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Waiting for more: the performance of domestic dogs (*Canis familiaris*) on exchange tasks

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Abstract Five domestic dogs (*Canis familiaris*) were tested in a cooperative exchange task with an experimenter, as previously tested in non-human primates. In the first task, the dogs exchanged to maximise payoffs when presented with food items of differing quality. All consistently exchanged lower-value for higher-value rewards, as determined by their individual food preference, and exchanges corresponded significantly with the spontaneous preferences of three dogs. Next, all subjects demonstrated an ability to perform two and three exchanges in succession, to gain both qualitative and quantitatively increased rewards (group mean = 72 and 92% successful triple exchanges, respectively). Finally, the ability to delay gratification over increasing intervals was tested; the dogs kept one food item to exchange later for a larger item. As previously reported in non-human primates, there was considerable individual variation in the tolerance of delays, between 10 s and 10 min for the largest rewards. For those who reached longer time lags (>40 s), the dogs gave up the chance to exchange earlier than expected by each subject's general waiting capacity; the dogs anticipated delay duration and made decisions according to the relative reward values offered. Compared to primates, dogs tolerated relatively long delays for smaller value rewards, suggesting that the socio-ecological history of domestic dogs facilitates their performance on decision-making and delay of gratification tasks.

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Introduction

Human economic systems of trade and cooperative exchange are built on the maximisation of gains and require advanced cognitive capacities, including the ability to delay gratification. Transactions may involve investments months or years in advance of any payoff. In contrast, non-human animals have long been regarded as impulsive, lacking in self-control and unable to plan for future events (Silverberg et al. 1998). In humans, but also in other species, the ability to maximise the gains received in a transaction is an adaptive strategy, with relevant underlying cognitive capacities shaped by selection. One of these capacities, the ability to inhibit prepotent responses and delay gratification, is crucial for complex goal-directed action (Kacelnik 2003).

The most commonly used paradigms used to study self-control in animals, reverse-reward and delay-choice tasks, both require a single decision at the start of the trial—to choose a smaller amount or to wait longer to gain larger rewards, respectively (e.g. Shifferman 2009). In contrast, delay-maintenance tasks require this decision to be maintained over the duration of the trial, requiring continued

behavioural inhibition of the prepotent response to eat the accessible reward, in order to maximise the gains received. The exchange paradigm is particularly interesting as it mimics an economic transaction; individuals are given a food item and then offered the choice to exchange for another food item differing in quality or quantity. Unique to delayed-exchange paradigms is the requirement to retain but not consume a reward for the duration of the trial in order to make an exchange. These tasks require not only the maintenance of the delay, but also acceptance of an initial loss; in addition to behavioural inhibition, this potentially represents a trade-off between the gains of engaging in trade on the one hand and the risks inherent in giving up a desired item on the other (Brosnan and Beran 2009).

Temporal discounting affects the duration of delays maintained; as duration increases, the subjective value of a reward decreases, reducing the willingness to wait (Mazur 1987). Impulsivity and temporal discounting are dynamic processes that can shape and sustain decisions in relation to the temporal distance of the goal. In delay-choice tasks, in which subjects can choose between a small immediate reward and more valuable delayed reward, most species choose equally between these reward options for delays of less than a minute (e.g. Amici et al. 2008; Mazur 1987; Stevens et al. 2005). Great apes compare favourably to humans when tested in similar circumstances, delaying gratification for 2 min, a result interpreted as indicating that the common ancestor to humans and great apes possessed an 'extended temporal horizon' (Rosati et al. 2007). When tested in delay-maintenance tasks (in which the smaller reward is accessible throughout so that the initial decision to wait can change during the delay period), chimpanzees can maintain inhibitory control to gain the larger but delayed reward (Beran et al. 1999). Delay maintenance is also tested using accumulation tasks, in which an accessible reward steadily increases in value (Beran 2002; Beran and Evans 2006); when provided opportunities for self-distraction, chimpanzees tolerate delays of up to 18 min to gain a maximum of 36 preferred food items (Evans and Beran 2007). Although it appears that great apes may have advanced capabilities to delay gratification, given the variation in self-control paradigms and differences in contextual factors (such as reward value), it can be difficult to establish meaningful cross-species comparisons (see Shifferman 2009, for a review of these issues in relation to reverse reward tasks).

To date, delay-maintenance tasks have primarily been used to explore self-control in non-human primates. However, research in species with a long history of evolutionary divergence from humans increasingly points to a convergence of complex cognitive abilities with those of higher primates (Emery and Clayton 2004; Roth and Dicke 2005:

in corvids; Miklosi 2007: in canids). Domestic dogs are a particularly interesting study species given their unique socio-ecological niche and the role of the domestication process in shaping cognition and behaviour (Hare et al. 2002, 2005; Kubinyi et al. 2007). Successful performances in cooperative tasks, complex conflict resolution and strategic social behaviour are evident in several *Canis* species (Cordoni and Palagi 2008; Möslinger et al. 2009; Palagi and Cordoni 2009), including the domestic dog (Cools et al. 2008; Gansloßer 2009; Horowitz 2009; Naderi et al. 2001; Rooney and Bradshaw 2006). The cognitive capabilities underlying *Canis* cooperation have been further shaped during the process of domestication in dogs (see Hare et al. 2002). For example, fox kits selectively bred for fearless and non-aggressive behaviours towards humans show dog-like skills in reading human communicative gestures, suggesting that the social cognitive evolution of dogs may be a by-product of selection for interspecific social contact (Hare et al. 2005).

The ability to delay gratification is critical for goal-directed behaviour (Mischel et al. 1974) and may be a prerequisite for making future-oriented decisions (Pelé et al. 2010a). Dogs demonstrate behaviours that are fundamental to successful goal-oriented cooperation, such as turn-taking in the initiation of joint actions during interactions with humans (Naderi et al. 2001). The ability to cope with a delay could therefore be expected to be advanced in social species that typically coordinate their activities and cooperate in social and ecological contexts. The long history of social interaction with humans could also shape such abilities in dogs, and their capacity for social anticipation may contribute to their behavioural synchronisation and cooperative processes with humans (Kubinyi et al. 2003). However, the cognitive mechanisms behind these apparently complex social behaviours in *Canis* species are yet to be explored. While there is some evidence that dogs are able to anticipate future events (Kubinyi et al. 2003), it is widely assumed that dogs 'live in the moment' (Byrne and Bates 2007; Csanyi 2006) and, unlike chimpanzees (Dufour and Sterck 2008; Mulcahy and Call 2006), there has been no investigation into their ability to plan for future needs.

Here, we investigate domestic dog abilities in a food exchange task with a human. The exchange paradigm has been used to examine decision-making processes, gain maximisation and the maintenance of delay of gratification, using a consistent methodology across several species of primates (capuchin monkeys, *Cebus apella*, Drapier et al. 2005; Pelé et al. 2010a; Ramseyer et al. 2006; chimpanzees, *Pan troglodytes*, Dufour et al. 2007; tonkean macaques, *Macaca tonkeana*, Pelé et al. 2010a; long-tailed macaques, *Macaca fascicularis*, Pelé et al. 2010b). In terms of the underlying cognitive mechanisms, this task has three

key components (1) an assessment of the relative value of rewards (qualitative and quantitative), (2) the inhibition of the prepotent response to eat the first item and the ability to return it (behavioural inhibition and flexibility) and (3) an estimation of the delay length to determine whether the delayed reward is worth the wait (temporal discounting and anticipation of the delay in relation to reward value). The experiments reported in this study replicate the exchange tasks previously tested in non-human primates and allow for direct cross-species comparisons.

Methods

Subjects and conditions

Five dogs participated: three females and two males; further details are provided in Table 1. Following Experiment 1B, one dog (Faye) was withdrawn from testing as pregnant. The dogs were all pets, although they had received various training by owners. Two dogs belonged to the researcher (RJL: Ellie and Jet), but none of the dogs had any prior experience of cognitive testing. Testing took place individually within their home environments. Participants were never deprived of food, and items offered during test trials were dietary treats. Testing sessions (6–12 trials) were completed between 3 and 6 days per week dependent on availability. Testing sessions were conducted by RJL and videotaped (with six exceptions due to technical difficulties), to allow accurate timing of events. Testing procedures adhere to UK legal requirements and ASAB guidelines for animal research (Association for the Study of Animal Behaviour 2006).

General training and testing procedure

The methodology of the exchange paradigm was adapted from previous primate studies and modified for domestic dogs; the key difference being the manner in which food items are taken by the subject, as dogs are required to use their mouth to select and hold food items. This difference

could potentially affect the dogs' inhibition of their spontaneous response to consume the food items (given that the food is already in the mouth) and their ability to retain the item for long periods of time (e.g. due to salivary responses). Nonetheless, a consideration of the ethological background of dogs, hunting and retrieving in their interspecific associations with humans and also carrying food for their young indicates that using the mouth to hold food is within the species capabilities.

Given the potential influence of prosocial tendencies of the dogs towards human interactants, we applied a series of measures to limit these. For example, instead of hand gestures (palm up to request objects) that the dogs may have previously learnt (within contexts in which social approval might also have been given), a container was used to receive exchanged items. The training to exchange via the use of the container was novel for all the dogs and only acquired in the context of the training phase of this study. In addition, the experimenter remained silent during testing (no verbal requests to exchange) and avoided eye contact with the dogs. No responses were made to success or failure to exchange so that neither approval nor disapproval was given to the subject during testing. In contrast to the lack of social feedback, the experimenter always delivered a food reward on each trial.

The dogs were first trained to exchange items with the experimenter, learning first to drop a non-food item into a container ($20 \times 10 \times 14$ cm) for a small reward (for details on training, see ESM 1). Each training session consisted of 10 trials/exchange attempts; training sessions were short in duration (approx. 5 min), one session per day, and occurred between 2 and 5 times per week. Subjects required between 11 and 20 (mean = 15) training sessions in total to reach testing criteria. For testing, food items differing in quality or quantity were used.

A wooden barrier was secured in a doorway with the experimenter on one side and subject on the other (Fig. 1a). A container was positioned on the experimenter's side and raised approximately 20 cm. The experimenter showed two food items, one in each hand, close enough for the dog to sniff (Fig. 1b). One item was held up for duration of the

Table 1 Subjects' characteristics at the start of the research

| Subject name	Sex	Age (years)	Breed	Training experience (as provided by owners)	Length of time with present owner	Familiar with RJL prior to research
Ellie	F	5	Working sheepdog	Obedience, agility, working trials	4 years	Yes[a]
Jet	M	1	Lurcher	Basic obedience	3 months	Yes[a]
Bailey	M	3	Border Collie	Obedience and agility	3 years	Yes
Bonnie	F	1	Springer Spaniel	Basic obedience	9 months	No
Faye	F	4	German Shorthaired Pointer	Working pointer	3 years	No

[a] Owned by RJL
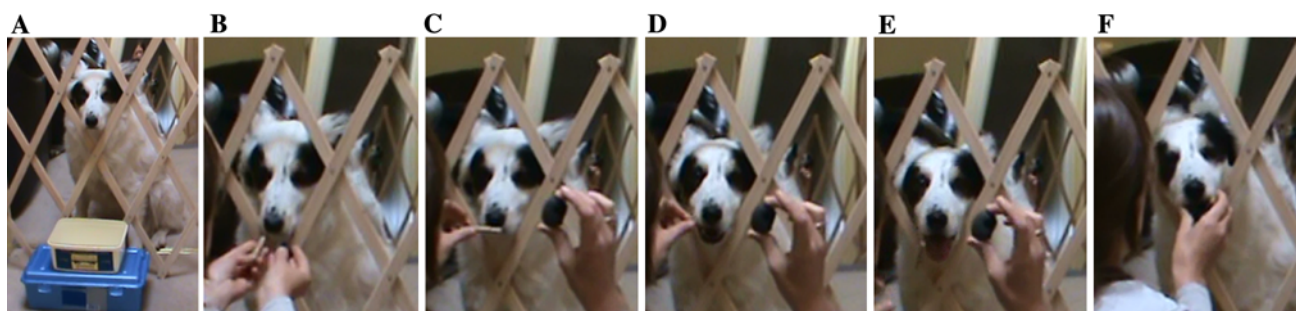
Fig. 1 An exchange sequence for foods differing in quality (see text for description)

trial, and the other item was given to the dog (Fig. 1c). The container was tilted towards the subject (Fig. 1d). If the dog dropped the initial item into the container (Fig. 1e), she/he received the alternative, displayed item (Fig. 1f).

If the subject returned only part of the item, it was returned to him/her and the trial ended without an exchange. All rejected items were placed into a 'bin' and not offered in subsequent trials. The intertrial interval was 10 s.

Experiment 1A: Food quality exchange

The dogs' decision-making processes in the exchange paradigm were initially examined with food items differing in quality. First, we assess whether they are capable of exchanging one food item for another, when they have to hold the first food item in their mouth before trading it for another one. Second, given their everyday compliance with human requests, we examine whether the dogs are compelled to perform an exchange when offered, regardless of the relative quality of the two items available. The level of correspondence between spontaneous preferences and exchange behaviour therefore allows us to evaluate whether exchanges are made primarily to gain more desirable food rewards.

Methods

Assessment of food preferences

Individual preferences for four food types were first assessed before these were tested in an exchange task (Drapier et al. 2005). The foods used were plain biscuit, charcoal biscuit, beef chew and cocktail sausage. All food items were dietary treats (i.e. all were consumed immediately if offered). The items used to assess food preferences were approximately half the size of those used during testing (approx. $1.5 \times 1.5 \times 0.5$ cm pieces). There were 12 trials per session; one session was conducted per day.

Given four food items, there were six possible combinations: each dog completed eight assessment sessions (96 trials), so that each combination was presented 16 times in total (half presented to the right, half to left, to avoid side bias). Items were presented on two identical plastic lids, to avoid associations with hands/food/begging. Subjects were shown and allowed to sniff the two items, held approximately in line with the dog's head at a gap in the barrier; then, the two items were lowered and moved laterally, so each item was presented to either side of the dog, at a gap in the barrier. These spontaneous choices were recorded on a data sheet following each trial.

Procedure

The food items were approximately $3 \times 1.5 \times 1$ cm, although items varied in shape. The four foods (as above) were presented in six combinations; there were 12 possible paired combinations. Each session contained 12 trials, randomised in order of food combinations presented and side of presentation of each item offered (left/right hand). Each subject completed 15 sessions with 12 trials per session; the six food combinations were each shown 30 times. Throughout testing, if an attempted exchange missed the container, the item was returned to the dog and a second attempt offered and if successful, an exchange was recorded.

Statistical analysis

Due to variability in food preferences and the small sample size and subsequent difficulty in testing for normality in these data, individual results were analysed using a nonparametric version of the Mantel Z statistic. Correlations between the preference matrix and exchange matrix were calculated using Dientz R statistic with alpha set at $P < 0.05$ (Matman programme, Noldus: deVries et al. 1993). This analysis compared the pattern of exchanges with spontaneous food preferences assessment.

Results and discussion

Although individual food preferences differed, all subjects consistently exchanged lower-value (plain and charcoal biscuits) for higher-value items (beef chew and cocktail sausage) and did not exchange high-value items for low-value ones (see Table 2 for preference and exchange matrices). Three subjects readily exchanged their second favourite for favourite food items (Jet 93%, Faye 90% and Bonnie 83%), while the other two (Ellie and Bailey) did so less consistently (40%). For the three female dogs, exchanges correlated with preferences (Dientz R: Ellie $r = 0.974$, $P = 0.04$; Faye $r = 0.894$, $P = 0.04$; Bonnie $r = 0.996$, $P = 0.04$); but not significantly so for either of the males (Jet $r = 0.798$, $P = 0.08$; Bailey $r = 0.788$, $P = 0.08$).

Experiment 1A indicates that dogs generally engaged in exchanges to obtain the best available items despite having

to initially receive the first food item in their mouth. They did not exchange high-value items for lower-value ones, a pattern only explained by the relative value of items presented and not with a general compliance to exchange when given the opportunity. As this pattern is comparable to those previously reported for non-human primates tested using the same procedure, the exchange task is appropriate for exploring the capacity for self-control in dogs too. Familiarity with the experimenter did not affect the dogs' response: both Faye and Bonnie (unfamiliar with the experimenter) showed a significant correspondence between their food preferences and exchange behaviour and also exchanged their second favourite for favourite item when making exchanges. The dogs that were more familiar with the experimenter did not perform as consistently, either showing a non-significant correspondence between preference and exchanges or being less consistent

Table 2 Food preferences and quality exchanges: correlations between the matrix of preferences and the matrix of exchanges for each individual

Subject	Food preferences				Food exchanges				Dietz R test	
	Items chosen by the subject (%)				Items chosen by the subject (%)				Correlation	Significance
	Plain	Charcoal	Chew	Sausage	Plain	Charcoal	Chew	Sausage		
Bailey									0.788	$P = 0.08$
Plain	–	81	75	94	–	100	100	100		
Charcoal	19	–	82	87.5	0	–	77	93		
Chew	25	19	–	87.5	0	23	–	60		
Sausage	6	12.5	12.5	–	0	7	40	–		
Bonnie									0.996	$P = 0.04$
Plain	–	25	94	100	–	30	93	100		
Charcoal	75	–	94	100	70	–	93	100		
Chew	6	6	–	87.5	7	7	–	83		
Sausage	0	0	12.5	–	0	0	17	–		
Ellie									0.974	$P = 0.04$
Plain	–	94	100	100	–	90	100	100		
Charcoal	6	–	62.5	81	10	–	63	83		
Chew	0	37.5	–	87.5	0	37	–	60		
Sausage	0	19	12.5	–	0	17	40	–		
Faye									0.894	$P = 0.04$
Plain	–	81	81	94	–	100	100	100		
Charcoal	19	–	87.5	94	0	–	90	100		
Chew	19	12.5	–	87.5	0	10	–	90		
Sausage	6	6	12.5	–	0	0	10	–		
Jet									0.798	$P = 0.08$
Plain	–	75	75	94	–	100	97	100		
Charcoal	25	–	37.5	75	0	–	23	97		
Chew	25	62.5	–	94	3	77	–	93		
Sausage	6	25	6	–	0	3	7	–		

Food preferences: Choice between 2 items presented simultaneously to the subject (column 1 and columns 2–5). Quality exchanges: decisions when offered an exchange between items (column 1 and columns 6–9)

in relinquishing their second favourite item for their favourite.

Experiment 1B: Successive exchanges

Successive exchanges require individuals to repeatedly inhibit food consumption to maximise their payoffs, as previously demonstrated in capuchin monkeys (Drapier et al. 2005). The dogs need to engage in multiple successive exchanges to reach the final goal (obtaining the highest quality or largest reward). Not only do the dogs need to inhibit food consumption for longer (the delay to the final reward is increased with each repetition of an exchange within a trial), but they are also required to re-evaluate the decision to exchange as the subsequent items increase in value.

We tested both qualitative and quantitative versions of the exchange task; value judgments may be easier for qualitative arrays but performance on quantitative exchanges may be more informative, given potential differences in the strength of individual food preferences. In addition, as the olfactory modality is dominant for gathering information in dogs, discriminating between different amounts of the same food type may be more difficult.

We tested the dogs' ability to perform successive exchanges, requiring the repeated inhibition of the impulsion to consume items either for two (double exchange condition) or three successive exchanges (triple exchange condition). Following the initiation of the exchange with a non-food item, rewards increase in quality or quantity with each exchange. The item obtained in the first exchange becomes the item to return in the next, and so on, with triple exchanges therefore requiring greater inhibition but offering more valuable final rewards. Testing involved successive exchange of food items differing first in quality and then in quantity.

Methods

The items that were to be exchanged were lined in order on a plastic lid (15 × 10 cm) within the dog's view. A non-food item (hard plastic object, used when training to exchange) was given to the dog and then the lowest value food item (1) was shown to the subject as an exchange opportunity. The dogs were offered food items of increasing value with each exchange; all ranks were based on individual preferences (4th, then 3rd favourite in double, followed by their favourite food type in triple exchanges). If the object was exchanged for food item 1, food item 2 was then shown to the dog as an exchange opportunity (held up on display). In triple exchanges, if item 1 was returned, item 2 was shown to the dog alongside

a higher-value food item (3), for which item 2 could be exchanged (see ESM 3: Video 1).

For quantitative exchanges, the procedure was as described above but with the same food type always presented, doubling in size for each subsequent exchange offered. Prior to testing, two 10-trial sessions were completed for a new food type, which would be expected to be highly valued by all subjects. This assessment followed the basic testing procedure described for the successive qualitative exchanges, but subjects were first given a small food item (a piece of chicken strip) and offered the opportunity to exchange it for twice the amount of the same type of food. The dogs made exchanges between 70 and 100% of trials in the second session. This novel desirable food type was then used in successive exchange test sessions. Pieces of chicken chew strips that could easily be doubled in quantity were used in successive exchanges (minimum size, 2 cm × 3 cm × 0.2 cm, to a maximum of 2 cm × 12 cm × 0.2 cm, i.e. the last item in the triple exchange condition was four times the initial item size).

Two 12-trial sessions were completed in the qualitative condition, one session of double exchanges followed by one session of triple exchanges. Following this, we conducted two 12-trial quantitative testing sessions in both the double and triple exchange conditions. If the subject performed at a high success rate in the successive quantitative exchange condition (i.e. >4 in the first 6 trials), sessions were divided to limit excessive food consumption (six trials per day).

Results and discussion

For qualitative exchanges, overall performance was higher in the double than the triple exchange condition (mean success double = 85%; mean triple = 72%). At the individual level, three dogs performed better at double than triple exchanges (Bailey double = 100%, triple = 67%; Ellie double = 100%, triple = 33%; Faye double = 92%, triple = 83%). One dog (Bonnie) performed better at triple (83%) than double (42%), and one dog was consistent across both types (Jet 92% for both).

Performance during quantitative sessions was lower for the double (mean = 78%) than triple exchange condition (mean = 92%). All individuals were more successful on the triple exchange task (Ellie double = 87.5%, triple = 100%; Bonnie double = 79%, triple = 100%; Jet double = 75%, triple = 92%; Bailey double = 71%, triple = 75%).

When presented with successive opportunities to exchange in Experiment 1B, all performed these exchanges rapidly (approx. 1 s per item), limiting the time in which they had to delay gratification and inhibit consumption of the smaller food item. Interestingly, both quality and

quantity of the reward were judged accurately by the dogs and their relative value taken into account when deciding to exchange or not. Although an order effect could explain the improved performance on the final test session (quantitative triple exchanges), there were no similar improvements across the two qualitative sessions; increased motivation could also explain this result as the final rewards on the triple exchange trials were double those offered on the double exchanges.

Together, the results of Experiment 1A and 1B indicate that neither a general tendency for compliance nor familiarity of the experimenter to the individual dogs readily explains their performance on these exchange tasks. All the dogs performed well when making successive quantitative exchanges, indicating that familiarity with the experimenter did not seem to differentially influence their performance. In sum, refraining from consuming the item already in their mouth to obtain a more valuable one indicates behavioural inhibition in dogs, and successive exchanges indicate at least some basic capacity to delay gratification over delays of a few seconds.

Experiment 2: The effects of quantity and duration on delayed exchanges

Dogs are expected to engage readily with exchange tasks with humans but direct evidence in relation to dogs' cognitive abilities when calculating decisions, delaying gratification or anticipating future events is lacking. Experiment 2 examines their capacity to anticipate food return and exert self-control in greater depth, by testing the maximum delays tolerated between receiving the initial item and the opportunity to exchange. Here, we systematically varied the relative value of the food item on offer, allowing the interaction between delay durations and reward values to be examined (as tested in primates: Dufour et al. 2007; Pelé et al. 2010a, b; Ramseyer et al. 2006). We investigated whether dogs, like primates, anticipate the length of the delay and make decisions about a future exchange early in the trial. Such a response pattern indicates that the decision to wait is based on a trade-off between reward quantity and expected costs of the waiting duration. Waiting times sustained by the primate species tested generally vary according to the relative value of food items ($2\times$, $4\times$ or $8\times$ the size of the initial item; but see Pelé et al. 2010a). We tested the dogs using quantitatively differing food items following the same proportions as previously tested in non-human primates.

Methods

The dogs were given a small food item to either consume or exchange for a larger item after a delay. The precise time lags between receiving initial items and offering an exchange were steadily increased across (not within) test sessions, starting with 2-s delays in the first phase, and increasing to 5, 10, 20 s etc. (maximum delay tested = 1,280 s). Items offered in exchange trials could be two times, four times or eight times the size of the initial item (2 cm $\times$ 3 cm $\times$ 0.2 cm). Within each session, different size values were presented randomly (randomisation completed in 12-trial blocks).

For each experimental testing phase (time lag), six sessions of eight trials were completed ($N = 48$ trials, 16 per size of return). Each time lag was tested until individual performance dropped to 0% return (over the 48 trials); the subject no longer tolerated the delay between receiving the initial item and the opportunity to exchange. The frequency of exchange, exact time points and types of 'giving up' (e.g. consumption of initial item) were recorded.

Procedure

The procedure was as described for the basic exchange testing procedure above, except a different container (22 cm $\times$ 20 cm) with a lid was used and exchanges could only be made when the lid was removed (i.e. an exchange opportunity was presented). The experimenter held her hand palm down over the lid during the delay to prevent the dogs removing the lid with their nose to 'create' an opportunity to exchange, as had been attempted during training sessions (see ESM 2 for further details on training). To avoid satiation and overfeeding, testing was reduced to four or six trials per session if larger rewards were obtained in initial trials. As in previous conditions, the larger food item remained fully visible in the experimenter's other hand for the duration of the waiting period. The experimenter monitored delay length using a stopwatch, avoided visual contact and did not make any response in relation to a dog's behaviour during trials, glancing up only to determine the time of 'giving up' if the delay was not maintained. When the waiting period had elapsed, the experimenter removed the lid of the container, and the dog was only then able to return the smaller item in order to receive the larger item. If the smaller item was consumed, the larger item was discarded and the trial ended. If the subject attempted to exchange the smaller item too soon, or broke it or consumed part of it, the smaller item was returned to the subject, the larger item discarded and the trial ended.

Statistical analyses

Statistics were conducted using Friedman ANOVA to test for a main effect of reward size on the rates of exchange. In addition, the timing of errors was analysed using the

Kaplan–Meier survival analysis (Bland and Altman, 1998). The Kaplan–Meier survival analysis is a statistical tool used to measure survival rates in a given population and obtain predictive measures. To test whether the dogs' timing of the decision to give up was related to the relative size of the larger food item, the analysis was performed on the giving up times for each size of return at each time lag ($N = 16$ trials per size per delay). The estimated (observed) probability of continuing to wait was calculated at each point in time that subjects gave up. This analysis included both the failure times and the times of successful return at the end of the trial (as censored data). In this analysis, the survival probability was expressed as the percentage chance of the subject waiting longer than the time already elapsed within a given trial. Against this observed survival function, the expected (exponential) distribution of giving up times was calculated (under the null hypothesis of a constant giving up chance). Thus, this expected distribution takes into account the general capacity to wait (based on individual performance). These expected and observed distributions were compared using an adjusted Kolmogorov–Smirnov test (Haccou and Meelis 1992); a statistically significant difference leads to the rejection of the null hypothesis. All reward sizes $2\times$, $4\times$ and $8\times$ the original item size ($N = 48$) were used to run the analysis on the times of error, from the 10-s time lag to the longest time lag tested for each individual.

The comparison between the observed and expected distributions indicates whether each dog was equally likely to give up at any point during the delay period, or they were more likely to give up near the onset or end of the trial. Consistently rejecting exchanges at the start of a trial is indicative of a decision not to wait for the reward size on offer, while doing so much later in the trial suggests difficulty tolerating the delay when attempting to maintain the delay of gratification.

Results

For all reward sizes combined (equal numbers of each size were presented across all time lags tested), during the initial testing with short waiting periods (2, 5 and 10 s), all four subjects performed exchanges at a high rate but this decreased as the waiting period increased (Mean 78% at 2 s, 71% at 5 s and 67% at 10 s). However, individual variation in performance also increased as time lags extended (SD = 7, 12 and 19 for 2-, 5- and 10-s delays, respectively). Maintaining delay of gratification over longer time lags was harder for some individuals than others; Bailey and Jet exchanged at maximum delays of 10 and 20 s, respectively, while Bonnie reached 320 s (5 min 20 s) and Ellie exchanged at 640 s (10 min 40 s; see Fig. 2). For the maximum durations tolerated during failed

attempts: Bailey's longest waiting duration was 18 s, although 20 s was once completed by returning only part of the original item; Jet's longest waiting duration was 39 s; Bonnie's was 600 s (10 min); Ellie's was 1090 s (18 min 10 s) before consumption of the initial food item.

We examined the effect of relative reward size ($2\times$, $4\times$ or $8\times$ initial reward size) on the likelihood of exchanging. As time lags extended, the relative size became increasingly relevant to the decision to wait (with the exception of Bailey; see Fig. 3). A Friedman test compared performance for the three different sizes in the last 3 time lags in which subjects made successful exchanges; as the dogs approached their maximum waiting period, significantly more exchanges were made for larger than for smaller returns ($Chi^2 (2) = 6.5$, $P = 0.04$).

To better understand the processes underlying delay-maintenance decisions, we investigated whether decisions to give up were made at the start or towards the end of the delay intervals, or randomly throughout. A Kaplan–Meier survival analysis indicated that all but one subject (Bailey) gave up significantly sooner than predicted by chance (Table 3). For Jet, early abandonment of exchange opportunities occurred for all sizes of return at the 40 s time lag, indicating delay intolerance and perhaps resulting from the extinction of exchange behaviours. However, 'giving up' times of Bonnie and Ellie revealed a different pattern. For the smallest returns, the decision not to wait was made earlier in the trial than would be expected by chance (according to each subject's general waiting capacity); at 40 and 80 s for Bonnie, and at 80, 160 and 320 s for Ellie (see Fig. 4). In contrast, when approaching their longest time lags tested, the decision not to wait was made early in the trial for even the largest returns (see Table 3; Fig. 4). For these two dogs, the decision not to wait occurred relatively early in the session, a pattern that emerged for the smallest return ($2\times$) at shorter delays but also for medium returns ($4\times$) as the delays extended, and then finally for the largest size rewards ($8\times$). This pattern indicates temporal discounting, with the subjective value of the future reward decreasing as the delay interval increases, so that the dogs are less likely to attempt to maintain delay of gratification.

Behavioural differences

The individual dogs displayed rather different behavioural responses during the waiting period (ESM 3: Videos 2, 3 and 4). Both Bailey and Jet continuously shifted the item in the mouth, which often resulted in disintegration of the item at longer delays. In contrast, Bonnie and Ellie held the food for more extended durations with very little movement of the mouth. Placing the food temporarily on the ground was observed in all subjects except Bailey.
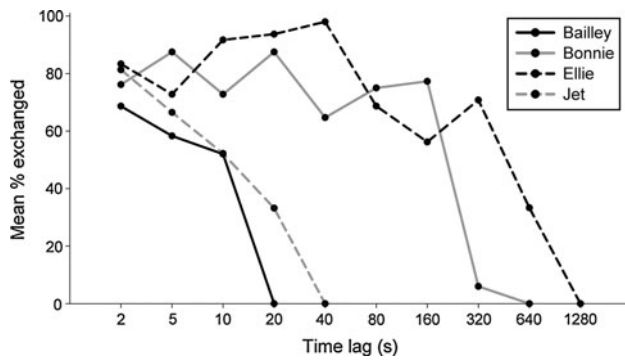
Fig. 2 Mean percentage of exchanges performed by each subject, at consecutive time lags

Differing behavioural responses were seen in the two most successful subjects: Bonnie typically engaged in rapid, circling locomotion (performed on 100% of delays maintained). She was sometimes seen placing the food item on the floor briefly, moving it with a forepaw, then picking it up and resuming the locomotory behaviour. In contrast, Ellie sat quietly with very little bodily movement (100% of delays maintained), and as the delays increased (beyond 80 s) she would frequently close her eyes for extended periods of time (e.g. 1 min). The subject would sometimes place the food item on the floor in her immediate area and leave it there for between 5 and 60 s, before picking it up and resuming a static position at the barrier.

Discussion

When offered opportunities to exchange on a qualitative or quantitative basis, the dogs made exchanges to maximise payoffs. Their exchange behaviour on quality trials corresponded closely with their food preferences. All dogs were also capable of exchanging these qualitatively different food items, or the same food type doubling in size, in two or three successive exchanges. These data demonstrate that domestic dogs display sufficient self-control to give up a small reward already in their possession in order to obtain a more highly valued and slightly delayed one. The dogs' performance on qualitative trials compared favourably with that of capuchins tested under similar conditions (Drapier et al. 2005), as the dogs' exchanges were more closely correlated to their spontaneous food preferences. Like capuchins, the dogs were also able to perform a quick sequence of consecutive exchanges (Drapier et al. 2005).

When delays were imposed before exchange opportunities, some individuals tolerated considerable delays, but delay maintenance was clearly dependent on the size of reward on offer. One dog was able to wait for over 10 min to exchange for the largest reward, demonstrating a high level of behavioural inhibition. When tested in the same conditions, for the same relative value returns (up to 8× the size), capuchin monkeys inhibited consumption for a maximum of 80 s (Pelé et al. 2010a; Ramseyer et al. 2006),
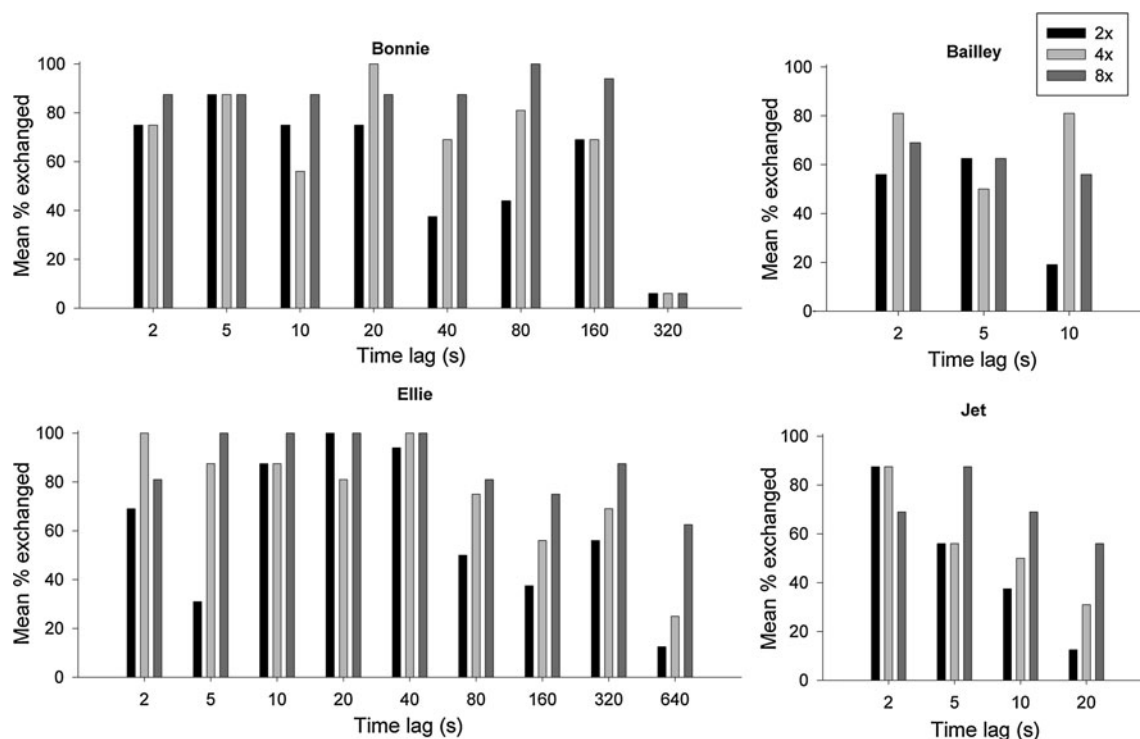

Fig. 3 Percentage of return according to the relative value of food items

Table 3 Maximum values obtained from the Kolmogorov–Smirnov statistical test used to compare the expected and observed distribution of giving up times

Time lag (s)	Subjects											
	Exchanging for 2 × returns				Exchanging for 4 × returns				Exchanging for 8 × returns			
	Bailley	Jet	Bonnie	Ellie	Bailley	Jet	Bonnie	Ellie	Bailley	Jet	Bonnie	Ellie
10	0.59	0.43	0.65	S	0.11	0.38	0.49	0.1	0.56	0.23	0.29	S
20	0.27 (N/S)	0.75	0.4	S	0.28 (N/S)	0.57	S	S	0.31 (N/S)	0.41	0.18	S
40	–	1.73*** (N/S)	1.78***	0.24	–	1.3** (N/S)	0.76	S	–	2.09*** (N/S)	0.47	S
80	–	–	1.68***	1.94***	–	–	0.58	0.96	–	–	S	0.24
160	–	–	0.47	2.22***	–	–	0.61	1.48***	–	–	0.18	0.74
320	–	–	2.38***	2.38***	–	–	2.45***	2***	–	–	1.63***	0.5
640	–	–	3.5***	2.63***	–	–	3.75***	2.48***	–	–	3.5***	1.18*
			(N/S)				(N/S)				(N/S)	
1280	–	–	–	3.75*** (N/S)	–	–	–	3.75*** (N/S)	–	–	–	3.69*** (N/S)

– = not tested

S = 100% success at this delay, N/S = Not successful at this delay

Critical value = 1.03 for $P < 0.05$. Critical value = 1.22 for $P < 0.01$. Critical value = 1.43 for $P < 0.001$

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

long-tailed and tonkean macaques for a maximum of 2 min 40 s (Pelé et al. 2010a, b) and chimpanzees for a maximum of 4 min (Dufour et al. 2007). The maximum waiting periods sustained by domestic dogs exceed those of other species tested in the exchange paradigm using similar reward values, ratios and durations. However, this may not reveal the maximum potential waiting period of domestic dogs; capuchins, macaques and chimpanzees were all able to substantially increase their tolerance of delays when offered rewards 40× the size of the initial item, tolerating delays of up to 2 min 40 s, 21 min and 8 min, respectively (Dufour et al. 2007; Pelé et al. 2010a, b). The delays sustained by the dogs also compare favourably to those of 4-year-old human children, who have a maximum tolerance of 5 min when tested in a delay-maintenance paradigm (Mischel et al. 1989).

As the dogs sustained delay lengths comparable to primates for smaller maximum returns, perhaps the dogs attributed more value to the food items received in exchange. Given the prosocial tendencies of dogs towards humans, it could be that social elements of the exchange task were intrinsically rewarding for the dogs, thereby having an additive effect on the reward value. Alternatively, as dogs are accustomed to performing tasks when requested to do so by a human, subjects may have attempted to comply by inhibiting consumption and enduring the waiting period. However, we were very cautious in avoiding experimenter behaviours that could have

influenced the dogs' actions. As dogs respond to the attentional state of humans (Call et al. 2003; Kundey et al. 2010), our procedures were aimed at reducing any potential social influence. On all trials, the dogs received a food reward but never received social feedback from the experimenter, regardless of whether they exchanged or not. Additionally, the results of Experiment 1A indicate that the dogs perceived that the experimenter was signalling an opportunity rather than a demand to exchange. Their exchanges maximised payoffs in accordance with their preferences; higher rewards were also available for *not* exchanging. If performance was primarily based on compliance, we might also expect that dogs could inhibit consumption for considerable delay durations, regardless of the reward on offer, but the individual variation in responses in Experiment 2 shows that this is not the case. Moreover, examination of 'giving up' times indicates strategic decisions based on relative reward size and duration, which is also not consistent with an interpretation based on inherent compliance. The dogs gave up earlier in the delay period than predicted by chance and did so in relation to the size of reward, which points to the critical role temporal discounting plays in their evaluation of future rewards; the subjective value of a reward decreased with the length of delay.

Given the relatively long delays maintained, dogs may have better inhibitory control than non-human primates. In addition, they may exhibit slower rates of temporal

Fig. 4 Comparing the distributions of observed and expected giving up times (expressed as a percentage probability of giving up, *Y* axis), according to the time elapsed in the trial (*X* axis) and the relative value of rewards (×2 and × 8): Bonnie (40 s delay) and Ellie (80 s delay)
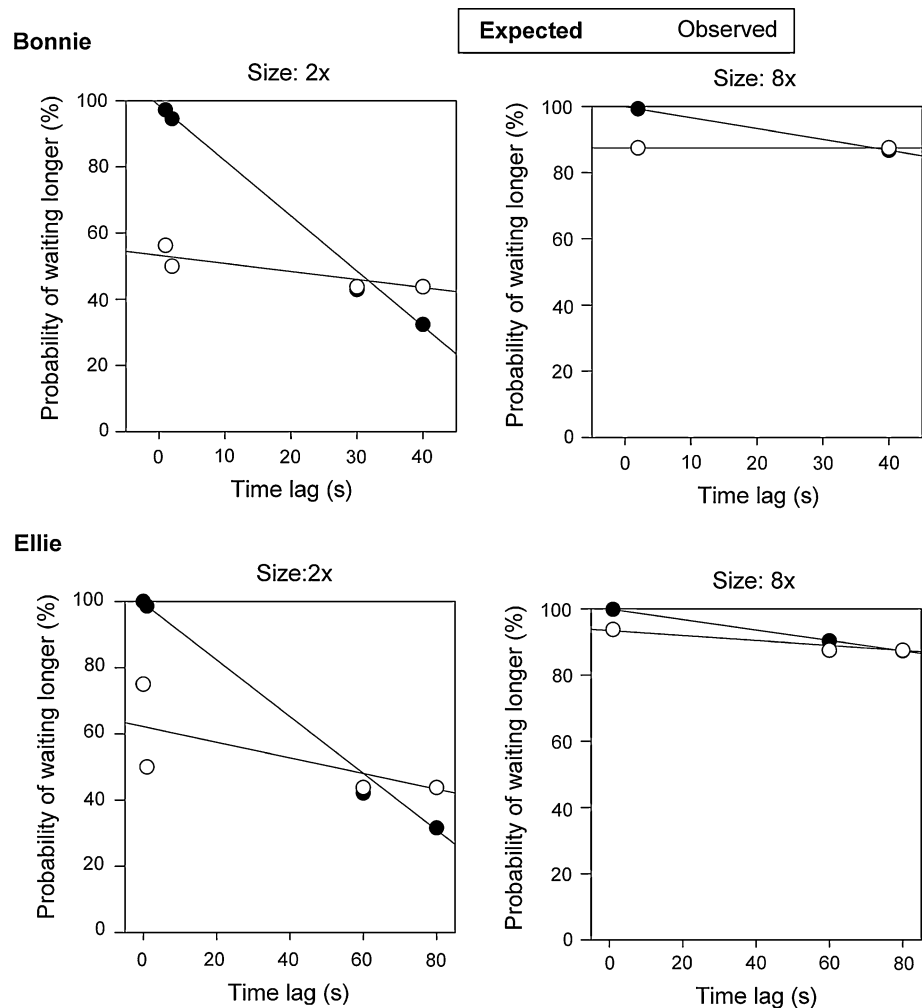
discounting in food contexts (Pelé et al. 2010a). Slower rates of temporal discounting on the exchange task could be partially attributed to dogs' prosocial tendencies; future research could examine this issue in greater detail, disentangling the role of each influence by employing an automated procedure (but see Beran and Evans 2006 for evidence that chimpanzee performance is comparable on social and automated versions of a delay-maintenance task). The exchange paradigm is designed to explore the mechanisms involved in cooperative exchange; it mimics an economic transaction, and therefore by its nature also involves a dynamic social interaction. In order to understand decision-making mechanisms at stake, participants need to be given opportunity to observe the contingencies within an interactive procedure that maintains ecological relevance.

The dogs mastered the contingencies of the exchange and made decisions early in trials based on an anticipation, of both the duration of the delay and the relative value of return expected. This suggests that the assumption that dogs 'live in the moment' (Byrne and Bates 2007; Csanyi 2006) should be reconsidered. Given the capacity to delay

gratification demonstrated by the dogs in this task, the time scale on which future-oriented decisions were made is of a considerable length. Dogs, like primates, are capable of foreseeing gains and losses, rather than being exclusively bound to the present (Dufour et al. 2007; Pelé et al. 2010a). This does not provide direct evidence that dogs are able to plan for the future, as they were working towards a current goal, but it suggests that dogs may possess the necessary cognitive capacities and highlights possibilities for further research on mental time travel in this species.

There were striking individual differences in performance between the dogs; this is reported in many species, across the different paradigms for testing self-control in humans and in other animals. Given the small sample size, it is difficult to identify personality or learning experiences which could explain such differences (e.g. Marshall-Pescini et al. 2008; Topál et al. 1997; Range et al. 2009). Given that owners can mislead their dogs in interactive tasks (e.g. by presenting divergent information, Kupán et al. 2011; Prato-Previde et al. 2008), it could be argued that all dogs tested should be equally unfamiliar with the

experimenter. However, examination of our results in relation to each dog's familiarity with the experimenter suggests this factor did not determine performance; for example, in Experiment 2, Ellie (familiar) and Bonnie (not familiar) maintained the longest delay durations. Instead, individual behavioural patterns during delays (see ESM 3) appear to facilitate behavioural inhibition. For example, chimpanzees employ behavioural strategies in delay of gratification tasks, with a direct relationship between the amount of self-distraction observed and the individual's ability to delay gratification (Evans and Beran 2007). Perhaps the related abilities of self-distraction and delaying gratification are not unique to primate species (see also Vick et al. 2010).

When examining the evolutionary origins of human sociality and intelligence, cooperation and reciprocal exchange are issues that are primarily studied using primates as models of early hominid behaviour (as a result of the closer genetic relationships), despite the likelihood that many factors leading to their development would be present in other vertebrate species (e.g. Bond et al. 2003; Westergaard et al. 2004). According to the social intelligence hypothesis, highly social animals (particularly those who form enduring social bonds) should show commensurate increases in cognitive abilities in response to the demands of their social environment (e.g. Dunbar and Shultz 2007). There is increasing evidence that social carnivores share similar advances in cognitive abilities with higher primates (Drea and Carter 2009; Dunbar 2009; Dunbar and Bever 1998; Palagi and Cordoni 2009), and the ecological relevance of cooperation for group-living predatory species is therefore also worth considering further (Byrne and Bates 2007; Stevens et al. 2005).

Moreover, the correlated by-product domestication hypothesis proposes that the enhanced socio-communicative abilities of domestic dogs result from selection against fear and aggression and in favour of dog–human social contact; this selection leads to individuals living without stress and behaving prosocially towards humans (because of high fear-aggression thresholds) subsequently having the highest fitness (Hare et al. 2005). This hypothesis relates to the present research from both ultimate and proximate perspectives. Domestication is likely to have further shaped *Canid* cooperative capacities, such as the ability to delay gratification, as these were adapted for interactions with humans. At the proximate level, it is also likely that in comparison with other species tested in self-control paradigms with a human experimenter, dogs are more eager and willing to engage and attempt to endure delays, at least partly as a result of their unique prosocial tendencies towards humans. For example, experimental studies have shown that when placed in a novel environment, dogs find the presence of a human companion even more effective in

reducing behavioural and physiological arousal than a canine companion (Tuber et al. 1996), and periods of human interaction can alleviate both behavioural and physiological signs of stress in shelter dogs (Hennessy et al. 1998, 2002a, b). Given that the human environment represents the natural socio-ecological niche of domestic dogs, their cooperative tendencies in food acquisition tasks (e.g. Bräuer et al. 2006) may result specifically from a history of relationships with humans; further research examining non-domesticated species could reveal which elements are shared among *Canids* and which are species unique.

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