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The ecology and evolution of patience in two New World monkeys

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Decision making often involves choosing between small, short-term rewards and large, long-term rewards. All animals, humans included, discount future rewards—the present value of delayed rewards is viewed as less than the value of immediate rewards. Despite its ubiquity, there exists considerable but unexplained variation between species in their capacity to wait for rewards—that is, to exert patience or self-control. Using two closely related primates—common marmosets (*Callithrix jacchus*) and cotton-top tamarins (*Saguinus oedipus*)—we uncover a variable that may explain differences in how species discount future rewards. Both species faced a self-control paradigm in which individuals chose between taking an immediate small reward and waiting a variable amount of time for a large reward. Under these conditions, marmosets waited significantly longer for food than tamarins. This difference cannot be explained by life history, social behaviour or brain size. It can, however, be explained by feeding ecology: marmosets rely on gum, a food product acquired by waiting for exudate to flow from trees, whereas tamarins feed on insects, a food product requiring impulsive action. Foraging ecology, therefore, may provide a selective pressure for the evolution of self-control.

Keywords: temporal discounting; impulsivity; rate maximization; tamarins; marmosets

1. INTRODUCTION

How individuals discount or devalue future rewards has intrigued economists, psychologists and behavioural ecologists under a number of different guises. Researchers studying temporal discounting often have subjects choose between small, immediate and large, delayed rewards to assess whether they can exhibit self-control by waiting for the delayed reward, or whether they discount the value of the delayed reward and select the immediate reward. Economists have examined discounting as a crucial factor in constructing models of how humans assign utility to rewards available over different time-scales (Frederick *et al.* 2002). Psychologists commonly use self-control paradigms to investigate the cognitive mechanisms associated with delayed gratification and impulsivity in humans and non-human animals (Logue 1988). Behavioural ecologists investigate rate maximization

to elucidate the role of evolutionary pressures influencing animal foraging ecology (Kacelnik 2003). These three perspectives converge in their finding that the speed with which individuals devalue delayed rewards (the ‘discounting level’) can vary tremendously between species, between individuals, across the lifetime of a single individual, and even in different contexts for the same individual. Why does this variation exist? Researchers suggest that some of this variation could result from differences in the rate of interruptions (Sozou 1998) or general cognitive ability (Tobin *et al.* 1996). Understanding the source of this variation could help elucidate the causes of impulsivity and self-control.

Here, we examine discounting behaviour in two cooperatively breeding New World monkeys—common marmosets and cotton-top tamarins. These species have comparable body and brain size, behaviour, mating systems and life history trajectories (table 1). Given the similarities and relatively close phylogenetic relationship between these species, one might not expect substantial differences in cognitive abilities such as discounting. A closer look at their foraging ecology, however, reveals one factor that might favour different discounting functions: in general, marmosets are significantly more gummivorous when compared with tamarins (approximately 70% versus 14% of feeding time, respectively; Snowdon & Soini 1988; Stevenson & Rylands 1988), whereas tamarins are more insectivorous. Gummivory requires scratching tree bark and then waiting for the sap to flow, while insectivory favours immediate acquisition of an ephemeral food source.

2. MATERIAL AND METHODS

To evaluate the discounting behaviour of both species, we used an adjusting-delay, self-control procedure (Mazur 1987). Captive-born subjects, with no foraging-relevant experience, chose between two tools, one containing a small, immediate reward and the other containing a large, delayed reward (figure 1). We presented each subject with a series of 15–32 experimental sessions composed of 10 choice trials. In each trial, a subject selected between two options, the ‘standard’ option of two food pellets with no delay and the ‘adjusting’ option of six food pellets with variable delay. Initially, there was no delay between pulling either tool and receiving access to the food. If the subject preferred the larger reward, we incremented the delay to the large reward by 1 s on the subsequent session. If the subject preferred the small reward, we decreased the delay to the large reward by 1 s. If the subject selected the two amounts equally often, the delay to the large reward remained the same. Using this method, we titrated the delay time to find each subject’s indifference point—the point at which subjects equally valued the smaller, immediate reward and larger, delayed reward (see Electronic Appendix).

3. RESULTS

On average, tamarins showed indifference between the amounts when the six pellets were delayed for a mean ($\pm$ s.e.) of 7.9 ± 0.6 s, whereas marmosets waited 14.4 ± 1.5 s (figure 2), a significantly longer delay ($F_{1,7} = 13.51$, $p < 0.01$). The indifference points for individual tamarins ranged from 5.6 to 9.8 s, and for marmosets from 10.0 to 19.0 s; the most self-controlled tamarin waited less than the most impulsive marmoset. We next turn to an analysis of why such species differences may have evolved.

Body condition (body weight/tibia length) did not significantly correlate with indifference points for

Table 1. Comparison of traits for tamarins and marmosets.

trait	cotton-top tamarins (<i>Saguinus oedipus</i>)	common marmosets (<i>Callithrix jacchus</i>)
body weight ^a	380 g ^b	280 g ^b
brain weight ^a	10 g	7.6 g
brain/body weight ratio ^a	0.026	0.027
lifespan ^c	11.7 yrs	13.5 yrs
home range size ^d	7.8–10 ha	0.5–5 ha
habitat ^d	lower to mid-canopy of Colombian rainforest	lower to mid-canopy of Brazilian rainforest
group size ^d	2–13	3–13
mating system ^d	monogamy, occasional polyandry	monogamy
parental care ^d	bi-parental care	bi-parental care
cooperative breeding ^d	yes	yes
twinning ^d	common	common
diet ^d	insects > fruit > gum	gum > insects > fruit
percentage time feeding on gum ^d	14% ^e	70%

^a Stephan *et al.* (1981).^b Note that these values are estimates from Stephan *et al.* (1981) to correlate with their measures of brain size. Weights for our subjects can be found in the Electronic Appendix.^c Ross (1991).^d Snowdon & Soini (1988) and Stevenson & Rylands (1988).^e No data available for *Saguinus oedipus*, therefore we used a measurement for closely related *Saguinus geoffreyi*.

either marmosets ($r^2 = 0.33$, $p = 0.31$) or tamarins ($r^2 = 0.01$, $p = 0.89$), excluding the influence of motivational state on choice behaviour. Some researchers suggest that the level of discounting may decrease with the ratio of brain size to body weight (Tobin *et al.* 1996). This explanation cannot account for our differences in discounting, as the brain : body ratio of tamarins (0.026) is almost identical to that of marmosets (0.027; Stephan *et al.* 1981).

To quantitatively assess how the marmosets and tamarins devalue rewards over time, we tested whether the patterns of discounting fit predictions made by the rate maximization model of discounting. Rate maximization theory predicts that foragers optimize the gain in reward per unit time (Stephens & Krebs 1986); therefore, individuals should maximize the fitness value (V) of a choice $V = A/(t+h)$, where A is the reward amount, t is the delay to reward following choice and h is the time required to process/handle the reward. Note that this function describes only short-term gain, omitting the time between choices. Despite its intuitive appeal, psychologists and behavioural ecologists have demonstrated that animals tend to ignore the inter-choice interval, maximizing intake over the short-term rather than the long-term (Bateson & Kacelnik 1996; Stephens & Anderson 2001). Rate maximization predicts indifference between the small and large rewards in our design when intake rate of the standard option equals that of the adjusting option: $A_s/(t_s+h_s) = A_a/(t_a+h_a)$. Given the values from table 2, we can estimate the predicted indifference point (t_a) if the subjects maximize intake rate. Because of differences in handling time between species, rate maximization predicts an indifference point of 8.6 s for tamarins and 6.6 s for marmosets (table 2). While the marmosets waited longer than expected by the rate maximization model ($t_8 = 4.5$, $p < 0.01$), the tamarins' mean indifference point did not differ from the rate maximization prediction ($t_{10} = -0.1$, $p = 0.91$). Thus, the tamarins appear to maximize their short-term intake rate,

whereas the marmosets have a longer time horizon, resulting in more self-controlled choices.

4. DISCUSSION

The striking difference in discounting behaviour between tamarins and marmosets is surprising given their close phylogenetic relationship and comparable biology. The two species share similar mating systems, group sizes, cooperative behaviours and general ecology (table 1). We suggest that a key difference between these species—their feeding ecology—may explain this difference.

Relative to other factors, ecological differences between species have been little explored as a selective pressure on discounting. As noted, one significant ecological difference between marmosets and tamarins is their diet. Although both species feed on fruit, marmosets specialize on plant exudates whereas tamarins focus more on insects (Coimbra-Filho & Mittermeier 1976; Snowdon & Soini 1988; Stevenson & Rylands 1988). Feeding on insects may require greater impulsivity to take advantage of ephemeral bouts of availability. Foraging on exudates has led to a number of specialized adaptations in marmosets such as modified teeth for gouging and modified digestive physiology (Coimbra-Filho & Mittermeier 1976; Harrison & Tardif 1994; Power & Oftedal 1996). Harrison & Tardif (1994) also contend that the concentrated nature of gum-exuding feeding sites may reduce gummivore home range sizes, possibly accounting for the differences between tamarins and marmosets. We contend that gummivory may have led to cognitive specializations as well. Because feeding on exudates requires waiting for gum and sap to ooze out of the plants, marmosets may have evolved the ability to value future rewards more than the insectivorous tamarins. Therefore, the self-control needed to feed on gums may have selected for a more general ability to delay gratification. The question remains: did selection increase impulsivity in

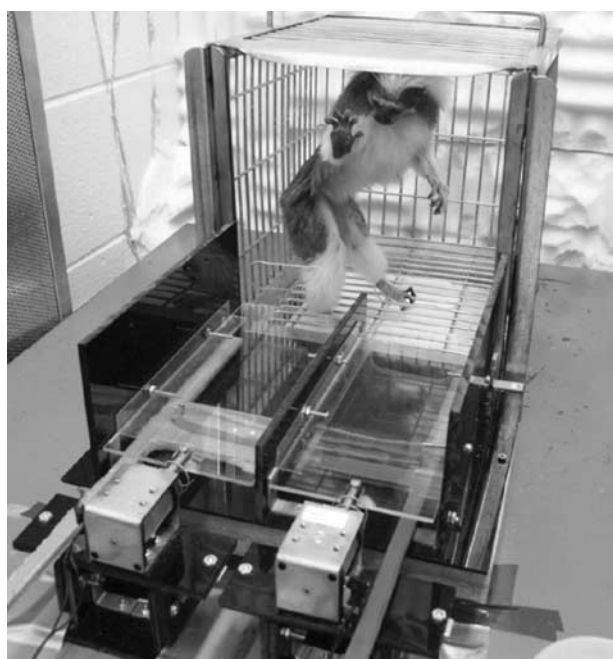


Figure 1. Experimental apparatus for discounting procedure. Both marmosets and tamarins experience the same choices: pulling one of two tools. One tool yielded two food pellets after no delay, and the other tool yielded six food pellets after a longer delay. Transparent Plexiglas covers prevented access to the pellets until the delay expired.

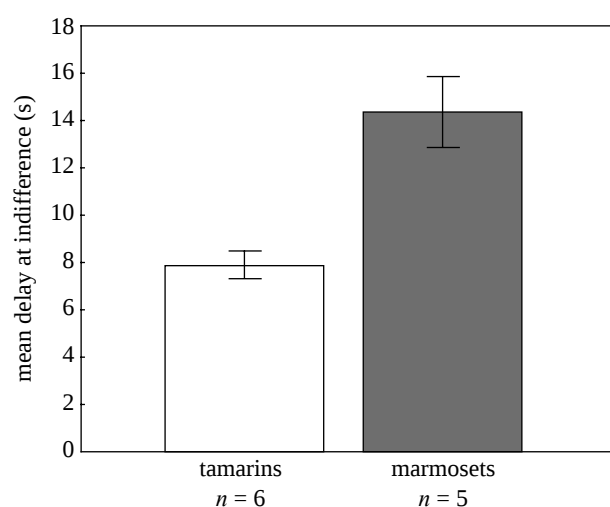


Figure 2. Species differences in discounting levels. Marmosets and tamarins differed in their indifference points with marmosets waiting almost twice as long for the six pellets than tamarins. The tamarin indifference point does not differ from that expected, but marmosets exhibit more self-control than predicted by short-term rate maximization. Error bars represent standard error of the mean indifference points.

tamarins, decrease it in marmosets, or both? Given our finding that tamarins' feeding rate maximizes but marmosets are more self-controlled than expected, it appears as though selection probably favoured self-control in the marmosets.

The role of feeding ecology in cognition has been documented in other species. Species that cache food have better spatial memory (Balda & Kamil 1989) and larger hippocampal volume (Basil *et al.* 1996)

Table 2. Summary of amounts, delays and indifference points.

	cotton-top tamarins (<i>Saguinus</i> <i>oedipus</i>)	common marmosets (<i>Callithrix</i> <i>jacchus</i>)
standard amount (A_s)	2 pellets	2 pellets
adjusting amount (A_a)	6 pellets	6 pellets
standard delay (t_s) ^a	0.1 s	0.1 s
standard handling time (h_s) ^a	10.7 s	8.3 s
adjusted handling time (h_a) ^a	27.1 s	18.5 s
predicted indifference point (t_a)—rate maximization ^a	8.6 s	6.6 s
observed mean indifference point	7.9 s	14.4 s

^a See Electronic Appendix for calculations of these estimates.

than closely related non-caching species. In addition, fruit-eating primates, such as spider monkeys, have larger brains than leaf-eating species such as howler monkeys, presumably to track spatial and temporal variation in fruit distribution (Milton 1981). The present study, however, provides the first indication that diet may influence animal discounting levels. If this model generalizes beyond the current findings, animals with long food processing times would exhibit more self-control than those with short processing times (but travelling time should not affect discounting). Therefore, we predict that species that must wait for food sources (e.g. gummivores, stalking predators) should have longer time horizons and lower discounting levels than species which immediately consume ephemeral food sources (e.g. frugivores, opportunistic predators); these ecological pressures may be so fundamental that even under captive conditions, innate species-specific differences are nonetheless maintained.

While highlighting differences in discounting levels between marmosets and tamarins in the context of foraging, our data do not necessarily imply a difference across all situations. In fact, selection may act on discounting levels in different contexts independently. For example, although tamarins and marmosets value food differently over time, they may value reproductive opportunities equally, given their similar mating systems. Yet, in more promiscuous systems in which each reproductive attempt is more valuable, individuals may act more impulsively in their mating decisions. Wilson & Daly (2004) provide data illustrating how discounting might interact with reproduction in humans by demonstrating that men discount monetary rewards more highly following the presentation of attractive female faces, but not unattractive faces. They conclude that the possibility of mating makes men more impulsive. Studies that correlate discounting levels across contexts are needed to determine the domain specificity of these cognitive adaptations.

One alternative explanation of our findings is that rather than having different discounting levels, tamarins and marmosets value the food differently—that is, perhaps marmosets value six pellets as more than

three times the value of two pellets and, therefore, will wait longer for them. While difficult to rule out, this alternative seems unlikely given that motivational measures which would temporarily influence value (such as body condition) did not correlate with individual indifference points. What remains are inherent differences in value functions between species, which are notoriously difficult to describe. Further work on varying quantities and qualities of food, as well as different methods of delaying access to food, is needed to disentangle the complex interaction between inherent value and temporal discounting.

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The supplementary Electronic Appendix is available at <http://dx.doi.org/10.1098/rsbl.2004.0285> or via <http://www.journals.royalsoc.ac.uk>.