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Crows and common ravens do not reciprocally exchange tokens with a conspecific to gain food rewards

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25 **Abstract**

26 Human economic transactions are based on complex forms of reciprocity, which
27 involve the capacities to share and to keep track of what was given and received over time.
28 Animals too engage in reciprocal interactions but mechanisms, such as calculated
29 reciprocity have only been shown experimentally in few species. Various forms of
30 cooperation, *e.g.* food and information sharing, are frequently observed in corvids and they
31 can engage in exchange interactions with human experimenters and accept delayed
32 rewards. Here, we tested whether carrion crows and common ravens would reciprocally
33 exchange tokens with a conspecific in an exchange task. Birds received a set of three
34 different types of tokens, some valuable for themselves, *i.e.* they could exchange them for a
35 food reward with a human experimenter, some valuable for their partner, and some
36 without value. The valuable tokens differed between the birds, which means that each bird
37 could obtain more self-value tokens from their partner's compartment. We did not observe
38 any active transfers, *i.e.* one individual giving a token to the experimental partner by placing
39 it in its beak. We only observed 6 indirect transfers, *i.e.* one individual transferring a token
40 into the compartment of the partner (3 no-value, 1 partner-value and 2 self-value tokens)
41 and 67 'passive' transfers, *i.e.*, one subject taking the token lying in reach in the
42 compartment of the partner. Individuals took significantly more self-value tokens compared
43 to no-value and partner-value tokens. This indicates a preference for tokens valuable to
44 focal individuals. Significantly more no-value tokens compared to partner-value tokens were
45 taken, likely to be caused by experimental partners exchanging self-value tokens with the
46 human experimenter, and therefore more no-value tokens being available in the
47 compartment. Our results presently do not provide empirical support for reciprocity in
48 crows and ravens, most likely caused by them not understanding the potential roles of

49 receiver and donor. We therefore suggest further empirical tests of calculated reciprocity to
50 be necessary in corvids.

51

52 **Keywords:** carrion crows, common ravens, cooperation, corvids, reciprocity, token
53 exchange

Introduction

Human societies show a high propensity of cooperation between unrelated individuals (Fehr & Fischbacher, 2003) and the inherent evolutionary instability of cooperation inspires a great amount of interest in researching these cooperative behaviours (Axelrod & Hamilton, 1981), because individuals are not expected to invest in a cooperative enterprise without a guarantee of net fitness returns. To date, the most prominent theory explaining human cooperation is reciprocal altruism, based on the idea of individuals engaging in actions that are costly for themselves expecting future returns (Maynard Smith, 1983; Trivers, 1971). The relationship between interaction partners plays a significant role regarding the complexity of cooperation. In symmetry-based cooperation, interactions without equivalent returns balance out over time between kin and long-term partners (Berghänel et al., 2011; Dunbar, 1980). In contrast, calculated reciprocity requires keeping a mental record of the debts owed and the favours given (de Waal & Luttrell, 1988), based on the expectancy of a return for every costly favour given. Emotions may as well modulate cooperative interactions. Attitudinal reciprocity has been suggested to take the partner's general social attitude into account (de Waal, 2000) and emotionally based bookkeeping allows long-term tracking of reciprocity without involving complex cognitive skills (Schino et al., 2007). Therefore, different forms of cooperative behaviour in nonhuman animals are expected to be based upon different cognitively challenging mechanisms depending on the complexity of the social system.

Despite the growing research effort on cooperation in animal societies in the recent decades, it is still unclear if and to what degree, some non-human animals are also capable of cooperative interactions based on reciprocal altruism (Taborsky, 2013). Observational

studies, particularly in primates, suggest reciprocity in grooming (Barrett et al., 1999; Gomes et al., 2009; Majolo et al., 2012; Molesti, 2017; Schino et al., 2007), grooming for food (de Waal, 1997), agonistic support (Watts, 2001), grooming for agonistic support (Carne et al., 2011), food sharing (Wilkinson, 1984) and allonursing (Engelhardt & Weladji, 2015).

Surprisingly few experimental studies test for direct reciprocity in non-human animals. In a token exchange task, individuals had to exchange tokens useless to themselves but valuable to an experimental partner, in order to exchange the token valuable to them for food with the experimenter. Two orangutans (*Pongo pygmaeus abelii*) actively gave numerous tokens valuable to the experimental partner and one of the orangutans routinely used gestures to request tokens while the other complied with such requests (Dufour et al., 2009). Similarly, requests for help in a reciprocal exchange paradigm have also been discussed in Norway rats (Schweinfurth & Taborsky 2018). A number of other primate species (Capuchin monkeys (*Sapajus apella*), Tonkean macaques (*Macaca tonkeana*), gorillas (*Gorilla gorilla*), bonobos (*Pan paniscus*), and chimpanzees (*Pan troglodytes*)) tested in a similar token exchange paradigm compared to the study in orangutans, failed to actively exchange tokens and if exchanges occurred, they were mostly of ‘passive’ nature, *i.e.* a subject brings a token near the common mesh wall and tolerates the partner to take it or ‘indirect’ exchanges, *i.e.* an individual places a token in the partner’s compartment without physical contact with the partner (Pelé et al., 2009; Pelé et al., 2010). In different experimental setups, *e.g.* instrumental cooperation tasks, food exchange or predator mobbing, rats, pied flycatchers (*Ficedula hypoleuca*), zebra finches (*Taeniopygia guttata*), vampire bats (*Desmodus rotundus*), chimpanzees and working dogs (*Canis familiaris*) cooperated more with previous cooperators compared to defectors (Gfrerer & Taborsky,

2018; Krams et al., 2008; Melis et al. , 2008; Rutte & Taborsky, 2008; St-Pierre et al., 2009), however direct reciprocity still requires to be studied in different species in order to gain further insight in the social and ecology requirements facilitating the evolution of reciprocal altruism in the wild (Taborsky 2013).

In the present study, we examined if two species of corvids, carrion crows (*Corvus corone corone*) and common ravens (*Corvus corax*) were able to engage in calculated reciprocity using the paradigm already used in several primate species (Dufour et al., 2009; Pelé et al., 2009; Pelé et al., 2010). Various forms of naturally occurring cooperation can be observed in different corvid species (*e.g.* coalition formation: (Heinrich, 1999), social support: (Emery et al. , 2007), resource or information sharing: (Bugnyar & Kotrschal, 2001; de Kort et al., 2006), and cooperative breeding: (Baglione et al., 2003; Woolfenden & Fitzpatrick, 1985). Cooperative propensities vary not only between but also within species, depending on socio-ecological factors (Clayton & Emery, 2007). Particularly in costly interactions (*e.g.* food sharing, agonistic encounters) corvids are very selective in choosing a certain partner (Emery et al., 2007; Fraser & Bugnyar, 2010), which hints at reciprocity. In corvids, long-term relationships are frequent, which makes symmetry-based reciprocity likely. But also, short-term cooperative interactions exist (Fraser & Bugnyar, 2011), which could be based on calculated reciprocity. Experimental studies on cooperative behaviour in corvids are scarce and it remains unclear whether mutualism or reciprocal altruism is involved (Massen et al., 2015b; Scheid & Noë, 2010; Seed et al., 2008). Subadult ravens and crows fail to transfer valuable tokens to conspecifics, when there is nothing to gain for themselves (Massen et al., 2015a; Horn et al. unpublished data) and food sharing in pinyon jays (*Gymnorhinus cyanocephalus*) is not based on short-term or long-term reciprocity

(Duque & Stevens, 2016). In cooperative contexts, ravens have been shown to memorise the outcome of an interaction with human experiments after a single interaction (Müller et al., 2017). In a prisoner's dilemma task, blue jays (*Cyanocitta cristata*) failed to behave reciprocally (Clements & Stephens, 1995). This is of special interest as the blue jay's inability to cope with a delay of gratification causes its failure to reciprocate (Stephens et al., 2002). Recently, this cognitive prerequisite of reciprocity has been successfully shown in crows and ravens (Dufour et al., 2012; Hillemann et al., 2014). Crows have also demonstrated to be sensitive to inequity in reward distribution and working effort (Wascher & Bugnyar, 2013) and learn to differentiate between reliable and unreliable cooperation partners (Massen et al., 2015b; Mueller et al., 2015; Wascher et al., 2015). This shows that corvids do possess cognitive abilities necessary for reciprocal altruism and this makes them ideal candidates to test this form of cooperation. Further, individuals responding stronger to unequal treatment initiate less affiliative behaviour in a group context (Wascher, 2015), indicating cognitive skills in crows facilitating cooperative behaviours.

In the present study, we expected the crows and ravens to learn to attribute different value of tokens for different individuals and to adapt their behaviour accordingly. By monitoring the occurrence of transfers, the value of tokens exchanged and the alternation of roles between individuals, we aimed to assess the extent to which crows and ravens may purposefully engage in reciprocal behaviours. We expect individuals to preferentially exchange self-value tokens with the human experimenter. Further, we expect crows and ravens to preferentially manipulate self-value and partner-value tokens, compared to no-value tokens. If crows and ravens engage in reciprocal altruism, we expect experimental partners to transfer partner-value tokens in a reciprocal way with each other.

150 Further, if focal individuals fully understand the value of different types of tokens, they
151 might preferentially cache partner-value tokens for future use.

Methods

Study subjects and housing

Subjects were 6 captive crows (5 carrion crows, *Corvus corone corone*, 1 hooded crow, *Corvus corone cornix*) at the Konrad Lorenz Forschungstelle (KLF), Austria and 2 captive ravens (*Corvus corax*) at Edinburgh Zoo, RZSS, UK. Birds were held in large outdoor aviaries, equipped with wooden perches, natural vegetation and rocks. An enriched diet consisting of fruit, vegetables, bread, meat and milk products was provided on a daily basis. Water was available *ad libitum*. For testing, subjects were voluntarily, *i.e.* they entered the experimental compartment on their own, separated in a familiar compartment.

Tokens

In the present experiment we used three different types of tokens. Tokens differed in form, material and colour, and some could be exchanged for food in the experiment. Tokens used were a triangle cut out of a blue plastic bottle screw-top, with the sides being about 1 cm long, a metal screw nut, about 1 cm in diameter and a wooden triangle, with sides approximately 2 cm long. In the experiment, subjects were initially given sets of 36 tokens, consisting of 12 items of each of the three types of tokens. In an initial training phase, tokens were associated as either (a) 'self-value' tokens, which the subject could exchange for a food reward with a human experimenter, (b) 'partner-value' tokens were valuable to the experimental partner and valueless to the subject, and (c) 'no-value' tokens were not valuable to any individual within an experimental dyad. Table 1 gives information about each subject's self-value tokens. Self-value tokens were associated semi-randomly for individuals, however experimental dyads were considered, *i.e.* individuals of a

dyad had to have different self-value tokens. The wooden triangle was assigned as the no-value token for all dyads.

Training Procedure

All the birds were trained to exchange an item against a food reward with a human experimenter and participated in different experiments applying this paradigm (Dufour et al., 2012; Wascher et al., 2012; Wascher & Bugnyar, 2013). The present experiments have been conducted by two human experimenters, TF and CAFW. At the beginning of each training session, 12 items of each token type were placed in the experimental compartment (Figure 1). A training session started with the experimenter requesting tokens by holding an open hand, with palm up, next to the fence and showing the reward in the other hand. Rewards were either mealworms or greaves, *i.e.* deep-fried pig grease, depending on the personal preference of the birds. When a subject gave a self-value token to the human experimenter, it received one piece of food reward, but did not receive a reward when transferring a partner-value or no-value token to the human experimenter. When receiving a token from the subject, the human experimenter placed the self-value tokens in one container and the partner-value and no-value token in a different container, to illustrate the difference in value to the subject. Once the bird had returned its 12 self-value tokens, the training session was over. A subject was considered trained when they succeeded in giving at least 90 % of the correct tokens first, during three consecutive sessions.

Testing Procedure

Testing took place in the same room as the training, divided into two testing compartments by a wire mesh through which subjects could interact and transfer tokens

199 with each other. In testing phase 1 (full set phase), we placed the same set of 36 tokens (12
200 self-value tokens for subject, 12 partner-value tokens, and 12 no-value tokens) in each
201 compartment. In the first part of a session, partners had the possibility to exchange self-
202 value tokens with the experimenter. Once both individuals had exchanged all 12 self-value
203 tokens, the experimenter left the room for 3 minutes (min) to not influence interactions and
204 possible transfers of tokens between subjects. After 3 min, the experimenter came back for
205 a minimum duration of 3 min to give birds the opportunity for further exchanges. A session
206 ended 3 min after the last interaction, *e.g.* begging or token manipulation. During the entire
207 session, subjects could interact through the mesh. Each dyad received twelve sessions, with
208 a maximum of two sessions per day. We tested all possible pairs of individuals (3 crow
209 dyads, 1 raven dyad), with the limitation that only individuals with different self-value
210 tokens could be tested together. Testing phase 2 (reduced set phase) was similar to phase 1
211 except individuals received 12 partner-value and 12 no-value tokens but no self-value
212 tokens. Here, food could only be gained at a trial if some transfers of valuable token had
213 occurred between partners. We expected this to motivate individuals to interact with their
214 partner as the only self-value tokens available for them were in the partner's compartment.
215 Two crow and one raven dyad were tested in this phase. Testing phase 3 (re-motivation
216 phase) was similar to phase 2, but the set of tokens comprised three self-value tokens in
217 addition to the 12 partner-value and 12 no-value tokens. This was done to increase
218 motivation of subjects to participate in the session. In addition, the experimenter did not
219 leave individuals on their own after all self-value tokens have been exchanged, but stayed
220 for three minutes after the last interaction with any token. Eight crow dyads were tested in
221 this phase. Different test phases have been designed to increase motivation to exchange
222 tokens between experimental partners, *e.g.* by reducing the number of self-value tokens.

223

224 *Video Processing*

225 Test sessions have been video-recorded and were analysed using Solomon Coder
226 version beta 17.03.22 (©András Péter, www.solomoncoder.com). The behaviours recorded
227 during testing sessions were (a) exchange with experimenter: a subject passes a token
228 through the mesh to the experimenter; (b) transfer with partner: a subject obtains a token
229 that was originally in its partner's compartment; we distinguished between 'passive
230 transfer', *i.e.* one subject taking the token from the compartment of the partner, facilitated
231 by the experimental partner dislocating the tokens closer to the wire mesh, *e.g.* by stepping
232 on them or moving them through beak movement. 'Indirect transfer', *i.e.* a token is placed
233 in the partner's compartment and 'active transfer', *i.e.* a token is placed directly into the
234 partner's beak; (c) manipulation of tokens: a subject is manipulating a token with its beak or
235 feet. (d) caching of tokens: a subject cached a token somewhere in its own compartment.
236 The frequency of all these behaviours were recorded.

237

238 *Data analysis*

239 All data were analysed using R version 3.5.3 (R Core Team 2015). We conducted
240 Friedman and Wilcoxon signed-rank tests to calculate whether subjects showed an initial
241 preference returning a specific token type more than others in the first training session.
242 Results of all tests are given two-tailed and significance was set to $\alpha = 0.05$. In order to
243 investigate how frequency of behaviour was affected by phase of the experiment and type
244 of token, we conducted four generalized linear mixed models (GLMMs) with poisson error
245 distribution. Models were calculated using the glmmADMB package (Skaug et al., 2013). The
246 response variables were exchanges with the human experimenter (GLMM1), passive

transfers between individuals (GLMM2), frequency of token manipulations (GLMM3) and frequency of caching a token (GLMM4). Experimental phase (1, 2 and 3), type of token (self-value, partner-value, no-value), and the interaction between phase and type of token was included as fixed factors. In models where the interaction between phase and type of token was non-significant it was subsequently removed from the model (Engqvist, 2005). For each model, we fitted individual identity as a random term to control for the potential dependence associated with multiple samples from the same individual.

Results

Initial training phase

Crows needed on average (\pm standard deviation) 7.66 ± 2.65 sessions and ravens on average 11.5 ± 3.53 sessions to reach the discrimination criterion, *i.e.* preferentially returning their self-value token to the human experimenter.

Exchange with experimenter and partner

Individuals gave more no-value tokens to the human experimenter compared to partner-value tokens in phase 3, but not the other experimental phases (Table 2; Figure 2).

In our experiment, we did not observe any active transfers, *i.e.* one individual giving a token to the experimental partner by placing it in its beak. We only observed 6 indirect transfers, *i.e.* one individual transferring a token into the compartment of the partner (3 no-value, 1 partner-value and 2 self-value tokens) and 67 'passive' transfers, *i.e.*, one subject taking the token from the compartment of the partner. More passive transfers occurred in phase 1 compared to phase 2, but not significantly different between phase 2 and 3 and

phase 1 and 3. Individuals took significantly more self-value tokens compared to no-value and partner-value tokens and significantly more partner-value tokens compared to no-value tokens (Table 2, Figure 3). Most of the transfers (indirect and passive) were observed by one individual (Klaus taking tokens from the other compartment in 56 out of 73 occasions).

Manipulation and caching of tokens

In order to investigate whether focal subjects showed a preference for a specific token type, we investigated whether they cached or manipulated certain types of tokens more than others. Individuals manipulated tokens more in phase 1 compared to phase 2, but no significant difference was found in frequency of manipulation between phase 2 and 3 as well as between phase 1 and 3. Individuals manipulated self-value tokens more often compared to partner-value and no-value tokens and no-value tokens more often compared to partner-value tokens (Table 2). Individuals cached no-value tokens more often compared to self-value tokens, but not significantly different to partner-value tokens and partner-value tokens compared to self-value tokens. Individuals cached significantly more in phase 1 compared to phase 3, but no significant difference was detected between phase 1 and 2 as well as between phase 2 and 3 (Table 2; Figure 4).

291 Discussion

292 Both, ravens and crows learned to distinguish their self-value tokens among three
293 different types of tokens. They preferentially exchanged those tokens with the
294 experimenter. The number of sessions required to reach the criterion for being considered
295 trained is comparable to those found in primates (Pelé et al., 2009; Pelé et al., 2010). We
296 recorded no active transfers between experimental partners and only a very limited number
297 of indirect transfers. Most of the transfers were passive transfers, so one individual taking a
298 token from the compartment of the partner, which was only possible for those tokens
299 placed close to the wire mesh. Our results are comparable to previous results in monkeys
300 and apes, except orangutans, which show calculated reciprocity in exchanges of tokens
301 (Dufour et al., 2009; Pelé et al. 2009; Pelé et al., 2010). Therefore, it has to be considered,
302 although orangutans exchanged tokens in a reciprocal way, the presented experimental
303 design might be too complicated for other species of non-human animals, as it requires
304 understanding of different values of tokens. The use of alternative paradigms, such as
305 instrumental cooperation tasks (Gfrerer & Taborsky, 2018; Rutte & Taborsky, 2007), might
306 be preferable. We further recommend future studies applying the token exchange paradigm
307 to consider introducing an additional training phase, during which the experimental
308 partners are trained to exchange tokens amongst themselves, as most species tested in the
309 paradigm until now, did not spontaneously start exchanging tokens amongst themselves.

310

311 Passive transfers were facilitated by the experimental partner dislocating the tokens
312 closer to the wire mesh, *e.g.* by stepping on them or moving them through beak movement.
313 Displacements have been accidental and no intend to move the tokens closer to the
314 experimental partner could be identified. Most of these passive transfers have been

conducted by one individual (Klaus; 56 out of 73 occasions), further supporting the view that the observed passive transfers do not reflect a general pattern of one individual giving tokens to an experimental partner. We suggest that rather than showing purposeful manipulation of the tokens valuable to their partners near the common mesh so that they could benefit from them, a parsimonious hypothesis is that the potential roles of receiver and donor in our experiment have not been understood by subjects. However, one interesting aspect regarding the passive transfers is the fact that the experience of being able to acquire valuable tokens from the compartment of the experimental partner, did not elicit any further behavioural interactions between subjects. Although in very low numbers, five out of nine experimental dyads experienced indirect transfers and three out of nine dyads experienced passive transfers. Therefore, more than half of the dyads had opportunities to learn about the possibility to exchange tokens between experimental partners. Common ravens previously have shown to memorise the outcome of cooperative interactions with human experiments after a single interaction (Müller et al., 2017), therefore it could have been expected that our crows and ravens learn to exchange with an experimental partner after a limited amount of interactions.

We did not find evidence for our crows and ravens to develop a preference, shown by transferring, exchanging, manipulating or caching more partner-value tokens compared to no-value tokens. A preference for specific type of tokens has previously been shown in primate studies, which describe subjects to attribute more value to types of tokens which have been observed to be valuable to other individuals (Brosnan & Waal, 2004; Pelé et al., 2009; Pelé et al., 2010). Object manipulation in common ravens has been previously shown to be socially facilitated, *i.e.* individuals to manipulate objects more which have been

previously manipulated by a social partner (Schwab et al., 2008), therefore we would have expected crows and ravens in the present study to develop a stronger preference to manipulate partner-value tokens more. Previous studies in ravens suggest enhanced social facilitation between affiliated individuals (Schwab et al., 2008). Due to the small sample size, we did not consider affiliation status between experimental pairs in the present study. In the first training session, we did find an initial preference for no-value tokens (wooden triangles) compared to any other token type and generally the number of interactions with tokens, *i.e.* manipulation, caching, passive transfers, did decrease in the course of the experiment, indicating the crows and ravens do lose interest.

The absence of active transfers makes it difficult to evaluate whether partners understood the potential value of the token to their experimental partner. Great apes, previously have been observed to engage in solicitation or the use of begging behaviours, such as pointing and holding-out-hand gestures (Dufour et al., 2009; Pelé et al., 2009; Yamamoto et al., 2009). We could not identify specific solicitation or begging behaviours in our focal individuals. Occasionally, we have observed individuals approaching their experimental partner and looking at the partner's tokens, however these behaviours were difficult to identify and did not occur regularly enough to be systematically analysed.

To summarise, although cooperative behaviours including the sharing of food has been described in corvids (de Kort et al., 2003; Emery et al., 2007) in our experiment, crows and ravens did not exchange tokens with each other. Similar experiments have previously shown that crows and juvenile ravens do not exchange tokens with experimental partners, when there is nothing to gain for themselves (Horn et al. unpublished data; Massen et al.,

363 2015a). A limited amount of indirect and passive transfers provided learning opportunities
364 for individuals, however they did not result in an increase in active and indirect transfers.
365 More studies are required to further examine the ability of corvids to engage in reciprocal
366 actions.

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368 Conflict of Interest: The authors declare that they have no conflict of interest

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528 Table 1: Subjects sex (M = male, F = female), age (year of hatching), self-value token and
 529 experimental partners in each experimental phase.

Subject	Sex	Age	Species	Self-value token	Dyads (phase 1)	Dyads (phase 2)	Dyads (phase 3)
Baerchen	M	2008	Carrion crow	blue plastic	Peter	NA	Resa, Peter, Gabi
Gabi	F	2007	Carrion crow	screw nut	Klaus	Klaus	Klaus, Baerchen
Gertrude	F	2011	Hooded crow	blue plastic	NA	NA	Resa, Peter
Klaus	M	2009	Carrion crow	blue plastic	Resa, Gabi	Resa, Gabi	Resa, Peter, Gabi
Peter	F	2007	Carrion crow	screw nut	Baerchen	NA	Gertrude, Baerchen, Klaus
Resa	F	2009	Carrion crow	screw nut	Klaus	Klaus	Klaus, Gertrude, Baerchen
Hugo	M	2003	Common raven	screw nut	Manon	Manon	NA
Manon	F	1990	Common raven	blue plastic	Hugo	Hugo	NA

530 NA: individual did not participate in this testing phase

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Table 2 Results of the generalized mixed linear model investigating factors affecting exchange behaviour with human experimenter. Significant values ($p \leq 0.05$) are highlighted in bold.

	Parameters	Estimate \pm SE	Z	p
Exchange with human experimenter	Intercept	1.98 \pm 0.35	5.53	<0.001
	Type of token	-0.98 \pm 0.19	-5.1	<0.001
	Phase 2	-18.44 \pm 2116	-0	0.993
	Phase 3	-0.01 \pm 0.23	-0.08	0.934
	Type of token*phase 2	16.89 \pm 211	0	0.993
Passive transfers	Type of token*phase 3	-1.21 \pm 0.47	-2.56	0.01
	Intercept	-0.71 \pm 0.53	-1.33	0.182
	Type of token (partner-value)	-1.86 \pm 0.64	-2.88	0.003
	Type of token (self-value)	0.92 \pm 0.28	3.27	0.001
	Phase 2	-2.1 \pm 0.47	-4.46	<0.001
Frequency of manipulation	Phase 3	-14.22 \pm 140.9	-0.1	0.919
	Intercept	-0.71 \pm 0.53	-1.33	0.182
	Type of token (partner-value)	-1.86 \pm 0.64	-2.88	0.003
	Type of token (self-value)	0.92 \pm 0.28	3.27	0.001
	Phase 2	-2.1 \pm 0.47	-4.46	<0.001
Frequency of caching	Phase 3	-14.22 \pm 140.9	-0.1	0.919
	Intercept	0.86 \pm 0.45	1.9	0.056
	Type of token (partner-value)	-0.1 \pm 0.16	-0.64	0.516
	Type of token (self-value)	-1.8 \pm 0.37	-4.78	<0.001
	Phase 2	0.18 \pm 0.18	0.98	0.322
	Phase 3	-1.1 \pm 0.23	-4.73	<0.001

Figure 1: Layout of the experimental set-up. Two testing subjects were separated by a common mesh (vertical dashed line). In the training and phase 1 of the experiment, each subject had the same number of tokens, 12 self-values, 12 partner-values and 12 no-values that were placed in each compartment out of reach of the partner. Tokens could be transferred through the wire mesh or exchanged with the human experimenter through an hole in the wire mesh (horizontal dashed line).

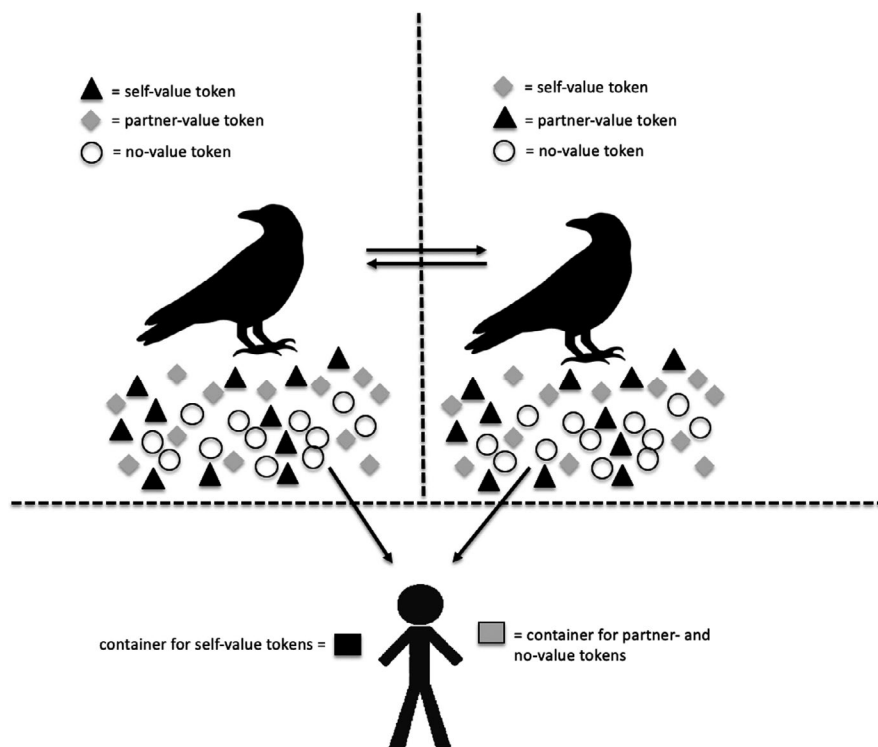


Figure 2: Number of tokens \pm standard deviation and actual data points, given to the experimenter in different experimental phases by each focal individual of a dyad. Dots represent individual data points and darker colours indicate overlapping data points.

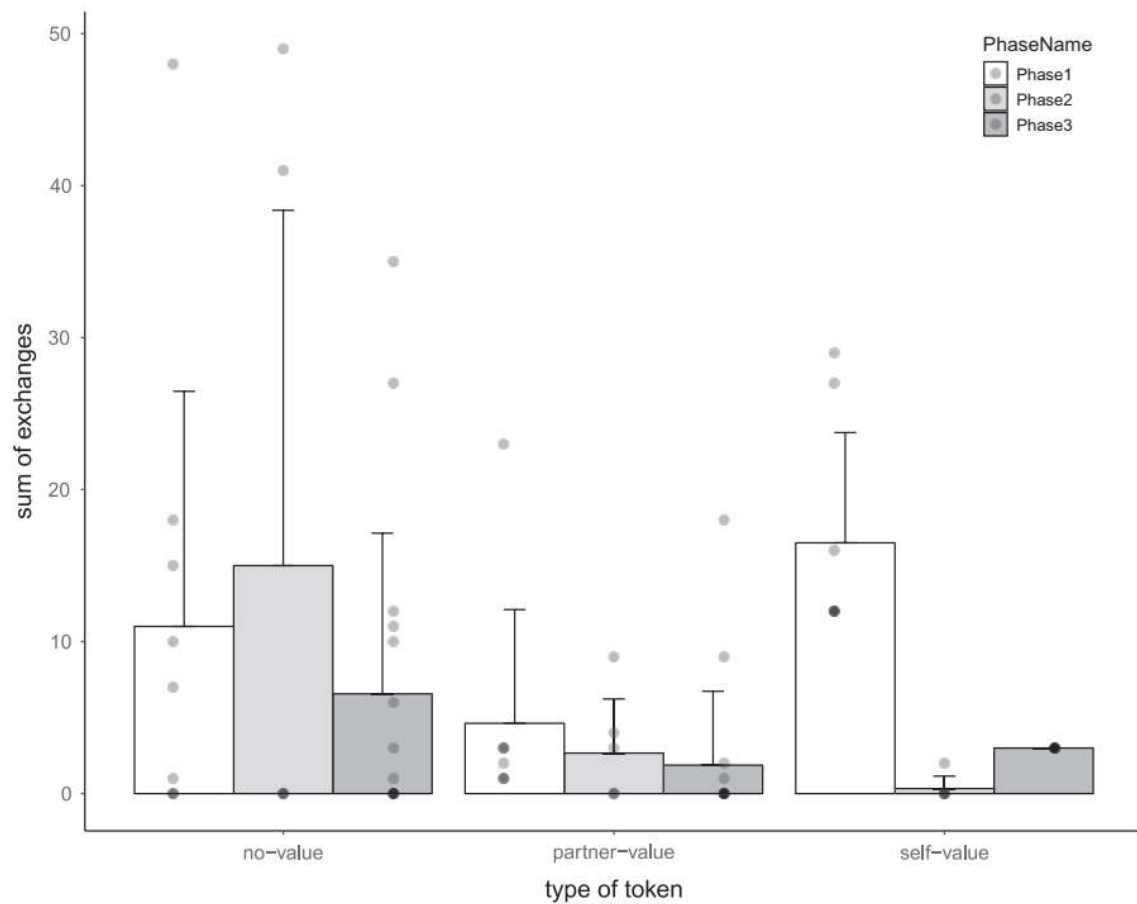
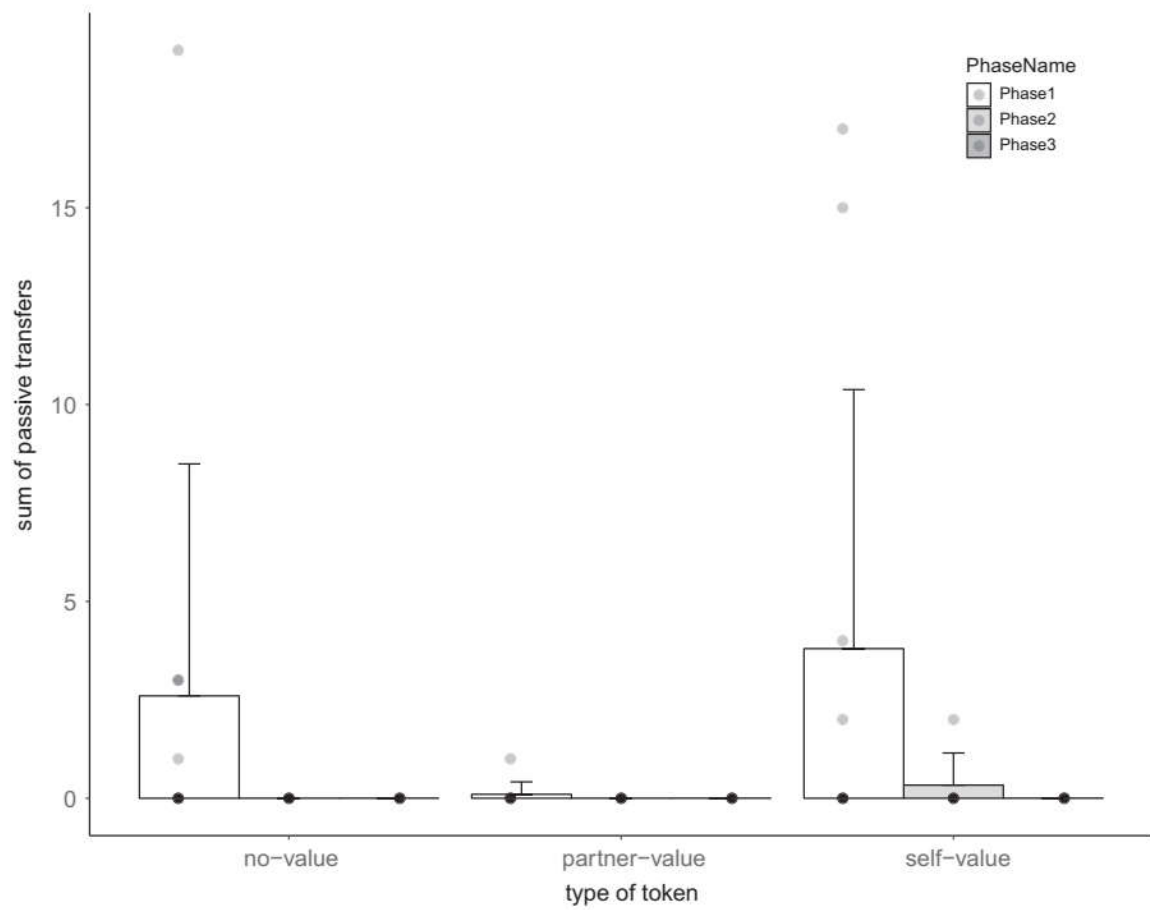
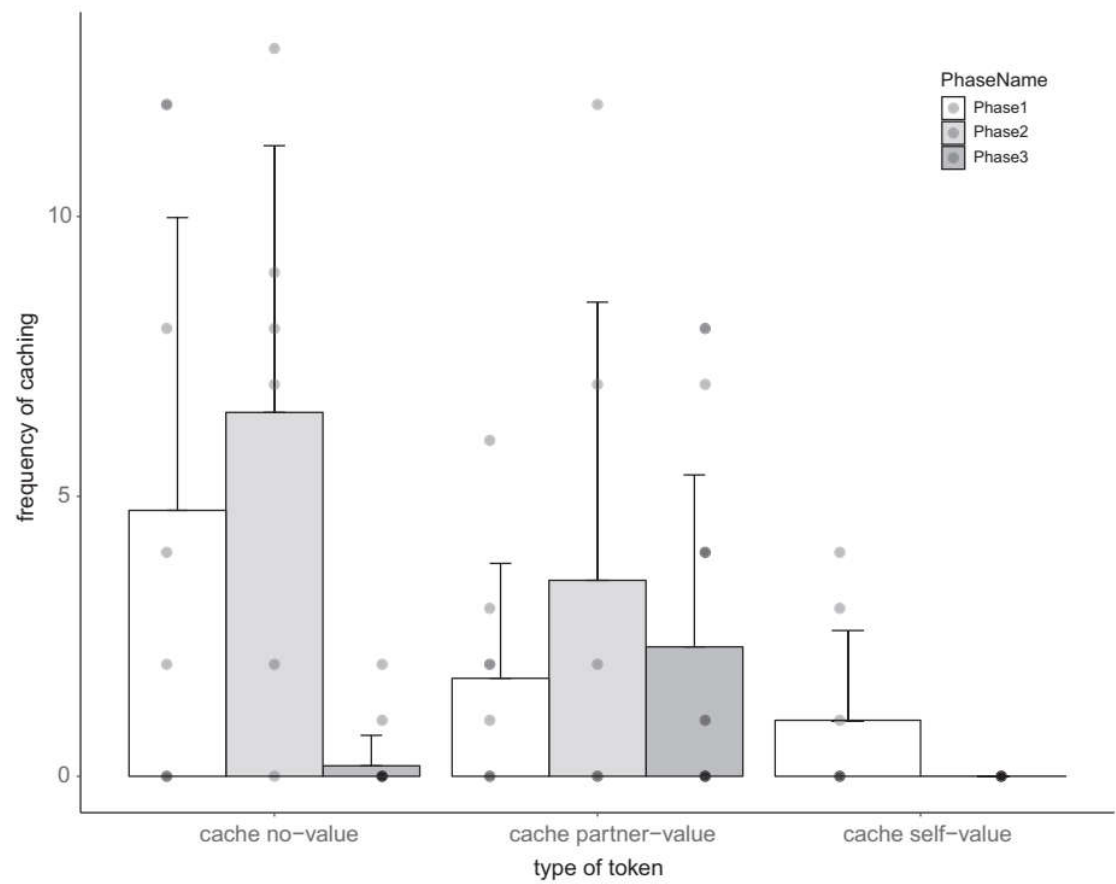


Figure 3: Sum of tokens taken by subjects from their partner's compartment (passive transfers) in each experimental phase \pm standard deviation.



579 Figure 4: Frequency of caching depending on token type and experimental phase \pm standard
580 deviation.



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