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Animal behaviour

Working dogs transfer different tasks in reciprocal cooperation

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Direct reciprocity can establish stable cooperation among unrelated individuals. It is a common assumption of direct reciprocity models that agents exchange like with like, but this is not necessarily true for natural interactions. It is yet unclear whether animals apply direct reciprocity rules when successive altruistic help involves different tasks. Here, we tested whether working dogs transfer help from one to another cooperative task in an iterated prisoner's dilemma paradigm. In our experiment, individual dogs received help to obtain food from a conspecific, which involved a specific task. Subsequently, the focal subject could return received favour by using a different task. Working dogs transferred the cooperative experience received through one task by applying an alternative task when they helped a previously cooperative partner. By contrast, they refrained from helping previously defecting partners. This suggests that dogs realize the cooperative act of a conspecific, which changes their propensity to provide help to that partner by different means. The ability of animals to transfer different tasks when helping a social partner by satisfying the criteria of direct reciprocity might explain the frequent occurrence of reciprocal cooperation in nature.

1. Introduction

Reciprocity is a mechanism explaining cooperation among unrelated individuals, where two or more social partners help each other in turn [1]. In direct reciprocity, the help one individual provides to another is contingent on help it has previously received from that partner. Animals have been reported to exchange a variety of services among each other in nature [2]. However, it is yet unclear whether they apply direct reciprocity rules in such mutual exchanges, which would prevent exploitation by cheating [1,3].

A standard assumption of reciprocal cooperation is that the same tasks are exchanged against each other, regardless of whether this is allogrooming [4], mutual food provisioning [5–7] or mobbing behaviour towards predators [8]. It seems cognitively more demanding to apply direct reciprocity rules when help is transferred between two different tasks. Nevertheless, reciprocal exchange often involves different tasks (reviewed in [2]). Here, we ask whether dogs apply direct reciprocity rules when returning received help to conspecifics by using alternative tasks.

Domestic dogs (*Canis familiaris*) interact socially with conspecifics and humans. They successfully perform cooperative tasks, resolve complex social conflicts and show strategic behaviour in interactions with conspecifics and humans [9]. Family dogs were shown to differentiate between familiar and unfamiliar conspecifics when exhibiting unconditional prosocial behaviour [10]. Even if dogs are kept separated from conspecifics as in the Swiss military, they share food in a reciprocal food exchange paradigm [7]. However, despite their capacity to solve cognitively demanding tasks, dogs prefer using simple rules for behavioural decisions if they are effective [7,11].

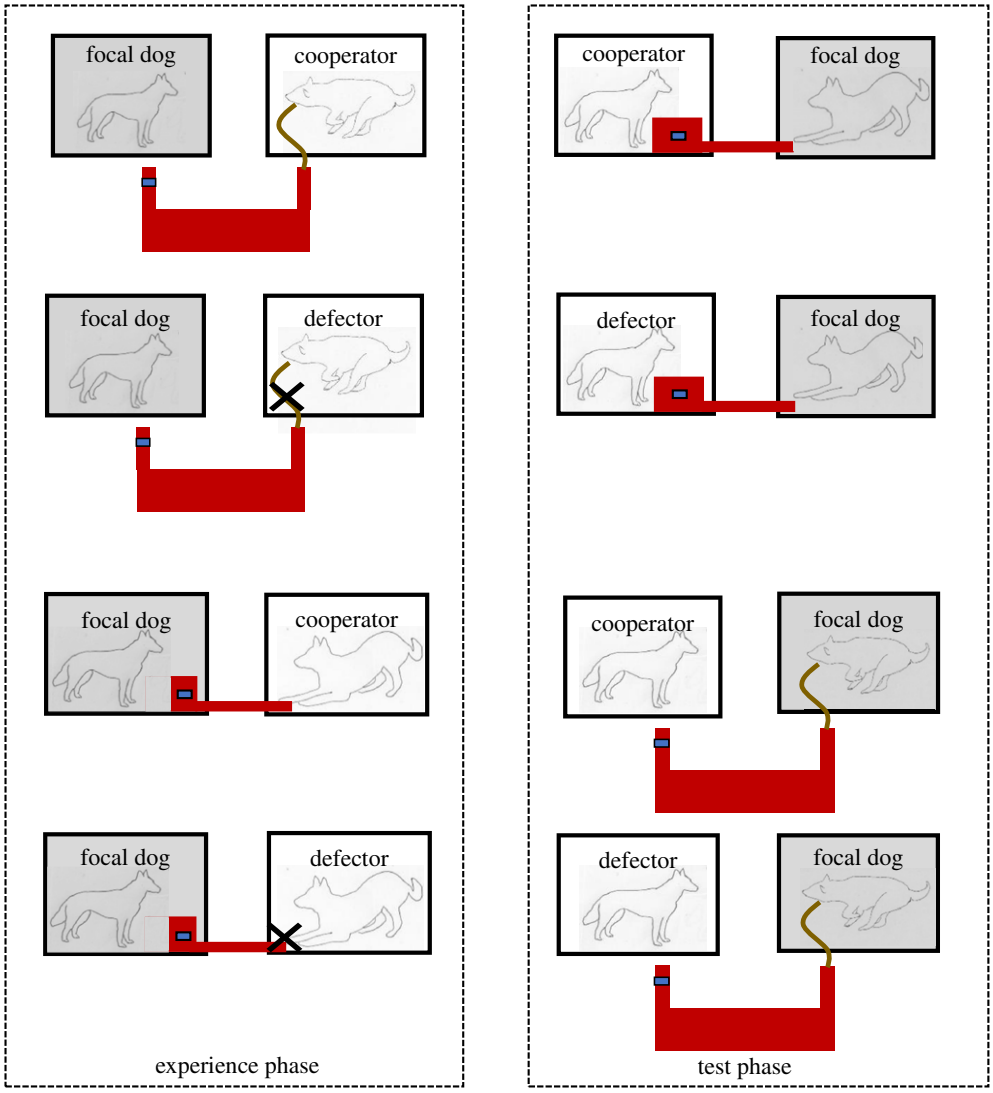

Figure 1. Experimental set-up to test whether working dogs transfer different tasks in reciprocal cooperation. On the first day (experience phase; left panel), focal dogs received either help by a cooperator or no help by a defector, by a mechanism involving either pulling a rope or pushing a lever. On the next day (test phase; same line in the right panel), they could help the same partner to get a food item by the alternative mechanism (pulling → pushing, pushing → pulling). The little blue rectangle denotes the food item provided to the respective experimental partner. (Online version in colour.)

In our experiment using a full-factorial design, working dogs of the Swiss military once received a food donation from a conspecific (cooperation experience treatment) and once did not (defection experience treatment), which involved a particular helping task. In the defection treatment, the focal subjects received the same amount of food as in the cooperation treatment, but here it was delivered not by the partner but by the experimenter who operated the apparatus accordingly. Subsequently, the focal dog's propensity was tested to donate food to the former cooperator or defector by using a different helping task. The first task involved pulling a rope which the dogs did with their muzzle, whereas the second task involved pushing a lever with their paws. If dogs realize the significance of cooperation instead of merely copying a social partner's behaviour, they should differentiate between a cooperator and a defector also when the tasks diverge between receiving and returning help.

2. Material and methods

(a) Subjects

We used 16 unrelated working dogs of the same breed (Belgian shepherd, Malinois; 11 uncastrated males and five castrated females) with a limited age range (13–48 months). All dogs took part in the trainings for the Swiss military service and had not met before the experiment. Four males were chosen to act as cooperators (2) and defectors (2), respectively; all other dogs served as test subjects.

(b) Pre-experimental training

The dogs learnt two alternative mechanisms by which they could donate food to a conspecific partner. The first mechanism involved pulling a rope that moved a wooden platform bearing a food item towards the partner [7]. The second mechanism involved pressing a lever that opened a box containing a food item for the partner. In both situations, the acting individual never received food itself, only its partner. Each dog was enclosed in a separate, adjacent kennel so that the donors could not get the reward from their partner. Two dogs were randomly selected from our 16 animals to serve as defectors; they were not taught to pull or push for a partner, but were habituated to the two rewarding situations like the other subjects. After 16 training days (two sessions lasting about 5 min per dog per day), all other dogs had learnt to pull and push alternatively for each other in both situations seven times in a row (cf. [7]). The four dogs used to provide experience to the 12 focal subjects (two cooperators and two defectors) had no interactions with the focal dogs before the experiment.

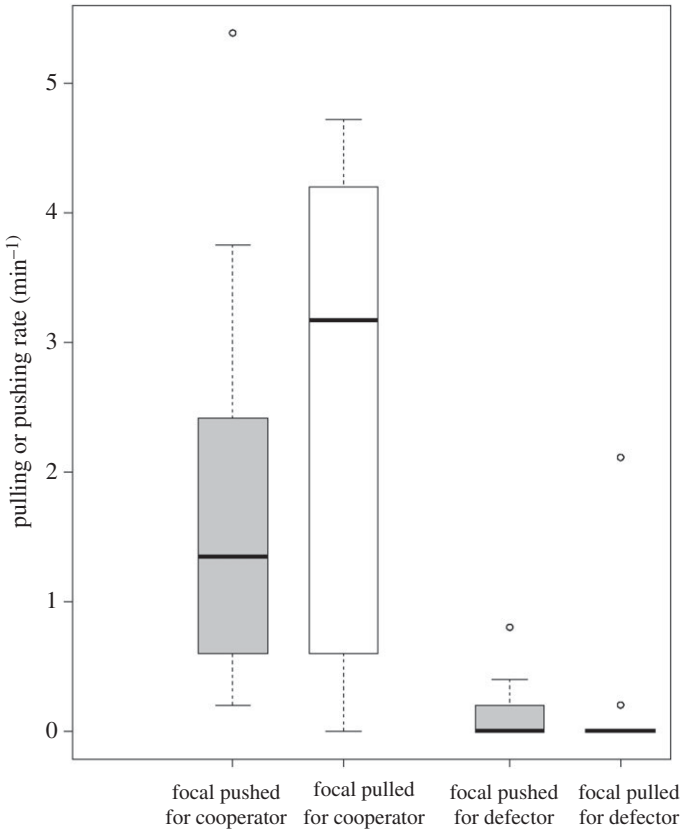

Figure 2. The transfer of alternative tasks in reciprocal cooperation among dogs. Focal subjects helped partners more often with either the pulling or pushing mechanism if these had helped them before with the alternative mechanism (cooperator treatment), than they helped partners that had not helped them before (defector treatment). Box-plots show pulling and pushing rates per minute (medians, interquartile ranges, whiskers (lowest and highest value that is not an outlier), outliers (values greater than 1.5 interquartile ranges away from the 25th and 75th percentiles)).

(c) Experiment

In a full-factorial design, each focal dog once received and once did not receive food provided by the partner by one mechanism in the experience phase, and it was subsequently enabled to provide food to the same partner by the alternative mechanism in the test phase (figure 1). The sequence of receiving experience with a cooperator or defector, and the two alternative provisioning mechanisms (pulling or pushing), were randomized. The focal dog had two experiences (one each with both mechanisms) with a cooperator or defector on the first day of the experiment, followed on the next day by one test with the respective previous experience provider and one control without a partner in the neighbouring kennel (electronic supplementary material, figures S1 and S2), again in randomized sequence. This procedure was repeated four times; i.e. on days 1, 3, 5 and 7, experience was provided by a cooperator or defector, and on days 2, 4, 6 and 8, the respective tests and controls were performed. Importantly, during the experience phase, the focal dog received the same number of food items, irrespective of whether it was combined with a cooperator or defector. The only difference was that in the cooperator treatment, the partner dog was providing the food items to the focal dog by operating the respective apparatus, whereas in the defector treatment, the same number of food items was provided to the focal dog by the experimenter, who pulled the rope or pushed the lever.

During the test, the focal dog had the opportunity to pull or push for donating food to its partner. In the control situation, the focal dog could again pull or push to produce food, but the neighbouring kennel was empty. The experience phases as well as the test and control phases lasted for 5 min or until a dog had pulled or pushed seven times (cf. [7]). During the test, the partner dog (cooperator or defector) was the same as in the experience phase on the previous day, i.e. partner A for the first 2 days, partner B for the following 2 days, partner C for days 5 and 6 and partner D for the last 2 days.

(d) Measured variables

We counted the numbers of pulls and pushes and measured the latencies to the first pull or push of the focal dogs. Additionally, we recorded the behaviour of the partners towards the focal dogs during the test phase. We included 'friendly' and 'begging' behaviours (described in the electronic supplementary material).

(e) Statistics

The pulling or pushing rates of focal dogs in the test trials as response variable were analysed with a linear mixed model, with focal dog as a random factor and the mechanism of help (pulling or pushing mechanism) and the friendly and begging behaviours of the partner as a fixed effect using the statistical software R (R Development Core Team 2009; v. 2.13.1). Two females could only participate in some of the tests owing to other use by the military that conflicted with the experiment. Hence, these two dogs were excluded from the statistical analysis ($N = 10$). The latency of focal subjects to the first pull or push was analysed with a survival analysis, where the partner's behaviour and the identity of the partner were included as random factors. The solo pulling control was compared with the test situation with a non-parametric Mann–Whitney *U*-test. We compared the partners' behaviours (friendly and begging) during the test phase between cooperators and defectors also with a Mann–Whitney *U*-test.

3. Results

Focal dogs helped a previous cooperator significantly more often than a previous defector, irrespective of the behaviour

these partners showed during the test phase ($p < 0.001$; figure 2). There was no significant difference in helping frequencies between the pulling and pushing tasks ($p = 0.119$). The friendly and begging behaviours of the partner enhanced the pulling propensity of focal dogs (begging: $p = 0.044$, friendly: $p = 0.045$; electronic supplementary material, table S1). Further, the dogs pulled significantly earlier for a cooperator than for a defector (d.f. = 7.53, $p \leq 0.001$; electronic supplementary material, figures S3 and S4).

In the solo control situation where focal subjects could *push* and the previous cooperator was absent, the dogs did not push at all, except two subjects which pushed either once or twice. The same was true in the control situation where the previous defector was absent (electronic supplementary material, figure S5). Similarly, in the solo control situation where focal subject could *pull* and the previous cooperator was absent, the dogs did not pull at all, except two subjects which pulled once. In addition, one dog pulled once and one dog pulled twice in the control situation where the previous defector was absent (electronic supplementary material, figure S6). Thus, the propensities to push or pull in the solo control differed from the situations in which the cooperator was present in the neighbouring kennel (pushing: $V = 55$, $p = 0.006$; pulling: $V = 36$, $p = 0.012$), but they did not differ significantly from the test situation in which the defector was present in the neighbouring kennel (pushing: $V = 6$, $p = 0.181$; pulling: $V = 1$, $p > 0.999$). Hence, there is no indication that the intrinsic tendencies to pull the rope or to push the lever had been influenced by the experimental experiences.

The duration of friendly behaviour shown towards the focal dog during the test situations did not differ between cooperators and defectors ($V = 17$, $p = 0.308$), whereas there was a slight tendency for cooperators to beg more often than defectors ($V = 69.5$, $p = 0.099$; minutes per test session: cooperators 0.256 ± 0.389; defectors 0.19 ± 0.589).

4. Discussion

When deciding to donate food to a social partner, working dogs apparently differentiate between cooperators and defectors, even when receiving and giving food donations involves divergent tasks. Focal subjects pulled and pushed more often and earlier for cooperators than for defectors. Thus, working dogs can apparently generalize cooperative experience by using a different task to pay back received help. This is clearly a social service, because the focal dogs hardly ever pulled or pushed in the control situation when the partner's kennel was empty.

Humans may also use different tasks when returning received favour [12]. Our results showing that dogs can trade different tasks among social partners in a variant of the iterated prisoner's dilemma might suggest that this ability is widespread in nature [2]. Reciprocal cooperation may not be as cognitively demanding as previously assumed [13,14]. In many different contexts, individuals remember the outcome of previous social encounters with a partner, which is, for instance, the basis for the establishment of social hierarchies [15]. Attitudinal reciprocity [16] is one mechanism proposed to explain the exchange of social services among partners: receiving help from a social partner is assumed to change the attitude towards this individual, thereby increasing the propensity to help that partner if cooperation is requested. This is in line with our result showing that friendly behaviour and help requests enhance the propensity that help will be given. Furthermore, previous studies have shown that dogs prefer using simple rules for behavioural decisions if they are effective [7,10]. This study did not aim to clarify motivational or cognitive mechanisms of reciprocal cooperation, but our results suggest that dogs might be promising subjects for such investigation.

It has been suggested that the transfer of social experience between contexts is under positive selection [17]. This study adds to the evidence that reciprocal exchange between different tasks and commodities among animals may be a common, yet understudied phenomenon [2].

Ethics. Authorization by the Swiss Federal Veterinary Office (licence BE82-11).

Data accessibility. Data are included in the electronic supplementary material.

Authors' contributions. N.G. and M.T. designed the study; N.G. carried out the experiments and statistical analysis. M.T. advised on data analysis. N.G. and M.T. wrote the manuscript. N.G. and M.T. approved the final version of the manuscript and agree to be held accountable for the content therein.

Competing interests. We declare we have no competing interests.

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