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1 **Crows and common ravens do not reciprocally exchange tokens with a conspecific to gain**  
2 **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

## 54 **Introduction**

55           Human societies show a high propensity of cooperation between unrelated  
56 individuals (Fehr & Fischbacher, 2003) and the inherent evolutionary instability of  
57 cooperation inspires a great amount of interest in researching these cooperative behaviours  
58 (Axelrod & Hamilton, 1981), because individuals are not expected to invest in a cooperative  
59 enterprise without a guarantee of net fitness returns. To date, the most prominent theory  
60 explaining human cooperation is reciprocal altruism, based on the idea of individuals  
61 engaging in actions that are costly for themselves expecting future returns (Maynard Smith,  
62 1983; Trivers, 1971). The relationship between interaction partners plays a significant role  
63 regarding the complexity of cooperation. In symmetry-based cooperation, interactions  
64 without equivalent returns balance out over time between kin and long-term partners  
65 (Berghänel et al., 2011; Dunbar, 1980). In contrast, calculated reciprocity requires keeping a  
66 mental record of the debts owed and the favours given (de Waal & Luttrell, 1988), based on  
67 the expectancy of a return for every costly favour given. Emotions may as well modulate  
68 cooperative interactions. Attitudinal reciprocity has been suggested to take the partner's  
69 general social attitude into account (de Waal, 2000) and emotionally based bookkeeping  
70 allows long-term tracking of reciprocity without involving complex cognitive skills (Schino et  
71 al., 2007). Therefore, different forms of cooperative behaviour in nonhuman animals are  
72 expected to be based upon different cognitively challenging mechanisms depending on the  
73 complexity of the social system.

74

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

78 studies, particularly in primates, suggest reciprocity in grooming (Barrett et al., 1999; Gomes  
79 et al., 2009; Majolo et al., 2012; Molesti, 2017; Schino et al., 2007), grooming for food (de  
80 Waal, 1997), agonistic support (Watts, 2001), grooming for agonistic support (Carne et al.,  
81 2011), food sharing (Wilkinson, 1984) and allonursing (Engelhardt & Weladji, 2015).

82

83 Surprisingly few experimental studies test for direct reciprocity in non-human  
84 animals. In a token exchange task, individuals had to exchange tokens useless to themselves  
85 but valuable to an experimental partner, in order to exchange the token valuable to them  
86 for food with the experimenter. Two orangutans (*Pongo pygmaeus abelii*) actively gave  
87 numerous tokens valuable to the experimental partner and one of the orangutans routinely  
88 used gestures to request tokens while the other complied with such requests (Dufour et al.,  
89 2009). Similarly, requests for help in a reciprocal exchange paradigm have also been  
90 discussed in Norway rats (Schweinfurth & Taborsky 2018). A number of other primate  
91 species (Capuchin monkeys (*Sapajus apella*), Tonkean macaques (*Macaca tonkeana*),  
92 gorillas (*Gorilla gorilla*), bonobos (*Pan paniscus*), and chimpanzees (*Pan troglodytes*)) tested  
93 in a similar token exchange paradigm compared to the study in orangutans, failed to actively  
94 exchange tokens and if exchanges occurred, they were mostly of 'passive' nature, *i.e.* a  
95 subject brings a token near the common mesh wall and tolerates the partner to take it or  
96 'indirect' exchanges, *i.e.* an individual places a token in the partner's compartment without  
97 physical contact with the partner (Pelé et al., 2009; Pelé et al., 2010). In different  
98 experimental setups, *e.g.* instrumental cooperation tasks, food exchange or predator  
99 mobbing, rats, pied flycatchers (*Ficedula hypoleuca*), zebra finches (*Taeniopygia guttata*),  
100 vampire bats (*Desmodus rotundus*), chimpanzees and working dogs (*Canis familiaris*)  
101 cooperated more with previous cooperators compared to defectors (Gfrerer & Taborsky,

102 2018; Krams et al., 2008; Melis et al. , 2008; Rutte & Taborsky, 2008; St-Pierre et al., 2009),  
103 however direct reciprocity still requires to be studied in different species in order to gain  
104 further insight in the social and ecology requirements facilitating the evolution of reciprocal  
105 altruism in the wild (Taborsky 2013).

106

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

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

140

141           In the present study, we expected the crows and ravens to learn to attribute  
142 different value of tokens for different individuals and to adapt their behaviour accordingly.  
143 By monitoring the occurrence of transfers, the value of tokens exchanged and the  
144 alternation of roles between individuals, we aimed to assess the extent to which crows and  
145 ravens may purposefully engage in reciprocal behaviours. We expect individuals to  
146 preferentially exchange self-value tokens with the human experimenter. Further, we expect  
147 crows and ravens to preferentially manipulate self-value and partner-value tokens,  
148 compared to no-value tokens. If crows and ravens engage in reciprocal altruism, we expect  
149 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.

## 152 **Methods**

### 153 *Study subjects and housing*

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

161

### 162 *Tokens*

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

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

177

### 178 *Training Procedure*

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

195

### 196 *Testing Procedure*

197 Testing took place in the same room as the training, divided into two testing  
198 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](http://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

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

254

## 255 **Results**

### 256 *Initial training phase*

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

260

### 261 *Exchange with experimenter and partner*

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

264

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

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

275

#### 276 *Manipulation and caching of tokens*

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

288

289

290

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



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

331

332           We did not find evidence for our crows and ravens to develop a preference, shown  
333 by transferring, exchanging, manipulating or caching more partner-value tokens compared  
334 to no-value tokens. A preference for specific type of tokens has previously been shown in  
335 primate studies, which describe subjects to attribute more value to types of tokens which  
336 have been observed to be valuable to other individuals (Brosnan & Waal, 2004; Pelé et al.,  
337 2009; Pelé et al., 2010). Object manipulation in common ravens has been previously shown  
338 to be socially facilitated, *i.e.* individuals to manipulate objects more which have been

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

348

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

357

358         To summarise, although cooperative behaviours including the sharing of food has  
359 been described in corvids (de Kort et al., 2003; Emery et al., 2007) in our experiment, crows  
360 and ravens did not exchange tokens with each other. Similar experiments have previously  
361 shown that crows and juvenile ravens do not exchange tokens with experimental partners,  
362 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.

367

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

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378 **References**

- 379 Axelrod, R., & Hamilton, W. D. (1981). The evolution of cooperation. *Science*, *211*, 1390–  
380 1396.
- 381 Baglione, V., Canestrari, D., Marcos, J. M., & Ekman, J. (2003). Kin selection in cooperative  
382 alliances of carrion crows. *Science*, *300*(5627), 1947–1949.
- 383 Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E., & Hill, R. A. (1999). Market forces predict  
384 grooming reciprocity in female baboons. *Proceedings of the Royal Society B: Biological  
385 Sciences*, *266*, 665–670.
- 386 Berghänel, A., Ostner, J., Schröder, U., & Schülke, O. (2011). Social bonds predict future  
387 cooperation in male Barbary macaques, *Macaca sylvanus*. *Animal Behaviour*, *81*(6),  
388 1109–1116. <https://doi.org/10.1016/j.anbehav.2011.02.009>
- 389 Brosnan, S. F., & de Waal, F. B. M. (2004). Socially Learned Preferences for Differentially  
390 Rewarded Tokens in the Brown Capuchin Monkey (*Cebus apella*), *118*(2), 133–139.
- 391 Bugnyar, T., & Kotrschal, K. (2001). Movement coordination and signalling in ravens (*Corvus  
392 corax*): an experimental field study. *Acta Ethologica*, *3*(2), 101–109.
- 393 Carne, C., Wiper, S., & Semple, S. (2011). Reciprocation and interchange of grooming,  
394 agonistic support, feeding tolerance, and aggression in semi-free-ranging Barbary  
395 macaques. *American Journal of Primatology*, *73*(11), 1127–1133.
- 396 Carter, G. G., Wilkinson, G. S., & Carter, G. G. (2013). Food sharing in vampire bats:  
397 reciprocal help predicts donations more than relatedness or harassment. *Proceedings  
398 of the Royal Society B*, *280*. <https://doi.org/https://doi.org/10.1098/rspb.2012.2573>
- 399 Clayton, N. S., & Emery, N. J. (2007). The social life of corvids. *Current Biology*, *17*(16),  
400 R652-656.
- 401 Clements, K. C., & Stephens, D. W. (1995). Testing models of non-kin cooperation:  
402 mutualism and the Prisoner's dilemma. *Animal Behaviour*, *50*(2), 527–535.
- 403 Clutton-Brock, T. (2009). Cooperation between non-kin in animal societies. *Nature*, *462*, 51–  
404 57.
- 405 de Kort, S. R., Emery, N. J., & Clayton, N. S. (2003). Food offering in jackdaws (*Corvus  
406 monedula*). *Naturwissenschaften*, *90*, 238–240.
- 407 de Kort, S. R., Emery, N. J., & Clayton, N. S. (2006). Food sharing in jackdaws, *Corvus  
408 monedula*: what, why and with whom? *Animal Behaviour*, *72*(2), 297–304.
- 409 de Waal, F. B. M. (1997). The chimpanzee's service economy: food for grooming. *Evolution  
410 and Human Behavior*, *18*, 375–386.
- 411 de Waal, F. B. M., & Luttrell, L. M. (1988). Mechanisms of social reciprocity in three primate  
412 species: Symmetrical relationship characteristics or cognition? *Ethology and  
413 Sociobiology*, *9*, 101–118.
- 414 de Waal FB. (2000). Attitudinal reciprocity in food sharing among brown capuchin monkeys.  
415 *Animal Behaviour*, *60*(2), 253–261.
- 416 Dufour, V., Pelé, M., Neumann, M., Thierry, B., & Call, J. (2009). Calculated reciprocity after  
417 all: computation behind token transfers in orang-utans. *Biology Letters*, *5*(2), 172–175.
- 418 Dufour, V., Wascher, C. A. F., Braun, A., Miller, R., & Bugnyar, T. (2012). Corvids can decide if  
419 a future exchange is worth waiting for. *Biology Letters*, *8*(2), 201–204.
- 420 Dunbar, R. I. M. (1980). Determinants and evolutionary consequences of dominance among  
421 female gelada baboons. *Behavioral Ecology and Sociobiology*, *7*(4), 253–265.
- 422 Duque, J. F., & Stevens, J. R. (2016). Voluntary food sharing in pinyon jays: the role of  
423 reciprocity and dominance. *Animal Behaviour*, *122*, 135–144.  
424 <https://doi.org/10.1016/j.anbehav.2016.09.020>

425 Emery, N. J., Seed, A. M., von Bayern, A. M. P., & Clayton, N. S. (2007). Cognitive adaptations  
426 of social bonding in birds. *Philosophical Transactions of the Royal Society of London.*  
427 *Series B, Biological Sciences*, 362(1480), 489–505.

428 Engelhardt, S. C., & Weladji, R. B. (2015). Evidence of reciprocal allonursing in reindeer,  
429 Rangifer tarandus. *Ethology*, 121, 245–259.

430 Engqvist, L. (2005). The mistreatment of covariate interaction terms in linear model analyses  
431 of behavioural and evolutionary ecology studies. *Animal Behaviour*, 70(4), 967–971.

432 Fehr, E., & Fischbacher, U. (2003). The nature of human altruism. *Nature*, 425(6960), 785–  
433 791.

434 Fraser, O. N., & Bugnyar, T. (2010). The quality of social relationships in ravens. *Animal*  
435 *Behaviour*, 79(4), 927–933. <https://doi.org/10.1016/j.anbehav.2010.01.008>

436 Fraser, O. N., & Bugnyar, T. (2011). Ravens reconcile after aggressive conflicts with valuable  
437 partners. *PloS One*, 6(3), e18118.

438 Gfrerer, N., & Taborsky, M. (2018). Working dogs transfer different tasks in reciprocal  
439 cooperation. *Biology Letters*, 14, 20170460.

440 Gomes, C. M., Mundry, R., & Boesch, C. (2009). Long-term reciprocation of grooming in wild  
441 West African chimpanzees. *Proceedings of the Royal Society B: Biological Sciences*,  
442 276(1657), 699–706.

443 Heinrich, B. (1999). *Mind of the raven*. New York: Harper Collins.

444 Hillemann, F., Bugnyar, T., Kotrschal, K., & Wascher, C. A. F. (2014). Waiting for better, not  
445 for more: Corvids respond to quality in two delay maintenance tasks. *Animal*  
446 *Behaviour*, 90, 1–10.

447 Horn, L., Bugnyar, T., & Massen, J. J. M. No proof for prosocial preferences in  
448 carrion/hooded crows' when tested in a token exchange paradigm. *Ethology*,  
449 submitted.

450 Koenig, W. D. (1988). Reciprocal altruism in birds: A critical review. *Ethology and*  
451 *Sociobiology*, 9(2–4), 73–84.

452 Krams, I., Krama, T., Igaune, K., & Mänd, R. (2008). Experimental evidence of reciprocal  
453 altruism in the pied flycatcher. *Behavioral Ecology and Sociobiology*, 62(4), 599–605.

454 Majolo, B., Schino, G., & Aureli, F. (2012). The relative prevalence of direct, indirect and  
455 generalized reciprocity in macaque grooming exchanges. *Animal Behaviour*, 83(3), 763–  
456 771.

457 Massen, J. J. M., Lambert, M., Schiestl, M., & Bugnyar, T. (2015a). Subadult ravens generally  
458 don't transfer valuable tokens to conspecifics when there is nothing to gain for  
459 themselves. *Frontiers in Comparative Psychology*, 6, 885.

460 Massen, J. J. M., Ritter, C., & Bugnyar, T. (2015b). Tolerance and reward equity predict  
461 cooperation in ravens (*Corvus corax*). *Scientific Reports*, 5, 1–11.

462 Maynard Smith, J. (1983). Game theory and the evolution of cooperation. In D. S. Bendall  
463 (Ed.), *Evolution from Molecules to Men* (pp. 445–456). Cambridge: Cambridge  
464 University Press.

465 Melis, A. P., Hare, B., & Tomasello, M. (2008). Do chimpanzees reciprocate received  
466 favours? *Animal Behaviour*, 76(3), 951–962.

467 Molesti, S. (2017). Evidence of direct reciprocity , but not of indirect and generalized  
468 reciprocity , in the grooming exchanges of wild Barbary macaques (*Macaca sylvanus*).  
469 *American Journal of Primatology*, 79, e22679.

470 Müller, J. J. A., Massen, J. J. M., Bugnyar, T., & Osvath, M. (2017). Ravens remember the  
471 nature of a single reciprocal interaction sequence over 2 days and even after a month.

472 *Animal Behaviour*, 128, 69–78.

473 Pelé, M., Dufour, V., Thierry, B., & Call, J. (2009). Token transfers among great apes (*Gorilla*  
474 *gorilla*, *Pongo pygmaeus*, *Pan paniscus*, and *Pan troglodytes*): Species differences ,  
475 gestural requests, and reciprocal exchange. *Journal of Comparative Psychology*, 123(4),  
476 375–384.

477 Pelé, M., Thierry, B., Call, J., & Dufour, V. (2010). Monkeys fail to reciprocate in an exchange  
478 task. *Animal Cognition*, 13(5), 745–751.

479 R Core Team (2015). R: A Language and Environment for Statistical Computing. Vienna,  
480 Austria: R Foundation for Statistical Computing. Retrieved from [http://www.r-](http://www.r-project.org/)  
481 [project.org/](http://www.r-project.org/)

482 Rutte, C., & Taborsky, M. (2007). The influence of social experience on cooperative  
483 behaviour of rats (*Rattus norvegicus*): direct vs generalised reciprocity. *Behavioral*  
484 *Ecology and Sociobiology*, 62(4), 499–505.

485 Scheid, C., & Noë, R. (2010). The performance of rooks in a cooperative task depends on  
486 their temperament. *Animal Cognition*, 13(3), 545–553.

487 Schino, G., di Sorrentino, E. P., & Tiddi, B. (2007). Grooming and coalitions in Japanese  
488 macaques (*Macaca fuscata*): partner choice and the time frame reciprocation. *Journal*  
489 *of Comparative Psychology*, 121(2), 181–188.

490 Schwab, C., Bugnyar, T., Schloegl, C., & Kotrschal, K. (2008). Enhanced social learning  
491 between siblings in common ravens, *Corvus corax*. *Animal Behaviour*, 75(2), 501–508.

492 Seed, A. M., Clayton, N. S., & Emery, N. J. (2008). Cooperative problem solving in rooks  
493 (*Corvus frugilegus*). *Proceedings. Biological Sciences / The Royal Society*, 275(1641),  
494 1421–1429.

495 Skaug, H., Fournier, D., Nielsen, A., Magnusson, A., & Bolker, B. (2013). Generalized Linear  
496 Mixed Models using AD Model Builder.

497 St-Pierre, A., Larose, K., & Dubois, F. (2009). Long-term social bonds promote cooperation in  
498 the iterated Prisoner's dilemma. *Proceedings of the Royal Society B*, 276, 4223–4228.

499 Stephens, D. W., McLinn, C. M., & Stevens, J. R. (2002). Discounting and reciprocity in an  
500 iterated Prisoner's Dilemma. *Science*, 298(5601), 2216–2218.

501 Schweinfurth, M., & Taborsky, M. (2018). Norway rats (*Rattus norvegicus*) communicate  
502 need, which elicits donation of food. *Journal of Comparative Psychology*, 132(2), 119–  
503 129.

504 Taborsky, M. (2013). Social evolution: Reciprocity there is. *Current Biology*, 23(11), R486–  
505 R488.

506 Team, R. D. C. (2015). R: a language and environment for statistical computing. R foundation  
507 for statistical computing. Retrieved from <http://www.r-project.org/>

508 Trivers, R. L. (1971). The evolution of reciprocal altruism. *The Quarterly Review of Biology*,  
509 46(1), 35–57.

510 Wascher, C. A. F. (2015). Individual performance in socio-cognitive tasks predicts social  
511 behaviour in carrion crows. *Behaviour*, 152, 615–634.

512 Wascher, C. A. F., & Bugnyar, T. (2013). Behavioral responses to inequity in reward  
513 distribution and working effort in crows and ravens. *PloS One*, 8(2), e56885.

514 Wascher, C. A. F., Dufour, V., & Bugnyar, T. (2012). Carrion crows cannot overcome  
515 impulsive choice in a quantitative exchange task. *Frontiers in Comparative Psychology*,  
516 3, 1–6.

517 Wascher, C. A. F., Hillemann, F., Canestrari, D., & Baglione, V. (2015). Carrion crows learn to  
518 discriminate between calls of reliable and unreliable conspecifics. *Animal Cognition*,

- 519 18(5).
- 520 Watts, D. P. (2001). Reciprocity and interchange in the social relationships of wild male  
521 chimpanzees. *Behaviour*, 139, 343–370.
- 522 Wilkinson, G. S. (1984). Reciprocal food sharing in the vampire bat. *Nature*, 308(8), 181–184.
- 523 Woolfenden, G. E., & Fitzpatrick, J. W. (1985). *The Florida Scrub Jay. Demography of a*  
524 *Cooperative-Breeding Bird*. New Jersey: Princeton University Press.
- 525 Yamamoto, S., Humle, T., & Tanaka, M. (2009). Chimpanzees help each other upon request.  
526 *PLoS ONE*, 4(10), e7416.
- 527

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

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

530 NA: individual did not participate in this testing phase

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

|   | Parameters                           | Estimate $\pm$ SE                  | Z            | p                |
|---|--------------------------------------|------------------------------------|--------------|------------------|
| <b>Exchange with human experimenter</b> | <b>Intercept</b>                     | <b>1.98 <math>\pm</math> 0.35</b>  | <b>5.53</b>  | <b>&lt;0.001</b> |
|   | <b>Type of token</b>                 | <b>-0.98 <math>\pm</math> 0.19</b> | <b>-5.1</b>  | <b>&lt;0.001</b> |
|   | 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            |
| <b>Passive transfers</b>                | <b>Type of token*phase 3</b>         | <b>-1.21 <math>\pm</math> 0.47</b> | <b>-2.56</b> | <b>0.01</b>      |
|   | Intercept                            | -0.71 $\pm$ 0.53                   | -1.33        | 0.182            |
|   | <b>Type of token (partner-value)</b> | <b>-1.86 <math>\pm</math> 0.64</b> | <b>-2.88</b> | <b>0.003</b>     |
| <b>Frequency of manipulation</b>        | <b>Type of token (self-value)</b>    | <b>0.92 <math>\pm</math> 0.28</b>  | <b>3.27</b>  | <b>0.001</b>     |
|   | <b>Phase 2</b>                       | <b>-2.1 <math>\pm</math> 0.47</b>  | <b>-4.46</b> | <b>&lt;0.001</b> |
|   | Phase 3                              | -14.22 $\pm$ 140.9                 | -0.1         | 0.919            |
|   | Intercept                            | -0.71 $\pm$ 0.53                   | -1.33        | 0.182            |
|   | <b>Type of token (partner-value)</b> | <b>-1.86 <math>\pm</math> 0.64</b> | <b>-2.88</b> | <b>0.003</b>     |
| <b>Frequency of caching</b>             | <b>Type of token (self-value)</b>    | <b>0.92 <math>\pm</math> 0.28</b>  | <b>3.27</b>  | <b>0.001</b>     |
|   | <b>Phase 2</b>                       | <b>-2.1 <math>\pm</math> 0.47</b>  | <b>-4.46</b> | <b>&lt;0.001</b> |
|   | 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            |
|   | <b>Type of token (self-value)</b>    | <b>-1.8 <math>\pm</math> 0.37</b>  | <b>-4.78</b> | <b>&lt;0.001</b> |
|   | Phase 2                              | 0.18 $\pm$ 0.18                    | 0.98         | 0.322            |
|   | <b>Phase 3</b>                       | <b>-1.1 <math>\pm</math> 0.23</b>  | <b>-4.73</b> | <b>&lt;0.001</b> |

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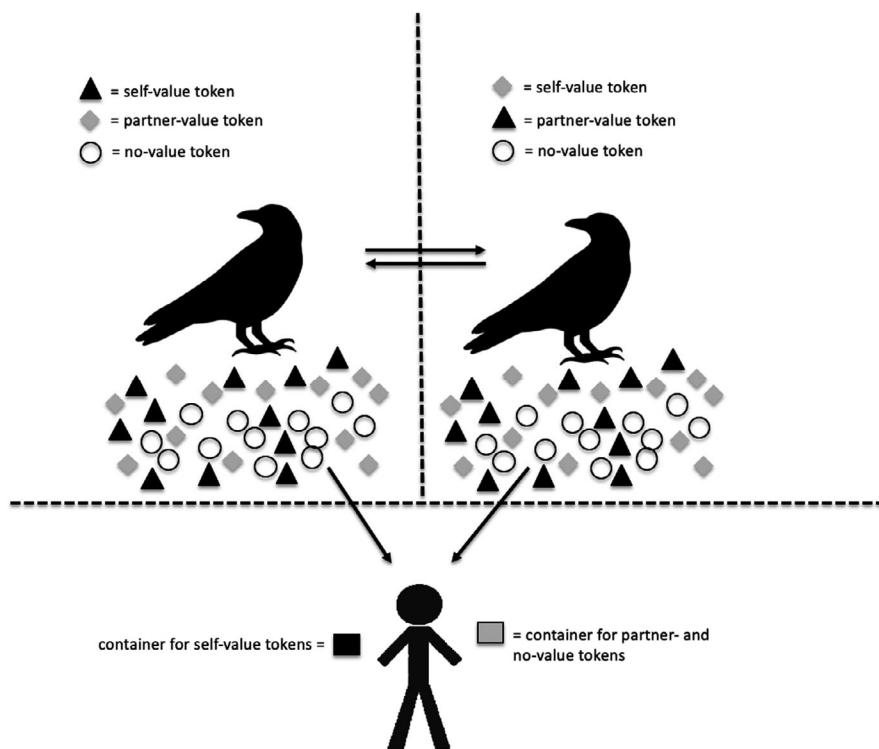
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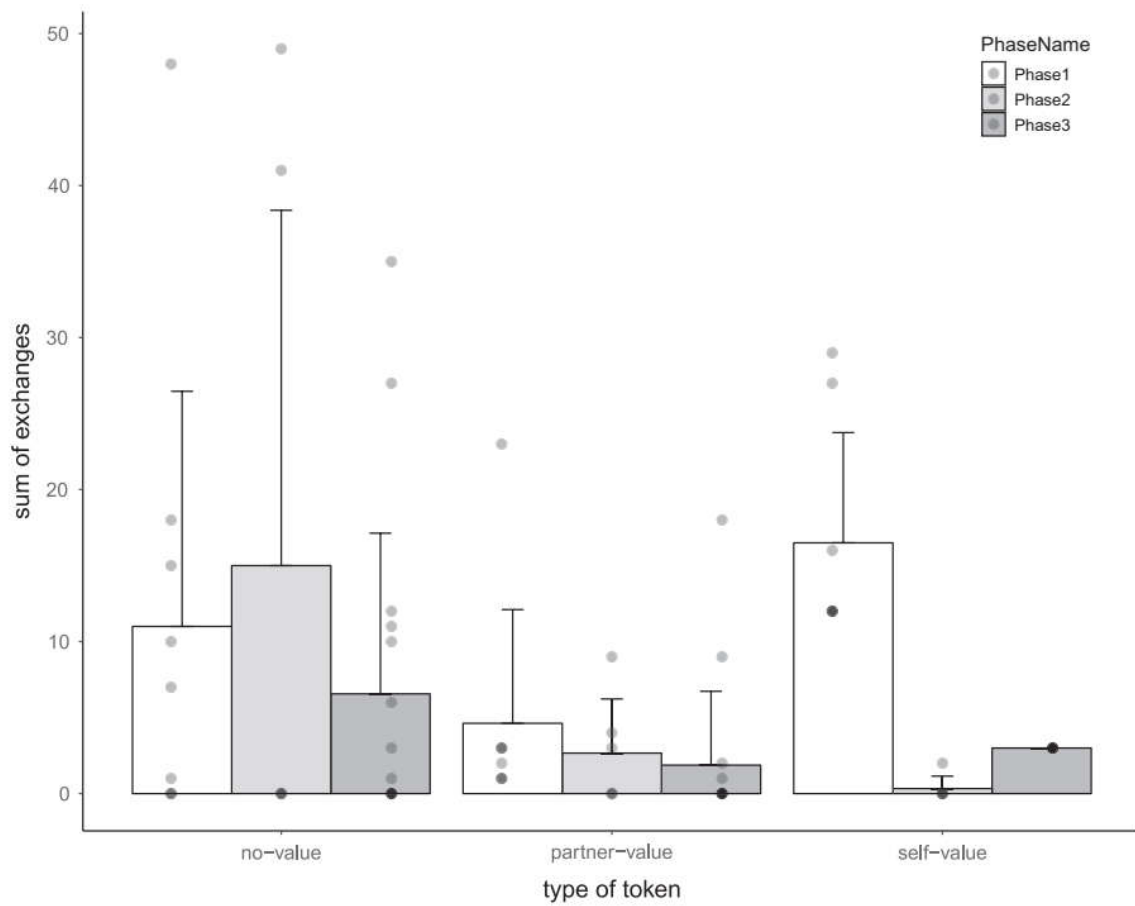
544 Figure 1: Layout of the experimental set-up. Two testing subjects were separated by a  
545 common mesh (vertical dashed line). In the training and phase 1 of the experiment, each  
546 subject had the same number of tokens, 12 self-values, 12 partner-values and 12 no-values  
547 that were placed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



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

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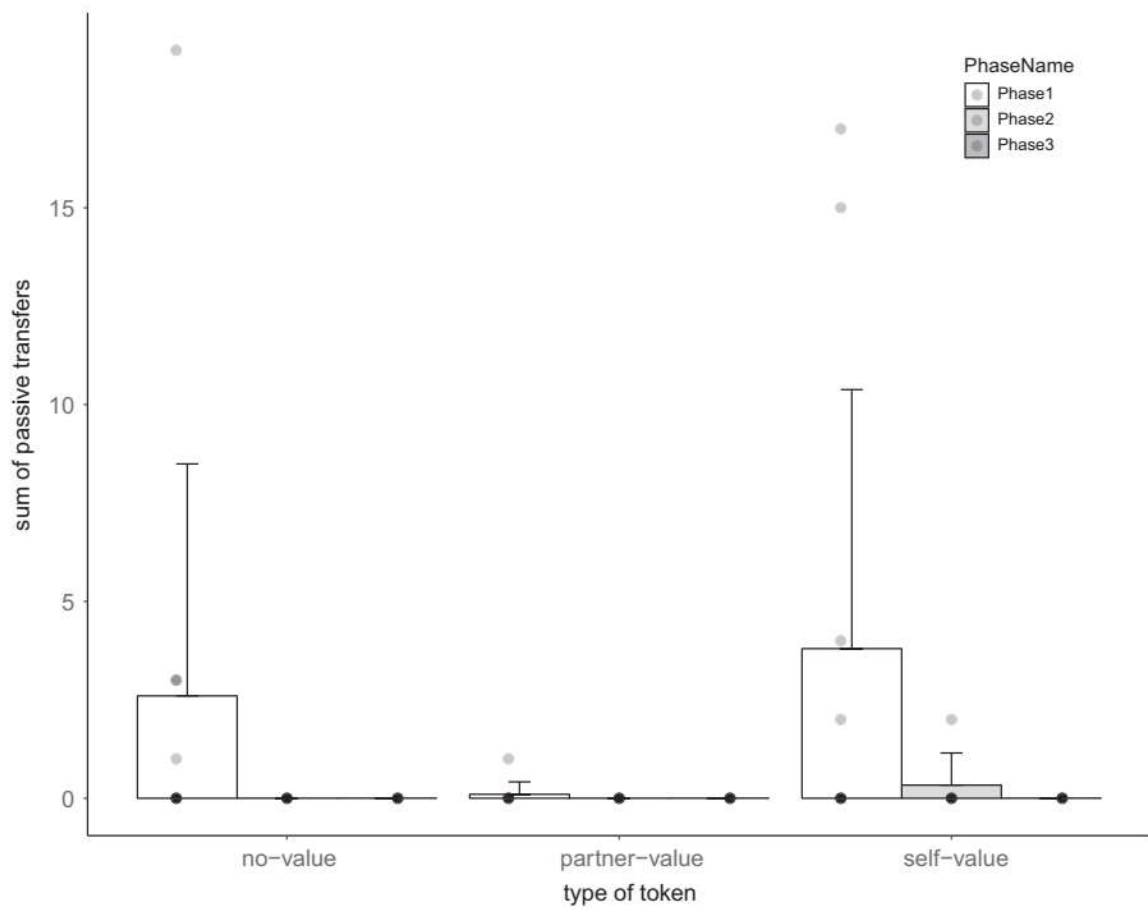
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568 Figure 3: Sum of tokens taken by subjects from their partner's compartment (passive  
569 transfers) in each experimental phase  $\pm$  standard deviation.

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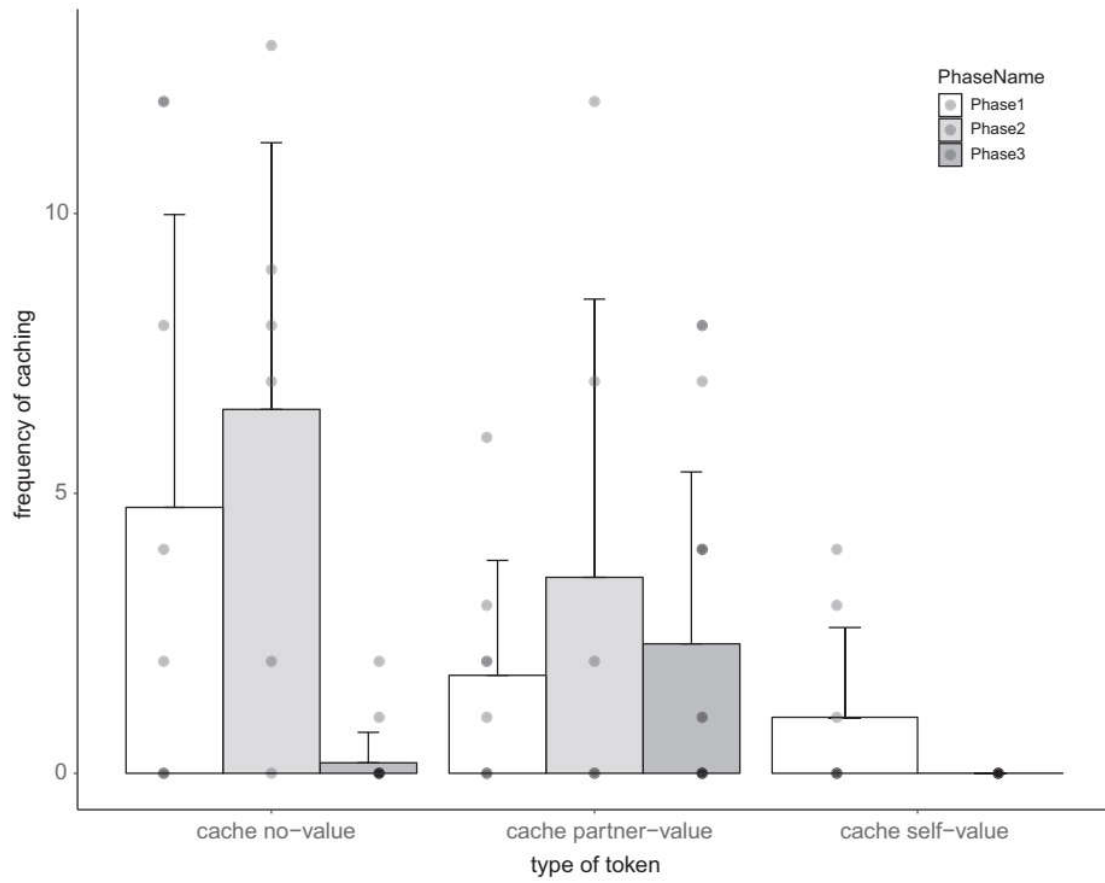
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579 Figure 4: Frequency of caching depending on token type and experimental phase  $\pm$  standard  
580 deviation.



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