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A fruit in hand is worth many more in the bush: Steep spatial discounting by free-ranging rhesus macaques (*Macaca mulatta*)

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A B S T R A C T

Decision making is one of the principal cognitive processes underlying goal-directed behaviour and thus there is justifiably strong interest in modeling it. However, many of these models have yet to be tested outside of the laboratory. At the same time, field work would benefit from the use of experimental methods developed in the laboratory to determine the causal relationships between environmental variables and behaviour. We therefore adapted a laboratory-derived experimental paradigm to test decision making in the wild. The experiment used an indifference-point procedure to determine the influence of both the amount and distance of food on choice behaviour. Free-ranging rhesus monkeys were given the choice between a smaller amount of food at a closer distance and a larger amount farther away. In four conditions, we held the closer amount constant across trials and varied the farther amount to determine the point at which the monkeys were indifferent to the choice alternatives. For example, in condition one, we used one piece of food at the closer location, and determined how many pieces would be equivalent in the farther location. Four different closer amounts were tested to obtain an indifference point curve, with the indifference amounts at the farther location plotted against the closer amounts. The slope of the obtained linear indifference curve was surprisingly high, suggesting that rhesus monkeys significantly discount food that is farther away. Possible reasons for this steep spatial discounting are discussed.

1. Introduction

Decision making is a key process governing goal-directed behaviour, and models of decision making attempt to characterize how cost and benefit parameters influence choice behaviour. For example, with respect to the *amount* of a positive reward such as food and the *delay* to receiving it, animals will discount the overall value of the reward if it is not immediately available (Fantino, 1969; Rachlin and Green, 1972; Ainslie, 1974; Mazur and Logue, 1978; Fantino and Davison, 1983; Mazur, 1987; Green and Myerson, 1996). Thus, when choosing between a smaller and larger amount of food, the smaller amount may be preferred if the larger would be received after a significant delay.

To quantify the effects of amount and delay on choice behaviour, evidence has been found for the following relationship:

$$V = \frac{A}{1 + KD} \tag{1}$$

where V is the subjective value of a given option, A is the reward amount, D is the delay to receiving the reward, and K is a free parameter that determines how steeply subjective value changes with delay (e.g. Mazur, 1987, 2000, 2007; Tobin and Logue, 1994). Thus, there is a positive linear relationship between the subjective value of a choice option and the reward amount, and a hyperbolic relationship between subjective value and delay to reward. The hyperbolic relationship captures the fact that the value of a choice option decreases as delay increases, with the discounting becoming less severe with longer delays.

For animals foraging in the wild, delay is often associated with travel distance—individuals normally must travel to obtain food, and traveling takes time and energy (Stephens and Krebs, 1986). Moreover, many choices are based on food sources at known locations and thus the evaluation of a given food source may depend explicitly on the travel distance to the source. One might therefore hypothesize that the relationship of distance to value may also be represented in Eq. (1), with distance replacing delay. That is, one would expect value to decrease with increasing distance, and the severity of this discounting might diminish with increasing distances. We will consider this formulation of the influence of distance on choice – where delay is replaced by distance in Eq. (1) – as Model 1 (see Bateson and Kacelnik, 1996; Janson, 2007).

Other studies have found evidence for the addition of a parameter to Eq. (1):

$$V = \frac{A}{1 + KD^B} \tag{2}$$

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where B is a scaling factor or represents other factors such as effort or risk (Mazur and Kralik, 1990; McKerchar et al., 2009; Rachlin, 2006). In this second model, we will again consider D to be distance to the food source.

We conducted the current study to determine whether the value of food at a distance is better represented by Model 1 or 2, in cases where animals are making discrete choices before traveling. The experiment was also conducted to determine if models of decision making developed in the laboratory apply to animal behaviour in more natural environments. This ecological validation is critical because laboratory research has uncovered important findings that have yet to be verified in the field. Furthermore, much of the research in the development of these models was conducted on pigeons and rats, and thus we also conducted the experiment to determine if such models also applied to an Old World monkey, the rhesus macaque (*Macaca mulatta*) (also see Hayden and Platt, 2007; Janson, 2007; Kim et al., 2008; Stevens et al., 2005a,b; Szalda-Petree et al., 2004; Tobin et al., 1996). Finally, the current experiment was conducted to test whether a specific experimental procedure used in the laboratory to quantify the relationship of economic variables to choice behaviour could also be used in the field: Mazur's (1987) indifference point procedure, described in Section 2.2. If successful, it would provide another experimental paradigm with quantitative rigor to study decision making in the wild (also see Janson, 2007).

2. Methods

2.1. Subjects

We tested adult and subadult male rhesus macaques on Cayo Santiago in Puerto Rico. Subadult males were males estimated to be between three and five years of age, whose body size was approximately as large as those of adult males, but whose testes had not completely descended.

2.2. Indifference point procedure

To test between the two models, we utilized an indifference point procedure (Mazur, 1987). The procedure is a popular means for testing decision-making models because it takes advantage of the fact that when one is indifferent between two choice alternatives, the equations for each alternative are set equal to each other, which cleverly removes value, V, a variable that is difficult to measure objectively, and leaves variables such as amount and distance that can be objectively measured. Additionally, it leads to specific indifference point function predictions that can be tested experimentally. The procedure works as follows: when an individual is indifferent between two choice options 1 and 2, the value, V_1, of option 1 is equal to the value, V_2, of option 2. Using Eq. (1), in the case in which $V_1 = V_2$, we have

$$\frac{A_1}{1+KD_1} = \frac{A_2}{1+KD_2} \quad (3)$$

If we then solve for A_2 as a function of A_1, we obtain

$$A_2 = \left(\frac{1+KD_2}{1+KD_1}\right) A_1 \quad (4)$$

Thus, the first model, Eq. (1), predicts that the indifference points A_2 are a linear function of the corresponding values of A_1, with a slope of $(1+KD_2)/(1+KD_1)$, and a y-intercept of zero. Following the same procedure, the second model, Eq. (2), also predicts a linear indifference point relationship, however, the predicted slope is $\left(1+KD_2^B\right)/\left(1+KD_1^B\right)$.

Evidence for species-typical discounting that likely evolved due to specific ecological or social conditions suggests that it is meaningful to obtain model parameters that capture the general discounting rate across individuals within a species (Green et al., 2004; Mazur, 2000, 2007; Rosati et al., 2007; Stevens et al., 2005a). Clear, systematic results from data collected across subjects would also support the concept of an overall species-typical effect. We therefore tested this possibility by conducting the experiment across multiple subjects. Nonetheless, to minimize individual differences, we tested peripheral males who in general share a comparable position in the social structure of the Cayo Santiago monkeys.

2.3. Test conditions

The experiment consisted of four conditions. In each condition, the amount of food at the closer location remained constant, and the amount at the farther location was increased or decreased across trials to determine the indifference point between the two alternatives – that is, to determine the amount at the farther location that would result in the monkeys, on average, choosing either location 50% of the time. Macintosh apples were used and cut into 1/16 slices. For Conditions 1–4, the amounts at the closer location were 1, 2, 3 and 4 slices, respectively. We used predetermined amounts for the farther location (see below), with ten trials per amount. It is important to note that we did not compile the results until after we conducted all trials of the experiment, thus we were essentially blind to the experimental outcome while conducting the experiment. Finally, to minimize repeated trials with specific monkeys, we tested different monkeys in every block of ten trials, and tested different individuals on any given day (systematically testing monkeys on different parts of the island throughout the day). Thus, no individual monkey should have been tested on more than six trials in the experiment.

2.4. Testing procedure

When we spotted a lone individual, we approached to a distance of 3.1 m (10 ft) and 4.6 m (15 ft) from the monkey, yielding a distance ratio of 1:1.5, and we positioned ourselves so that we formed a 90° angle with the monkey as the vertex (Fig. 1). The two distances were switched at regular intervals across trials from left to right of the monkey, such that each was to the left and right five times within every 10 trials. Once in position, we simultaneously knelt on our right knees, and placed a tray on the ground (white, 30.5 cm length × 20.3 width × 2.5 thickness, rectangular Styrofoam boards attached to a wicker place mat underneath to keep the trays from blowing away) (Fig. 1).

We then removed the apple slices from our backpacks and presented them simultaneously to the monkey. After the monkey had clearly looked at both options, we simultaneously placed the food items down on the trays, stood up, turned around and walked away from the trays. The monkeys typically took a straight line to one of the two trays immediately after we stepped away from them. If a monkey did not touch at least one of the apple slices of a choice alternative, either due to approaches by conspecifics or other intervening factors (e.g. a loud noise), the trial was considered a "no response" and aborted; 11% of trials were aborted. The entire procedure took approximately 10–15 s. When the number of slices was 12 or more we presented them to the monkeys in a clear zip lock bag and then laid them out on the trays after removing them from the bag. The monkeys' behaviour did not appear to be affected by the clear bags themselves, and the systematic results support this lack of effect.

The testing procedure was developed during initial pilot testing. Since the monkeys on Cayo Santiago are generally not afraid of the experimenters, we chose distances at which the monkeys typically refrained from approaching until after the experimenters stepped back. In addition, we chose an angle between the two alternatives in