



# Translational research into intertemporal choice: The Western scrub-jay as an animal model for future-thinking



James M. Thom<sup>a,b</sup>, Nicola S. Clayton<sup>b,\*</sup>

<sup>a</sup> Department of Philosophy, King's College London, Strand, London WC2R 2LS, UK

<sup>b</sup> Department of Psychology, University of Cambridge, Downing Street, Cambridge CB2 3EB, UK

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## ABSTRACT

Decisions often involve outcomes that will not materialise until later, and choices between immediate gratification and future consequences are thought to be important for human health and welfare. Combined human and animal research has identified impulsive intertemporal choice as an important factor in drug-taking and pathological gambling. In this paper, we give an overview of recent research into intertemporal choice in non-human animals, and argue that this work could offer insight into human behaviour through the development of animal models. As an example, we discuss the role of future-thinking in intertemporal choice, and review the case for the Western scrub-jay (*Aphelocoma californica*) as an animal model of such prospective cognition.

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## 1. Intertemporal choice

Choices are ubiquitous in the lives of all animals, and the consequences of these choices will often be subject to delay or clouded in uncertainty. Consider foraging behaviour – an animal feeding at a poor patch may need to abandon that patch in prospect of richer resources elsewhere. To do so, the animal must weigh the predictable and immediate benefits of continuing to feed against potential future payoffs at another patch. These *intertemporal choices* are similarly common in modern human life, and can have socially important consequences (e.g. Critchfield and Kollins, 2001), such as drug-taking and addiction (Bickel et al., 2007).

Studies of intertemporal choice in humans most commonly take the form of questionnaires offering hypothetical choices between delayed and immediate sums of money (e.g. Rachlin et al., 1991;

Green et al., 1999b; Kirby et al., 1999). For example, “Would you prefer \$50 immediately or \$100 in six months?”. Similar methods are also used to assess risky decision-making (e.g. Rachlin et al., 1991; Green et al., 1999a). Translational research in animal models such as rats and pigeons has adapted these methods to examine choices for real food rewards (e.g. Green et al., 2010). There is reason to think that the tasks adopted in this work tap some of the same processes as their human counterparts, despite substantial methodological differences. Both human and non-human studies reveal inconsistencies in choice whereby immediate payoffs are especially preferred (e.g. Green et al., 1997, 2010). For example, many people favour \$50 immediately to \$100 in six months, but would opt for \$100 in a year over \$50 in six months, despite the differences in delay and reward magnitude being identical in the two choices (Ainslie and Haendel, 1983). If couched in terms of *discounting* – delay-dependent decay in the subjective value of a payoff – the rate of decay is better modelled by a hyperbolic function than an exponential constant-decay function (see Green and Myerson, 1996 for overview). These findings also apply to choices

\* Corresponding author. Tel.: +44 01223 3 33559; fax: +44 01223 333564.  
E-mail address: [nsc22@cam.ac.uk](mailto:nsc22@cam.ac.uk) (N.S. Clayton).

under conditions of risk, which is sometimes understood in terms of ‘probabilistic discounting’ (e.g. Green et al., 1999a).

Intertemporal choice may be important in conditions associated with poor health choices, which typically involve underweighting of the long-term consequences of immediately gratifying behaviours such as drug-taking. Human individual differences reflect this, with heroin addicts (Kirby and Petry, 2004; Kirby et al., 1999), cocaine users (Bornovalova et al., 2005; Kirby and Petry, 2004), smokers (Bickel et al., 1999; Ohmura et al., 2005), and alcoholics (Vuchinich and Simpson, 1998) showing more impulsive monetary intertemporal choice than healthy controls. Translational research in rats has identified impulsive intertemporal choice as a predictor of the acquisition of cocaine self-administration (Perry et al., 2005), and has identified pharmacological factors associated with pre-morbid individual differences (e.g. Dalley et al., 2007). Similarly, animal work has offered clear insight into the effects of recent exposure to cocaine on intertemporal choice (Mendez et al., 2010; Roesch et al., 2007). Taken together, this research implicates intertemporal choice as an important component in the development and maintenance of drug addiction (Bickel et al., 2007).

Similar work underlines the importance of intertemporal choice in gambling behaviour, in the absence of any drug to alter a subject’s decision-making faculties following exposure. Impulsivity in intertemporal choice correlates positively with severity of pathological gambling behaviour in humans (Alessi and Petry, 2003), as well as with suboptimal gambling-like choice in pigeons (Laude et al., 2014a).

## 2. Translational research

Suboptimal decision-making in pigeons has been presented as an analogue of human pathological gambling (see Zentall, 2014 for a comprehensive review). The utility of this analogue rests on the identification of causal factors in pigeon choice that could plausibly underpin similarly maladaptive human behaviour. For example, Zentall and Stagner (2011) identified signalling of wins and losses by conditioned reinforcers as important in maintaining suboptimal choice, and noted that human gambling often involves such signals prior to receipt of an actual reward (e.g. matching numbers on a lottery ticket or pictures on the wheel of a slot machine). Pigeons show a reduction in inhibitory responses to loss signals over time (Laude et al., 2014b), which could support the development of problem gambling in humans. Further research has also highlighted contextual factors affecting pigeon suboptimal choice, which could be predictors of human gambling behaviour, including environmental enrichment (Pattison et al., 2013) and the animal’s motivational state during testing (Laude et al., 2012).

The use of animal models to complement work with human subjects is common in the behavioural sciences. We believe this approach has significantly improved our understanding of the psychology of human pathological behaviours, such as habitual drug use and problem gambling. The validity of animal data for human models depends upon similarities between the species in both the relevant behaviour and in the mechanisms proposed to underpin that behaviour. In the case of human and pigeon suboptimal choice, the mechanism we discussed above is a reduction in inhibitory responses to conditioned reinforcers. Because both pigeons and humans associate signals with reinforcement, this mechanism is worthy of consideration as a causal factor in human gambling behaviour. This would not be the case were Pavlovian conditioning a process unique to pigeons. We therefore face a difficulty in applying translational research to instances of behaviour that depend upon psychological processes thought to have no analogue in the rest of the Animal Kingdom. Typically these processes are asserted to be unique to humans, to have evolved within the *homo* lineage

following its split from the chimpanzees, and to be associated with an expanded prefrontal cortex. Examples of processes described as such have included those underpinning languages, the physical understanding required to make and use tools, cognition for negotiating complex social environments, and the ability to think about the future.

The rest of this manuscript focuses on attempts at translational research into intertemporal choice in non-human subjects. We first give an overview of the methods used in this research. Then we consider the importance of *future-thinking* – sometimes described as unique to humans (e.g. Suddendorf and Corballis, 1997 but see Corballis, 2012) – for intertemporal choice. Finally, we address the case for translational research into future-thinking in intertemporal choice, and describe a potential animal model – the Western scrub-jay (*Aphelocoma californica*).

## 3. Comparative studies in intertemporal choice

The last fifteen years have seen published a large number of studies examining intertemporal choice in a range of different species, including monkeys (e.g. Tobin et al., 1996; Stevens et al., 2005a,b), great apes (e.g. Beran, 2002; Rosati et al., 2007), corvids (e.g. Dufour et al., 2012; Hillemann et al., 2014; Thom and Clayton, 2014), dogs (Leonardi et al., 2012), cockatoos (Auersperg et al., 2013), and fish (e.g. Mühlhoff et al., 2011). The methodologies used in these studies vary tremendously, but most can be described as either *delay-choice* tasks that ask subjects to point to their preferred reward (e.g. Rosati et al., 2007; Stevens et al., 2005a), or *delay-maintenance* tasks that require subjects to inhibit action while waiting for a delayed payoff (e.g. Beran, 2002; Evans and Beran, 2007) (analogous to the ‘marshmallow’ task often used in children). The main difference between these task types is that delay-maintenance tasks offer the subject the opportunity to take an immediate payoff at any point in the delay to the larger payoff, whereas delay-choice tasks do not. Other tasks offer variations on these themes, like *hybrid-delay* tasks that ask subjects to make an initial choice and then give them the opportunity to renege while waiting (Paglieri et al., 2012; Beran et al., 2013), *delayed exchange* tasks in which the subject actually receives the immediate payoff at the onset of the delay and must return it at the end to get the larger/more valuable payoff (e.g. Dufour et al., 2012; Wascher et al., 2012), and *delay-distance* tasks that apply delay as the time taken to travel to a reinforcer in order to mimic foraging conditions (Mühlhoff et al., 2011; Stevens et al., 2005b).

The above lists are not exhaustive, but should illustrate the broad range of task types and subject species being used. Species comparisons have allowed insight into the ecological pressures acting on intertemporal choice mechanisms. For example, Stevens and colleagues compared performance by two New World monkeys – common marmosets (*Callithrix jacchus*) and cotton-top tamarins (*Saguinus oedipus*) – on delay-choice (Stevens et al., 2005a) and delay-distance (Stevens et al., 2005b) tasks. While marmosets are gummivorous, and must wait for sap to flow from trees, cotton-top tamarins feed primarily on insects for which they range over much greater distances than marmosets. On the delay-choice task, the marmosets were willing to wait longer for a larger reward than were the cotton-top tamarins, consistent with the requirements of their feeding ecology. Conversely, the cotton-top tamarins were willing to tolerate greater delays than the marmosets in the delay-distance experiment, where the delays were implemented as travel times conflated with distance-to-food. Stevens et al. (2005b) conclude that the requirement for cotton-top tamarins to range extensively in search of insects drove the evolution of patience for delays associated with travel distance.

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