the eight remaining individuals, three out of the five who started with the *Exchange* condition performed more “bring-back” responses in the *Exchange* than in the *Release* condition,

although only Limbuko showed a clear-cut difference between the two. In contrast, all the three subjects who started with the *Release* condition, reliably produced more “bring-back” responses in the *Exchange*, than in the *Release* conditions. Gertrudia displayed the smallest difference between the two conditions (two trials), but solved the task for the first time on the eighth trial and then displayed two consecutive “bring-back” responses on trials 13 and 14, suggesting a late acquisition of the task. Table 2 gives a summary of subjects’ performances in the two conditions.

Overall, eight subjects solved the task in the *Exchange* condition and were given food rewards after successful exchanges. Additionally, three individuals (Limbuko, Ulindi, Dokana) showed a clear differential response between conditions by producing more “bring-back” responses in the *Exchange* than in the *Release* conditions. Considering the performance at the species level, we found that both the condition and the species affected the overall rate of the “bring-back” response (Fig. 1), with the chimpanzees differing from the two other ape species ( $N = 13$ ; best fitting model: AIC = 288.5, see Online Resource 3; chi-square tests for the log-likelihood ratios, best fitting model—null model,  $p = 0.030$ ). The apes produced “bring-back” responses significantly more often in the *Exchange* than in the *Release* conditions (Wald test,  $z = -2.98$ ,  $p = 0.003$ ), and chimpanzees did so to a lesser extent than bonobos and orangutans (Wald test,  $z = -2.79$ ,  $p = 0.005$ ). Online Resource 4 provides an illustration of the task.

### Effect of the order of presentation of the conditions

The order of presentation of the conditions and the species affected the overall rate of “bring-back” responses (Fig. 2), with the chimpanzees differing from the two other ape species ( $N = 13$ ; best fitting model: AIC = 278.9, see Online Resource 5; chi-square tests for the log-likelihood ratios, best fitting model—null model,  $p < 0.001$ ). Subjects who first received the *Release* condition produced significantly less “bring-back” responses in the *Release* than in the *Exchange* conditions, compared to subjects who received the *Exchange* condition first; with the interaction between the order of presentation of the conditions and the condition being significant (Wald test,  $z = -3.32$ ,  $p < 0.001$ ).

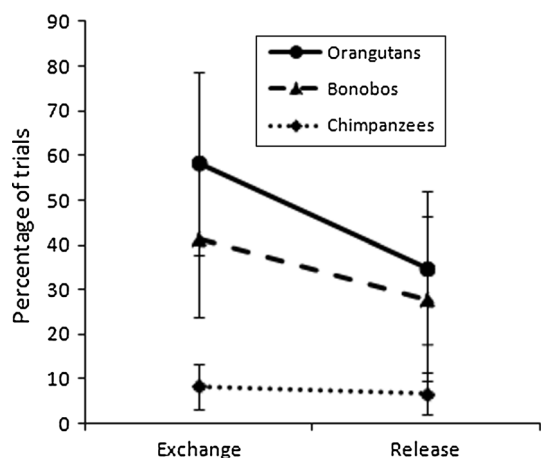
The number of “bring-back” responses scored by the two groups of subjects, i.e., ER and RE, differed significantly in the *Release* condition only (Permutation test, *Release*:  $t = 2.03$ ,  $p = 0.040$ ; *Exchange*:  $t = 0.95$ ,  $p = 0.371$ ;  $N = 13$ ). The effect of the condition was stronger for the subjects who began with the *Release* condition than for those apes who began with the *Exchange*

**Table 2** Summary of the subjects' performances

Subjects	Exchange condition			Release condition		
	Number of "bring-back" responses <sup>a</sup>	Trial no.	Mean number of tokens brought back <sup>b</sup>	Number of "bring-back" responses <sup>a</sup>	Trial no.	Mean number of tokens brought back <sup>b</sup>
<b>Bonobos</b>						
Joey	13/15	1–6, 9–15	1.38	14/15	1, 2, 4–15	1.64
Limbuko	10/15	1, 3–5, 7, 8, 12–15	4.00	5/12	1, 4, 5, 8, 12	2.60
Kuno	0/10		0.00	0/11		0.00
Ulindi	6/15	6–8, 10, 12, 14	1.00	0/15		0.00
Yasa	0/15		0.00	0/15		0.00
<b>Chimpanzees</b>						
Jahaga	0/15		0.00	0/15		0.00
Gertrudia	3/15	8, 13, 14	2.33	1/15	7	1.00
Alex	0/15		0.00	0/15		0.00
Alexandra	2/15	1, 7	4.00	3/15	7, 14, 15	5.00
<b>Orangutans</b>						
Bimbo	0/15		0.00	0/15		0.00
Dokana	13/15	1, 3–7, 9–15	1.85	2/15	2, 6	1.50
Pini	13/15	1–9, 11, 13–15	9.38	11/15	1–3, 5, 6, 8, 9, 11–14	5.00
Padana	9/15	1–3, 6, 10–14	2.78	8/15	3, 6, 8–15	11.00

<sup>a</sup> Trials where at least one valuable token had been collected in room A and later brought back from room B to room A

<sup>b</sup> The mean was only calculated over trials where a "bring-back" response was scored



**Fig. 1** Mean percentage ( $\pm$ SEM) of "bring-back" responses (i.e., trials where at least one valuable token had been collected and brought back to room A) according to the condition

condition (Fig. 3). Owing to this order effect that could have affected subjects' performance in the second part of the study (16 s trials), we compared subjects' initial performance during the first 16 trials as a function of the condition they received (*Exchange*:  $N = 7$ ; *Release*:  $N = 6$ ). Subjects involved in the *Exchange* condition produced significantly more "bring-back" responses than subjects in the *Release* condition (Permutation test,

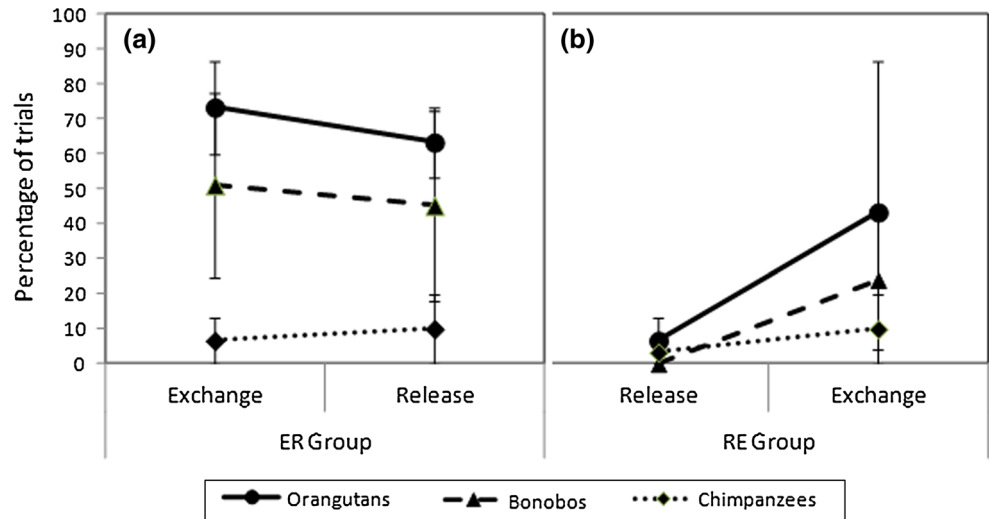
$t = 2.11$ ,  $p = 0.049$ ) during the first 16 trials of the study (Fig. 3).

#### Selectivity for valuable tokens

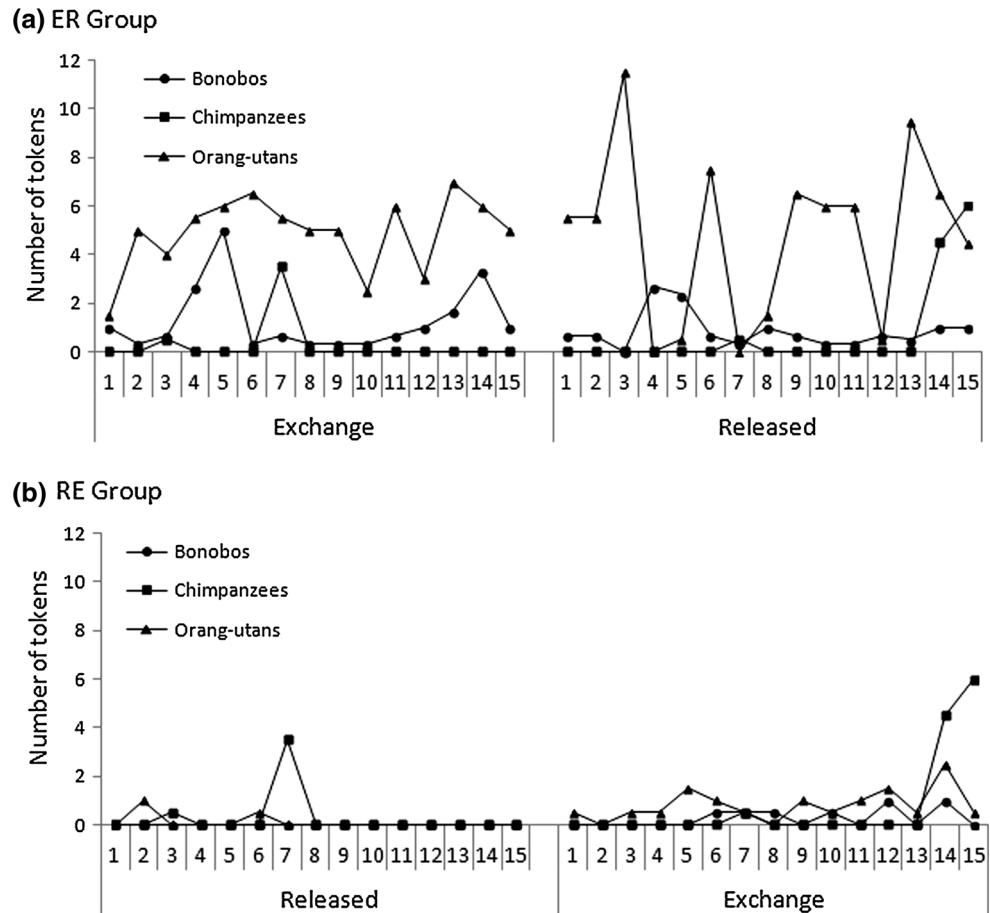
During the collection period, the apes collected valuable tokens significantly above chance in the *Exchange* condition (Binomial tests; theoretical probability  $p = 1/3$ , all apes,  $N = 13$ ,  $p < 0.001$ ; bonobos,  $N = 5$ ,  $p = 0.006$ ; chimpanzees,  $N = 4$ ,  $p < 0.001$ ; orangutans,  $N = 4$ ,  $p < 0.001$ ), and in the *Release* condition, except the bonobos (Binomial tests; theoretical probability  $p = 1/3$ , all apes,  $N = 13$ ,  $p < 0.001$ ; bonobos,  $N = 5$ ,  $p = 0.547$ ; chimpanzees,  $N = 4$ ,  $p < 0.001$ ; orangutans,  $N = 4$ ,  $p < 0.001$ ). The apes were not more selective for collecting the valuable tokens in the *Exchange* than in the *Release* condition (Fisher exact probabilities tests: all apes,  $N = 13$ ,  $p = 0.768$ ; bonobos,  $N = 5$ ,  $p = 1$ ; chimpanzees,  $N = 4$ ,  $p = 1$ ; orangutans,  $N = 4$ ,  $p = 0.773$ ; Fig. 4a).

At the end of the waiting period, all apes except the chimpanzees brought back valuable tokens from room B to room A significantly above chance in the *Exchange* condition (Binomial tests; theoretical probability = number of valuable tokens saved in room B/number of all tokens saved in room B; all apes,  $N = 13$ ,  $p < 0.001$ ; bonobos,  $N = 5$ ,  $p < 0.001$ ; orangutans,  $N = 4$ ,  $p < 0.001$ ; chimpanzees,  $N = 4$ ,  $p = 1$ ), and in the *Release* condition

**Fig. 2** Mean percentage ( $\pm$ SEM) of “bring-back” responses as a function of subjects’ group. **a** ER group (*Exchange* then *Release*), **b** RE group (*Release* then *Exchange*)

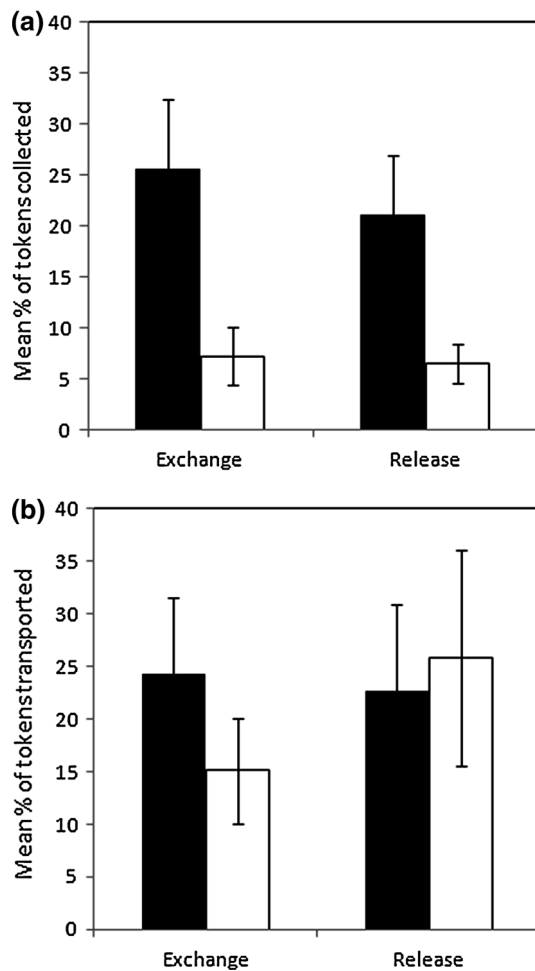


**Fig. 3** Mean number of valuable tokens transported back to room A. **a** ER group (*Exchange* then *Release*), **b** RE group (*Release* then *Exchange*)



(Binomial tests; theoretical probability = number of valuable tokens saved in room B/number of all tokens saved in room B; all apes,  $N = 13$ ,  $p < 0.001$ ; bonobos,  $N = 5$ ,  $p = 0.022$ ; chimpanzees,  $N = 4$ ,  $p = 0.016$ ; orangutans,  $N = 4$ ,  $p < 0.001$ ). The apes were not more selective for transporting the valuable tokens in the *Exchange* than in the *Release* condition (Fisher’s exact probabilities test: all

apes,  $N = 13$ ,  $p = 0.201$ ; chimpanzees,  $N = 4$ ,  $p = 0.164$ ; orangutans,  $N = 4$ ,  $p = 1$ ; Fig. 4b), except the bonobos that brought back higher proportions of non-valuable tokens in the *Release* (mean %  $\pm$  SEM =  $34 \pm 19.0$ ) than in the *Exchange* (mean %  $\pm$  SEM =  $15 \pm 7.4$ ) conditions and similar proportions of valuable tokens in the two conditions (mean %  $\pm$  SEM<sub>Exchange</sub> =  $19 \pm 10$ ; Mean



**Fig. 4** Selectivity for valuable and non-valuable tokens; **a** proportion (mean  $\pm$  SEM) of tokens collected in room A (i.e., out of the initial available amount of 12 valuable and 24 non-valuable tokens), **b** proportion (mean  $\pm$  SEM) of tokens transported back from rooms B to A (out of the amount available in room B). *Solid bars* valuable tokens, *open bars* non-valuable tokens

$\% \pm \text{SEM}_{\text{Release}} = 17 \pm 11$ ; Fisher exact probabilities test:  $N = 4$ ,  $p = 0.047$ ).

## Discussion

The present results confirm that great apes can generate future action plans to secure future needs (i.e., a token to be exchanged for food) they are not currently experiencing. Our task revealed species differences, with bonobos' and orangutans being more skillful than chimpanzees in the context of token exchange. For these two species, planning extended beyond the context of tool use, which contradicts the hypothesis of domain-specificity in non-human species (e.g., Suddendorf and Corballis 2007, 2010). Moreover, three subjects exhibited transport of valuable tokens more often in the condition where they could exchange them for food compared to the condition where they could not. To

some extent, this suggests that great apes can flexibly adjust their planning behavior when there is a change in their future needs.

We argue that the future-oriented behavior of these apes is a genuine case of future planning. Indeed, to solve the task, the apes had to collect valuable tokens in room A, transport them in room B, keep them in this room during the waiting period, pick them up again, and then transport them back at the end of the waiting period in room A before the sliding door was closed after them. Note that the apes could no longer go back to room B (to pick up forgotten tokens for example) once the experimenter had entered the testing area. Thus, any “bring-back” response was the result of a complex behavioral sequence formed by several actions (some of which were not directly reinforced) and that had to be performed in a specific order. It is conceivable that the apes formed an association between picking up valuable tokens from the floor and obtaining food rewards during the training. In this respect, the apes' selective collection of valuable tokens was not surprising. Furthermore, one could argue that apes solved the task because the sight of the tokens elicited the exchange response. Although this argument would hold for collecting tokens, there is no reason why it should also elicit their transport to room B. Recall that token transport had not been explicitly trained, and it was never rewarded in room B. Moreover, neither the food nor the human partner was present in the testing area, something that could signal the impending food exchange opportunity.

Alternatively, one could argue that token transport might have occurred by association as a mere by-product of the apes' high interest in valuable tokens. In other words, the apes might have solved the task by moving the token by chance and getting rewarded for it. One difficulty with this explanation is that the required responses and the reinforcement for their production are substantially separated in time. The shape of the acquisition curves is also problematic for this explanation. More specifically, associative learning would predict a gradual increase or decrease in the apes' performance. However, this is not what we observed. Individuals presented with *Exchange* first, who were likely to form such an association, displayed a stochastic pattern rather than a gradual decrease in “bring-back” responses once presented with the *Release* condition (see Fig. 3). Likewise, individuals that received the *Release* condition first should have produced bring-back responses on first trials followed by rapid extinction. Additionally, some of them later solved the task despite a “counter-exposure” of never being rewarded for 16 consecutive sessions. Consequently, it is unlikely that associative learning solely accounts for the apes' planning behavior.

This study further showed that some individuals were capable of adjusting their future-oriented behavior



depending upon experimental contingencies. In humans, updating planned actions with upcoming information appears to be a difficult component of planning since it imposes a high cognitive load on working memory (Petrides 1994; Owen 1997). To date, scrub jays had been shown to use upcoming information about decaying rates of cached food to adjust their cache preferences at recovery time 1 day later (Clayton et al. 2003). Squirrel monkeys are also sometimes capable of reversing their initial strategy according to future outcomes (McKenzie et al. 2004; Naqshbandi and Roberts 2006). Crucially, three individuals (two bonobos and one orangutan) reliably brought valuable tokens back to room A more often in the *Exchange* than in the *Release* conditions. One orangutan (Pini) and one bonobo (Limbuko) also brought back a substantially greater number of tokens in the *Exchange* than in the *Release* condition. Such a flexible behavior in non-human primates' future planning has never been reported to date. Importantly, differential responses between *Exchange* and *Release* conditions were visible from the first 16 trials; with individuals involved in the *Exchange* condition producing more “bring-back” responses than the apes involved in the *Release* condition. However, individuals' flexibility in adjusting behavior to conditions was higher for those individuals who had begun with the *Release* rather than the *Exchange* conditions. One tentative explanation of this order effect is that collecting and saving tokens was possibly less costly for the apes than not doing so (in case an opportunity for exchanging them for food arose). Thus, compared with individuals who had received the *Release* condition first, individuals who had begun with the *Exchange* condition may have been less likely to stop collection and transport “just in case” an opportunity reappeared. Perhaps informing the apes about the condition they were about to receive, for instance, by using explicit time cues such as morning *Exchange* versus afternoon *Release*, may have produced clearer differences between *Exchange* and *Release* conditions. However, this would have involved the use of a cue that may have eliminated the need to recall what took place in previous sessions. Note that the effect of condition that we observed here was possibly weakened by the time the apes spent adjusting to the contingencies of each condition, given that apes could only rely on their personal memories of what happened the days before. Nevertheless, our findings show that apes can adjust their behavior depending on whether they will have an opportunity to exchange tokens later on.

It is worth noting that we found high individual variability in planning responses. This is not surprising given that we tested an unusually large sample size in comparison to other studies of future planning in non-human primates. Individual differences can be partly explained by a lack of interest from some individuals in the study, i.e., five apes

never collected any tokens. Despite this variability, our results highlight that individual chimpanzees, individual orangutans and individual bonobos differentially attended to the task, suggesting that species differences in regard to future planning may exist. Individual orangutans appeared to understand the temporal components of the task better than the other species. Three out of the four orangutans scored very highly, producing “bring-back” responses in 60–87 % of the trials in the *Exchange* condition. Individual orangutans and bonobos also displayed the best adjustment to the conditions, whereas chimpanzees failed to distinguish the two conditions and failed to appreciate the temporal components of the task. However, chimpanzees were the most selective for the valuable tokens and hardly ever collected non-valuable tokens throughout the study. Bonobos were less accurate in selecting valuable tokens, but this depended on the condition. They definitely collected and transported more valuable tokens in the *Exchange* condition, but reversed their preferences in the *Release* condition, suggesting they knew *which* tokens they needed to solve the task and *when* precisely they did and did not need them. In the same vein, orangutans were the ones bringing the largest numbers of tokens back in room B, though only one orangutan (Pini) maximized her benefit by bringing back all or most of the correct tokens in room B. These findings highlight that behavioral adjustments to the immediate contexts can take different forms and suggest that individuals from the three species differentially attended to the multiple components of the planning task.

The fact that most apes brought back a small number of valuable tokens is reminiscent of the tactic deployed by macaques and capuchins tested with a comparable task (Bourjade et al. 2012). Three monkeys completed 10–33 % of the trials bringing back only one valuable token each time. Thus, the monkeys focused on a strategy to get food, but failed to understand that they could maximize their gains by bringing several tokens back instead of one. One tentative interpretation is that the apes attribute food quality differently from quantity and only optimize reward quality. This would be consistent with the results of previous studies in monkeys (Silberberg et al. 1998; Anderson et al. 2008) and corvids (Dufour et al. 2012; Wascher et al. 2012; Hillemann et al. 2014). Notably, in the previous work with great apes, saving and transporting only one tool (i.e., a stick with bonobos and orangutans: Mulcahy and Call 2006; a hook with chimpanzees: Dufour and Sterck 2008), or only one token (e.g., Osvath and Persson 2013), was sufficient to gain the maximum amount of food. Bringing back several exemplars of the same tokens might have represented an extra cognitive load for most individuals of the present study, in comparison to previous experiments using one tool or one token (Mulcahy and Call 2006; Osvath and Osvath 2008; Osvath and Persson 2013).

Thus, one explanation is that the general relationship established between tokens and food on a qualitative level may be easier to grasp than the quantitative relationship between each token and each piece of food, albeit the latter was obviously achieved by some orangutans.

Interestingly, the token-exchange task may thus reveal species differences that had not been detected with the tool-use task. Hence, the single experimental design, i.e., derived from the “Spoon test” (Tulving 2005) and used to test for planning abilities of the three species in two different domains (i.e., tool-use task: Mulcahy and Call 2006; Dufour and Sterck 2008; token-exchange task: this study), allows us to compare species’ performances across tasks (and thus contexts). Consistently with our results, orangutans performed better than the two other species in the tool-use task (solving 37–94 % of trials; Mulcahy and Call 2006) and showed comparable performances across tasks (solving 60–87 % of trials in this study). The bonobos however, performed better in our study (solving 40–87 % of trials) than in the tool-use task (solving 12–44 % of trials; Mulcahy and Call 2006), perhaps due to a general knowledge of the testing procedure. In fact, three bonobos (Kuno, Joey, Limbuko) and one orangutan (Dokana) of this study had been involved in the former tool-use planning task (Mulcahy and Call 2006). However, one bonobo (Ulindi) and two orangutans (Pini, Padana) of the present study also obtained high scores in the token-exchange task, suggesting that previous experience with the procedure was not necessary to solve the task. Chimpanzees successfully planned the token-exchange task in 13–20 % of trials and the tool-use task in 29–64 % of trials (Dufour and Sterck 2008) and were therefore more successful with tools. Importantly, the chimpanzees of our study were not familiar with the testing procedure, which might have been a cause of differential performances with the other species. However, Dufour and Sterck (2008) also tested naïve chimpanzees’ planning abilities with a token-exchange task and obtained results very similar to ours. In contrast, Osvath and Persson (2013) recently reported that two chimpanzees and one orangutan could collect one token and transport it to exchange it for food 15 min later in 50–58 % of trials. This suggests that shortening the delay between collection and exchange might render the task more tractable for the chimpanzees.

The reasons why chimpanzees mostly fail to plan for a future token-exchange (collaborative) task while they succeed with tools (e.g., Dufour and Sterck 2008; Osvath and Osvath 2008) are not completely clear. One possibility is that chimpanzees may be more limited than the other ape species in their planning skills outside functional contexts in which they excel, such as tool use. In this respect, future planning in chimpanzees might rather be domain-specific, although variable performances between individuals and studies invite to cautiousness until this is investigated

further. Alternatively, chimpanzees’ results in planning for a token exchange that implies a social component may be explained by differential prosocial tendencies with other species. While orangutans have pseudo-solitary lifestyle, forming individual-based fission–fusion societies where individuals group temporarily for social purposes (Mitani et al. 1991; Van Schaik 1999), chimpanzees form larger parties dominated by male–male bonds and high feeding competition (Nishida 1990; Boesch 1996). In particular, female chimpanzees with offspring are relatively solitary to avoid feeding competition (Goodall 1986; Chapman et al. 1995; Stumpf 2007) and social bonds are also weaker and less affiliative than in bonobo societies (Stanford 1998). In contrast, female bonobos establish and maintain strong affiliative bonds with one another, are more likely to cooperate, and to approach and mate with strangers (Parish 1996; Furuichi 2011). In that respect, chimpanzees’ reliance on collaboration with a partner might have been selected against (Jaeggi et al. 2010), which would arise in stark contrast with bonobos that are able to share with strangers in experimental contexts (Tan and Hare 2013), and with orangutans that can give tokens to others (Pelé et al. 2009) and exchange them reciprocally better than any other ape species to date (Dufour et al. 2009). There is also accumulating evidence that chimpanzees perform better in competitive than in cooperative cognitive tasks (Hare 2001; Hare and Tomasello 2004), take selfish decisions (Jensen et al. 2006), and discriminate helping from non helping homospecific (Melis et al. 2006) and hetero-specific (Subiaul et al. 2008) partners. These collective findings suggest that chimpanzees may have quickly learned that the experimenter was unwilling to give the food from the very first trial (where they did not bring tokens back) in our study. Future research may address whether this particular response reveals a more general trend of the species for avoiding prosocial activities (Jaeggi et al. 2010), for instance in devising an experimental paradigm that requires the chimpanzees to collaborate at various times in the future for outcompeting a human or another conspecific (Hare 2001).

Suddendorf and Corballis (2010) stressed that “diverse contexts are necessary to demonstrate the flexibility that is so characteristic of human foresight” (p. 296). This study provides some evidence that at least bonobos and orangutans can plan beyond traditional individually centered tasks such as tool use and engage in tasks such as token exchange that also possess a social component. Whether chimpanzees are more limited than other species in this regard is something that needs to be confirmed in future studies. At this stage, our results provide a missing link of domain-general flexibility of great apes future planning, although the true extent of this flexibility remains to be determined.

**Acknowledgments** The research was supported by a grant from the *Agence Nationale de la Recherche* (ANR-08-BLAN-0042-01). We thank Hanna Petschauer for her valuable assistance throughout the study.

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