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Effect of orbitofrontal cortex lesions on temporal discounting in rats

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Abstract

Although choices of both humans and animals are more strongly influenced by immediate than delayed rewards, methodological limitations have made it difficult to estimate the precise form of temporal discounting in animals. In the present study, we sought to characterize temporal discounting in rats and to test the role of the orbitofrontal cortex (OFC) in this process. Rats were trained in a novel intertemporal choice task in which the sequence of delay durations was randomized across trials. The animals tended to choose a small immediate reward more frequently as the delay for a large reward increased, and, consistent with previous findings in other species, their choice behavior was better accounted for by hyperbolic than exponential discount functions. In addition, model comparisons showed that the animal's choice behavior was better accounted for by more complex discount functions with an additional parameter than a hyperbolic discount function. Following bilateral OFC lesions, rats extensively trained in this task showed no significant change in their intertemporal choice behavior. Our results suggest that the rodent OFC may not always play a role in temporal discounting when delays are randomized and/or after extensive training.

Keywords

orbitofrontal cortex; intertemporal choice; temporal discounting; delayed reward; decision making

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1. INTRODUCTION

Humans and other animal species preferentially choose an immediate reward over a similar, but more delayed reward, suggesting that the subjective value of a reward is discounted as a function of its delay. Temporal discounting in humans has initially been proposed to be exponential, such that the subjective value is discounted at the same rate during the entire delay (Samuelson, 1937). However, subsequent empirical studies have repeatedly shown that temporal discounting in humans is better described by a hyperbolic discount function than by an exponential function (Rachlin et al., 1991; Green and Myerson, 2004). Similar results have been reported for rats (Mazur, 2007; Mazur and Biondi, 2009) and pigeons (Rodríguez and Logue, 1988; Mazur and Biondi, 2009), suggesting that hyperbolic temporal discounting might be a universal form of value discounting across different animal species. However, previous studies in rats and pigeons have employed the adjusting delay procedure (Mazur, 1987) or block-wise variation of delay durations (e.g., Kheramin et al., 2002; Mar et al., 2011). Such procedures often lead to choices that are non-stationary or serially correlated across trials, which can potentially lead to biases in estimating temporal discount functions (Cardinal et al., 2002). By contrast, recent behavioral studies in monkeys have employed an intertemporal choice task with symbolic cues and randomized reward delays, and have shown that their choice behavior is in general more consistent with hyperbolic than exponential discounting of subjective values (Kim et al., 2008; Hwang et al., 2009; Cai et al., 2011).

The first goal of this study was to estimate the precise form of temporal discount function in rodents, using a novel intertemporal choice task in which the sequence of delay durations was randomized across trials. The results showed that a hyperbolic discount function accounted for the rat's temporal discount function better than an exponential function. The second goal was to examine the role of orbitofrontal cortex (OFC) in temporal discounting during intertemporal choice of rats. OFC lesions are known to induce impulsive choice behavior in humans (Bechara et al., 2000; Berlin et al., 2004). Neural activity in the monkey OFC is also correlated with temporally discounted values (Roesch and Olson, 2005). However, previous lesion studies in rats have yielded conflicting results on this matter. Following OFC lesions, the rate of temporal discounting increased (Kheramin et al., 2002; Mobini et al., 2002; Rudebeck et al., 2006), decreased (Winstanley et al., 2004), did not change (Mariano et al., 2009), or varied depending on the extent of lesions (Mar et al., 2011) and the presence or absence of a distinct cue bridging the delay between choice and reward delivery (Zeeb et al., 2010). In the present study, we tested the effect of OFC lesions on the rat's temporal discount functions that were estimated more accurately than in the previous studies. In particular, to distinguish the OFC role in learning response-outcome contingency (Walton et al., 2010) from its contribution to temporal discounting, we extensively trained rats before the lesions. We found that OFC lesions did not make a significant change in temporal discounting of rats.

2. MATERIALS AND METHODS

2.1. Subjects

Seven young male Sprague-Dawley rats (approximately 9~11 weeks old, 390~400 g) were used. The animals were individually housed in a colony room and initially allowed free access to food and water with extensive handling for 1 week. Their body weight was gradually reduced to 80~85% of their free-feeding weight by water deprivation and maintained at this level throughout the study. Experiments were performed in the dark phase of a 12-h light/dark cycle. The experimental protocol was approved by the Ethics Review Committee for Animal Experimentation of the Ajou University School of Medicine.

2.2. Apparatus

The animals were trained on a six-arm maze that was made of black acrylic (Fig. 1). The maze had five goal arms and one start arm. The length of each arm was 35 cm and the width was 8 cm (overall dimension: 100×100 cm). Each goal arm had a white opaque door, but the start arm had a transparent door so that the animals could discover available choices (i.e., closed vs. open arms) while they were confined in the start arm. The maze was elevated 30 cm from the floor with 10 cm-high walls along the start arm and 2 cm-high walls along the rest of the maze. Water was delivered at the ends of the five goal arms (20 or 40 μ l) and the start arm (20 μ l) by solenoid valves. Navigation of the animal was monitored by seven photobeam sensors that signalled the animal's arrival at the goal locations (i.e., reward sites) and return to the start arm. Monitoring of animal behavior and water delivery were automatically controlled by a personal computer using LabView software (National Instruments, TX).

2.3. Behavioral Task

Rats were presented with four different pairs of choices. The animals were allowed to choose freely between the arm that would deliver a small reward (20 μ l of water) and one of the other four arms that would deliver a large reward (40 μ l of water) in each trial. In some sessions (type S0), the length of the delay associated with the small reward was 0 s, and the lengths of the delay associated with the large reward were 0, 3, 6 and 9 s. In the remaining sessions (type S3), the delays for both small and large rewards were increased by 3 s. In other words, the length of the delay associated with the small reward was 3 s, and the lengths of the delay associated with the large reward were 3, 6, 9 and 12 s. The number of free-choice trials in each daily session was 80 (20 trials for each choice pair) and the sequence of choice pairs was randomized.

At the beginning of each trial, the doors of the small reward arm and one large reward arm slid down (i.e., opened) in turn while the animal was confined in the start arm. The sequence of door opening was constant for a given session (the small reward arm opened earlier or later than a large reward arm), but reversed in the next session. The door of the start arm slid down immediately after opening of the second goal-arm door, enabling the animal to navigate to either goal arm. The open doors of the two goal arms slid up (i.e., closed) when the animal reached a reward site. Water was then delivered and the door of the chosen arm slid down (opened) after a given delay (0, 3, 6, 9 or 12 s) following the arrival of the animal at a reward site. The doors of the chosen arm and the start arm were closed when the animal returned to the start arm. The next trial began after 0, 3, 6 or 9 s of an inter-trial interval. The length of the inter-trial interval varied according to the delay for the chosen goal so that the sum of the reward delay and inter-trial interval was constant across trials. This prevented the animals from adopting a strategy to increase the rate of reward by choosing the small and more immediate rewards. The inter-trial interval did not include the latency to make a choice or the latency to consume reward and return to the central compartment, so that it was disadvantageous for the animals to spend time unnecessarily for these processes. None of these measures was significantly affected by the OFC lesions (*t*-test, *p*>0.05 for all comparisons).

2.4. Training

Animals were divided into two groups according to the location of the small reward goal (group 1, *n*=4 animals, the small reward goal was the leftmost arm; group 2, *n*=3 animals, the small reward goal was the center arm; Fig. 1). The animals were initially allowed to navigate on the maze freely and to obtain water reward until they were well acquainted with the reward locations (1 day, maximum 1 hour). They were then trained in forced-choice trials with no delay (30-150 trials per daily session; 1-5 days). One of the doors of the five

goal arms slid down in a pseudorandom manner after the animal returned to the start arm and then the door of the start arm opened immediately, allowing the animal to navigate to the open goal arm. The reward was delivered immediately when the animals reached a reward site. The next phase of training was a mixture of forced- and free-choice trials without a delay (80 trials per daily session; 1-7 days). After 40 trials of forced-choice, the animals went through 40 free-choice trials in which they were allowed to choose freely between the small reward and a large reward arm in each trial. When the animals almost exclusively chose the large reward arms over the small reward arm, reward delay was imposed and the task was switched back to exclusive force-choice trials (80 trials per daily session). The initial delays were 0.5 or 1 s for those three arms that would eventually deliver a large reward with a 3-, 6- or 9-s delay for session type S0. The reward delays for these three arms were gradually increased by 0.5 or 1 s until they became 3 s (1-2 days). Then the animals were trained in a mixture of forced- and free-choice trials (40 trials each) until they chose the three large delayed reward arms with similar probabilities in free-choice trials (1-5 days). The task was then switched back to exclusive force-choice trials (80 trials per daily session), and the reward delays were gradually increased to 6 s for the two arms that would eventually deliver a large reward with a 6- or 9-s delay for session type S0 (1-3 days). The animals were trained again in a mixture of forced- and free-choice trials (40 trials each) until they chose the two large delayed reward arms with similar probabilities in free-choice trials (1-5 days). The task was switched again to exclusive force-choice trials (80 trials per daily session), and the reward delay was gradually increased to 9 s for the arm that would eventually deliver a large reward with a 9-s delay for session type S0 (1-2 days). Next, for those animals that would be tested in session type S3 first (n=2), delays for the five goal arms were gradually increased until they reached 3 s for the small reward arm and 3, 6, 9 or 12 s for the large reward arms (1 day). Inter-trial interval was then introduced so that the duration of each trial was roughly the same, and the animals were trained as in the testing phase (10 forced-choice and 80 free-choice trials per daily session) until their choice frequency for a large delay reward decreased monotonically as a function of delay in a given session type (S0 or S3) for at least five consecutive days (7-28 days).

2.5. Testing

The animals were tested with two or three repetitions of alternating type-S0 and type-S3 session blocks, both before and after OFC lesions (10 forced-choice and 80 free-choice trials per daily session), with the order of session types reversed for each animal after OFC lesions. The last five days of the training period were regarded as the first session block of the testing period. Five animals were tested with type S0 first (e.g., S0-S3-S0-S3-lesion-S3-S0-S3-S0), whereas two animals were tested with type S3 first (e.g., S3-S0-S3-S0-lesion-S0-S3-S0-S3). Testing in the same session type (i.e., S0 or S3) continued for multiple days until the animal's choice frequency for a large delay reward decreased monotonically as a function of delay for at least five consecutive days (5-21 days). The animals went through one forced-choice session (80 trials) before post-lesion testing began. In forced-choice trials, only one of the five goal arms was available in each trial in a pseudorandom manner.

2.6. OFC lesions

The animals were deeply anesthetized by intraperitoneal injection of 50 mg/kg sodium pentobarbital and placed on a stereotaxic frame. Small burr holes were drilled on the skull to remove bones over the infusion sites, and 0.1 M quinolinic acid dissolved in 0.1 M phosphate buffer (pH 7.0~7.4) was infused into each injection site using a 33 gauge needle and a 10 μ l Hamilton syringe that was mounted on the stereotaxic frame. In one rat, 0.25 μ l of quinolinic acid was injected into each of three locations in each hemisphere (AP +4.0, ML $\pm$ 0.8, DV -3.4; AP +3.7, ML $\pm$ 2.0, DV -3.6; AP +3.2, ML $\pm$ 2.6, DV -4.4 mm), and, in the other six animals, 0.4 μ l of quinolinic acid was injected into each of two locations in

each hemisphere (AP +3.7, ML ± 1.2 , DV -4.8; AP +3.7, ML ± 2.8 , DV -4.4 mm). Infusions were made at a rate of 0.2 μ l per min, and the needle was remained in place for 3 min after infusion to ensure the diffusion of quinolinic acid. The burr holes in the skull were covered with bone wax, and the skin was sutured. The animals were allowed to recover for at least 10 days following surgery before post-operative training began. A sham lesion group was not included because preliminary results indicated no significant effect of OFC lesions on the animal's choice behavior.

2.7. Histology

At the completion of behavioral testing, animals were overdosed with sodium pentobarbital and perfused transcardially with 0.1 M PBS followed by 4% paraformaldehyde. The brains were removed, postfixed in 4% paraformaldehyde, and transferred to 30% sucrose solution. After being cut on a freezing microtome, coronal sections (40 μ m) were stained with cresyl violet

2.8. Data analysis

Four different discount functions were fit to the choice data from each animal. The exponential discount function was given by

$$DV(A, D) = A \exp(-kD),$$

and the hyperbolic discount function was given by

$$DV(A, D) = \frac{A}{1+kD},$$

where $DV(A, D)$ is temporally discounted value, A is the magnitude of reward (20 or 40 μ l), D is the delay (s), and k indicates the steepness of the discount function (s^{-1}). In addition, the q -exponential function (Cajueiro, 2006; Hwang et al., 2009) was given by

$$DV(A, D) = \frac{A}{(1 + (1 - q)kD)^{1/(1-q)}},$$

and the beta-delta (β - δ) discount function (Laibson, 1997; McClure et al., 2004) was given by

$$\begin{aligned} DV(A, D) &= A, \text{ for } D=0, \text{ and} \\ DV(A, D) &= A\omega \exp(-kD), \text{ for } D>0, \end{aligned}$$

where q and ω are additional model parameters. Therefore, compared to the exponential and hyperbolic discount functions, these latter two models each includes one additional parameter.

For all models, the probability that the animal would choose the small immediate reward, $P(S)$, was given by the Boltzmann distribution as follows:

$$P(S) = \frac{\exp\{\beta DV(A_s, D_s)\}}{\exp\{\beta DV(A_s, D_s)\} + \exp\{\beta DV(A_L, D_L)\}},$$

where A_S and A_L represent the reward magnitudes associated with the small- and large-reward targets, respectively, D_S and D_L represent the delays associated with the small- and large-reward targets, respectively, and β is the inverse temperature that defines the degree of randomness in animal's choices. The parameters of the discount functions (k , q and ω) and the inverse temperature (β) were estimated separately for the entire behavioral data obtained before (42–69 sessions) or after (26–47 sessions) OFC lesions for each animal based on a maximum likelihood procedure as described elsewhere (Patiwan, 2001; Hwang et al., 2009). Performances of the models were compared using the Bayesian information criterion (BIC) which penalizes the number of model parameters more strongly than does the Akaike's information criterion, and it was normalized by the number of trials (BIC/ N , where N is the number of trials).

2.9. Statistical test

Two-way ANOVA was used to test effects of delay duration and OFC lesions on the animal's choice of a small immediate vs. a large delayed reward separately for each session type (S0 and S3). Wilcoxon signed rank test was used to compare model parameters before and after OFC lesions. A p -value <0.05 was used as the criterion for a significant statistical difference.

3. RESULTS

3.1. Extent of lesions

Fig. 2 shows schematic representations of the largest (light gray), medium (dark gray), and the smallest (black) OFC lesions ($n=7$ animals). As shown, quinolinic acid injections consistently produced extensive damages to the medial, lateral, ventral and dorsolateral OFC (Paxinos and Watson, 1998).

3.2. Choice behavior

The animals performed $2,263 \pm 711$ and $2,343 \pm 440$ trials in S0 and S3 sessions, respectively, before the OFC lesions, and $1,371 \pm 451$ and $1,474 \pm 206$ trials in S0 and S3 sessions, respectively, after the OFC lesions (mean $\pm$ SD). When the delays for the small and large rewards were the same, all animals almost always chose the large reward. This was true both before and after OFC lesions, regardless of the delay for the small reward (before lesions, S0 sessions, $99.8 \pm 0.0\%$; S3 sessions, $99.9 \pm 0.0\%$; after lesions, S0 sessions, $99.8 \pm 0.0\%$; S3 sessions, $99.8 \pm 0.0\%$; mean $\pm$ SD), demonstrating the animal's strong preference for a large reward when the delays are equal for small and large rewards. However, the frequency for the animals to choose the small reward increased monotonically as the delay for the large reward increased (Fig. 3). Moreover, how the animal's preference for the small reward changed with reward delays was not influenced by OFC lesions (two-way ANOVA with repeated measure, session type S0, main effect of delay, $F(3,18)=20.99$; $p<0.01$; main effect of lesions, $F(1,6)=0.38$; $p=0.541$; effect of delay $\times$ lesion interaction, $F(3,18)=0.16$; $p=0.925$; session type S3, main effect of delay, $F(3,18)=29.24$; $p<0.01$; main effect of lesions, $F(1,6)=0.02$; $p=0.883$; effect of delay $\times$ lesion interaction, $F(3,18)=0.05$; $p=0.985$).

3.3. Model comparison

We compared the goodness of fit for several different discount functions using the BIC (Fig. 4 and Table 1). When only the exponential and hyperbolic discount functions were compared, the hyperbolic discount function better accounted for the animal's choice behavior in the majority of cases (10 out of 14 cases, 78.6%; before OFC lesions, 6 out of 7 animals; after OFC lesions, 4 out of 7 animals). However, when we compared all four discount functions, the models with two-parameter discount functions (q -exponential and

beta-delta functions) were in general superior to those with single-parameter discount functions (exponential and hyperbolic functions) in explaining the animal's intertemporal choice behavior. The animal's choices were best accounted for by the beta-delta function in 7 cases (50%; 4 animals before and 3 animals after OFC lesions), by the q -exponential function in 6 cases (42.9%; 3 animals before and 3 animals after OFC lesions), by the exponential function in 1 case (7.1%; 1 animal after OFC lesions), and never by the hyperbolic function. Furthermore, none of the model parameters was significantly influenced by the OFC lesions for any of the four discount functions (Wilcoxon signed rank test, exponential function, k , $p=0.578$; β , $p=0.578$; hyperbolic function, k , $p=0.813$; β , $p=1.000$; q -exponential function, k , $p=1.000$; q , $p=0.813$; β , $p=1.000$; beta-delta function, k , $p=1.000$; ω , $p=0.469$; β , $p=1.000$; Fig. 4 and Table 1).

4. DISCUSSION

The first goal of the present study was to determine the precise form of temporal discounting in rodents while avoiding methodological complications associated with the adjusting delay procedure. To accomplish this, all reward delays were explicitly signalled to the animals by the arm locations (rather than requiring the animals to estimate them through experience) and their sequence was randomized across trials in our task. Hence, our task was free from the problem of serial correlation or non-stationarity in the animal's choices. In our novel five goal-arm intertemporal choice task, rats preferred the small immediate reward more strongly as the delay for the large reward increased, which can be parsimoniously explained by the models of temporal discounting. Also, rats' choice behavior was better accounted for by a hyperbolic than an exponential discount function, which is consistent with the majority of previous studies on intertemporal choice in humans and animals (see Introduction). The average value of the k parameter for the hyperbolic discount function (0.21 before and 0.20 s^{-1} after lesions) was comparable to previously reported values in rats (0.03-0.57 in studies using adjusting delay procedures; Richards et al., 1997; Green et al., 2004; 0.328 in a study using block-wise binary choices; Kheramin et al., 2002), but somewhat smaller (i.e., less steep discounting) than the values obtained from pigeons (0.21-2.24 in studies using adjusting delay procedures; Mazur, 2000; Green et al., 2004), and monkeys (0.14-1.32; Hwang et al., 2009). However, model comparisons using BIC showed that the hyperbolic discount function was inferior to two-parameter discount functions (q -exponential and beta-delta functions) in explaining the animal's choice behavior. A recent study in primates (Hwang et al., 2009) has also found that these so-called quasi-hyperbolic discount functions are in general superior to exponential and hyperbolic discount functions in explaining the animal's intertemporal choice behavior (but see Mazur, 2007). Underlying neural processes for this quasi-hyperbolic discounting are unknown. One possibility is that temporal discounting is influenced by logarithmic time perception. Namely, exponential discounting combined with logarithmic time perception produces a q -exponential function (Takahashi et al., 2008; Hwang et al., 2009).

The second goal of this study was to examine effects of OFC lesions on temporal discounting of rats in our novel intertemporal choice task. We found no significant effect of OFC lesions on the animal's intertemporal choice behavior, which suggests that the intact OFC is not always needed for temporal discounting. Previous studies have found steeper temporal discounting in rats with OFC lesions that were tested without pre-training in an intertemporal choice task (Kheramin et al., 2002; Mobini et al., 2002). However, considering that the OFC plays a critical role in correctly associating responses and their outcomes (Walton et al., 2010), it is possible that the animal's intertemporal choice behavior was altered as a by-product of the animal's impaired abilities to learn response-outcome contingency. Indeed, although rats made more impulsive choices following OFC lesions even with pre-training in a single-duration intertemporal choice task, their choice behavior

became indistinguishable from that of control animals once they had a chance to associate available choice options with their outcomes by equating delays of the two options (Rudebeck et al., 2006). Also, a recent study (Mar et al., 2011) has shown that initial changes in intertemporal choice behavior following OFC lesions (Winstanley et al., 2004) disappeared with extended training.

Several different accounts have been advanced to explain inconsistent outcomes of OFC lesions in rats. For example, Kheramin et al. (2002) proposed that OFC lesions may increase the rate of time discounting as well as sensitivity to the ratio of reward magnitudes, so that OFC lesions could facilitate or suppress impulsive choices depending on relative magnitudes and delays of alternative reward options. However, it is often difficult to estimate how the preference for delayed reward is influenced by the reward delay and magnitude separately, because in most animal studies, including ours, the magnitudes for immediate and delayed rewards are fixed. Therefore, whether and how the OFC contribution to the animal's preference for delayed reward changes with these two factors need to be explored more systematically in future studies. Mariano et al. (2009) suggested that the presence or absence of prominent sensory cues during choice and delay may be an important factor in determining the effects of OFC lesions on inter-temporal choice behavior. They argued that salient sensory cues for small vs. large rewards may help develop strong cue-reward value associations, so that after the OFC lesions, the animals more frequently rely on habitual responses to choose large delayed over small immediate rewards. It is unclear whether this account can explain our results, because physical appearances of all target arms were similar, hence the amount of delay/reward was signalled by its location rather than a distinct cue in our study. Nevertheless, we cannot rule out the possibility that the animals associated a distinct location/arm with a specific amount of delay and reward before lesions so that the location/arm information acted as a cue preferentially guiding the animal's choices. Zeeb et al. (2010) also proposed that the presence or absence of a distinct sensory cue bridging the delay between response and delivery of larger rewards may be an important factor determining the direction of OFC lesion effects; a distinct cue during the delay may act as a conditioned reinforcer permitting strong association between the cue and large rewards and biasing the animal's choice toward large delayed rewards. Under this scenario, delay-specific cues during the reward delays would reduce animal's baseline impulsivity, and OFC lesions would lead to more impulsive choices, whereas the opposite pattern would be expected without such cues. The fact that we found no significant change in temporal discounting following OFC lesions is therefore inconsistent with this possibility. However, the absence of a distinct sensory cue for the larger rewards in our task may have contributed to the finding that OFC lesions did not increase impulsive choices.

In a recent study, lesions selective to the lateral and medial OFC made rats more and less impulsive, respectively, whereas whole OFC lesions induced only a transient change that disappeared with extended training (Mar et al., 2011). In the present study, we trained the animals before whole OFC lesions longer than in any of the previous studies (30-35 sessions each consisting of 80 trials) and verified that their choice behavior was stable (i.e., choice frequency for a large delayed reward decreased as a function of delay for at least five consecutive days). Testing the animals with these procedures, we found no significant effect of whole OFC lesions on the animal's temporal discounting. Although our results can be explained by opposite effects of lateral and medial OFC lesions on intertemporal choices (Mar et al., 2011), they are also consistent with the possibility that the OFC is not required for temporal discounting per se during intertemporal choice as long as the animals had enough chance to learn response-outcome contingency. They are also in line with the findings from previous physiological studies in monkeys that neural signals for temporally discounted values are distributed in multiple areas of the brain such as the dorsolateral prefrontal cortex (Kim et al., 2008), posterior parietal cortex (Louie and Glimcher, 2010),

dorsal striatum and ventral striatum (Cai et al., 2011). Brain imaging studies have also found blood oxygenation level-dependent signals related to temporally discounted values in multiple areas of the brain (McClure et al., 2004; Tanaka et al., 2004; Kable and Glimcher, 2007; McClure et al., 2007; Luhmann et al., 2008). It is possible that the information about temporally-discounted values was provided by these brain structures other than, or in addition to, the OFC in guiding the animal's choice in our task. In addition, it is notable that neural activity related to temporally discounted values has been found in the monkey OFC (Roesch and Olson, 2005), but not in the rat OFC (Roesch et al., 2006), which is also in line with our finding that the OFC is not critically involved in guiding choice behavior based on temporally-discounted values in rats.

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Abbreviations

OFC	orbitofrontal cortex
BIC	Bayesian information criterion

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Highlights

1. Temporal discounting of the rat was studied using a novel inter-temporal choice task
2. Rat's choices were better explained by hyperbolic than exponential discount functions
3. Two-parameter discount functions were superior to single-parameter discount functions
4. Orbitofrontal cortex lesions did not alter rat's inter-temporal choice behavior

Figure 1. Intertemporal choice task. The circles denote reward delivery sites. Either 20 (small circles) or 40 μl (large circles) of water was delivered. The numbers above each goal arm denote reward delays in session type S0 (upper) and S3 (lower). Left, group 1 animals (n=4); Right, group 2 animals (n=3).

Figure 2.

The extent of OFC lesions. Left, OFC lesions were reconstructed at different anterior-posterior levels. The largest (light gray shading), medium (dark gray shading) and smallest (black shading) lesions are indicated. The numbers indicate anterior-posterior coordinates in reference to bregma (mm). Modified with permission from Elsevier (Paxinos and Watson, 1998). Right, Example photomicrographs showing typical lesions of the OFC.

Figure 3. Choice behavior. The graphs show the probability for the animals to choose the small-reward goal (ordinate, $P(S)$) as a function of the delay for the large-reward goals (abscissa) before and after OFC lesions. Circles and triangles denote behavioral data obtained from S0 and S3 sessions, respectively. Lines indicate predictions of different models that are indicated in different colors. Solid and dotted lines denote model fitting to the data obtained from S0 and S3 sessions, respectively. The data for individual animals are shown separately. Error bars, SEM.

Figure 4.

Effect of OFC lesions on model parameters. Shown are estimated parameters and normalized BIC for four different models before and after OFC lesions. Open circles, model parameters and normalized BIC for individual animals. Filled circles and error bars, their mean and SEM.

Values of estimated model parameters. Shown are estimated parameters and normalized BIC (BIC/*N*) for four different models before and after OFC lesions (mean±SEM).

Table 1

Before lesions					
Model	K	β	q	w	BIC/ <i>N</i>
Exponential	0.12±0.01	0.28±0.02			0.79±0.05
Hyperbolic	0.21±0.03	0.45±0.06			0.71±0.04
q-exponential	0.28±0.04	0.46±0.05	-0.45±0.34		0.68±0.04
β-δ	0.09±0.01	0.46±0.05		0.75±0.04	0.67±0.04

After lesions					
Model	K	β	q	w	BIC/ <i>N</i>
Exponential	0.10±0.01	0.34±0.07			0.73±0.09
Hyperbolic	0.20±0.03	0.45±0.09			0.71±0.05
q-exponential	0.29±0.08	0.45±0.06	-0.59±0.67		0.63±0.06
β-δ	0.08±0.01	0.45±0.06		0.81±0.06	0.63±0.06